

OXFORD

BIOLOGY

# bumblebees

behaviour, ecology,  
and conservation

DAVE GOULSON



SECOND EDITION

# Bumblebees

*This page intentionally left blank*

# Bumblebees

## Behaviour, Ecology, and Conservation

Second Edition

DAVE GOULSON

OXFORD  
UNIVERSITY PRESS

OXFORD

UNIVERSITY PRESS

Great Clarendon Street, Oxford OX2 6DP

Oxford University Press is a department of the University of Oxford.  
It furthers the University's objective of excellence in research, scholarship,  
and education by publishing worldwide in

Oxford New York

Auckland Cape Town Dar es Salaam Hong Kong Karachi

Kuala Lumpur Madrid Melbourne Mexico City Nairobi

New Delhi Shanghai Taipei Toronto

With offices in

Argentina Austria Brazil Chile Czech Republic France Greece

Guatemala Hungary Italy Japan Poland Portugal Singapore

South Korea Switzerland Thailand Turkey Ukraine Vietnam

Oxford is a registered trade mark of Oxford University Press  
in the UK and in certain other countries

Published in the United States

by Oxford University Press Inc., New York

© Dave Goulson 2010

The moral rights of the authors have been asserted

Database right Oxford University Press (maker)

First published 2003

This edition 2010

All rights reserved. No part of this publication may be reproduced,  
stored in a retrieval system, or transmitted, in any form or by any means,  
without the prior permission in writing of Oxford University Press,  
or as expressly permitted by law, or under terms agreed with the appropriate  
reprographics rights organization. Enquiries concerning reproduction  
outside the scope of the above should be sent to the Rights Department,  
Oxford University Press, at the address above

You must not circulate this book in any other binding or cover  
and you must impose the same condition on any acquirer

British Library Cataloguing in Publication Data

Data available

Library of Congress Cataloging in Publication Data

Data available

Typeset by Newgen Imaging Systems (P) Ltd., Chennai, India

Printed in Great Britain

on acid-free paper by

MPG Biddles Ltd., King's Lynn, Norfolk

ISBN 978-0-19-955306-8 (Hbk.) 978-0-19-955307-5 (Pbk.)

1 3 5 7 9 10 8 6 4 2

# Contents

<b>Preface</b>	ix
<b>Acknowledgements</b>	xi
Chapter 1: Introduction	1
1.1 Evolution and phylogeny	2
1.2 The life cycle	5
Chapter 2: Thermoregulation	13
2.1 Warming up	13
2.2 Controlling heat loss	16
2.3 Thermoregulation of the nest	18
Chapter 3: Social Organization and Conflict	21
3.1 Caste determination	22
3.2 Division of labour	25
3.3 Sex determination	34
3.4 Control of reproduction and queen–worker conflicts	34
3.4.1 Timing of reproduction	37
3.4.2 Matricide	39
3.5 Sex ratios in ‘true’ bumblebees	40
3.6 Sex ratios in <i>Psithyrus</i>	43
Chapter 4: Finding a Mate	45
4.1 Territoriality	45
4.2 Nest surveillance	46
4.3 Hilltopping	46
4.4 Scent-marking and patrolling	47
4.5 Inbreeding avoidance	50
4.6 Evolution of male mate-location behaviour	51
4.7 Queen-produced sex attractants	51
4.8 Monogamy versus polyandry	52
Chapter 5: Natural Enemies	57
5.1 True predators	57
5.2 Parasitoids	62
5.2.1 Conopidae (Diptera)	62
5.2.2 Sarcophagidae (Diptera)	64

vi Contents

5.2.3 Braconidae (Hymenoptera)	65
5.2.4 Mutilidae (Hymenoptera)	65
5.3 Parasites and commensals	66
5.3.1 Viruses	66
5.3.2 Prokaryotes (Bacteria and others)	66
5.3.3 Fungi	67
5.3.4 Protozoa	67
5.3.5 Nematodes	70
5.3.6 Mites (Acarina)	71
5.3.7 Other commensals	73
5.4 The immune system of bumblebees	73
5.5 Social parasitism	75
5.5.1 Nest usurpation	75
5.5.2 Social parasitism by drifting workers	76
5.5.3 Cuckoo bees ( <i>Psithyrus</i> )	77
Chapter 6: Foraging Economics	81
6.1 Foraging range	84
6.1.1 Measuring foraging range	86
6.1.1.1 Marking experiments and direct observation	86
6.1.1.2 Modelling foraging range	87
6.1.1.3 Homing experiments	88
6.1.1.4 Radar tracking	91
6.1.1.5 Mass-marking and pollen analysis	92
6.1.2 Do bumblebees forage close to their nests?	94
6.1.3 Differences between bumblebee species	95
6.1.4 Management implications	97
Chapter 7: Exploitation of Patchy Resources	101
7.1 The ideal free distribution	102
7.1.1 Search patterns within patches	102
7.1.2 Non-random choice of patches	106
7.2 The marginal value theorem	107
Chapter 8: Choice of Flower Species	113
8.1 Learning and flower constancy	114
8.1.1 Explanations for flower constancy	115
8.1.2 Can flowers be cryptic?	120
8.2 Infidelity in flower choice	123
8.3 Variation in learning ability	124
8.4 Coping with deceptive unrewarding flowers	125
8.5 The influence of pollen quality on flower choice	126

Chapter 9: Intraspecific Floral Choices	131
9.1 Direct detection of rewards	131
9.2 Flower size	132
9.3 Flower age	132
9.4 Flower sex	133
9.5 Flower symmetry	134
9.6 Floral scent	135
9.7 Thermal rewards	135
9.8 Motivation and choosiness	136
Chapter 10: Foraging Cues Gained from Other Bees	137
10.1 Communication in the nest	137
10.2 Visual responses to other bees on flowers	140
10.3 Scent marking of flowers	140
10.3.1 Repellent versus attractant marks	146
10.3.2 The evolution of scent marking	147
Chapter 11: Competition and Niche Differentiation in Bumblebee Communities	151
Chapter 12: Bumblebees as Pollinators	161
12.1 Pollination of crops	162
12.1.1 Honeybees versus bumblebees	163
12.1.2 Approaches to enhancing bumblebee pollination	165
12.2 Pollination of wild flowers	171
12.2.1 Nectar robbing	172
Chapter 13: Conservation	177
13.1 Causes of declining bumblebee numbers	181
13.1.1 Loss of habitat	181
13.1.2 Pesticides	186
13.1.3 Impacts of non-native bees and commercial beekeeping	188
13.1.4 Population structure and habitat fragmentation	191
13.1.5 Do bumblebees suffer from inbreeding depression?	198
13.2 Why are some bumblebee species still abundant?	199
13.3 Consequences of declining bumblebee numbers	204
13.4 Conservation strategies	206
13.4.1 Enhancing bumblebee diversity in farmland	206
13.4.1.1 Field margin management and wildflower strips	206
13.4.1.2 Restoring and maintaining species-rich grasslands	210
13.4.1.3 Providing nest sites	211
13.4.1.4 Organic farming	212



viii Contents

13.4.2 The importance of urban areas	213
13.4.3 Translocations and reintroductions	215
13.5 Summary	216
<b>Chapter 14: Bumblebees Abroad: Effects of Introduced Bees</b>	<b>219</b>
14.1 Competition with native organisms for floral resources	221
14.1.1 Effects on foraging of native organisms	222
14.1.2 Evidence for population-level changes in native organisms	225
14.2 Competition for nest sites	227
14.3 Introgression with native bees	228
14.4 Transmission of parasites or pathogens to native organisms	228
14.5 Effects on pollination of native flora	231
14.6 Pollination of exotic weeds	233
14.7 Summary and conclusions	235
<b>References</b>	<b>239</b>
<b>Index</b>	<b>311</b>

# Preface

'Everybody knows the burly, good-natured bumblebee. Clothed in her lovely coat of fur, she is the life of the gay garden as well as the modestly blooming wayside as she eagerly hums from flower to flower'

F.W.L. Sladen (1912)

So begins *The Humble-bee*, the first book ever written on bumblebees, and it is hard to better as an opening passage. With their large size, furry, colourful bodies and slow, buzzing, slightly clumsy flight, bumblebees are among the most endearing and welcome of insect visitors to the garden. They enjoy an enviable popularity compared to most insect fauna, for the buzz of foraging bumblebees is intimately associated in our minds with warm summer days and flower-filled meadows. They are widely recognized as being beneficial through their role in pollination, and bumblebees are most reluctant to mar their reputation by stinging; most species only do so when very hard pressed. Despite their familiarity, there is a great deal that we do not know about bumblebees. Many species are hard to distinguish from one another, rendering fieldwork difficult and discouraging amateur interest. Their nests are exceedingly hard to locate, so that those of some species have never been found. Fundamental aspects of the behaviour of many species, such as mating, have never been seen.

Bumblebees have been in decline for perhaps 60 years, but this has only recently caught the attention of the general public. Recent collapses in managed honeybee populations have also raised the profile of bees in the public consciousness, and there are now probably few members of the general public in western Europe and North America who are not at least dimly aware that bees are having problems. However, all too often the issues are poorly understood, and rather few people are clear as to the difference between honeybees and bumblebees (many folk think there is just one species of bee!). Given the key roles that bees play as pollinators of crops and wildflowers, and the need for concerted action at the landscape scale if we are to effectively conserve these essential organisms, it is vital that ways be found to involve the wider public in conservation efforts. If we can subtly change the ways we farm, garden, and how local government organizations manage land, we can save our bees. It is not too late. But there is much to do if we are to get the message across. The intention in writing this book was in part to try to draw attention to the importance of conserving dwindling bumblebee populations, and to summarize the state of knowledge with regard to what we need to do to conserve them.

That was not my only motivation. Bumblebees have always been popular subjects for scientific study, but research has accelerated in recent years, notably in the United Kingdom, Japan and North America. Many new discoveries have been made with regard to their ecology and social behaviour, but this information is widely dispersed in the

literature. The past 20 years has also seen the commercialization of bumblebee breeding for pollination, and the invasion of new parts of the globe by bumblebee species, with potentially far-reaching consequences. The first edition of this book was written in 2002. Since then, more than 700 new scientific papers on bumblebees have been published. In some fields, such as population genetics, there have been substantial advances. Here I attempt to summarize and update our understanding of the ecology of these fascinating and charismatic organisms, and identify some of the many gaps that remain in the hope of stimulating further research.

A plea for forgiveness is necessary at this point for I am sure that I have made numerous mistakes when attempting to synthesize and explain the work of others. I must also apologize for biases that I inevitably show in my coverage of different topics; some will feel that I dwell for too long on conservation and other applied issues such as impacts of non-native bumblebees on the environment. This simply reflects my particular interests and also my belief that action is needed; it is probably not going too far to say that if humans are to thrive in the future, and have anything like the standard of living that we in the developed world enjoy today, then we simply have to look after our bumblebees. With dedication and a little luck perhaps we can conserve the 'burly, good-natured bumblebee' for future generations to enjoy.

# Acknowledgements

I am indebted to the work of others who long ago laid the foundations for the study of bumblebees. In particular *The Humble-bee* by Sladen (1912, reprinted in 1989), *Bumblebees* by Free and Butler (1958) and *Bumblebees* by Alford (1975) are invaluable reference works. Prys-Jones and Corbet (1991) provide an excellent and accessible introduction to the subject which helped to stimulate my interest in bumblebees. I am also grateful to Ben Darvill, Kirsty Park, Gillian Lye, Steph O'Connor, Penelope Whitehorn, Nicky Redpath, Lynne Osgathorpe, Juliet Osborne, James Cresswell, Paul Williams, Mick Hanley, Mairi Knight, Matt Tinsley, Mike Edwards and many others for invaluable discussions.

This book is dedicated to my two boys, Finn and Jedd, at ages 7 and 5 already keen hunters of woogermice and bumblebees.

*This page intentionally left blank*

# 1

---

## Introduction

Bees (Superfamily Apoidea) belong to the large and exceedingly successful insect order Hymenoptera, which also includes wasps, sawflies and ants. There are currently approximately 25,000 known species of bee, belonging to over 4,000 genera, and undoubtedly many more remain to be discovered. All bees are phytophagous, feeding primarily on nectar and pollen throughout their lives. While many other insects feed on nectar or pollen as adults, very few do so throughout their development. This is simply because pollen and nectar, although nutritious, are sparsely distributed in the environment, and immature insects cannot fly from flower to flower to collect them (they do not have wings). In bees, the adult females gather the food for their offspring, so that the offspring themselves do not need to be mobile. In fact, the larval stage is maggot-like and generally rather feeble, being defenceless and capable of only very limited movement; they are entirely dependent on the food reserves provided for them. To facilitate the gathering of floral resources the mouthparts of adult bees are modified into a proboscis for sucking nectar, and in many species the hind legs of females are modified for carrying pollen (Michener 1974).

As in the wasps (from which bees evolved), bee social behaviour spans a broad spectrum from solitary species, to those that live in vast colonies containing tens of thousands of individuals. The social species are more familiar, and it is not widely appreciated that by far the majority of bee species are solitary. In terms of nest architecture and behaviour, they are similar to many solitary wasps (the obvious difference being that wasps generally provision their nests with animal prey). Some bee species within the Halictidae and Anthophoridae exhibit primitively social behaviour, living in small colonies in which the females may switch between roles as workers or queens. Approximately 1,000 bee species are classed as eusocial (having a non-reproductive worker caste), although the distinction between primitively social species and eusocial species is sometimes blurred. The most advanced eusocial bees are all within the Apidae, notably *Apis* (honeybees) and the tropical stingless bees (Meliponinae).

Bumblebees (which also belong to the Apidae) are often described as primitively eusocial, because their social organization is said to be simpler than that of the honeybee. Unlike the Meliponinae and *Apis*, most bumblebee species have an annual cycle, with queens single-handedly founding nests. However, some tropical species of bumblebee initiate new colonies by swarming, in a way similar to honeybees (Garófalo 1974). Temperate species exhibit nest homeostasis, tightly regulating the temperature within

## 2 Bumblebees

the nest (Alford 1975), and it has recently been discovered that bumblebee workers do communicate with regard to food sources (Dornhaus and Chittka 2001; Dornhaus *et al.* 2003), attributes normally associated with advanced sociality. Thus, the tag of ‘primitively eusocial’ is probably misleading (although perhaps I am unnecessarily defending my favourite insects!).

Bumblebees are all fairly large compared with the majority of bee species (or indeed most other insects), and most are covered in dense fur. Owing to this combination of size and insulation, bumblebees are capable of endothermy, and they are well adapted for activity in cool conditions (Heinrich 1993). It is thus not surprising that bumblebees are largely confined to temperate, alpine and arctic zones. They are found throughout Europe, North America and Asia (Plate 1). They become scarce in warmer climates such as the Mediterranean, although atypical species are found in the lowland tropics of south-east Asia and Central and South America. The mountain chains running through North and South America have allowed these primarily northern temperature organisms to cross the equator, and moderate species diversity is to be found in the Andes. In the Himalayas, they are generally only found at altitudes above about 1,000 m rising to 5,600 m (Williams 1985a). Species richness peaks in the mountains to the east of Tibet and in the mountains of central Asia (Williams 1994). In Europe, species richness tends to peak in flower-rich meadows in the upper forest and subalpine zones (Rasmont 1988; Williams 1991; Goulson *et al.* 2008b).

### 1.1 Evolution and phylogeny

It is widely accepted that the bees probably first appeared in the early cretaceous approximately 130 million years ago (mya), in association with the rise of the angiosperms (Milliron 1971; Michener 1979; Michener and Grimaldi 1988). Bees evolved from predatory wasps belonging to the Sphecoidea, and indeed primitive bees can be difficult to distinguish from Sphecoid wasps. The earliest known fossil bee is of the stingless bee *Trigona prisca* (Meliponinae), found in amber dating from 74 to 94 mya (Michener and Grimaldi 1988). However, this is an advanced eusocial species so it is reasonable to suppose that a great deal of bee evolution occurred in the 50 million years from the beginning of the Cretaceous to the time when this fossil lived (Michener and Grimaldi 1988).

The earliest fossils attributed to *Bombus* date from the Oligocene (38–26 mya), but we do not know when the group arose (Zeuner and Manning 1976). Inevitably, the fossil record for bumblebees is exceedingly sparse, for such large insects are unlikely to be caught in amber. Estimates based on a molecular phylogeny suggest an early divergence of bumblebee lineages 40–25 mya, perhaps corresponding to a period of global cooling at the Eocene–Oligocene boundary that may have favoured cold-adapted insects such as bumblebees (Hines 2008). It seems most probable that bumblebees arose in Asia, because this is still the area of greatest bumblebee diversity (notably the mountains bordering Tibet to the east, and the mountains of central Asia). Bumblebees probably

dispersed westwards from Asia through Europe, to North America probably about 20 mya and finally to South America about 4 mya (Williams 1985a; Hines 2008).

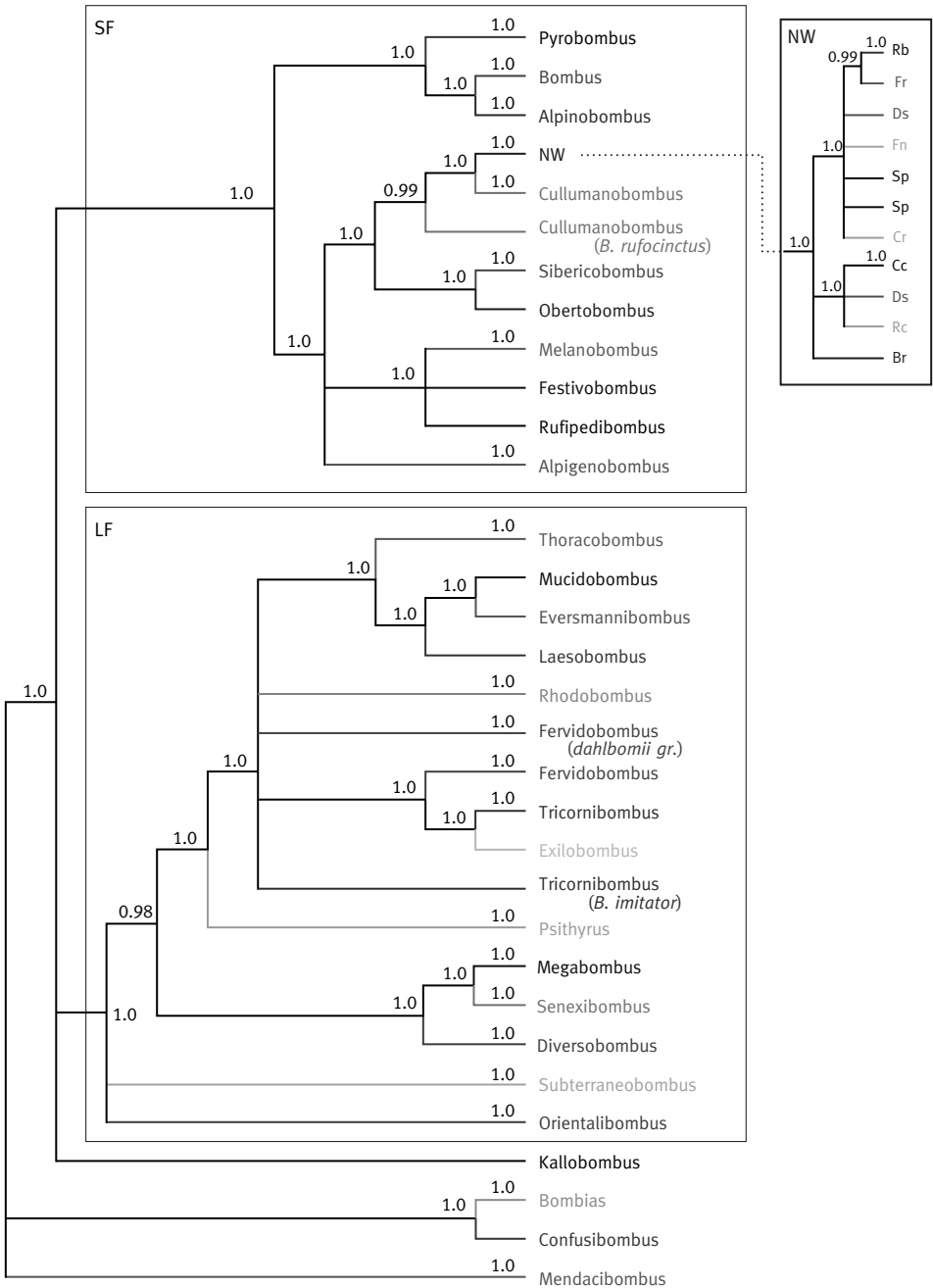
The world bumblebee fauna consists of approximately 250 known species, and it is reasonable to assume that the majority of species have now been discovered (unlike most other invertebrate taxonomic groups) (Williams 1985a, 1994, 1998; Pedersen 1996). Recent classifications place all of the known species in a single genus *Bombus* (meaning 'booming'). The majority of these species are known as 'true' bumblebees, and have a social worker caste which is more or less sterile (they cannot mate but can lay unfertilized eggs that develop into males). The remaining 45 or so species are known as cuckoo bumblebees, and were formerly placed in a separate genus *Psithyrus* (meaning 'murmuring'). These are inquilines that live within the nests of the true bumblebees (they are often described as parasites but strictly speaking this is not accurate, because they do not feed upon their hosts, but only on the food gathered by their hosts). It is now clear that cuckoo bees have a monophyletic ancestry and belong within the genus *Bombus*, so that *Psithyrus* is now regarded as one of many *Bombus* subgenera (Plowright and Stephen 1973; Pekkarinen *et al.* 1979; Ito 1985; Pamilo *et al.* 1987; Williams 1985a, 1994; Cameron *et al.* 2007).

Various subdivisions of the genus *Bombus* have been attempted in the past, many of which have subsequently been discarded. Bumblebee taxonomy is notoriously tricky because as a group they are morphologically 'monotonous' (Michener 1990). Early classifications depended heavily on coat colour patterns (Dalla Torre 1880, 1882), but these are now generally regarded as being of limited value, particularly because most species exhibit considerable colour variation both within and between populations, and also because there often seems to be convergent evolution of coat colour driven by Müllerian mimicry (where two or more harmful species mimic one another's warning signals) (Plowright and Owen 1980; Williams 1991). Such is the confusion in bumblebee nomenclature that there are on average 11 synonyms for each currently recognized species, with *B. lucorum* having over 130.

Classifications based on male genitalia proved to be more useful in assigning species to subgenera (Krüger 1917; Skorikov 1922), but there was little agreement on the relationships between these subgenera until the recent application of molecular tools (Kawakita *et al.* 2004; Cameron *et al.* 2007). In the most comprehensive study to date, Cameron *et al.* (2007) sequenced four nuclear and one mitochondrial gene for 218 bumblebee species and produced a highly resolved phylogeny that supported most of the existing subgenera on the basis of morphological characters (Fig. 1.1). This work suggests that almost all bumblebee species can be assigned to one of two major clades, a 'short-faced' clade and a 'long-faced' clade, which broadly correspond with the previous division of the genus *Bombus* into two sections, *Odontobombus* and *Anodontobombus* (Krüger 1920). These phylogenetic relationships are of relevance to ecologists and conservationists because they correspond with differences in ecology between species. For example, *Bombias* and *Mendacibombus* have a distinctive nest-building behaviour; *Megabombus* generally have very long tongues and favour deep flowers; *Thoracobombus* tend to nest



## 4 Bumblebees



**Figure 1.1** Bumblebee phylogeny showing only the subgeneric relationships with strong support (PP = 0.95). Values on branches are Bayesian posterior probability values. *Abbreviations:* SF, Short-faced clade; LF, Long-faced clade; NW, New World clade; Rb, Robustobombus; Fr, Fraternobombus; Ds, Dasybombus; Fn, Funebribombus; Sp, Separatobombus; Cr, Crotchiibombus; Cc, Coccineobombus; Rc, Rubicundobombus; and Br, Brachycephalibombus. From Cameron *et al.* (2007).

just above the soil surface in tussocky grasses (Williams *et al.* 2008). In many cases very little is known about the ecology or behaviour of particular species, but having a reliable phylogeny at least makes it possible to make informed predictions as to what is most likely, on the basis of known relatives.

Molecular approaches have also proved to be valuable at lower taxonomic levels, revealing the presence of species that could not be detected by traditional methods. The United Kingdom has probably the best studies with regard to bumblebee fauna in the world, yet remarkably a common and widespread species, the aptly named *Bombus cryptarum*, remained undetected until 2005 because it is morphologically very similar to *B. lucorum* (Bertsch *et al.* 2005; Murray *et al.* 2008). It seems probable that there are other such cryptic species remaining to be detected.

## 1.2 The life cycle

Detailed descriptions of the life cycle of bumblebees have been given elsewhere (notably in Alford 1975), and are repeated in brief here. In general, *Bombus* species have an annual life cycle. Queens emerge from hibernation in late winter or spring, and at this time of the year they can often be seen searching for suitable nest sites. The timing of emergence differs markedly between species; some, such as *B. terrestris*, emerge early in February or March while others, such as *B. sylvarum*, emerge as late as May or June (Alford 1975; Prys-Jones 1982). Most temperate species emerge gradually over several months, but arctic and subarctic species such as *B. frigidus* tend to emerge synchronously, within 24 h of the first appearance of willow catkins (Vogt *et al.* 1994). Presumably, this is an adaptation to the very short season in these regions, in which late emerging queens would not have time to rear a colony.

The sites chosen for nesting also vary between species, both in terms of the habitat type in which they are located and in their position (Richards 1978; Svensson *et al.* 2000; Kells and Goulson 2003; Osborne *et al.* 2008b). Gardens seem to support unusually high densities of bumblebee nests, with an estimated mean of 36 Ha<sup>-1</sup> in the United Kingdom (Osborne *et al.* 2008b). In farmland, linear features such as hedgerows, fence lines and woodland edge tend to have more bumblebee nests (20–37 nests Ha<sup>-1</sup>) compared with non-linear features such as woodland or grassland (11–15 nests Ha<sup>-1</sup>) (Osborne *et al.* 2008b). Some bumblebee species always nest underground using pre-existing holes, very often the disused burrows of rodents (e.g. *B. lucorum*, *B. terrestris*). Other species such as those belonging to the subgenus *Thoracobombus* nest on or just above the surface of the ground within tussocks of grass or other dense vegetation, and again tend to use abandoned summer nests of small mammals. In the arctic, where insulation is presumably of great importance, *B. polaris* and *B. hyperboreus* commonly use old lemming nests. A few bumblebee species such as *B. pratorum* are opportunistic, employing a variety of nest sites both above and below ground, including old birds' nests, squirrels' dreys and artificial cavities. *B. hypnorum*, a European species that has expanded its range in recent years and invaded the United Kingdom, has the common name of tree

## 6 Bumblebees

bumblebee for it prefers to nest in holes in trees, using old birds' nests. Its recent success may in part be due to the ready availability of bird nest boxes which it readily utilizes. In Turkey, *Bombus niveatus* has been found to regularly oust redstarts (*Phoenicurus phoenicurus*) from their nests in nest boxes, causing the birds to abandon the site, even sometimes when they have eggs or chicks (Rasmont *et al.* 2008a). I have received anecdotal records of bumblebees driving tits from their nest in the United Kingdom, which is all the more remarkable because tits are known to depredate bumblebees. How common this phenomenon is and which bumblebee species show it is unknown.

The reason that bumblebees often use old nests constructed by other creatures is that they require a supply of moss, hair, dry grass, feathers or other insulating material from which they form the nest. These materials are arranged into a ball within which is a central chamber with a single entrance. Bumblebees generally do not gather their own nesting material, at least not by flying with it back to the nest. However, they will expend considerable effort in dragging materials from nearby into the nest, and in rearranging existing nesting materials. The unusual Amazonian species *Bombus transversalis* will cut and drag leaves back to the nest to form a rainproof roof (Taylor and Cameron 2003).

The queen provisions the nest with pollen, and moulds it into a lump within which she lays her eggs. Generally, between 8 and 16 eggs are laid in this first batch. The pollen lump is covered on the outside with a layer of wax (secreted from the ventral abdominal surface of the queen) mixed with pollen. The queen also forms a wax pot by the entrance to the nest, in which she stores nectar. She incubates her brood by sitting in a groove on top of the pollen lump, maintaining close contact between the lump and her ventral surface (Fig. 1.2). Queens generate a great deal of heat during this period, maintaining an internal temperature of 37–39°C, which enables them to maintain a brood temperature of about 30–32°C (Heinrich 1972a,b). The eggs hatch within about 4 days, and the young larvae consume the pollen. At this early stage, they live together within a cavity inside the pollen, known as the brood clump. In addition to incubating the brood, the queen has to forage regularly to provide a sufficient supply of pollen. It seems probable that this is one of the most delicate stages of the bumblebee life cycle, when a shortage of forage in close proximity or inclement weather could cause the young queen and her colony to perish.

Bumblebees can be divided into two groups according to the way that the larvae are fed. In the so-called pocket makers [which broadly correspond with the long-faced clade of Cameron *et al.* (2007)], fresh pollen is forced into one or two pockets on the underside of the growing brood clump, forming a cushion beneath the larvae on which they graze. The larvae continue to feed collectively. In the later stages of larval development, the queen pierces holes in the wax cap over the clump and regurgitates a mixture of pollen and nectar onto the larvae. In the 'pollen-storers' (Cameron *et al.*'s short-faced clade), the brood clump breaks up and the larvae build loose individual cells from wax and silk within which they live until they pupate. They are fed individually for most of their development on regurgitated pollen and nectar. There seems to be a marked



**Figure 1.2** Queen of *B. lapidarius* incubating the brood clump in her newly founded nest. Incubation is energetically expensive. The nectar pot is placed just in front of the queen so that she can replenish her energy reserves without losing contact with the brood clump. It seems probable that this stage of the life cycle is precarious since the queen must leave the nest to replenish her nectar reserves, but in early spring nectar-rich flowers tend to be few and far between.

difference in the ease with which bumblebee nests can be reared in captivity which corresponds with the distinction between pocket makers and pollen-storers. The latter group includes all of the species that are regularly reared for commercial use, whereas pocket makers are notoriously difficult to rear. As a result of this, our knowledge of bumblebee ecology is heavily biased towards pollen-storers such as *B. terrestris*.

The larvae have four instars. After approximately 10–14 days of development they spin a strong silk cocoon and pupate. It takes a further 14 days or so for the pupae to hatch, so that the total development time is about 4–5 weeks, depending on temperature and food supply (Alford 1975). The queen continues to incubate the growing larvae and pupae, but those near to the centre of the brood clump are kept warmer than those on the periphery. As a result they grow larger and emerge slightly before larvae that develop on the outside. When the first batch of larvae pupate (and hence no longer need feeding), the queen will generally collect more pollen and lay further batches of eggs. When the pupae hatch, the adults must bite their way out of the cocoon, often aided by the queen. In newly enclosed bumblebees, the hairs are entirely white at first, giving them a ghostly appearance; they develop their characteristic coloration after about 24 h. The first batch of offspring are almost invariably workers. Within a few days of their emergence the queen ceases to forage, presumably because this is a hazardous occupation and her survival is more important to the colony than that of her daughter

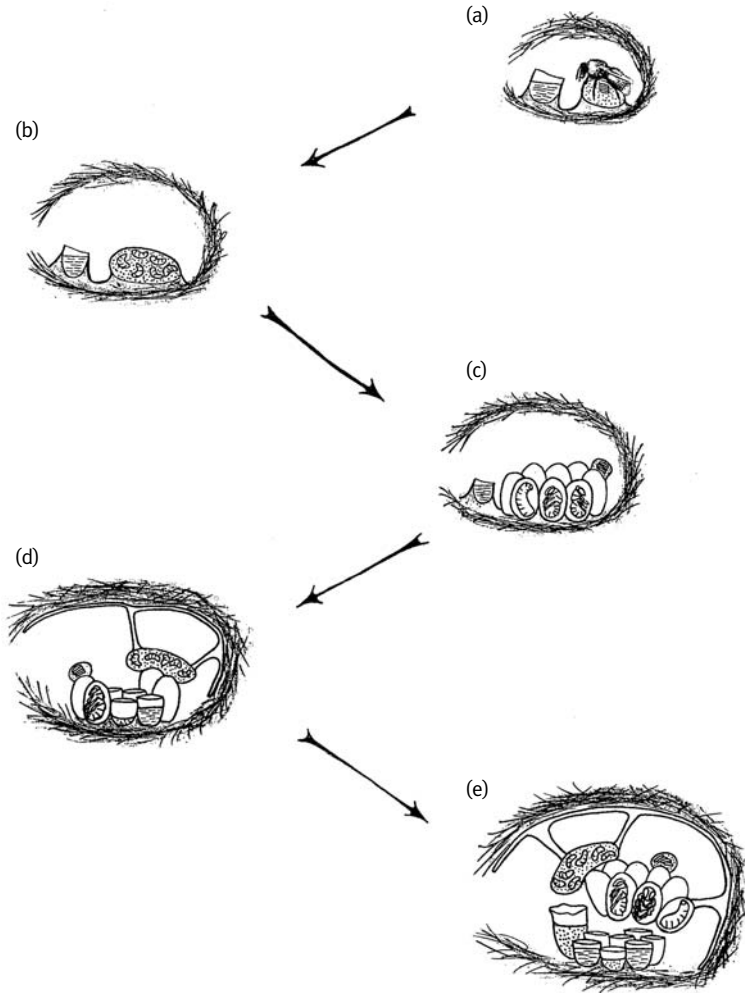
## 8 Bumblebees

workers. This duty is taken over by some of the new workers, while others help her tend to the developing broods.

From this point onwards nest growth accelerates; the nest can increase in weight by 10-fold within 3–4 weeks (Goulson *et al.* 2001) (Fig. 1.3). Several more batches of workers are usually reared, although the size to which the nest grows varies greatly between species. Estimates of worker longevity also vary between species and between studies, from 13.2 days for *B. terricola* to 41.3 days for *B. morio* (Chapter 5). Foragers have a shorter life expectancy than nest bees (Chapter 3). Surplus pollen and nectar may be stored in the empty cocoons from which workers have emerged. The temperature of the nest is regulated (Chapter 2); considerable heat can be generated by the workers if necessary, and they keep the brood warm by pressing their bodies against it. They may also ventilate the nest by fanning their wings near the entrance. Prior to emergence of the workers, Cumber (1949a) reported temperatures of 20–25°C in the nest cavity, increasing to 30–35°C at the height of nest development. Temperature fluctuations are also greater during early stages of colony development, with variation by no more than about 2.5°C once many workers are present (Hasselrot 1960).

The failure rate of colonies seems to be very high, although data are sparse. For example, of 80 *B. pascuorum* nests in southern England followed by Cumber (1953) only 23 produced any new queens (a further 9 produced only males). Similarly, of 36 *B. lucorum* nests placed out in the field by Müller and Schmid-Hempel (1992b), only 5 produced queens. These studies ignore the early stages of colony founding during which colony failure is probably more frequent. Colonies may die out for many reasons; for example because of high rates of parasitism, or they may be destroyed by predators (e.g. badgers) or agricultural practices (e.g. mowing for hay). Availability of a succession of suitable flowers is also vital if colonies are not to starve; Bowers (1985a) found that colonies frequently died out if founded in particular subalpine meadows with a low availability of flowers.

If the nest attains sufficient size, at some time between April and August, depending on the species, the nest switches to the rearing of males and new queens. Some species such as *B. polaris* that live in the arctic where the season is very short rear only one batch of workers before commencing the production of reproductives (Richards 1931). In contrast, colonies of *B. terrestris* can grow to contain up to 350 workers (Goulson *et al.* 2001). The duration of nest growth and the size that it attains is not just determined by climate. Within any one region a range of different strategies can be found. In Europe, *B. pratorum* and *B. hortorum* nests last for about 14 weeks from founding, compared to about 25 weeks for the sympatric *B. pascuorum* (Goodwin 1995) (Fig. 1.4). In general, no more workers are reared once the colony switches to producing reproductives. The main factor that triggers the switch is thought to be the density of workers in the nest, or perhaps more specifically the ratio of workers to larvae, although it is probably under the control of the queen (Chapter 3). Developing queens require more food over a longer period than worker larvae, so they can only be produced if sufficient food is available, and if there are sufficient workers to feed the larvae. Nests are founded over



**Figure 1.3** Nest development of a generalized *Bombus* species. (a) The queen finds a nest within a ball of dry grass, moss and animal hair. She constructs a single nectar pot, and lays her first batch of eggs within a brood clump of pollen mixed with nectar and surrounded by a layer of wax. (b) The eggs hatch and the larvae consume the brood clump. The queen alternates incubating the brood with foraging for further nectar (to fuel incubation) and pollen (for the growing larvae). (c) As they near pupation the larvae spin individual silken cells, and cease to feed. Those near the centre of the brood tend to pupate first. Once her first batch of larvae cease to feed, the queen will lay another batch of eggs in a brood clump constructed on top of the pupal cells (top right). (d) The first workers emerge. They take over foraging, and also aid the queen in caring for further batches of brood. Old pupal cells are recycled as further nectar pots. A wax cover is often constructed over the nest. (e) The nest grows rapidly as the work force expands. Surplus pollen may be stored in specially constructed tall cells (left). After a variable number of worker broods have been reared, the nest switches to production of new queens and/or males.



**Figure 1.4** A maturing *B. pascuorum* nest under moss, showing large numbers of queen pupae. Photograph by Sue Thomas.

a prolonged period in spring, but the production of new queens and drones appears to be approximately synchronized (which means that late-founded nests have shorter durations) (Pomeroy and Plowright 1982; Müller and Schmid-Hempel 1992a).

In Hymenoptera, the males are haploid and females are diploid, so males are produced from unfertilized eggs. This means that the queen can control the sex of her offspring. Workers may also lay eggs, but because they have not mated any eggs that they lay must be male. At the point when the colony switches to rearing of reproductives, some workers often lay eggs, but it seems that generally rather few males are fathered by workers. Owen and Plowright (1982) estimated that 19% of males were the offspring of workers in *B. melanopygus*, but in *B. hypnorum* (a potentially atypical polyandrous species) all males were produced by the queen (Paxton *et al.* 2001). The number of males and queens reared by a colony varies greatly, and is largely determined by nest size; small nests may rear no reproductives. Moderate-sized nests often rear only males, whilst only the largest nests produce both males and queens (Schmid-Hempel 1998).

The young queens leave the nest to forage, returning at intervals and at night, but they do not usually provision the nest. They consume large quantities of pollen and nectar, and build up substantial fat reserves. Males play little part in the life of the colony, although their presence does help keep the brood warm; after a few days within the colony they leave, never to return. Once they have left the nest, the males occupy themselves with feeding on flowers (often rather sluggishly), and with searching for a mate (Chapter 4). The mate location behaviour is unusual. In most *Bombus* species, males deposit pheromone in a number of places in the early morning, choosing leaves, prominent stones, fence posts or tree trunks. They then patrol these sites on a regular flight circuit during the day (Darwin 1865; Sladen 1912). Often a succession of males will adopt more or less the same route, so that a continuous stream of males can be observed at any one point. The pheromone is produced by the labial gland, and consists of a complex mixture of organic compounds, mainly fatty acid derivatives and terpene

alcohols and esters (Kullenberg *et al.* 1973). Each bumblebee species employs a different blend, and the scents of some species are readily detectable by the human nose (Sladen 1912). Different species also patrol at different heights, for example, *B. lapidarius* tends to patrol circuits at treetop level, while *B. hortorum* patrols within a meter of the ground (Bringer 1973; Svensson 1979). Presumably, species-specific pheromones and distinct patrolling heights facilitate young queens in identifying a mate of the correct species. However, mating is rather rarely observed in the wild in bumblebees, and young queens have never been observed to be attracted to the pheromone-marked circuits of males (Alford 1975). Further studies are required to examine exactly where bumblebee courtship and mating usually takes place in natural situations.

Direct observation and dissection of queens suggests that in most bumblebee species they mate only once (Röseler 1973; Sakagami 1976; Van Honk and Hogeweg 1981). This has been confirmed by molecular studies of a range of European bumblebee species which demonstrated that the offspring of a single queen are usually full siblings (Estoup *et al.* 1995; Schmid-Hempel and Schmid-Hempel 2000). However, queens of some species including *B. hypnorum* and *B. huntii* do mate up to three times (Hobbs 1967a; Röseler 1973; Estoup *et al.* 1995). After mating, young queens may continue feeding for a while but before long they begin to search for suitable hibernation sites. As with nest sites, preferences vary between species, but generally queens in the United Kingdom are said to prefer north-facing banks with loose soil (Alford 1975). In contrast, subarctic species probably prefer south-facing sites where snow melts first, so that they are stimulated to emerge from hibernation as soon as conditions are favourable (Vogt *et al.* 1994). Bumblebees are not well equipped for digging, and those queens that I have observed entering hibernation have all dug down into soft, disturbed soil. In gardens they often use the relatively loose compost in flower pots. In more natural settings mole hills may be important in providing suitable disturbed sites.

Once they have found a site, the queen rapidly digs down a few centimetres (again, the preferred depth varies between species) and forms a small oval chamber in which she will remain until the following spring. They survive during this long period of inactivity on substantial fat reserves that fill their abdominal cavity; queens that have not laid down sufficient reserves will perish (e.g. in *B. terrestris* the critical weight is about 0.6 g; Beekman *et al.* 1998). This period of dormancy may begin as early as May in some species, and so it is perhaps misleading to refer to it as hibernation (although for simplicity the term is retained here).

Once the males and young queens have departed, the nest rapidly degenerates. The remaining workers are old and become lethargic. The foundress is usually worn out and expires. Parasites and commensals consume what remains of the comb, and soon very little remains.

It has long been suspected that some species, such as *B. jonellus*, *B. pratorum* and *B. frigidus*, may sometimes have more than one generation per year (Alfken 1913; Hobbs 1967a; Douglas 1973; Alford 1975). Their colonies typically come to an end rather early, in about May, yet sometimes fresh workers are seen foraging late in the summer. Whether



these are the result of new queens taking over their mother's nest, or founding new nests of their own has not been established, but Alford (1975) deems the former to be more likely.

There appear to have been some changes in the life cycle of *B. terrestris* in recent years. In New Zealand, where the species is not native, nests can persist through the winter (Cumber 1949b), presumably because the climate is milder than in England (the origin of the New Zealand population). In North Africa and Corsica, this species is active mainly in the winter (Ferton 1901; Sladen 1912), demonstrating that it possesses considerable phenological flexibility. In 1990, workers of *B. terrestris* were found in January and February in Devon (south-west England) (Robertson 1991). More recently, *B. terrestris* appears to have become more or less continuously brooded in the southern half of England; I have observed queens founding nests in December, and workers are seen all winter during warmer weather. Recent records collected by the Bumblebee Conservation Trust suggest that the phenomenon is spreading steadily northwards, and at the time of writing has spread as far as the north midlands (Leicester and Birmingham). Authoritative works on bumblebees such as Sladen (1912) and Alford (1975) make no reference to this, suggesting that it is probably a recent phenomenon. There are few or no native flowers available at this time of year; all visits are to exotic garden plants. It is presumably no coincidence that these observations are at present confined to the southern half of England, where the winters are milder. This switch to continuous generations may have been favoured by changes in the climate, and by the availability of exotic flowers providing nectar and pollen through the winter.

The small number of bumblebee species that live within the lowland tropics of south-east Asia and South America have atypical life histories. There is no annual cycle, and nests can reach a very large size and contain several thousand workers (Michener and Laberge 1954; Michener and Amir 1977; Brian 1983). As many as 2,500 new males and queens can be produced by a single nest of *B. incarum* in Brazil (Dias 1958). In the Brazilian species *B. atratus*, new queens supersede the foundress, and new colonies may be initiated by swarming in the same way as honeybees (Garófalo 1974).

Cuckoo bumblebees (subgenus *Psithyrus*) have annual life cycles similar to those of typical temperate bumblebee species, except that instead of founding their own nest and rearing workers, they steal a nest from a 'true' bumblebee (Chapter 5). *Psithyrus* females emerge later from hibernation, and search for young nests of other *Bombus* species (strictly speaking female *Psithyrus* are not queens because there is no worker caste). Once located, they enter the nest, kill the queen, and take over her role. The bumblebee workers continue to forage and tend to the brood. The *Psithyrus* female lays eggs that develop into either new breeding females or males. Mate location behaviour and hibernation are similar to other *Bombus* species.

# 2

---

## Thermoregulation

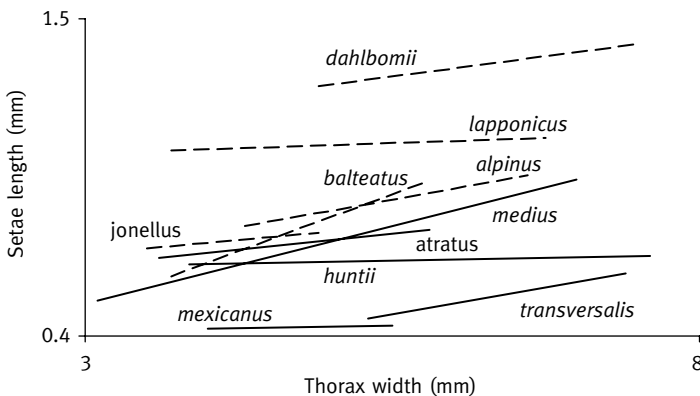
As recently as the 1960s, it was widely believed that insects were all essentially ectothermic, so that their body temperature remained close to ambient temperature unless they used external heat sources (generally solar radiation) to heat themselves. Thanks largely to studies of North American moths and bumblebees carried out by Bernd Heinrich in the 1970s, this is now known to be very far from the truth (see particularly Heinrich 1979b). Although many insects, particularly the small species, are unavoidably ectothermic due to their large surface area to volume ratio, larger flying insects such as sphingid moths, dragonflies and bumblebees can generate considerable quantities of metabolic heat, and use this to maintain stable body temperatures many degrees above the ambient temperature. Indeed, they would be entirely unable to fly without this ability. Much of what follows is based on the work of Heinrich. Readers wishing to know more are directed to his excellent book '*Bumblebee Economics*' (Heinrich 1979b), and to two more recent general texts on insect thermoregulation, '*The Hot-Blooded Insects*' (Heinrich 1993) and '*The Thermal Warriors*' (Heinrich 1996).

### 2.1 Warming up

At rest, bumblebees generally have an internal temperature close to ambient. In the temperate regions where most species live, ambient temperatures in the spring and summer generally fall within the range of 5–25°C. However, to generate the power needed for flight, bumblebees need to raise the temperature of their flight muscles to above 30°C (sphingid moths operate at even higher temperatures around 47°C) (Heinrich 1971). To do so, they generate heat through shivering the flight muscles, and probably also through substrate cycling in the flight muscles (Newsholme *et al.* 1972). In bumblebees, the upward and downward strokes of the wings are each driven by two sets of powerful muscles that in flight contract alternately. During warm-up, they contract at the same time, generating heat but little or no movement (Heinrich 1979b). As they warm-up, so the speed of contractions can increase, generating yet more heat. Balancing this, heat loss increases as the temperature difference between the thorax and the surrounding air (the temperature excess) increases. The minimum muscle temperature required for flight varies greatly between species; some moths that fly in the winter can fly (albeit very weakly) with a thorax temperature of 0°C (Heinrich and Mommsen 1985). In bumblebees the minimum is about 30°C, although the optimum thorax temperature

is probably closer to 40°C (Heinrich 1972a,c,d, 1975a, 1993). It seems certain that different bumblebee species, which vary in size, hairiness and the climate to which they are adapted, have different minimum body temperatures at which flight can occur, but most species have not been investigated. Certainly, species from warmer climates tend to have short hair, while those from high altitudes or latitudes tend to be very woolly in appearance with much longer hairs (Peat *et al.* 2005a; Fig. 2.1).

There is an alternative school of thought with regard to the source of heat generated during warm-up in bumblebees. Newsholme *et al.* (1972) argued that muscle shivering is not necessary, and that bumblebees are able to burn sugars to generate heat in the flight muscles through substrate cycling. They demonstrated that a key enzyme in this process, fructose biphosphatase, has unusually high activity in the flight muscles of bumblebees (Newsholme *et al.* 1972; Prys-Jones and Corbet 1991). In non-flying bumblebees, the rate of substrate cycling is inversely related to ambient temperature, enabling the bees to maintain a stable internal temperature when inactive (Clark *et al.* 1973; Clark 1976). The amount of this enzyme that is present varies greatly between species, and levels appear to correlate with foraging behaviour: bumblebee species such as *B. lapidarius* with high enzyme activity tend to forage on large inflorescences (Newsholme *et al.* 1972; Prys-Jones 1986). It is proposed that while feeding on an inflorescence these species save energy by allowing their body temperature to drop. However, once the flower is depleted (or if they are attacked by a predator), they need to generate heat rapidly to take off, and they do so through substrate cycling. In contrast, species such as *B. hortorum* tend to feed on solitary flowers, and so when foraging they are almost continuously in flight. Since flight generates heat, they have less need for a rapid warm-up mechanism, and thus have lower enzyme levels. A recent study of seven North



**Figure 2.1** Size-related thoracic hair length in 10 species of *Bombus* from two climatic extremes. These linear regression lines show a general positive relationship between hair length and thorax width. Cold climate species are represented by dotted lines and hot climate species by solid lines; note that cold-adapted species have longer hairs than those from warm climates. From Peat *et al.* (2005a).

American species found that fructose biphosphatase is only found at high levels in one of these species (*B. rufocinctus*), but it is not clear whether these interspecific differences correspond with differences in foraging behaviour, or why North American species should tend to have lower levels than European species (Staples *et al.* 2004).

Although Newsholme's argument is plausible and rather neat, Heinrich (1979b) pointed out that thermogenesis in the proven absence of muscle shivering had never convincingly been demonstrated in any insect, while warm-up in bumblebees always seems to be associated with flight muscle action potentials. Shivering in bumblebees is not externally visible, so it is actually quite hard to prove that they are not doing it. Surholt *et al.* (1990) attempted to do precisely this, by using a highly sensitive vibration monitoring system to detect muscle contraction in bumblebees during warm-up. They were unable to detect consistent shivering, although some usually occurred at the start of warm-up. In subsequent experiments (Surholt *et al.* 1991), they apparently demonstrated that the rates of substrate cycling were sufficient to account for observed levels of heat production in bumblebees. However, at about the same time, Esch *et al.* (1991) were performing a delicate experiment in which they mounted a tiny mirror onto the scutellum of *B. impatiens* onto which they shone a light. The reflected light was picked up using a photovoltaic cell partially obscured so that only a downward-pointing triangle of the cell surface was exposed. The tiniest movements of the scutellum (and the mirror) resulted in movement of the position of the light beam on the cell. Any upward movement would result in the light beam falling on a broader portion of the exposed triangle of the cell, generating more voltage. Conversely, downward movement produced less voltage. Using this hypersensitive set-up they demonstrated shivering during all stages of thermogenesis, as evinced by movement of the scutellum. Calculations by Staples *et al.* (2004) suggest that even in bumblebee species with high levels of fructose biphosphatase, the amount of heat that could be generated by substrate cycling would contribute less than 10% of that needed to maintain flight activity in typical ambient air temperatures. Whether this finally lays to rest the substrate cycling hypothesis remains to be seen, for there is still the intriguing cross-species correlation between foraging behaviour and enzyme levels to explain. In addition, demonstrating that shivering *is* taking place does not prove that bees are not also generating heat through substrate cycling. Even a small amount of heat produced through substrate cycling might be important at air temperatures marginal to bee activity. Given the marked differences between bumblebee species, it would be interesting to examine fructose biphosphatase activity in a broader range of species from diverse subgenera, and also to examine enzyme levels in queens which are active early in the year and have the formidable task of single-handedly keeping their brood warm.

Whatever the mechanism of thermogenesis, it is certainly true that bumblebees do generate considerable internal heat one way or the other. Of course there must be a limit to the heat that they can generate, and thus there must be a lower limit to the ambient temperature at which they can fly. This limit is determined by the temperature excess that a bee can maintain, which in turn depends on the rate at which it can

generate heat and the rate at which heat is lost. Heat balance of any organism can be described by the following equation:

$$\frac{dH}{dt} = M - C(T_b - T_a)$$

The change in heat per unit time (i.e. the left-hand side of the equation) depends on the amount of heat that is produced ( $M$ ) and the amount that is lost. The latter depends on the conductance of the body ( $C$ ) and the temperature difference between the body temperature ( $T_b$ ) and the ambient temperature ( $T_a$ ). The amount of heat that can be generated is broadly determined by the muscle mass, which is linearly related to the mass of the bee. The conductance is strongly dependent on the surface area of the bee, and on the degree of insulation. Larger bees have a lower surface area to volume ratio, and thus we would expect them to be able to maintain a higher temperature excess, all else being equal (Stone and Willmer 1989). Bumblebees such as *B. polaris*, which are unusually large and well insulated, are capable of maintaining a temperature excess of 30°C or more, and so can forage at ambient temperatures close to freezing (Vogt and Heinrich 1994). Similarly, queens of *B. vosnesenskii* and *B. edwardsii* can sustain continuous flight in ambient temperatures ranging from 2°C to 35°C. However, workers are considerably smaller and are unable to maintain an adequate body temperature for flight in air temperatures below 10°C (Heinrich 1975a). Bumblebee workers vary considerably in size, and in general it is the larger workers that do most of the foraging (Goulson *et al.* 2002b). One likely explanation for this alloethism is that larger foragers can operate at lower ambient temperatures. They can thus begin foraging earlier in the day, and on cold days. They are also less likely to become grounded when out foraging should the temperature drop.

Fascinatingly, recent evidence suggests that bumblebees adjust their thoracic temperature depending on their motivation to forage: when visiting flowers that are particularly rewarding, either in terms of nectar or pollen, they exhibit a higher thoracic temperature than conspecifics foraging in identical conditions but collecting less valuable food (Nieh *et al.* 2006; Mapalad *et al.* 2008). For example, Nieh *et al.* (2006) found that foraging *Bombus wilmattae* were hotter the higher the sucrose concentration of the nectar they were collecting. Presumably when collecting high-quality food it is worth bearing the extra cost of maintaining a higher thoracic temperature to enable the bee to gather the reward quickly.

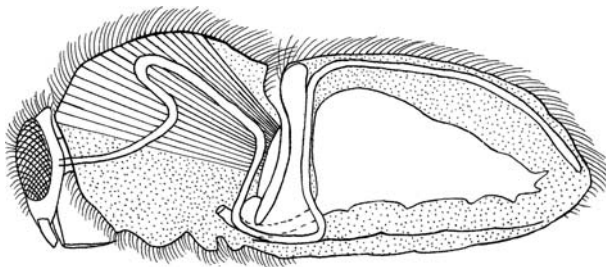
## 2.2 Controlling heat loss

Most endothermic vertebrates tend to maintain roughly even temperatures throughout their body, although the extremities may be a little cooler. In those insects that thermoregulate, body temperatures are generally very uneven. Large flying insects often maintain an elevated and stable thorax temperature, but the rest of the body may

be substantially cooler. In flying bumblebees, the abdomen is typically 10–15°C cooler than the thorax (Heinrich 1979b), a phenomenon that has been beautifully illustrated in bumblebees by the use of infrared imaging (Volynchik *et al.* 2006). This imaging technique reveals that the centre of the thorax contains a hotspot that is more than 20°C warmer than ambient and 10°C warmer than the abdomen.

Heat loss from the thorax to the abdomen is reduced by the narrow waist (the petiole) separating the two, and by an insulating air sac in the anterior section of the abdomen where it contacts the thorax (Fig. 2.2). However, the bumblebee heart pumps haemolymph forward from the abdomen to the thorax, from where it flows backwards through the body tissues to the abdomen. Without this flow of fluid to carry carbohydrates to the muscles, flight would not be possible for long. Yet haemolymph circulation should lead to rapid heat transfer between the thorax and the abdomen. Heinrich (1979b) suggested that the petiole acts as a countercurrent heat exchanger. Cool haemolymph in the heart flows forwards from the abdomen, and in the petiole is forced into intimate contact with the warm haemolymph flowing backwards from the thorax. Inevitably, heat will be transferred between the two as they pass alongside each other, so that rather little heat is lost to the abdomen.

Just as there must be a minimum temperature at which insects can fly, so there is also a maximum. In bumblebees, the maximum thoracic temperature that they can tolerate is about 42–44°C (Heinrich and Heinrich 1983a,b). Here, large size can act against an individual. Flight necessarily generates heat, so that a temperature excess is unavoidable. The larger the insect, the more heat is generated, and the less surface area (proportionally) is available through which to lose it. Thus queens and large foragers are liable to overheat at high ambient temperatures (Heinrich 1975a, 1979b). This presumably explains, at least in part, why most bumblebee species are found in cool climates. Interestingly, this may also explain why the most common element of bumblebee colour patterns worldwide is a black band across the centre of the thorax, the part of the



**Figure 2.2** Diagrammatic longitudinal section of a bumblebee, showing features involved in thermoregulation (redrawn from Heinrich 1979a). Heat is produced by the flight muscles in the thorax. The thorax is well insulated on the outside with a dense furry coat, and heat loss to the abdomen is minimized by the narrow petiole, thought to act as a heat exchanger, and by insulating air sacs in the abdomen.

insect that gets hottest during flight. The small number of bumblebees that occur in lowland neotropical forests are also largely black, and Williams (2007) suggests that dark colour may aid the radiation of excess heat.

At moderately high ambient temperatures, large insects such as bumblebees and dragonflies can avoid overheating by shunting heat from the thorax to the abdomen, which increases the surface area from which heat can be dissipated (Heinrich 1976c). If, as Heinrich (1979b) argues, the petiole acts as a countercurrent heat exchanger, how can this be achieved? The size of the aperture between the thorax and the abdomen is controlled by the ventral diaphragm; when it contracts, the aperture widens. However, when the thoracic temperature approaches 44°C (the approximate lethal limit), several marked physiological changes take place (Heinrich 1979b). Heart beat amplitude increases and the frequency halves, while the frequency of contraction of the diaphragm increases and steadies to match that of the heart. The abdomen also begins to pump at the same frequency (about 350 beats per minute). This leads to alternating pulses of haemolymph between the thorax and the abdomen. As the abdomen expands, the diaphragm contracts, drawing a pulse of hot haemolymph from the thorax into the abdomen. As the abdomen contracts, and the heart beats, a pulse of cool liquid flows forwards into the thorax. During each pulse, little or no liquid flows in the opposite direction, so the heat exchange system ceases to operate.

At very low ambient temperatures, shunting heat from the thorax to the abdomen may serve a quite different purpose to avoidance of overheating. *B. polaris* is the northernmost social insect in the world, reproducing well within the Arctic circle. It is a large, unusually hairy bumblebee that is able to exist in regions where, even in the height of summer, ambient temperatures rarely exceed 5°C (Vogt and Heinrich 1994; Heinrich 1996). As we have seen, all bumblebees have to maintain a high thoracic temperature to remain active. However, Vogt and Heinrich (1994) demonstrated that, unlike other bumblebees that inhabit temperate regions, queens of *B. polaris* also maintain a stable and elevated abdominal temperature (>30°C). They found that this enables them to develop eggs within their ovaries quickly, something that is presumably important in the short Arctic summer. Workers and males of this species have no eggs to develop, and their abdomens are substantially cooler.

### 2.3 Thermoregulation of the nest

Depending on the latitude at which they live, bumblebee queens have approximately 2–7 months to found a nest, rear a force of perhaps several hundred workers, and then produce the next generation of reproductives. To compress this cycle into such a short space of time, the immature stages must be incubated to hasten their development. Heating of the abdomen before egg laying may be confined to species that inhabit cold climates, but heating of the abdomen to incubate the brood is found in all bumblebees that have been examined. Once the first batch of eggs has been laid the queen spends a considerable amount of time incubating them. She builds the brood clump with a

groove on the dorsal surface in which she sits, allowing for close contact between the brood and the ventral surface of her abdomen and thorax (Heinrich 1974). While incubating she produces heat in her thorax, and distributes this to the abdomen by pulsing contractions of the abdomen (Heinrich 1979b). Heinrich (1974) found that *B. vosnesenskii* queens can maintain a brood temperature up to 25°C above ambient temperature even in the absence of insulation. The amount of heat transferred to the brood is controlled by adjusting the rate of heat transfer from the thorax to the abdomen; in this way, a stable brood temperature can be maintained under fluctuating ambient conditions.

Incubation is undoubtedly costly. Silvola (1984) estimated that a *B. terrestris* queen uses about 600 mg of sugar per day at temperatures typical for central Europe, and that to obtain this she may visit up to 6,000 flowers. Of course in her absence the brood will rapidly cool, so availability of plentiful, rewarding flowers near to her nest is vital.

Incubation of the brood is aided by the nest site and construction. Queens of some species choose south-facing banks in which to nest, and build their nest above the soil surface where it is exposed to solar warming. Others nest underground, using the insulation provided by abandoned rodent's nests. Whether nesting above or below ground, the queen uses the materials that are available to construct an insulated ball within which the brood is reared. As the nest grows this may be supplemented with a wax cap which traps warm air. Once workers are available, they too will incubate the brood. The more workers that are available, the more stable the nest temperature (Seeley and Heinrich 1981). In established nests, the temperature is remarkably stable at around  $30 \pm 1^\circ\text{C}$ . Active incubation may become unnecessary as a colony grows, since the activity of many bees can produce sufficient heat to warm the nest. Indeed, large colonies may overheat, at which point some workers switch to fanning the brood with their wings (Vogt 1986). At these times, part of the wax cap may also be removed from the nest. Workers also fan the nest in response to rising  $\text{CO}_2$  levels (Weidenmüller *et al.* 2002).

The thermoregulatory capacity of established bumblebee nests is impressive. I once attempted to kill a commercial colony of *B. terrestris* by placing it in its entirety in a domestic freezer at  $-30^\circ\text{C}$ . After 24 h, I returned to find the colony alive and buzzing loudly; the workers had gathered into a tight clump over the brood and were presumably shivering at maximum capacity. The queen was hidden in their centre. Subsequent experience has shown that briefly anaesthetizing the nest with  $\text{CO}_2$  before placing it in the freezer is much more effective.

Although no workers appear to specialize entirely in nest thermoregulation, this task is adopted more readily by some bees than others. It seems that individual bees differ in the threshold at which they respond to either declining or rising temperatures (Weidenmüller 2004; Gardner *et al.* 2007). As nest temperature increases, bees with the lowest threshold for fanning behaviour begin to do so (O'Donnell and Foster 2001; Weidenmüller 2004). If the nest continues to get warmer, bees with higher thresholds switch to fanning as well. Conversely, if nest temperature is low, some bees begin to incubate brood. If the temperature drops further, more bees switch to incubation. Lifetime effort on fanning and incubation are positively correlated, so that bees that do



one tend also to engage in the other. Bees with high thresholds may rarely if ever engage in thermoregulatory behaviour under natural conditions; these individuals presumably specialize in other tasks such as foraging. By containing a range of individuals with varying thresholds, the colony responds appropriately to thermal challenge, allocating effort to thermoregulation as required and not overcompensating for falling or rising nest temperatures. What is not known is how the threshold for each bee is determined, and how a range of thresholds can be present among a group of very closely related workers.

Foragers of social insects such as bumblebees and honeybees have an advantage over solitary species with regard to warming up, for they can exploit the warm environment of the nest. Internal heat production is slow at low temperatures, so that it may take a long time for a bee to become warm enough to fly (and at very low temperatures they may be entirely unable to do so). Warming up is a costly activity, for during warm-up energy is being expended without any rewards being accrued. Thus the shorter the duration the better. Bumblebee nests are insulated and maintained at a temperature close to 30°C through metabolic heat production, so that foragers have little trouble attaining flight temperature in the cool temperatures of early morning. In contrast, solitary species may be unable to forage until much later in the day. It has been suggested that this may give social bees a competitive advantage by enabling them to gather the bulk of floral resources before solitary bees are able to begin foraging (many flower species produce nectar at night so that nectar levels are highest first thing in the morning and subsequently decline through exploitation by bees).

# 3

---

## Social Organization and Conflict

With their fat and furry appearance, their slow, meandering flight amongst flowers and their docile behaviour, it is easy to dismiss bumblebees as charming but dim. Examination of a nest might confirm this opinion; it is, in appearance, a ramshackle affair compared to that of the honeybee. The pupal cells, honey pots and larvae are haphazardly arranged. Housekeeping is poor—bees often defecate in and close to the nest, and the nest is often overrun with parasites and commensals. For these reasons, and because of the difficulties involved in finding bumblebee nests, researchers were slow to investigate the bumblebee social system. Bumblebee workers were considered to be generalists, each carrying out all tasks rather than dividing up the work in the efficient way that, for example, ants or honeybees do. Similarly, although the honeybee waggle dance has been known for many years, it was erroneously assumed that bumblebees did not communicate about sources of forage (Dornhaus and Chittka 1999). However, in recent years interest in the social life of the bumblebee has undergone a renaissance. Perhaps in part because some species can now be bred in the laboratory (or the nests bought from commercial suppliers), in the past 20 years bumblebees have been used for studies of diverse topics including queen–worker conflict, caste determination, polyandry and parasite resistance, and alloethism. This work is revealing that, despite their bumbling appearance, the social life of the bumblebee is every bit as complex as that of other eusocial insects.

Before delving further into the social organization of bumblebees, a brief explanation is required regarding the slightly odd genetic system possessed by bumblebees and other hymenopterans. Most familiar organisms, including ourselves, are diploid, meaning we have two copies of each chromosome, and hence two copies of every gene. Gametes (sex cells) are formed by a special cell division process known as meiosis, during which the chromosome pairs are separated so that each gamete has just one copy of each (hence the gamete is haploid). Fusion of two gametes (sperm and egg) restores the full complement of two copies of each chromosome and thus forms a viable organism. Hymenopterans (and some other organisms) do something rather different. Females are typically diploid, and produce eggs by meiosis, just as do familiar diploid organisms such as ourselves. However, males are haploid (usually), and formed from an *unfertilized* egg. Hence, these organisms are known as haplodiploids.

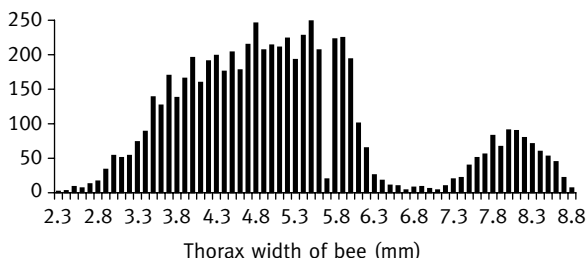
This has all sorts of interesting consequences: females can produce male offspring without ever mating; by controlling whether eggs are fertilized, females can control

whether they lay eggs that will become sons or daughters; all sperms produced by a male are genetically identical to one another and to every cell in the male's body. Perhaps the most relevant quirk of this system is that sisters are unusually highly related to one another. Relatedness (technically, the number of genes shared by common descent) is measured by the coefficient  $r$ . For normal sisters in diploid organisms,  $r = 0.5$ ; they share 50% of each other's genes by common descent. In contrast, in hymenopterans, full sisters share 75% of their genes. This means that a worker bee is more closely related to her sister ( $r = 0.75$ ) than she is to her own daughter ( $r = 0.5$ ). This, in essence, is what predisposes hymenopterans to evolving sociality: a bee, wasp or ant nest is a (sometimes vast) group of sisters helping their mother produce yet more sisters. All else being equal, given the choice between producing her own daughter or helping to produce a sister, a female hymenopteran should choose the latter.

### 3.1 Caste determination

Bumblebees exhibit marked variation in size (Plate 3). Queens are the largest caste and, in pollen-storers such as *Bombus terrestris* (see Chapter 1), the size distribution of females is strongly bimodal, with little overlap between the size range of queens and that of other workers (Fig. 3.1). However, size is not a reliable indicator of caste since, in some species, particularly the pocket-making species, there is a considerable overlap (Plowright and Jay 1968). Structurally, queen and worker bumblebees are identical in all other aspects of their external morphology. The most striking difference between queens and workers is in the size of their fat deposits; workers have very little fat, particularly in their abdomen, leaving plenty of room for the honey stomach, an enlargement of the oesophagus in which nectar can be stored on foraging trips. In contrast, in young queens the abdomen is largely full of fat. This leads to queens being heavier for their size than workers (Richards 1946; Cumber 1949a).

What determines whether a female bee becomes a worker or a queen? All eggs are capable of developing into either, regardless of when they are laid during colony development. Thus even the very first batch of eggs laid in a nest can be induced to



**Figure 3.1** Frequency histogram of numbers of the different castes of *B. terrestris*, grouped by thorax width. On the basis of all the bees in 28 fully developed nests ( $n = 6,371$ ) (D.G., unpublished data).

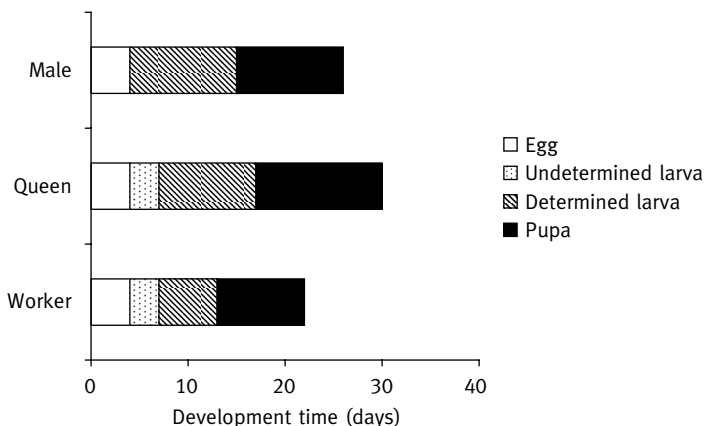
develop into queens (Sladen 1912; Free 1955c). In honeybees, prospective queens are fed royal jelly which is nutritionally richer than the food given to larvae destined to become workers (Haydak 1943; Brian 1965b). Some authors have suggested that in bumblebees there may be similar differences in the types of food fed to queens versus workers. Lindhard (1912) proposed that the diet of future queens was supplemented with masticated eggs, although this was never substantiated. After their initial period of feeding on pollen within the brood clump, larvae are fed on a mixture of pollen and nectar, combined with proteins secreted by the adult bees (Pereboom 2000). These proteins are probably mainly invertase and amylase produced in the hypopharyngeal gland (Palm 1949; Pereboom 2000). This mixture is regurgitated on to the larvae as a droplet. Ribeiro (1994, 1999) suggested that future queens receive additional glandular secretions, but these have not been identified and this remains speculative. In terms of the total protein, pollen and carbohydrate in the food mixture, larvae of all castes receive the same proportions (Pereboom 2000). In fact, nurse bees often feed queen, worker and male larvae in rapid succession using the same crop content (Katayama 1973, 1975). It thus seems unlikely that there can be qualitative differences in the food received by larvae of different castes.

There are differences in the way that sexual broods are fed in pocket-making species. Worker larvae are fed for most of their development on pollen deposited in pollen pockets. In comparison, male larvae and those destined to become queens are fed on regurgitated food from an earlier age (Alford 1975). Some authors have suggested that caste determination is simply a matter of how much food the larvae receive (Röseler and Röseler 1974; Alford 1975; Ribiero *et al.* 1999). Increasing the frequency of feeding makes larvae more likely to develop into queens in *B. pascuorum* (Reuter 1998), but not in *B. terrestris* (Pereboom 1997). Feeding rate is presumably dependent on the ratio of workers to larvae, and this is strongly correlated with queen production in *B. terricola*, *B. perplexus* and *B. ternarius* (Plowright and Jay 1968). However, measurement of growth rate of future queens versus workers revealed no difference in *B. terricola* (Plowright and Pendrel 1977) and, contrary to expectation, queens of *B. terrestris* developed more slowly during their early instars than workers of the same age (Ribeiro 1994). This is clearly not what we would expect if future queens were fed more than future workers. Larvae that are to become queens are fed more frequently (Röseler and Röseler 1974; Alford 1975; Ribiero *et al.* 1999) but, as Pereboom (2000) points out, the period of rapid feeding of future queens in *B. terrestris* is after the point at which worker larvae have ceased to feed (i.e. caste has already been determined). By experimentally starving larvae, Pereboom *et al.* (2003) demonstrate that *B. terrestris* larvae produce a cue when hungry that stimulates workers to feed them, suggesting that the rate at which larvae are fed might at least partially be controlled by the larvae themselves rather than the workers.

It is now generally accepted that, in *B. terrestris* at least (but perhaps not in pocket makers such as *B. pascuorum*), caste is determined early in larval development. The queen appears to excrete a pheromone to which larvae are sensitive at an age of about 2–5 days; if it is present they enter an irreversible pathway towards development as

workers (Röseler 1970, 1991; Cnaani *et al.* 1997, 2000). If this pheromone is not present, the larvae become queens (Röseler 1991; Cnaani and Hefetz 1996; Pereboom 1997, 2000; Ribeiro *et al.* 1999). The pheromone has not yet been identified, but the evidence for its existence is convincing (e.g. Alaux *et al.* 2006; Lopez-Vaamonde *et al.* 2007). It seems that the pheromone is not airborne, but is transmitted directly by contact from bee to bee and from adults to larvae. Röseler (1970) found that larvae separated from the queen by a fine mesh developed into queens, but if workers were regularly moved from the queen's side to the side the larvae were on, then the larvae developed as workers. Although the identity of the pheromone is not known, it seems that it probably acts by suppressing the production of juvenile hormone, and low levels of juvenile hormone lead to larvae moulting earlier and at a smaller size. Topical applications of juvenile hormone to first or second instar larvae of *B. terrestris* results in them developing into queens (Bortolotti *et al.* 2001), and natural levels of juvenile hormone and ecdysteroids are higher in larvae destined to become queens than in larvae destined to be workers (Cnaani *et al.* 1997, 2000; Hartfelder *et al.* 2000).

Pheromone signals of this sort are probably not enforceable (Seeley 1985a; Keller and Nonacs 1993). If it were in the best interests of the larvae to develop as queens we would expect them to do so (Bourke and Ratnieks 1999). Perhaps attempting to develop into a queen during the early stages of colony development is a poor strategy for a larva to adopt, for if insufficient workers are available to feed her then the prospective queen would be small, and small queens are likely to die during hibernation (Beekman *et al.* 1998). It seems likely that the pheromone signal from the queen is the best indication that the larvae have as to their optimal course of development.



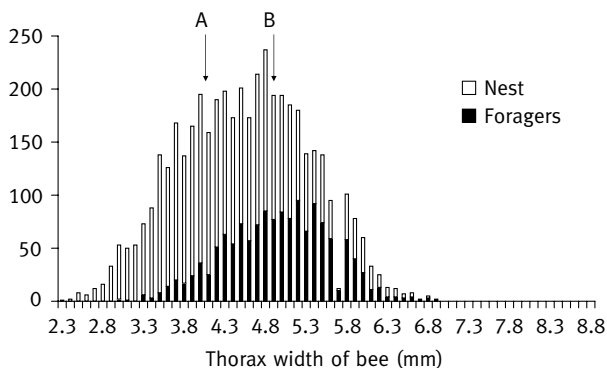
**Figure 3.2** Development time periods of workers, males and new queens of *B. terrestris* (development time taken from Duchateau and Velthuis 1988) (see Shykoff and Muller 1995). At hatching, diploid larvae have the potential to become either workers or queens, but after about 3 days their pathway becomes determined.

Whatever the details of the mechanisms involved in caste determination, once caste has been determined, larvae that are destined to become queens enter a different developmental pathway and continue to feed for longer than those that become workers, thus attaining a much greater size (Cnaani *et al.* 1997). They also have a longer pupal development (Frison 1928, 1929; Röseler 1970) (Fig. 3.2).

### 3.2 Division of labour

Within the worker caste there is great variation in size, even within single bumblebee nests. For example, thorax widths of workers of *B. terrestris* range from 2.3 to 6.7 mm and body mass varies eightfold from 0.05 to 0.40 g (Fig. 3.3). *B. terrestris* is a pollen-storer; worker size variation is even greater amongst the pocket-making species (Pouvreau 1989). Size variation of such magnitude is extremely rare in other insects, and is not found in other social bees; for example, workers of honeybees, *Apis mellifera*, are markedly uniform in size, particularly within single colonies. So why do bumblebee workers vary so greatly in size?

In the very first batch of workers reared by a queen, the only source of warmth is provided by the queen herself who incubates the brood. Larvae situated closest to the incubation groove in which the queen sits tend to grow larger than those further away (Alford 1975). For subsequent broods the nest temperature is likely to be more even, because it is regulated by a number of workers. However, in pocket-making bumblebee species (*Odontobombus*), groups of larvae live and feed within a wax covered chamber on pockets of pollen provided by workers. It is likely that the position of larvae within the group affects how much food they receive (they may actually compete for food), so that some grow larger than others (Sladen 1912; Cumber 1949a). This would explain why workers of pocket-making species vary more in size than do pollen-storers (Alford 1975; Pouvreau 1989). In pollen-storers such as *B. terrestris*, larvae spend most of their



**Figure 3.3** Frequency histogram of numbers of worker bees grouped by thorax width. Frequencies for bees caught in the nest ( $n = 3,077$ ) are stacked on top of those for foragers ( $n = 1,417$ ). The mean sizes of each group are indicated by arrows. From Goulson *et al.* (2002b).

development in individual silk cells, and are fed directly on droplets of nectar and pollen mixes, regurgitated by the adults directly on to the body of each larva (Alford 1975). The size attained by larvae is directly proportional to the amount of food they are given (Plowright and Jay 1968; Sutcliffe and Plowright 1988, 1990). Thus in this group of bumblebees, the size of new workers is under the direct control of the bees rearing them (Ribeiro 1994). Yet as we have seen, even pollen-storer workers exhibit an eightfold variation in mass. It seems implausible that this is the result of sloppy parenting skills, the accidental neglect of some larvae at the expense of others; if having a workforce of uniform size were advantageous one would expect mechanisms to have evolved which would ensure an equitable distribution of food, or prevent larvae from pupating until they reached the required size. Given that larvae are reared in a controlled environment by a team of specialized workers, it seems far more likely that this size variation has an adaptive function; that colonies benefit from rearing workers of a range of sizes.

What might this benefit be? The most obvious comparable instance of size variation in the worker caste of social insects occurs in some ant and termite species. Here, size is related to behaviour, with individuals of particular sizes specializing in particular tasks; a phenomenon known as alloethism. For example, in leaf-cutter ants of the genus *Atta*, the largest workers are soldiers, specializing in nest defence against mammals; medium-sized workers forage for food, while the smallest workers tend the fungus garden and initiate alarm responses along trails near the nest (Hughes *et al.* 2001).

Polyethism, the behavioural specialization of individual workers on particular tasks, is thought to be the key feature underlying the phenomenal ecological success of the eusocial insects (Wilson 1990). The same can be said of humans; we each specialize in particular tasks, such as carpentry, hairdressing, farming, or the study of insects, in which we build up expertise. The benefits of such a system are obvious; if they are not clear, try asking an accountant to reshoe your horse. In bumblebees, there is disagreement in the literature as to whether they exhibit polyethism. The traditional view is that individuals exhibit little behavioural specialization. They do not exhibit the clear age-based polyethism characteristic of honeybees (*A. mellifera*) (in which young workers do jobs in the nest and switch to foraging as they age), and workers regularly switch between foraging and performing tasks within the nest (Free 1955a; Van Doorn and Heringa 1986; Cameron and Robinson 1990). However, this view is questionable; there is abundant evidence that bumblebee workers do exhibit polyethism. Young adults only perform within-nest tasks and are more likely to become foragers as they become older (Pouvreau 1989; O'Donnell *et al.* 2000; Silva-Matos and Garófalo 2000). Wax in bumblebees is secreted on the underside of the abdomen, beginning on the second day after adult emergence but declining after the first week (Röseler 1967). Since wax is only required within the nest, young workers are predisposed towards nest maintenance tasks. In terms of age-related polyethism, the only difference between honeybees and bumblebees is that, in bumblebees, the age at which individuals switch to foraging is variable and some workers never become foragers. Young foragers generally collect nectar and tend to switch to collecting pollen as they age (Free 1955a), perhaps because collecting and

handling pollen is a more complex task than collecting nectar; Raine and Chittka (2007a) found that *B. terrestris* workers took three times as long to learn to gather pollen as they did to learn to extract nectar even from morphologically complex flowers.

Bumblebees probably do exhibit more behavioural plasticity than honeybees. Individuals can switch between tasks in response to colony requirements; for example, nest bees will switch to foraging if the foragers are experimentally removed or if nectar reserves are artificially removed (Kugler 1943; Free 1955a; Pendrel and Plowright 1981; Cartar 1989). Similarly, when nectar reserves are removed, foragers switch from pollen to nectar collection, and vice versa (Free 1955a; Cartar 1989; Plowright and Silverman 2000). Just as individual bees differ in the threshold temperature at which they begin incubating or fanning the brood (Chapter 2), individuals also differ in the threshold level of resources within the colony to which they respond (Van Doorn 1987; Cartar 1992a). Specialized foragers bring most food to the nest, while the majority of within-nest tasks are carried out by bees that primarily stay in the nest (O'Donnell *et al.* 2000). Just as in humans, specialists are presumably more efficient at their tasks; workers that are primarily foragers occasionally do within-nest tasks, but they do so much less quickly than specialized nest bees (Sakagami and Zucchi 1965; Cartar 1992a; O'Donnell and Jeanne 1992).

In addition to foraging and brood maintenance there is at least one other task that workers perform. Large nests of *B. lucorum*, *B. terrestris*, *B. hypnorum* and probably many other species generally have one or more guard bees that sit within the nest entrance and scrutinize foragers as they enter the nest (Free 1958) (Fig. 3.4). Using marked bees in *B. terrestris* colonies, we have found that the same individual carries out



**Figure 3.4** Guard bees sit inside the entrance of a *B. hypnorum* nest. This species commonly uses bird nest boxes, as here, and naturally nests in holes in trees, from which it gets the common name of tree bumblebee. Photograph by Juliet Osborne.



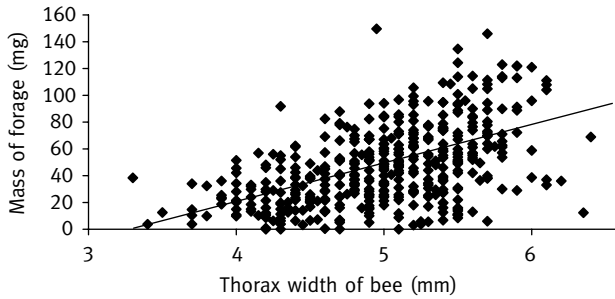
this task for many days (D.G., pers. obs.). Thus bumblebee workers clearly do exhibit a range of behavioural specializations.

Do these differences in behaviour relate to size (i.e. is there alloethism within bumblebee colonies)? It was long ago noticed that foragers of a range of bumblebee species appear to be larger, on average, than bees that remain in the nest (Colville 1890; Sladen 1912; Meidell 1934; Richards 1946; Cumber 1949a; Brian 1952; Free 1955a). In samples of 4,794 *B. terrestris* workers from 28 nests, we have found that nest bees are consistently smaller than foragers (mean thorax widths  $4.34 \pm 0.01$  and  $4.93 \pm 0.02$  (mm  $\pm$  SE), respectively; Fig. 3.3) (Goulson *et al.* 2002b). It seems that the difference in average size between foragers and nest bees comes about because large workers tend to switch from within-nest tasks to foraging at an earlier age, while the very smallest workers never switch to foraging (Pouvreau 1989). Even in captive nests of *B. huntii* in which the workers do not have the option to go foraging, thermoregulation of the brood is largely carried out by the smallest workers (Gardner *et al.* 2007). Thus bumblebees do exhibit alloethism.

Why then do larger workers tend to be foragers and small bees tend to look after the brood? In leaf-cutter ants, the explanation for alloethism is partially obvious; the large soldiers with their huge jaws are far better equipped to inflict damage on an attacking predator such as an armadillo than their smaller siblings [although the full explanation for alloethism in leaf-cutter ants is far more complicated than this; see Hughes *et al.* (2001) for a discussion]. For bumblebees, it is not immediately obvious why larger bees might be better suited to foraging.

Rather than trying to explain why foragers are large, Free and Butler (1959) suggested an explanation as to why nest workers should be small; they argued that they would be better able to manoeuvre within the cramped confines of the nest. In a test of this hypothesis, Cnaani and Hefetz (1994) experimentally manipulated the size of nest workers of *B. terrestris* to create nests with only large or small workers. They demonstrated that larvae reached a larger size when tended by large workers, compared to when they were tended by an equal number of small workers. However, this does not fully refute the hypothesis that small bees are better able to work within the nest, for a fairer comparison would have been between larvae tended by an equal biomass consisting of either a few large workers or many small ones. One cannot help but suspect that, in this situation, many hands may well make light of the work and produce larger offspring. This experiment remains to be done, but even if it did find that small bees are advantageous within the nest, it would still not explain why large worker bees are reared at all. We also need to demonstrate a positive advantage for large size in foragers.

A number of possible explanations for the larger size of foragers have been proposed. Free and Butler (1959) suggested that large workers could carry more forage. This is intuitively obvious and subsequent experiments have confirmed it to be true. If foraging *B. terrestris* are captured as they return to the nest, and the mass of forage measured, there appears to be a more or less linear relationship between the thorax width of the forager and the mass of forage they are carrying (Goulson *et al.* 2002b) (Fig. 3.5). The mass of forage, calculated as a proportion of the body mass of the bee, did not vary with body

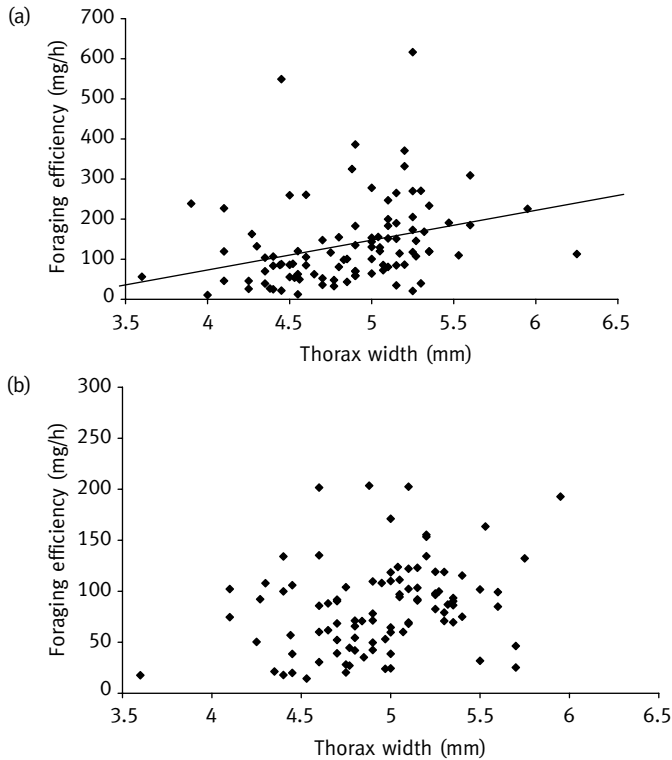


**Figure 3.5** Relationship between mass of foraging *B. terrestris* workers and the mass of forage (pollen and nectar combined) that they bring back to the nest in a single foraging trip. From Goulson *et al.* (2002b).

size, with bees carrying on average a mass of pollen and/or nectar equivalent to 23.1% of their unladen body mass (remarkably, the heaviest load recorded amounted to 77.1% of the unladen body mass of the bee).

Although larger foragers can carry more food, this does not explain why foragers are large. Presumably, the cost to the colony of rearing a worker is approximately proportional to its size. For example, for every worker of 250 mg the colony could have reared two workers of 125 mg. The single large bee or the two small bees would each be expected to bring back about 58 mg of forage per trip, but it seems likely that the single large bee would take much longer to do so (for it would have to single-handedly visit twice as many flowers as each of the small bees). Few studies have examined foraging efficiency with respect to size. As noted earlier, Stout (2000) found that smaller workers of *B. terrestris* and *B. lapidarius* were better able to trigger the complex flowers of *Cytisus scoparius* than were large workers and were also faster at handling flowers that had previously been triggered. Morse (1978b) found no differences in the foraging speeds of large and small workers of *B. vagans* foraging on *Vicia cracca*. To test whether large workers do bring back more food per unit time than small workers, we arranged *B. terrestris* nests so that bees leaving or entering the nest walked over the pan of a balance, enabling us to record both the duration of each foraging trip and the net mass gained during foraging (Goulson *et al.* 2002b). The data demonstrated that larger bees are more efficient foragers when collecting nectar, but not pollen (Fig. 3.6). However, whether the greater efficiency of larger bees is sufficient to offset their greater rearing costs is doubtful.

Why might larger bees be able to gather nectar more quickly? Pouvreau (1989) suggested that larger workers are at an advantage in foraging because they have longer tongues and are able to feed on deeper flowers [the relationship between overall size and tongue length is proportional (Medler 1962a,b; Pekkarinen 1979; Goulson *et al.* 2002b)]. However, having a long tongue is not necessarily an advantage. Bees with short tongues can forage more quickly on shallow flowers (Plowright and Plowright 1997). In fact, the most common bumblebee species in the United Kingdom are all relatively



**Figure 3.6** Relationship between foraging efficiency (mass of forage gathered per time spent foraging) and thorax width. On the basis of 98 *B. terrestris* foragers from 3 nests. From Goulson *et al.* (2002b). Trips were recorded as pollen gathering if pollen was visible in the pollen baskets of returning bees. (a) Nectar gathering trips. (b) Pollen gathering trips (in which nectar may also have been gathered).

short-tongued species, where most long-tongued species are on the brink of extinction (Edwards 1999). If having a long tongue provided an automatic advantage, we would expect foragers to have evolved longer tongues, not a larger size.

Another possibility is that larger bees (which have larger eyes) may have greater visual acuity, and so be better able to find flowers and reduce search times (Spaethe and Chittka 2003). The visual acuity of bumblebees is greater than that of honeybees (which are smaller) (Macuda *et al.* 2001). Kapustjanskij *et al.* (2007) demonstrate that the larger eyes and larger individual ocelli of large *B. terrestris* workers enable them to see and fly at lower light intensities than their smaller sisters, which should presumably enable them to forage earlier in the morning or later at night. There is some evidence that, in addition to size, larger workers have morphological adaptations that suit them to foraging. For example, large workers of *B. terrestris* have disproportionately smaller limbs, which may reduce heat loss (Peat *et al.* 2005a). They also have disproportionately more

olfactory sensilla on their antennae (i.e. they occur at higher density), which results in their antennae giving a higher electroantennogram response to a given odour, and in turn enables the bee to make correct choices based on lower concentrations of odour cues than are needed by smaller sisters (Spaethe *et al.* 2007).

Morse (1978a) suggested that large size may enable workers to forage over greater distances. According to Free (1955b), large bumblebee *species* tend to go on foraging trips of longer duration than smaller species and thus may cover larger distances. However, there have been no studies of the distance or duration of foraging trips in relation to size variation within species and, in general, very little is known of the foraging range of bumblebees (see Chapter 6). Similarly, we do not know how flight speed relates to size; if larger bees fly faster then this clearly would provide some advantage in foraging. The relative flight speeds of foragers in relation to their size have never to my knowledge been examined. Cresswell *et al.* (2000) calculated the upper limit of the foraging range of bumblebees to be about 10 km, this being the maximum distance from which a bee foraging for nectar could return with a net profit. The limit is imposed by the rate at which energy is burned on the flight back to the nest; this must be less than the total amount of energy that can be contained in the honey stomach. The energetic cost of foraging is approximately proportional to weight (Heinrich 1979b), and it has been shown that the amount of nectar that can be carried is proportional to weight. If the assumptions of Cresswell's model are correct then the maximum foraging distance of foragers should be independent of body size.

Yet another possibility relates to predation. Foraging is a dangerous task that probably increases worker mortality in social insects (Van Doorn 1987; O'Donnell and Jeanne 1995; O'Donnell *et al.* 2000). Silva-Matos and Garófalo (2000) found that worker mortality in the tropical bumblebee *B. atratus* was strongly correlated with frequency of foraging. Similarly, longevity of workers of *B. diversus* is longer in queenless colonies in which little foraging occurs, compared to those with queens, queenright colonies (Katayama 1996). Estimates of worker longevity vary between species and studies, from 13.2 days for *B. terricola* (Rodd *et al.* 1980) to 41.3 days for *B. morio* (Garófalo 1976; see also Brian 1952, 1965a; Goldblatt and Fell 1987; Katayama 1996). However, mark recapture studies of *B. vagans* and *B. terricola* visiting patches of flowers suggest that foragers rarely live for more than a week or two (Morse 1986b). Garófalo (1976) estimated the mean longevity of *B. morio* nest bees to be 72.6 days, compared to 36.4 days for specialist foragers. Foraging appears to reduce the ability of *B. terrestris* workers to encapsulate foreign bodies (suggesting that they have less resistance to parasitoids) (König and Schmid-Hempel 1995). It seems likely that larger bees are less prone to predation, particularly by spiders, than small bees (it is common to observe bumblebees caught temporarily in spider webs but they usually manage to break free). Conversely, the conopid fly *Sicus ferrugineus*, which attacks bees while they are foraging on flowers, preferentially parasitizes large workers (Schmid-Hempel and Schmid-Hempel 1996a). If, overall, large bees do have a longer life expectancy as foragers, then sending larger bees out to forage may be the safest option

for the colony. No data are available on the longevity of foragers in relation to size; this would be an interesting and relatively straightforward area for study.

Perhaps one of the most promising candidate explanation for alloethism in bumblebees relates to thermoregulation. Free and Butler (1959) pointed out that larger workers would be better able to forage in adverse weather. All bees are limited to foraging within a particular temperature range and, in general, the lower limit of this range shifts downwards as body size increases (Stone and Willmer 1989). For example, queens of *B. vosneskii* and *B. edwardsii* can sustain continuous flight in ambient temperatures ranging from 2°C to 35°C, but workers are unable to maintain an adequate body temperature for flight below 10°C (Heinrich 1975a). It seems that all bumblebees, from the smallest workers to the largest queens, have to maintain their thoracic temperature within the range 31–42°C to be able to fly (interestingly, males often feed on massed flowers and allow their temperature to fall below this range) (Heinrich and Heinrich 1983a,b). Thus, larger foragers are presumably able to become active at lower ambient temperatures than small foragers but, conversely, they are more prone to overheating in warm weather (Heinrich 1975a, 1979b). Indeed, these are arguments used to explain why bumblebees are superior pollinators to honeybees in cool climates and why the distribution of bumblebees is largely confined to temperate regions. The nest itself is maintained at a more or less constant temperature, so individual-level thermoregulation is not an issue for bees working within the nest. Neat though this theory is, the only attempt to test whether workers of different sizes tend to forage in different weather conditions suggests that they do not (Peat and Goulson 2005). We observed whether *B. terrestris* foragers exhibiting approximately an order of magnitude variation in mass differed in when they foraged according to ambient temperature, which during the study period varied from 13°C to 29°C. One might predict that 13°C might be too cool for the smallest foragers, and 29°C too hot for the largest, but in fact the mean size of bee leaving the nest was entirely unaffected by air temperature.

If thermoregulation were the explanation for alloethism in bumblebees, one might predict that the queen should rear a few large foragers early in the season but that workers reared in summer should be smaller. Several studies have examined changes in worker size during the season, with variable results. Knee and Medler (1965) found an increase in worker size for three American species late in the season. Plowright and Jay (1968) found an increase in worker size as the season progressed in some species but not in others. Röseler (1970) describes an initial decline in the mean size followed by a general increase in *B. terrestris*. No clear pattern emerges and it seems that foragers are not, in general, larger early in the season. Of course the sizes produced may not be the optimum with regard to thermoregulation, particularly if the colony is constrained by a shortage of pollen. This is particularly likely to be the case in early spring when the queen has to single-handedly gather food for her offspring. With regard to the first batch of workers, it is also possible that there is a trade-off between producing few large offspring, each of which would be well adapted to foraging in cool spring temperatures, or producing more smaller offspring, which would be poorer at thermoregulating. A

risk-averse queen might choose the latter strategy for it reduces the variance in the proportion of workers that might be lost to predation (i.e. she avoids putting all her eggs in a small number of large baskets).

The hypotheses proposed to explain why foragers are larger than nest bees are not mutually exclusive, and a combination of factors is likely to be responsible. They do not, however, address why there is so much size variation between foragers (Fig. 3.3). If it is in some way advantageous for foragers to be large and for nest bees to be small, why is there not a bimodal size distribution? It may be that having foragers of a range of sizes allows them each to specialize in flower types appropriate to their morphology and so improves overall foraging efficiency of the colony while minimizing intra-colony competition. Different size classes do tend to visit different flower species (Cumber 1949a; Heinrich 1976a; Morse 1978b; Inouye 1980a; Barrow and Pickard 1984; Johnson 1986). For example, Cumber (1949a) found that large workers of *B. pascuorum* tended to visit *Lamium album*, which has a deep corolla, while the smaller workers visited *Lamiastrum galeobdolon*, which has a substantially shallower corolla. Overall, the mean corolla depths of the different flower species visited varies in accordance with the tongue lengths of different sized workers (Prys-Jones 1982). Interestingly, Johnson (1986) found that it was only the large foragers of *B. ternarius* and *B. pennsylvanicus* that selected deeper flowers. The smaller foragers visited both deep and shallow flowers. Johnson (1986) suggests that this may be because the small bees were primarily nest bees that had been forced to forage due to a food shortage in their colonies, and thus they were inexperienced. An alternative explanation might be that small bees can operate at a profit on a lower reward per flower (because of their lower metabolic costs), so they can profitably visit deep flowers from which they cannot extract all of the nectar.

Studies have also found that there are differences in the mean size of foragers engaged in gathering pollen versus those that gather nectar, but they do not agree in the direction of this difference. Some studies have found that it is the larger foragers that tend to collect pollen, while the smaller foragers collect nectar (Brian 1952; Free 1955a; Miyamoto 1957; Pouvreau 1989), while Goulson *et al.* (2002b) found the reverse. It may be that the size of bees specializing in each of these tasks depends on which flowers are locally available. The structure of particular flowers suits bees of a particular size; for example, small foragers of *B. terrestris* and *B. lapidarius* are better able to trigger flowers of *C. scoparius* (Stout 2000). Since these flowers only provide pollen, we might expect pollen gatherers to tend to be small in nests situated near to patches of flowering *C. scoparius*. Thus, the relative sizes of pollen and nectar gatherers may vary between nests and at different times of the year according to the flowers that are locally available. Having foragers of a range of sizes enables both resources to be gathered efficiently.

It would be possible to test whether having foragers of a range of sizes is beneficial to bumblebee colonies by artificially varying the size distribution of workers in experimental nests. Young workers can readily be moved between colonies, so that it would be possible to create colonies with only large or small workers, or with a range of sizes, and then measure nest growth and foraging efficiency.

### 3.3 Sex determination

*Is this wretched demi-bee,  
Half-asleep upon my knee,  
Some freak from a menagerie?  
No! It's Eric the half a bee!*  
Monty Python (1976)

The sex of Hymenoptera is determined in an unusual way, using a system known rather dauntingly as parthenogenetic arrhenotoky (Crozier and Pamilo 1996). As we have seen, fertilized eggs develop into diploid females (they get one copy of each chromosome from each parent, as in most diploid organisms), while unfertilized eggs develop into haploid males (they only have one copy of each chromosome). Actually, it is slightly more complex than this. In many Hymenoptera (including bumblebees), individuals are male if they are homozygous at one or more sex-determining loci (Paxton *et al.* 2000). Heterozygotes at this locus are females. Since haploids are inevitably homozygous at all loci, all haploids are males. But it is quite possible for a diploid to be homozygous at this particular loci; such individuals develop as males.

In *B. terrestris*, it appears that only one locus is involved (Duchateau *et al.* 1994). This is also the case in honeybees and many other bee species that have been examined (Mackensen 1951; Woyke 1963, 1979; de Camargo 1979; Kukuk and May 1990). In fact, use of a single sex-determining locus seems to be the norm in most Hymenoptera (Cook and Crozier 1995). The fewer loci involved, the more likely it is that diploid males will occur. Diploid males appear to have very low fertility in bumblebees (Duchateau and Mariën 1995). In honeybees, diploid male larvae are consumed by workers, but in bumblebees they are reared to adulthood (Plowright and Pallet 1979; Duchateau *et al.* 1994). Their production is thus particularly undesirable because it places a burden on the colony for no gain. For any queen that is unfortunate enough to mate with a male carrying a copy of the sex-determining gene that is identical to one of her own two copies, half of her workers will develop as diploid males, and since they do no work then half of her workforce is effectively lost. Such colonies are very unlikely to survive. Hence negative frequency dependent selection operates at the sex-determining locus; any allele that is common is selected against because queens carrying it are more likely to end up in matched-pair matings. Thus in a healthy outbred population we would expect a large number of rare alleles, rendering the probability of matched-pair matings remote. In the only species studied to date, *B. terrestris*, there are thought to be at least 46 alleles at the sex-determining locus (Duchateau *et al.* 1994). Diploid male production is likely to become a problem in small, inbred populations (see Chapter 13).

### 3.4 Control of reproduction and queen–worker conflicts

Social Hymenoptera with an annual life cycle generally produce new reproductives at the end of the colony cycle (Wilson 1971; Michener 1974), and bumblebees are no exception. There is thought to be a trade-off between maximum colony growth and

reproduction, constrained by impending ecological (often seasonal) changes that will soon make conditions unsuitable for either. Limiting reproduction to the end of the cycle ensures that the largest possible workforce is present to rear reproductives (Oster and Wilson 1978). In bumblebees, one might expect that declining floral availability in the autumn would be the factor limiting colony development yet colonies of many species disband long before the end of the flowering season (e.g. in the case of *B. pratorum*, colonies begin reproducing as early as April and generally die off by mid-June). It is probably mounting pressure from parasitoids that become more abundant as the season progresses that curtails their development (Schmid-Hempel *et al.* 1990).

The early, pre-reproductive phase of colony development in bumblebees is generally harmonious, but in the later reproductive phase violent, even fatal, conflicts may occur between members of the colony. Some workers within a colony become more aggressive than others, both towards intruders and to their siblings, and these individuals tend to show a greater degree of ovarian development (Free 1958; Foster *et al.* 2004). These bees are generally nest bees rather than foragers, perhaps because foraging reduced opportunities for reproduction (Foster *et al.* 2004). Late in the development of the colony, such workers will sometimes construct egg cells and lay their own (unfertilized and thus male) eggs. The foundress queen will retaliate by eating these eggs and then laying her own in the egg cells (Free *et al.* 1969). In turn, the workers may eat the queen's eggs, often doing so as she is laying them (Van Honk *et al.* 1981; Duchateau and Velthuis 1989; Bloch and Hefetz 1999). Egg-eating by workers has frequently been observed in a range of bumblebee species including *B. lapidarius*, *B. terrestris*, *B. lucorum* and *B. fervidus*, so is probably a widespread phenomenon (Plath 1923a; Free 1955c). Eggs are generally only eaten within the first 24 h after being laid (Huber 1802). Perhaps after this time it becomes impossible for either the queen or workers to distinguish between their own eggs and those of others. Workers may also throw larvae out of the nest at this time, although the identity of these larvae has not been established (Pomeroy 1979). Egg-eating leads to fights within the nest and, on occasion, the queen may be killed by her own workers (Van Honk *et al.* 1981; Van Doorn and Heringa 1986; briefly reviewed in Bourke 1994).

What causes this conflict? The answer lies at least in part in the unusual patterns of relatedness found within Hymenoptera due to their haplodiploid sex determination. In the vast majority of bumblebee species, the queen mates only once (Estoup *et al.* 1995; Schmid-Hempel and Schmid-Hempel 2000) and colonies are founded by single queens. The sons of the colony queen carry 50% of their mother's genes, whereas the sons of workers (the queen's grandsons) carry only 25% of her genes. Thus, we expect the queen to favour rearing her own sons rather than allowing her daughters to lay their own eggs. However, from the point of view of the workers, their own sons carry more of their genes (50%) than do their brothers (25%). Even their nephews (the sons of other workers) are more closely related to them (sharing 37.5% of their genes) than are their brothers (incidentally, patterns of relatedness become far more complicated in species where queens mate more than once, or as in some ant species where nests may be founded by more



than one queen). The interests of the queen and of the workers are opposed; each would prefer to rear their own sons (Hamilton 1964; Trivers and Hare 1976).

Almost all studies of colony development and conflicts in bumblebees have been of *B. terrestris*. In this species, the onset of conflicts within the colony (known as the competition point) appears to be closely correlated with the time when the colony commences rearing new reproductives (Van der Blom 1986; Van Doorn and Heringa 1986; Duchateau and Velthuis 1988). Up to this point, the foundress queen appears to produce a pheromone that induces diploid larvae to develop as workers rather than queens (Röseler 1970, 1991). If she dies or is removed, workers will often rear new queens and lay their own eggs earlier than would otherwise occur. Similarly, suppression of the queen by an invading cuckoo bumblebee (*Psithyrus*) can induce workers to lay eggs. Müller and Schmid-Hempel (1992b) monitored nests of *B. lucorum* for attack by *Psithyrus* and removed any *Psithyrus* females within 3 days of their arrival. Nests that had been briefly attacked produced significantly more males, suggesting that even this very brief suppression of queen dominance can lead to significant worker reproduction. In contrast, if *Psithyrus* remain in the nest, they suppress worker ovarian development to a similar degree to an undisturbed queenright colony (Vergara *et al.* 2003).

Why does colony harmony break down at the competition point? What prevents workers from laying eggs earlier? Duchateau and Velthuis (1988) and Röseler (1991) hypothesize that worker aggression steadily increases until eventually the queen loses her dominance and ceases production of the pheromone. They argue that it is the pheromone that inhibits worker reproduction. It has been experimentally demonstrated that the queen does cease pheromone production at this time. Young female larvae placed with a queen taken from a colony before the competition point become workers, whereas if they are placed with a queen from a colony which has passed the competition point they become queens (Cnaani *et al.* 2000).

As Bourke and Ratnieks (2001) point out, there is a flaw in the argument put forward by Duchateau and Velthuis (1988) and Röseler (1991). Suppression of worker reproduction by a pheromone is unenforceable; selection would favour workers that ignored this signal and laid eggs anyway, if it were in their interests to do so. Other authors have also disputed the suggestion that worker reproduction is inhibited by a queen pheromone and have provided some experimental evidence against this idea (Keller and Nonacs 1993; Bloch *et al.* 1996; Bloch 1999; Bloch and Hefetz 1999). It seems unnecessary to argue that the switch to rearing reproductives should be forced upon the queen, since it is in her interests to do so at some point. Bourke and Ratnieks (1999, 2001) suggest a subtly different interpretation. They hypothesize that the queen ceases pheromone production of her own volition (rather than because she is being oppressed by the workers). Workers do not lay eggs before this time because it is not in their interests to do so; worker reproduction early in the colony cycle would slow colony growth (because males do not work) and reduce production of full sisters (who are more closely related to workers than their sons).

Interestingly, there is evidence that ovarian development in young workers is prevented by the presence of the queen and, also, by the presence of dominant workers in the absence of a queen (Röseler and Röseler 1977; Röseler *et al.* 1981; Bloch *et al.* 1996; Bloch and Hefetz 1999). Perhaps attempting to develop a reproductive capacity is a dangerous strategy for a young worker since it will place her in conflict with older colony members. Queens and dominant workers seem able to recognize, and are more aggressive towards, workers with developed ovaries (Van Doorn and Heringa 1986; Duchateau 1989; Röseler and Van Honk 1990). Ovarian development in workers is reversible: Alaux *et al.* (2007) demonstrated that if egg-laying workers were placed in colonies in the pre-competition point phase, they tended to revert to sterility, but only if they came into direct contact with the queen.

### 3.4.1 Timing of reproduction

*B. terrestris* colonies differ greatly in the timing of the reproductive phase. Some colonies switch from rearing workers to rearing reproductives at a relatively early stage in colony development, about 10 days after the emergence of the first adult workers (Duchateau and Velthuis 1988; Duchateau *et al.* 2004). These colonies produce mostly males. Other colonies switch later, about 24 days after emergence of the first workers, and these tend to produce mainly new queens. In both colony types, the competition point occurs about 31 days after emergence of the first workers. Thus in early-switching colonies, the competition point does not occur until about 21 days after the queen commences laying male eggs. In contrast, in late-switching colonies, the competition point occurs about 7 days after the first eggs are laid that are destined to become new queens (Duchateau and Velthuis 1988).

Bourke and Ratnieks (2001) suggest that the timing of the switch is under the control of the queen. In early-switching colonies, she commences laying male eggs while presumably continuing to release the pheromone that prevents female offspring from developing into queens. They argue that workers are unable to detect that they are rearing males until the male larvae are about 10 days old (15 days after the eggs were laid). Since it is probably not in the interests of workers to lay their own eggs before the switching point and they are not able to detect that this has occurred for 15 days, we would expect a substantial delay between the point at which reproductives are first produced and the onset of the competition point in early-switching colonies. Attempts to test whether workers are indeed only able to detect male larvae at an age of 10 days, by adding male larvae of varying ages to colonies, suggests that this is not so (Lopez-Vaamonde *et al.* 2004). Regardless of the age of the larvae, worker reproduction did not begin until 19 days after male larvae were added. The reason why workers do not begin egg laying earlier remains obscure, since it would appear to be in their interests to do so.

Once the workers detect the presence of male larvae, they could throw them out of the nest and attempt to replace them with their own offspring. However, it seems that they rarely do so, and this may be because earlier emerging males can be expected to

enjoy higher mating success providing that there are queens available for them to mate with (Bulmer 1983). Since the sons of workers would be at least 15 days younger than those of the queen, their expected mating success may be much lower. Also, the queen's sons are nearing the completion of their development by the time workers begin egg laying (timing of development taken from Duchateau and Velthuis 1988). If the workers lay their own eggs at this point, they will not have hatched until after the oldest of the queen's sons have pupated. Thus they will not be in direct competition for food and so, for the workers, there is little or nothing to be gained from destroying the first male larvae that they detect.

Consider now late-switching colonies. Here the switch is presumably determined by the queen ceasing to produce the pheromone that prevents female larvae from developing into queens (Cnaani *et al.* 2000; Bourke and Ratnieks 2001). Experimentally increasing the number of workers in the nest can bring forward the production of new queens (Bloch 1999), suggesting that the queen's decision as to when to cease pheromone production is flexible and dependent on the availability of a sufficiently large work force to rear new queens (which require more food than workers). Larvae are sensitive to the queen's pheromone at about 2–5 days old (7–9 days after their eggs were laid). The workers commence laying their own eggs about 7 days after the first eggs that are destined to become queens are laid (Duchateau and Velthuis 1988). As Bourke and Ratnieks (2001) point out, this corresponds precisely with the presumed time at which the queen ceases pheromone production.

Neat though these explanations for the timing of onset of the competition point are, there are some anomalies that require further investigation:

- a. Bloch (1999) found that in a few early-switching colonies, the competition point *preceded* the switching point. Bourke and Ratnieks (2001) put this down to worker error.
- b. As Bourke and Ratnieks (2001) concede, their hypothesis falls 6 days short of explaining the 21 day lag generally observed between the switching point and the competition point in early-switching colonies. These 6 days cannot be explained by the time needed for ovary development in workers, for Duchateau and Velthuis (1989) demonstrated that the ovaries of some workers are fully developed before the switching point (and in late-switching colonies egg laying by workers occurs very promptly).
- c. It is not clear why workers should lay their own eggs in late-switching colonies. Their sons are likely to compete for food with the developing queens [remember that the workers are more closely related to the new queens ( $r = 0.75$ ) than they are to their own sons ( $r = 0.5$ )]. Also, given the strong male bias in the ratio of males to new queens found in many bumblebee populations (Beekman and Van Stratum 1998) and the probable early male advantage discussed earlier, the expected reproductive success of worker-produced males in late-switching colonies is very low. Bourke and Ratnieks (2001) suggest that competition between worker-produced males and future queens is minimal since the colony has plentiful resources at this time. Lopez-Vaamonde

*et al.* (2003) provide a neat test of this hypothesis; by selectively removing either egg-laying or non-egg-laying workers from paired colonies, they demonstrate that egg laying by workers has no measurable impact on the production of new queens. This does of course beg the question as to why the queen does not lay more diploid eggs, and so increase production of new queens? If the colony has sufficient resources to rear worker-laid males, then it could presumably rear more future queens instead.

Overall, Bourke and Ratnieks' hypothesis fits the available data reasonably well and is certainly the closest we have yet come to a full explanation for the reproductive strategies adopted by bumblebee nests. It would be very useful to obtain data on other species, since almost all studies to date have focussed exclusively on *B. terrestris*. Identification of the queen pheromone would be invaluable, for it would enable experimental manipulations to test various aspects of the hypothesis [unfortunately, analysis of queen exocrine secretions suggests that there are at least 500 candidate compounds; Hefetz *et al.* (1996) and Urbanova *et al.* (2008)]. Also, at present, there are few data on the proportion of bumblebee males that are produced by workers and as to how skewed parentage of worker-produced males is towards the more dominant individual workers. Such data could be obtained easily using established microsatellite markers (Estoup *et al.* 1995, 1996) and would provide further insight into the degree of control which queens and workers each have over colony reproduction.

### 3.4.2 Matricide

Matricide has frequently been observed in the later stages of colony development in a range of bumblebee species (reviewed in Bourke 1994). It appears to be the result of a gradual process whereby conflict between the queen and workers steadily increase, resulting in a loss in queen condition and, sometimes, ultimately leading to her death. Why is this in the interests of the workers? Bourke (1994) considers the conflicting pressures on workers with regard to matricide in detail, although at this time it had not become apparent that *B. terrestris* colonies adopt one of two alternative reproductive strategies. In colonies specializing in male production, one would expect competition to be most fierce. If workers kill the queen they may well increase their own chances of reproducing and, since their sons ( $r = 0.5$ ) are more valuable to them than their brothers ( $r = 0.25$ ), matricide may be their best strategy. However, in early-switching colonies the queen generally lays some diploid eggs (which develop into queens) towards the end of colony development, so that matricide still has a cost to workers in terms of lost sisters. In late-switching colonies, matricide would seem to be a poor strategy for workers, because it will prevent the production of a (potentially large) number of fertile sisters ( $r = 0.75$ ), and trade them instead for sons ( $r = 0.5$ ). Unfortunately, no data are available on the frequency of matricide in early-switching versus late-switching colonies.

The optimum strategy for workers may well depend on the condition of the queen, as well as her decision to switch early or late. If her reproductive potential has been reduced through injury or parasitism, this may favour matricide. Since injury may occur

during queen–worker conflict over male production, there may be positive feedback; conflict reduces the queen’s condition which, in turn, pushes the optimum worker strategy towards further conflict leading to matricide. If the queen’s condition becomes sufficiently low it may actually benefit her to die, rather than to continue fighting with her daughters (who in her absence will produce more of her grandsons) (Bourke 1994).

### 3.5 Sex ratios in ‘true’ bumblebees

The population sex ratio in bumblebees varies greatly but is thought to exhibit a strong male bias (reviewed in Bourke 1997; see also Beekman and Van Stratum 1998). A male bias is unexpected in social Hymenoptera. Kin selection theory predicts that in a colony founded by a monogamous queen, workers should favour a 3:1 investment (females to males) because they share three times as many genes with sisters as they do brothers, while the queen should favour equal investment in both sexes since she is equally related to both (Trivers and Hare 1976). Neither the queen nor the workers should benefit from a male-biased sex ratio.

So why are bumblebee sex ratios seemingly male biased? Possible explanations have been considered in depth by Bourke (1997) and Beekman and Van Stratum (1998). The answer must be linked to the frequency with which colonies adopt an early-switching or late-switching strategy, because the former produce mostly males and the later mostly new queens. Bourke and Ratnieks (2001) argue that queens adopt an early-switching, male-producing strategy with a probability of 0.5 (observation of natural nests suggests that about half are early-switching and half are late-switching; Duchateau and Velthuis 1988). If the queen chooses to adopt a strategy of producing males then the workers have no choice but to comply, since they cannot lay their own diploid eggs (Bulmer 1981). If half of all colonies specialize in male production, then it is in the interests of both the queens and workers in remaining colonies to specialize in queen production (Bourke and Ratnieks 2001). A very similar system is thought to operate in the ant *Pheidole desertorum* (Helms 1999). This argument is plausible but appears to contradict that made earlier that, in late-switching colonies, the workers commence rearing their own male offspring as soon as they detect the switching point. Also, it does not explain why bumblebee sex ratios are often male biased. A number of compatible explanations have been proposed (see Bourke 1997), of which the most plausible are outlined as follows:

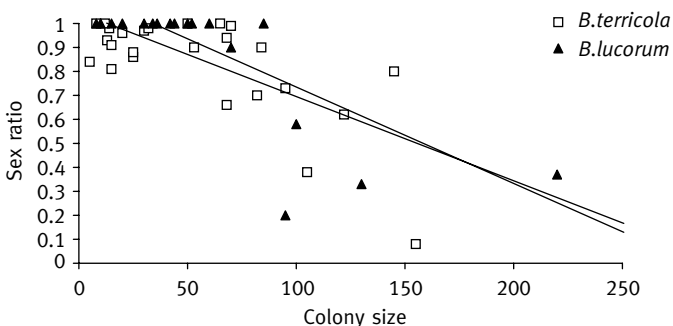
- (a) Perhaps the simplest explanation for male-biased sex ratios is that males are cheaper to produce (Beekman and Van Stratum 1998). Fisher (1930) predicted that most organisms should invest equally in sons and daughters, not that most organisms should produce equal numbers of sons and daughters. In bumblebees, males are markedly smaller than queens and so are cheaper to rear. For example, in *B. terrestris* the weight ratio of males to queens is 1:2.1 (Owen *et al.* 1980; Duchateau and Velthuis 1988). When the calorific value is taken into account, the differential is even

greater, at about 1:3.3 for mature new queens (Beekman and Van Stratum 1998). All else being equal, we would expect colonies that specialize in male production to rear about three times as many males as a colony specializing in queen production can rear queens. However, both Bourke (1997) and Beekman and Van Stratum (1998) conclude that this alone is not sufficient to account for observed population sex ratios.

- (b) Worker reproduction can, in theory, lead to male-biased sex ratios, particularly if one worker can monopolize reproduction. Bourke (1997), however, argues convincingly that this is highly unlikely to lead to male bias of the magnitude that is frequently found. For most species, we have little information as to what proportion of males produced by colonies are the offspring of workers; Owen and Plowright (1982) detected 19% of males to be worker-laid in *B. melanopygus*. The ready availability of microsatellite markers has recently made the detection of worker-produced males much easier. Using this approach on *B. hypnorum* (a potentially atypical polyandrous species), Paxton *et al.* (2001) found that all 267 males from 12 nests were produced by the queen yet Brown *et al.* (2003b) studying the same species found that 19.6% of 1,304 males from 10 colonies were the offspring of workers. Takahashi *et al.* (2008b) detected that approximately 5% of workers were worker-produced in *B. ignitus*. Even in artificial *B. terrestris* nests created by placing queens with unrelated workers, 95% of males were produced by the queen (Alaux *et al.* 2004). Worker reproduction in colonies in which the queen has died prematurely (e.g. due to infection by parasites) may contribute to male-biased sex ratios for, in this position, workers have no choice but to rear sons (Owen *et al.* 1980; Takahashi *et al.* 2008b). However, rates of orphaning that have been recorded are probably not adequate to explain observed male biases (Bourke 1997).
- (c) Bulmer (1981, 1983) demonstrated that male-biased sex ratios can arise because of protandry. Protandry (the emergence of males before new queens) has been recorded in a range of bumblebee species, and appears to be the norm (Hobbs 1964b; Pomeroy and Plowright 1982; Shelly *et al.* 1991; Foster 1992; Müller *et al.* 1992; reviewed in Bourke 1997). Although there are no data on mating frequency in relation to emergence time, it seems likely that early-emerging males enjoy greater mating success than do late-emerging males, since the former have more opportunities to encounter virgin queens during their lifetime. Bulmer's models predict that, for individual colonies, a male-biased sex ratio can be optimal under certain conditions (particularly if male production is under the control of the queen).
- (d) Beekman and Van Stratum (1998) develop Bulmer's (1983) model further by demonstrating that, under conditions of low resource availability, the best strategy for a colony is to produce males, because male size is probably not closely linked to their reproductive success, whereas in new queens an adequate size is crucial for surviving hibernation. Thus a stressed colony should produce males, while a colony with plentiful resources can afford to produce new queens. Certainly, studies of *B. melanopygus*, *B. terricola* and *B. lucorum* have found that it is large bumblebee

colonies that produce mostly queens, while small colonies tend to produce mainly males (Owen *et al.* 1980; Owen and Plowright 1982; Müller *et al.* 1992) (Fig. 3.7). In contrast, other studies of *B. lucorum*, *B. terrestris* and *B. hypnorum* found no such relationship (Müller *et al.* 1992; Paxton *et al.* 2001). Artificially induced stress on colonies of *B. terrestris* did not result in a switch to male production, but actually resulted in the production of fewer males and had no effect on the number of new queens produced (Müller and Schmid-Hempel 1992a). Interestingly, Duchateau *et al.* (2004) found that in *B. terrestris*, hibernation duration of the founding queen strongly influenced whether colonies switched early or late, with queens that had hibernated for longer tending to switch earlier, although it must be noted that the range of hibernation durations was artificially large. In early-switching colonies, worker production is curtailed by the queen. Whether she does so as a result of perceived resource availability, or for other reasons, is not known. The propensity of queens that have spent a long time in hibernation to switch early may reflect an inbuilt biological clock, for nests must produce reproductives at approximately the same time as other nests. Clearly, the success of early-switching versus late-switching depends on what other colonies are doing. If early-switching is triggered unconditionally by low resource availability then, in poor years, we would expect the vast majority of colonies to produce mainly males, which would lead to very low reproductive success.

None of the models presented above, however, adequately explain the highly variable sex ratios that appear to exist both within and between species. Much of the work to date has been theoretical; empirical studies are conspicuously rare and biased towards one species, *B. terrestris*. Much of the empirical work has been carried out on laboratory-reared colonies, and given that hibernation duration is now known to have a strong influence on colony sex ratio (Duchateau *et al.* 2004), and queens used in laboratory



**Figure 3.7** Relationships between the sex ratio of offspring produced by colonies and colony size for two bumblebee species, *B. terricola* (data from Owen and Plowright 1982) and *B. lucorum* (data from Müller *et al.* 1992). Sex ratio is defined here as the number of males divided by the total number of sexuals produced.

studies are often hibernated for unnatural periods, it could be argued that we have rather few data on sex ratios of bumblebees under natural conditions.

### 3.6 Sex ratios in *Psithyrus*

In contrast to the remainder of the genus *Bombus*, sex ratios of the subgenus *Psithyrus* appear to be female biased, although the data available are rather sparse and based on laboratory studies (Fisher 1992; see also Bourke 1997). Since *Psithyrus* have no worker caste to influence what happens in the colony, we would predict equal investment in sons and daughters, leading to a numerical bias towards male offspring. *Psithyrus* also appear to be protandrous, which should further increase male bias (Bulmer 1983). Fisher (1992) suggested that female bias may result from local mate competition among males, in which the reproductive success of males is reduced by competition between brothers (Hamilton 1967). However, given that *Psithyrus* have very similar mate location behaviours to other *Bombus* species (see Chapter 4), it is not clear why *Psithyrus* should be any more prone to local mate competition (Bourke 1997). An alternative explanation is that the sex ratio in *Psithyrus* is influenced by the behaviour of the host workers and queen. Both may reproduce after invasion by a *Psithyrus* female (Fisher 1987, 1992). Interestingly, the total ratio of new sexuals (*Psithyrus* females to *Psithyrus* males plus host males) may be similar to the ratio produced by the unparasitized host (Fisher 1992). Because of reduced queen dominance (or her death), the sex ratio of reproductives produced by the hosts is heavily male biased and it has been suggested that the female bias shown by *Psithyrus* represents the 'balance' left if workers rear an overall sex ratio appropriate to the unparasitized colony (Fisher 1992). However, this suggests that the *Psithyrus* female is unable to exert much influence over colony reproduction (for in this explanation the female bias in *Psithyrus* offspring is maladaptive), which seems unlikely given her dominance. Also, the female bias in *Psithyrus* offspring occurs even when the hosts do not reproduce (Fisher 1992). Far more research into the interactions between *Psithyrus* and their hosts is needed if we are to unravel the underlying strategies of *Psithyrus* reproduction.



*This page intentionally left blank*

# 4

---

## Finding a Mate

Mating in bumblebees is observed infrequently in the wild. However, the pre-mating behaviour of the males is often conspicuous, and has been the subject of many studies. At least four distinct mate-location strategies have been recorded in different bumblebee species.

### 4.1 Territoriality

Males of some *Bombus* species station themselves by a prominent landmark (either perched or hovering) and await a female. It appears that they search visually for queens, and they have unusually large compound eyes to facilitate this. Despite their large eyes, the males are clearly not able to distinguish queens from other organisms at a distance, since they will readily chase after any small flying organism, including birds. At least eight species of bumblebee are known to use this system of mate location; two from Europe (*B. confusus* and *B. mendax*) (Saunders 1909; Krüger 1951; Schremmer 1972), three from North America (*B. nevadensis*, *B. griseocollis* and *B. rufocinctus*) (Frison 1917; Hobbs 1965a; Alcock and Alcock 1983; O'Neill *et al.* 1991) and three from Asia (Williams 1991). O'Neill *et al.* (1991) describe the behaviour of the North American species in detail. Males stake out territories, usually centred on a prominent perch such as a fence post or tree. They dart out from their perch at passing insects, and if they encounter a queen they attempt to grasp her in mid-air with their legs; if successful the couple often continue in flight (and are then lost from view), but sometimes they fall to the ground. Observations of couples that fall to the ground suggest that copulation rarely ensues; more frequently, the queen escapes by crawling away through dense vegetation. Males are faithful to their territories for long periods, up to 26 days. However, they fight fiercely over territories, and resident males are frequently ousted. Fights can lead to severe injuries (Williams 1991). The territories are not based on resources that might be expected to attract females, often containing no flowers at all. Different species tend to choose different positions in which to perch; for example, *B. nevadensis* prefers open sunny areas and *B. griseocollis* favours shaded spots near large trees.

Territorial species also deposit scent-marks on vegetation within their territory, usually doing so early in the day (Alcock and Alcock 1983; O'Neill *et al.* 1991). The compounds deposited originate in the labial gland (Kindl *et al.* 1999). In *B. confusus* they

have been identified, and consist primarily of geranylcitronellol and (Z)-9-octadecenyl acetate (Hovorka *et al.* 1998). These marks presumably serve to either attract females and/or repel other males, but this has not been examined.

The distinctive large compound eyes of males of all species that are known to be territorial are very likely to be indicative of this type of mate-location behaviour; for example, *B. regeli*, *B. niveatus*, *B. morrisoni* and *B. crotchii* also have large eyes (Kruger 1951; O'Neill *et al.* 1991), but their mating system has not yet been examined.

## 4.2 Nest surveillance

Males of at least six *Bombus* species (*B. subterraneus*, *B. californicus*, *B. sonorus*, *B. fervidus*, *B. muscorum* and *B. ruderarius*) have been seen to stake out the entrance to nests from which young queens are about to emerge (Smith 1858; Tuck 1897; Krüger 1951; Lloyd 1981; Free 1987; Villalobos and Shelly 1987; Foster 1992; Darvill *et al.* 2007). Many males may be observed outside each nest, and they seem readily able to distinguish between queens and workers, suggesting that queens have a distinctive odour (see later). When a queen emerges, the males may fight furiously (Smith 1858). They may even pursue queens into the nest and mate with them there (Tuck 1897; Krüger 1951). Where several nests are available within a small area, males may regularly fly between them (Svensson 1980). Until very recently, it was not clear whether the males outside a nest had themselves emerged from that nest, although hanging around near one's natal nest attempting to mate with one's sisters might seem like a poor strategy (see Section 4.5). However, microsatellite typing of male and worker *B. muscorum* demonstrated that none of the males surveying a nest were sisters of the females within, indicating that males actively avoid opportunities that might lead to sib matings (Darvill *et al.* 2007).

## 4.3 Hilltopping

I have recently observed what appears to be hilltopping behaviour in bumblebees. Hilltopping is a well-known behaviour in some butterflies, wasps and flies, and has been observed in at least one bee species, the carpenter bee *Xylocopa varipuncta* (Alcock and Smith 1987). Males congregate at the highest point in the local area, and any female that is ready to mate has simply to fly uphill to encounter a choice of mates. Males of both *B. lucorum* and *B. sylvestris* can sometimes be observed in moderate to large numbers at the top of hills in Scotland. The sites where this occurs are conspicuously lacking in any floral resources and are typically cold and windswept, so it is hard to conceive what the bees are doing there if they are not attempting to locate a mate. However, as is generally the case in studies of bumblebee mate-location behaviours (if indeed this is one), I have not observed young queens visiting these hilltops.

#### 4.4 Scent-marking and patrolling

The males of many species of *Bombus* (including the subgenus *Psithyrus*) patrol regular circuits, in a manner similar to the trap-lining behaviour of foragers. This appears to be by far the most common mate-location mechanism in bumblebees. The behaviour was described in 1851 by Newman, and subsequently by Darwin (1886), who enlisted the help of his children in studying patrolling of *B. hortorum* males in his garden in Kent. He noticed male bees flying along regular routes, usually following hedgelines, and pausing at intervals by the trunk of a tree, fencepost or other prominent landmark, sites he called 'buzzing places'.

The routes remain the same for a considerable time, and the buzzing places are fixed within an inch. I was able to prove this by stationing five or six of my children each close to a buzzing place, and telling the one farthest away to shout out "here is a bee" as soon as one was buzzing around. The others followed this up, so that the same cry of "here is a bee" was passed on from child to child without interruption until the bees reached the buzzing place where I myself was standing (Darwin 1886).

Numerous bees follow the same route, so that a constant stream of males pass by, all going in the same direction.

We now know that each buzzing place has been marked with a pheromone, placed there by the male in the early morning, and replenished after rain (Alford 1975). Kullenberg *et al.* (1973) observed that the pheromone is smeared onto the chosen object and others nearby using the mandibles, aided also by the proboscis and the underside of the body. Awram (1970) suggested that the beard found on the mandibles of males of many species of bumblebees may be adapted as a brush for this purpose.

The pheromones differ between species, and are often detectable by the human nose (Frank 1941). They are secreted primarily from the labial glands (Kullenberg *et al.* 1973). The constituents of these pheromones have been examined in great detail in a sequence of studies conducted in Sweden, focusing predominantly on Scandinavian species, and recently by a group working in the Czech Republic. These studies have revealed that they consist largely of blends of fatty acid derivatives and terpene alcohols and esters (Stein 1963; Bergström *et al.* 1968; Calam 1969; Kullenberg *et al.* 1970; Svensson and Bergström, 1977, 1979; Bergström *et al.* 1981, 1996; Cederberg *et al.* 1984; Descoins *et al.* 1984; Svensson *et al.* 1984; Lanne *et al.* 1987; Appelgren *et al.* 1991; Bergman *et al.* 1996; Bergman and Bergström 1997; Valterová *et al.* 2001; Urbanová *et al.* 2001). The blend is generally species-specific, usually with one or two major components. For example, *B. terrestris* uses primarily 2,3-dihydro-6-*trans*-faresol with smaller amounts of geranyl-citronellol, while the closely related *B. lucorum* uses a markedly different blend based on ethyl dodecanoate and ethyl tetradecenoate (Bergström *et al.* 1981). Although most research has focused on identifying compounds present in the labial glands, analysis of scent-marks on leaves, and of volatiles in the air around marked leaves, confirm that the same compounds are deposited (Bergman and Bergström 1997).

These compounds may have value in taxonomic studies. Differences have been found between light and dark forms of *B. lucorum* (Bergström *et al.* 1981), perhaps indicating the presence of cryptic species (interestingly, allozyme data from Scandinavia also suggest that *B. lucorum* may contain two species; Pamilo *et al.* 1984). Similarly, labial gland pheromone analysis indicated the presence of two species within samples of *B. lapponicus* from Scandinavia, one of which was subsequently identified as *B. monticola* (Svensson and Bergström 1977; Svensson 1979).

The effects of male scent-marking compounds on female behaviour are poorly known. On rare occasions females have been recorded as being attracted to scent-marked objects (Free 1971; Svensson 1979, 1980), and thus they presumably encounter a male and mate. Very few bioassays of the effects of male scent-marks on queen behaviour have been carried out, and we do not really know how they work (Free 1987). In the carpenter bee, *X. varipuncta*, similar compounds act as long-range attractants to females (Minckley *et al.* 1991), and this seems their most likely function. But in addition to attracting queens, do they have arrestant or aphrodisiac effects? This would appear to provide a relatively straightforward opportunity for further study.

Presumably, the species-specific nature of the male pheromone blend facilitates females in locating males of the correct species. It seems that this may be further ensured by the height of the circuit marked by the males. Bringer (1973) and Svensson (1980) found that males of each species tend to mark and circuit objects at particular heights; thus, for example, *B. hortorum* and *B. (P.) sylvestris* tend to remain within 1 m of the ground. In contrast, *B. lapidarius*, *B. terrestris* and *B. lucorum* may follow routes at tree-top level, up to 17 m (Haas 1949; Awram 1970). However, as Prys-Jones and Corbet (1991) point out, these studies do not take into account the different habitat preferences of the species which may constrain the height of features that are available. There are records of *B. lapidarius* and *B. lucorum* patrolling near ground level in habitats without trees (Krüger 1951). On Salisbury Plain (United Kingdom), an extensive area of grassland with few trees or shrubs, I have seen male *B. lapidarius* scent-marking grass stems no more than 70 cm tall. Different species of bumblebee also tend to visit different sorts of landscape feature; for example, *B. hortorum* chooses dark hollows, *B. lapidarius* chooses the highest points that are available, and *B. terrestris* visits a range of points along shrubs and trees (Fussell and Corbet 1992b). On a larger scale, different species occupy different habitats. Thus in combination, the habitat, height and location of focal points and the pheromone blend all serve to prevent interspecific hybridization. In a study of *Bombus* communities in northern Scandinavia, Bergström *et al.* (1981) found that species that had similar pheromone blends always differed in the habitat they occupied and/or in the height at which males patrolled. Comparable results have also been described for the subgenus *Psithyrus* (Cederberg *et al.* 1984). The importance of evolved differences in mate-location behaviour as a barrier to hybridization is nicely illustrated by the recent introduction of *B. terrestris* to Japan. Here, *B. terrestris* regularly encounter the closely related *B. hypocrita*, a native Japanese species which is not normally sympatric with *B. terrestris*. Interspecific matings currently account for 30% of matings by *B. hypocrita*

queens, and such females all fail to found a viable colony (Kanbe *et al.* 2008). We might predict the rapid evolution of mechanisms to prevent interspecific matings given this strong selective pressure.

The patrolling routes followed by males are said to be more or less linear (Alford 1975). In *B. hortorum*, Frank (1941) found one particular route to be 300 m long and consisted of 28 marked points, varying from 30 cm to 33 m apart. An individual male was observed to repeat this circuit 20 times within an hour. In between circuits, or when the weather becomes unfavourable, males tend to feed and rest on flowers. It seems that an ability to detect the scent-marks is essential to males during the development of a patrolling circuit, but once they have learned the route they continue to follow it using visual cues. Removal of antennae from inexperienced males prevents them from patrolling on a regular route, but once the route is established bees remain able to follow it even if their antennae are removed (Awram 1970; Free 1987). Indeed, these bees re-marked the route on every circuit, suggesting that their inability to detect the scent stimulated them to replenish it.

When patrolling, the males always pause at more or less precisely the same points in space (sometimes known as the focal points). Yet the scent is applied over a number of objects up to 3 m from this point, suggesting that it acts primarily as a long-range attractant (Free 1987). When several males are visiting the same scent-mark, they usually pause at slightly different focal points. Presumably these are chosen arbitrarily, and visual cues used to locate them. One might imagine that it is at this moment, while the male hovers close to the scent-marks, that queens attracted to the scent and the male locate one another.

Remarkably, the same scent-marking points and patrolling routes are often used in successive years, as occurred in Darwin's garden (Darwin 1886; Svensson 1979). Whether this is because some scent remains or simply because the sites are particularly suitable in some way is not known. Interestingly, the features marked by males are rarely if ever flowers. In contrast, males of many species of solitary bee commonly scent-mark flowers to attract females (Kullenberg 1956; Haas 1960). It has been suggested that the move to scent-marking other objects evolved in bumblebees to minimize confusion over potential partners (Awram 1970). Flowers attract workers, which are generally very similar to queens in appearance, so that a male patrolling marked flowers may waste much time attempting to mate with workers (something that is obviously not a problem for solitary bee species lacking a worker caste).

An intriguing feature of male behaviour is that often a number of males will adopt similar or overlapping routes, so that a stream of individuals can be observed passing by (Alford 1975). This has been observed particularly frequently in *B. hortorum* (Darwin 1886). This is in marked contrast to the territorial behaviour of other *Bombus* species (described earlier). Indeed, the pheromones deposited by patrolling species appear to be attractive to other males (Kullenberg 1956); for example, if leaves scent-marked by males of *B. (P.) bohemicus* are moved to new locations they attract further males, which deposit more scent in the vicinity (Kullenberg 1973). Similarly, if crushed heads of males

are smeared on to leaves, further males of the same species can be attracted in substantial numbers (Free 1987). In fact, attraction of males to male scent-marks has been recorded far more frequently than attraction of queens.

One might intuitively expect that males would do better by actively avoiding each other and establishing their own distinct routes. However, a system whereby many males are attracted to the same places may benefit females by providing an opportunity for mate choice; since females of most species only mate once (while males can mate many times), it is particularly important for a female to choose a high-quality male. Unfortunately, since female attraction to male circuits, and subsequent mating, have so scarcely been recorded (Free 1971; Svensson 1979), we can only speculate as to exactly what happens and how it may have evolved. Perhaps a single male cannot deposit enough pheromone to attract females; by only responding to multiple pheromone marks, females might ensure themselves a choice of males. Alternatively, a female may only mate once she has had the opportunity to evaluate several potential partners, so a male circuiting on his own would not obtain a mate.

It is odd that mating has been so rarely observed in bumblebees. Free (1971) suggests that pairs may immediately leave the patrolling route, to avoid encounters with further males, but this has not been observed. In cage situations bumblebees readily mate, and males show little discrimination, enthusiastically attempting to mate with sisters (Whitehorn *et al.*, in prep.) or queens of other species.

Another as yet unexplained phenomenon is that mate-location behaviour is very rarely seen in some common bumblebee species. For example, *B. pascuorum* is abundant in much of Europe, but has only very rarely been seen patrolling (and has never been seen to use other mate-location mechanisms) (Awram 1970; Fussell and Corbet 1992b). Similarly, *B. (P.) vestalis* is generally the most common *Psithyrus* species in southern United Kingdom, and males can be exceedingly abundant, yet we have no records of its mating behaviour. One cannot help but suspect that there may be other mating systems used by bumblebees that are not easily observed (perhaps they take place in the canopy of trees). There is clearly need for further research on this fascinating but poorly understood subject.

## 4.5 Inbreeding avoidance

Foster (1992) demonstrated that *B. frigidus* (and possibly also *B. bifarius*) preferentially mated with non-siblings when confined in flight cages with a choice of potential partners. Similarly, Whitehorn *et al.* (in prep.) found that virgin queen *B. terrestris* took significantly longer time to mate when confined in cages with brothers than when confined with unrelated males. Inbreeding frequently results in offspring of reduced fitness (reviewed in Frankham *et al.* 2002), and in bumblebees it is likely to lead to the production of diploid males with low or zero fertility (see Section 3.3). Experimentally inbred colonies of *B. atratus* showed reduced growth compared to outbred colonies (Plowright and Pallet 1979). Inbred, diploid male producing colonies of *B. terrestris* rapidly died

when placed in field situations while outbred colonies fared much better (Whitehorn *et al.*, in prep.) (see also Chapter 13). There are thus clear benefits to be gained by avoiding mating with siblings. However, Foster (1992) found that in contrast to *B. frigidus*, both *B. californicus* and *B. rufocinctus* readily mated with siblings. He suggests that this variation between species may correspond to their mating system. Males of *B. californicus* and *B. rufocinctus* both use nest surveillance to find mates, and genetic studies of *B. muscorum*, another species that uses nest surveillance, demonstrate that males do not survey their own nest (Darvill *et al.* 2007). If this is also true of *B. californicus* and *B. rufocinctus* then they are unlikely to encounter sisters, and have no need for an inbreeding avoidance mechanism. In contrast, *B. frigidus*, *B. bifarius* and *B. terrestris* are patrollers, and may frequently encounter sibling queens. In these circumstances, a means of detecting and avoiding siblings is beneficial.

## 4.6 Evolution of male mate-location behaviour

Surprisingly, the distribution of different mate-location behaviours does not appear to correspond to phylogeny. Even allowing for some errors in the phylogeny, it seems certain that some of these behaviours must have evolved more than once. For example, when compared against the phylogeny of Cameron *et al.* (2007), bumblebees that are territorial fall into five separate subgenera. Similarly, the patrolling species fall within eight subgenera (O'Neill *et al.* 1991). These two behaviours clearly have much in common. The scent-marking compounds produced by both groups appear to be similar; for example, one of the main components of the scent-mark of the territorial *B. confusus* is geranylcitronellol, which is also a major component of the scent-marks of the patrolling species *B. hypnorum* and *B. lapponicus* (Bergström *et al.* 1981; Hovorka *et al.* 1998). In both groups the compounds are secreted by the labial glands, and are applied mainly in the morning (Kullenberg *et al.* 1973; Kindl *et al.* 1999). However, it is not obvious which mating behaviours are primitive and which are derived, or how species could readily switch between a territorial system with fierce male–male interactions to a patrolling system where males actively seek out sites being used by other males. It is easier to imagine how nest surveillance could evolve into patrolling behaviour (or vice versa), since species which use nest surveillance have been observed to patrol regular circuits between nests. Both systems include tolerance of other males, at least until a queen is available for mating. Mating systems are extremely variable within the Apoidea, and so provide little information as to what the mating system of the ancestral bumblebee might have been.

## 4.7 Queen-produced sex attractants

It seems that queens also produce pheromones which stimulate mating attempts by males. If virgin queens are tethered close to a focal point they usually attract males which attempt to mate with them, but if they are tethered a few meters away they



are ignored by males (Free 1971). This suggests that males are only capable of detecting queens over short distances, and probably do so visually (Awram 1970; Free 1971). However, after the initial approach it seems that queen odour is necessary to stimulate the male to attempt copulation, for they will not attempt to copulate with workers, other males, or old, mated queens (Free 1971). By experimentally removing body parts, Free (1971) demonstrated that the source of the pheromone was probably the head (males rarely attempted to mate with decapitated queens!). Van Honk *et al.* (1978) subsequently deduced that the pheromone is probably produced by the mandibular gland. Males rarely attempt to mate with queens in which the mandibular gland has been destroyed, but can be encouraged to do so by smearing these queens with mandibular gland secretions. Elicitation of mating behaviour by males also seems to require visual cues, for Krieger *et al.* (2006) found that dummies impregnated with solvent extracts of queen odours attracted males but that the males did not attempt to mate. In *B. terrestris*, it seems that the pheromone consists of a blend of saturated and unsaturated fatty acids, ethyl- and methyl esters of the fatty acids, heptacosene, 2-nonanone, and geranyl geraniol (Krieger *et al.* 2006), synthetic blends of which also stimulate male mating behaviour.

#### 4.8 Monogamy versus polyandry

Eusocial behaviour, where some individuals never attempt to reproduce but devote their energies to helping others to reproduce, is very rare in nature. Outside of the Hymenoptera, it is found in a handful of arthropods (notably the termites) and in one obscure mammal, the naked mole rat. Yet in the Hymenoptera it is common, and is thought to have evolved independently on a number of occasions (Hölldobler and Wilson 1990). Eusociality appears to be contrary to the Darwinian view of natural selection, and in fact its occurrence was of great concern to Darwin; he was never able to fully reconcile it with his belief that natural selection operated at the individual level. Hamilton (1964) was the first to provide a convincing explanation for eusociality in evolutionary terms. He argued that by helping relatives to breed, an organism was passing on its own genes indirectly (a behaviour now known as kin selection). Related individuals may thus be united by the common interest of passing on their shared genes. A crucial part of Hamilton's theory was that the effectiveness of helping relatives to reproduce as a means of passing on genes depends on the degree of relatedness; all else being equal, helping a close relative is a better strategy than helping a distant one.

An interesting consequence of haplodiploid sex determination (see Chapter 3) is that full sisters are more closely related to each other than is generally the case; on average, they can expect to have 75% of their genes in common, whereas in most organisms full sisters share 50% of their genes. This predisposes them to cooperate, and is thought to be one major reason why Hymenoptera have repeatedly evolved eusociality, whilst it remains rare in other organisms. However, thus far we have only considered the situation where sisters share both parents. Although the majority of social insects have

female mating frequencies close to one, in some social Hymenoptera the queens mate many times: the so-called ‘supermaters’ (Boomsma and Ratnieks 1996). For example, queens of *Apis* spp. may mate with 50 or more males during their nuptial flight (Seeley 1985a; Moritz *et al.* 1995; Oldroyd *et al.* 1995). This can greatly reduce the relatedness of their offspring; half sisters share only 25% of their genes.

What are the pros and cons of single versus multiple mating? Mating with a number of males is presumably costly to the queen in terms of time and exposure to predators (Moritz 1985; Crozier and Pamilo 1996). On the other hand, multiple mating provides the queen with a substantial reserve of sperm, which may be particularly important if she is long-lived (Cole 1983). It may set up the opportunity for sperm competition and thus result in better genes for her offspring. Multiple mating may also render the colony less vulnerable to pathogens and parasites (Sherman *et al.* 1988). Social behaviour predisposes organisms such as bees or ants to epizootics of such organisms, for they live at high densities and have frequent contact with siblings. Parasites and pathogens have long been suspected to act with positive frequency dependence, so that rare host genotypes are less likely to be infected (Haldane 1949; Hamilton 1980). Thus genetic variability within a colony of a social organism, created by multiple mating of the foundress, is likely to reduce the impact of parasites (Tooby 1982; Hamilton 1987; Sherman *et al.* 1988). Experimental tests with bumblebees support this hypothesis; infections of the protozoan parasite *Crithidia bombi* spread more slowly among unrelated workers than among related workers (Shykoff and Schmid-Hempel 1991a,b). Similarly, under field conditions, colonies of *B. terrestris* with artificially enhanced genetic variability have fewer parasites (Liersch and Schmid-Hempel 1998; Baer and Schmid-Hempel 2001).

Possibly the biggest constraints on mating behaviour are imposed by the social structure of the colony. Single mating promotes cooperation between workers, but may lead to conflicts between the queen and her workers over the sex ratio of the offspring that are reared (Crozier and Page 1985; Ratnieks and Boomsma 1995). Conversely, multiple mating reduces queen–worker conflict but reduces the incentive of daughters to cooperate with each other, leading to conflicts between daughters over resource allocation and reproductive opportunities (Crozier 1979; Boomsma and Grafen 1991; Pamilo 1991; Sundström 1994).

In contrast to honeybees, it seems that queens of most bumblebee species are monogamous in natural situations (although in a few species, notably *B. hypnorum*, queens do mate more than once, and polyandry seems to be more common in North America than in European species) (Röseler 1973; Estoup *et al.* 1995; Crozier and Pamilo 1996; Schmid-Hempel and Schmid-Hempel 2000; Paxton *et al.* 2001; Payne *et al.* 2003). Thus, the workers are generally full siblings and are (on average) 75% related to each other. This should render bumblebee colonies particularly susceptible to epizootics of parasites and pathogens. Unlike honeybees, bumblebee colonies are also likely to be more prone to queen–worker conflict over offspring sex ratios, but less prone to worker–worker conflicts. So why do bumblebees and honeybees differ so markedly in their mating behaviour?

The number of times a queen bumblebee mates may be constrained by the selfish interests of males (Brown and Baer 2005). In honeybees, mating is extremely rapid (taking only a few seconds; Winston 1987) and takes place in flight. In contrast, bumblebees mate while resting on the ground or sometimes high up in vegetation (Fig. 4.1). They have occasionally been observed to fly (propelled by the efforts of the queen while the male hangs limply), but are very clumsy. Lie-Pettersen (1901) records beating numerous pairs of copulating *B. terrestris* and *B. pascuorum* from the foliage of deciduous trees. Copulation is in general prolonged, lasting from 10 to 80 min in those species that have been studied (Alford 1975; Van Honk *et al.* 1978; Foster 1992; Duvoisin *et al.* 1999). Mean duration appears to be about 36–44 min. During this period, the pairs are presumably very vulnerable to attack, since they are both unable to move quickly and the queen is unable to sting.

Why does copulation take so long in bumblebees? Duvoisin *et al.* (1999) demonstrated that most of the sperm is successfully transferred within the first 2 min of copulation in *B. terrestris*. For reasons that remain to be explained, males transfer far more sperm to the female than she could possibly ever need (reviewed by Baer 2003). During the remainder of the time, the male transfers a gelatinous plug to the female genital tract, which completely fills the bursa copulatrix. The plug consists of a mixture of palmitic, linoleic, oleic and stearic acids, and a cyclic peptide, cycloprolylproline, a compound not known from any other insect species (Duvoisin *et al.* 1999; Baer *et al.* 2000). None of the components of the plug appears to be necessary for successful fertilization, for artificial transfer of sperm alone enables queens to successfully found healthy colonies. The plug persists within the queen for up to 3 days, and appears to partially block sperm transfer if she mates again during this time (although plugs placed in queens artificially are not very effective at blocking sperm; Sauter *et al.* 2001). Duvoisin *et al.* (1999)



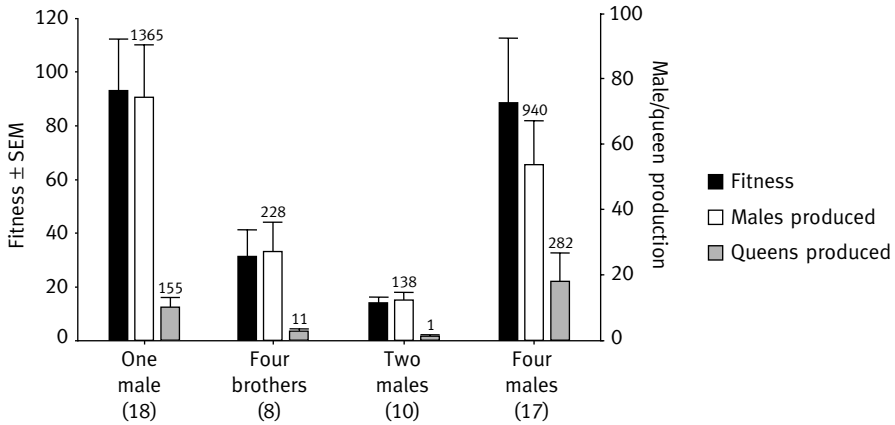
**Figure 4.1** Mating *B. lapidarius* observed on the windowsill of a garden shed. Pairs remain in copula for up to 80 min, but despite this mating pairs are rarely observed in the wild. Photograph by Michael Gibbins.

conclude that the prolonged copulation is probably imposed on the queen by the male. It serves to prevent her from remating until the male's sperm have reached the spermatheca (which takes 30–80 min). It also allows transfer of the plug which hampers further mating. The male genitalia gain a powerful grip on the queen's sting apparatus, so much so that attempting to artificially remove the male often results in his genitalia being ripped off (Baer 2003). Hence, it seems unlikely that the queen can forcibly displace him during mating.

In other insects, peptides in accessory secretions of males serve to reduce receptivity in females (Chen *et al.* 1988). Baer *et al.* (2001) conducted experiments in which they transferred components of the sperm plug to queen *B. terrestris* and examined their willingness to remate. Their working hypothesis was that cycloprolylproline was the most likely active component of the plug. Contrary to expectation, only linoleic acid inhibited further mating, and this compound did so effectively for at least 1 week. A further reason for males enforcing extended copulation on queens may therefore be to allow time for this inhibitory effect to come in to play. Baer *et al.* (2001) did not test whether the other compounds played some other role such as blocking sperm from subsequent males. It would seem to be a simple evolutionary step for females to ignore the linoleic acid signal if it were in their interests to do so. Perhaps it is not worthwhile for a bumblebee queen to attempt to mate a second time, since it will commit her to another lengthy copulation which may provide her with little sperm due to the presence of the plug. Interestingly, in the polyandrous bumblebee *B. hypnorum*, the mating plug is much shorter-lived than in *B. terrestris*, lasting for just 6–12 h (Brown *et al.* 2002).

There are other differences between honeybees and bumblebees that may influence the strength of selection pressures operating on queens with regard to how many times they mate. Bumblebee nests are much smaller in size and of shorter duration compared to honeybee nests, both of which will tend to make bumblebees less prone to epizootics than honeybees. Honeybee colonies can persist for many years, and during this period it is inevitable that some of the thousands of workers will bring pathogens back to the nest. Conversely, bumblebee nests generally last for only a few months, and the period of intense worker activity may last for only a few weeks. With luck, a bumblebee nest may entirely escape attack by a serious pathogen before the new reproductives have been reared. Thus, the need for genetic variability within colonies may be less. There are a small number of tropical bumblebees that have large, perennial nests similar to those of honeybees (Michener and Laberge 1954; Dias 1958; Michener and Amir 1977; Brian 1983; Hines *et al.* 2007). It would be interesting to examine whether these species are also monogamous.

The recent development of artificial insemination techniques in bumblebees makes it possible to inseminate bumblebee queens with sperm from more than one male, and study the consequences (Baer and Schmid-Hempel 2000). Baer and Schmid-Hempel (2001) inseminated *B. terrestris* queens with sperm from one, two or four unrelated males, or four brothers, and placed the resulting colonies out in the field in Switzerland. Colonies produced by singly mated queens had the highest reproductive success



**Figure 4.2** Reproductive success of colonies of *B. terrestris* according to treatment. The foundress queens had been artificially inseminated with sperm from one, two or four unrelated males, or four brothers. Colonies were then placed out in the field in Switzerland. Fitness is defined as the number of queens produced multiplied by two, plus the number of males. From Baer and Schmid-Hempel (2001).

(Fig. 4.2). Colony fitness appeared to follow a U-shaped function, being lowest when queens were mated twice. The mechanism underlying this result has not yet been established, but Baer and Schmid-Hempel (2001) speculate that low levels of multiple mating may lead to high levels of conflict between workers of different patriline within the nest, reducing colony fitness. Whatever the cause, it seems that bumblebee queens may be constrained by an adaptive valley, beyond which high fitness could be achieved. Unexpectedly, in a follow-up to this experiment Baer and Schmid-Hempel (2005) found that artificially inseminating a queen with sperm from multiple males had a significant and direct effect on queen fitness through reducing hibernation survival, although the mechanism underlying this effect remains somewhat mysterious. In conjunction with the costs of multiple mating imposed by males through prolonged mating duration and use of sperm plugs, these effects may make it very difficult for bumblebee queens to escape monogamy.

*B. hypnorum* is one of very few bumblebee species in which multiple mating by queens regularly occurs. Although many queens are monogamous, some mate two or more times (Schmid-Hempel and Schmid-Hempel 2000; Paxton *et al.* 2001). Molecular studies by Paxton *et al.* (2001) indicate that one male predominates fathering of the offspring (mean 69%), perhaps due to a partially effective sperm plug. It would be interesting to examine the consequences of multiple mating for colony fitness and social organization in this species in more detail.

# 5

---

## Natural Enemies

*Dave Goulson and Mark J.F. Brown*

Bumblebees are attacked in various stages of their life cycle by a diverse range of predators, parasites and parasitoids. The importance of these organisms is perhaps best illustrated by the vigour of bumblebees when they are freed from their natural enemies. In New Zealand, four bumblebee species were introduced in 1885 from the United Kingdom, and only three of their many parasites were accidentally introduced with them (Donovan and Wier 1978). Two of these bumblebee species (*B. subterraneus* and *B. ruderatus*) are now extinct or nearly so in the United Kingdom. In contrast, all four species are flourishing in New Zealand, and they often occur at extraordinary densities, far greater than those observed in their natural range, suggesting that elsewhere their numbers are held in check by natural enemies. Similarly, successful colonization of Tasmania by *B. terrestris*, which is both inbred (Schmid-Hempel *et al.* 2007) and lacks most parasites (Allen *et al.* 2007), provides further support for this parasite-release hypothesis.

In general, spectacularly little is known about the biology of most bumblebee parasites and parasitoids. In particular, the microorganisms and mites associated with bumblebees have received very little attention, and no doubt many have yet to be discovered. For those that have been identified and named, in the vast majority of cases almost nothing is known of their distribution, host range, and the impact that they have on the population dynamics of their hosts. Alford (1975) provides detailed descriptions of the life cycles of some species, focussing particularly on the United Kingdom. More recently, Schmid-Hempel (1998) provides an excellent review of the parasites of bumblebee and other social insects. These reviews serve primarily to illustrate the enormous gaps in our knowledge; there is great scope for further work. What follows is a description of the biology of the better known and more abundant natural enemies of bumblebees, but the list is far from comprehensive.

### 5.1 True predators

Foraging bumblebees are generally said to have few 'true predators', organisms that kill and consume many preys during their lives (*sensu* Thompson 1982). For this reason, it has often been argued that foraging bumblebees are not constrained in their behaviour by predation (Pyke 1978a) (e.g. they do not spend time looking around for predators in the way that, say, an antelope might). Paradoxically, bumblebees are among the most

obvious warningly coloured organisms in northern temperate zones. There is clear evidence for colour pattern convergence among groups of species in North America, Europe and Kashmir, presumably a result of Müllerian mimicry (in which harmful species mimic one another's warning signals to predators) (Plowright and Owen 1980; Williams 1991, 2007) (Plate 5). Some species are very variable in colour across their geographic range, so that different individuals may resemble a series of other bumblebee species. Very often, species with near-identical patterns are rather distantly related (e.g. *Psithyrus* species are often similarly coloured to their hosts). Williams (2007) described a particularly notable example of mimicry in bumblebees: *B. rufofasciatus* and *B. kashmirensis* are morphologically distinct and from different subgenera, but co-occur at high altitude on the southern and eastern edges of the Tibetan plateau. Workers appear near-identical in flight, with a red tail tipped with white. In *B. rufofasciatus* the white and red are formed from separate bands of red and white hairs, while in *B. kashmirensis* the same effect is achieved by hairs which are white at the base and red at the tip. Such convergent patterns are hard to explain without invoking significant predation pressure in the present or in the recent past.

Male bumblebees do not have a sting, so are presumably automimics of females of their own or other species (Mallet 1999), although interestingly males often differ quite obviously from females in their colour pattern. Perhaps there is a conflict between sexual selection and mimicry, although it has been argued that mate choice is unlikely to involve discrimination on the basis of colour in bumblebees (Free 1971; Williams 1991, 2007). If this is so, it is hard to explain why males and females differ in colour, since this makes it easy for visually hunting predators to learn to selectively attack the undefended males.

In temperate regions, the main true predators of bumblebees are probably birds and spiders. The literature contains rather few records of predation by birds. Shrikes are said to be particularly partial to bumblebees (Owen 1948). Grönlund *et al.* (1970) found that bumblebees may make up to 40% of the total food intake of the great grey shrike, *Lanius excubitor* in the autumn in Finland, but shrikes are generally uncommon birds. Spotted flycatchers (*Muscicapa striata*) occasionally take bumblebees, removing the sting by wiping the bee against a branch (Davies 1977). In southern Europe, bee-eaters (*Merops apiaster*) do likewise. Great tits (*Parus major*) have been recorded catching and eating bumble bee queens that have been feeding on lime trees (Saunders, 1907); the nectar makes the bees drowsy and therefore presumably easy to catch. Similarly, Alice Forster Johnson (2002) observed a great tit foraging on bumblebee queens at their overnight roosting site (a tree trunk) in Finland. The bird topped and tailed the bees, removing their sting and head, and then fed on the contents of the abdomen and thorax before discarding the corpses below the tree. This suggests that feeding by great tits on bumblebees is a widespread behaviour, but that it relies on bees being drowsy and therefore relatively easy to catch. The Bumblebee Conservation Trust (a UK-based charity) receives occasional reports from members of large numbers of bumblebee corpses being discovered, usually beneath flowering trees, and invariably neatly dissected with

a hole in the thorax and/or head and the contents removed (Fig. 5.1). This seems to be particularly common in spring where *Salix* bushes can attract large numbers of queens. The predation events themselves are rarely observed, but great tits seem to be the most common culprit. In 2008, Anne-Marie Smout observed a family of great tits (*P. major*) consuming more than 100 bumblebees in a garden in Denmark. There is an obvious parallel with the blue tit (*P. caeruleus*) in which, during the 1950s, the entire UK population learned to pierce the aluminium seals of milk bottles so that they could drink the cream. The behaviour is believed to have been learned by observation and therefore quickly spread through the population. It would seem that certain individual tits discover how to handle bumblebees, perhaps when they encounter a torpid individual during cold weather, and that this behaviour is copied by other individuals. However, these predation events appear to be short-lived and relatively scarce, perhaps because tits are only able to attack bumblebees effectively when they are feeding on flowers of woody shrubs on which the birds can perch close to the flowers. Such plants tend to have a short flowering period and for most of the year bumblebees feed primarily on herbaceous plants where presumably it is harder for birds to tackle them.

Most spider webs are too flimsy to catch bumblebees, but Plath (1934) observed that the North American species *Argiope aurantia* frequently caught bumblebees, and it is not uncommon to see bumblebee corpses in webs spun by some of the larger European spider species (Fig. 5.2). The larger crab spiders such as *Misumena vatia*, which do not spin a web but rather wait on flowers for their prey, are also capable of catching bumblebees (Plath 1934), but the rates of predation are low (Morse 1986b).

Perhaps the main arthropod predators of foraging bumblebees are the robber flies (Diptera: Asilidae). Robber flies are active fliers that catch flying prey in the air with their



**Figure 5.1.** Bird-predated bumblebee. The thorax has been neatly opened and the flight muscle pecked out. This is often the work of the great tit, *Parus major*.





**Figure 5.2.** Some larger spider species occasionally catch bumblebee workers and males, as here.

powerful legs. The larger robber fly species are capable of taking smaller bumblebees, and some species such as *Proctacanthus hinei* and *Mallophora bomboides* prey extensively on bumblebees (Bromley 1934). Interestingly, *M. bomboides* is also a Batesian mimic of its main prey, *Bombus americanorum* (Brower *et al.* 1960) (in Batesian mimicry a harmless species has evolved to mimic the warning coloration of a harmful species, so gaining protection from predators). Published records of predation on bumblebees by robber flies appear to be confined to North America (Brown 1929; Fattig 1933; Bromley 1936, 1949).

Beewolves (neither bees nor wolves but in fact wasps belonging to the Sphecidae) can be major predators of honeybees and other smaller bee species but have rarely been observed to take bumblebees. However, Dukas (2005) reported heavy bumblebee predation in the vicinity of a nest aggregation of the bee wolf *Philanthus bicinctus* in Wyoming, with up to 850 captured bumblebees being returned to the wasp nest aggregation per hour. This led to substantially depressed bumblebee density and reduced pollination of local flowers over an area of approximately 50 km<sup>2</sup>. Despite this dramatic example of predation by beewolves on bumblebees, we are aware of no other records from elsewhere. Overall it seems probable that predation on foraging bumblebees is infrequent, but clearly on occasion it can be severe.

Bumblebee nests are attacked by a number of predators which may have a significant impact on their populations. In the United Kingdom, nests are frequently destroyed by badgers (*Meles meles*), which entirely consume the brood, comb, and most of the adult bees (Alford 1975). In North America, skunks (*Mephitis mephitis*) are similarly destructive (Plath 1923b, 1934). Other nest predators are said to include foxes (*Vulpes vulpes*) (Southern and Watson 1941), moles (*Talpa europea*), weasels (*Mustela nivalis*)

(Sladen 1912), shrews (*Sorex* spp.) and voles (*Clethrionomys* and *Microtus*) (Alford 1975). In Iceland, bumblebee nests may be a major food source for mink (*Mustela vison*) (Prys-Jones *et al.* 1981). Newman (1851) estimated that two thirds of bumblebee nests in England were destroyed by the field mouse (*Apodemus sylvaticus*). However, in general we have very little quantitative data on predation rates by any of these organisms.

One predator which is undoubtedly of great importance is the wax moth, *Aphomia sociella* (Lepidoptera: Pyralidae). This species only occurs in the nests of bumblebees, and was said by Hoffer (1882–1883) to be one of their most serious enemies. The moth lays batches of eggs in the nest, and the gregarious larvae indiscriminately consume the comb, larvae and pupae (Fig. 5.3). They spin silken tunnels which presumably protect them from the adult bees. The bees appear to have no effective defence against them, and in heavy infestations the nests are entirely destroyed (D.G., pers. obs.). The larvae overwinter in a ball of tubular cocoons near the destroyed nest. They pupate in the spring, and give rise to adults from June onwards (Alford 1975). This moth appears to be particularly abundant in gardens in southern England, where I have found infestation levels in nests of *B. terrestris* of up to 80%. Since much lower infestation levels (~20%) were found in nests situated in farmland, this suggests that bumblebee populations may be higher in gardens than elsewhere (Goulson *et al.* 2002a). This moth is



**Figure 5.3.** Wax moth (*Aphomia sociella*) larvae can be exceedingly destructive in bumblebee nests, chewing through wax, food stores and brood. Heavy infestations rapidly destroy the nest.

known to be an important predator in mainland Europe (Hoffer 1882–1883; Hasselrot 1960; Pouvreau 1967), and has been introduced to North America (Forbes 1923).

Interestingly, bumblebee species vary greatly in their enthusiasm for nest defence. Some species, including *B. terrestris*, *B. muscorum* and *B. hypnorum*, are notoriously aggressive (Alford 1975; Schmid-Hempel 1998). They readily attack intruders near to their nest, which they will bite and sting simultaneously. Often workers will pursue intruders for some distance (D.G., painful pers. obs.). In contrast, species such as *B. pratorum* and *B. pascuorum* are remarkably docile. Their nests can be destroyed yet they will make little effort to defend them. This variation in behaviour does not follow taxonomic boundaries (e.g. *B. pascuorum* and *B. muscorum* are close relatives), and remains unexplained. We also have rather little idea how frequently bumblebees manage to repel nest predators. Rather impressively, the tropical bumblebee *B. transversalis* has been seen to defend its nest successfully against attack by army ants (Ramirez and Cameron 2003), but whether bumblebees successfully defend their nests against other predators such as voles or badgers is not known.

## 5.2 Parasitoids

Parasitoids are specialized organisms that develop on or in the body of their host, and successful development of the parasitoid invariably causes the death of the host (thus distinguishing them from parasites). They belong almost exclusively to the Hymenoptera and Diptera. A great deal is known about some parasitoids, notably the Hymenopteran parasitoids that attack agricultural pests. Rather less is known about parasitoids of social insects.

### 5.2.1 Conopidae (Diptera)

At least four genera of conopids attack bumblebees: *Conops*, *Myopa*, *Physocephala* and *Sicus* (Smith 1959, 1966, 1969). Conopids are parasitoids of all adult bees, queens, workers and males (Postner 1952; Alford 1975; Schmid-Hempel and Schmid-Hempel 1989). In Europe, hibernated queens fly too early to be attacked, but in Canada, queens of late-emerging species are attacked by *Physocephala texana* (Hobbs 1965b, 1966a,b), and in Switzerland, new summer queens can be parasitized before mating and hibernation (Schmid-Hempel and Schmid-Hempel 1989). The life cycle of conopids is described in detail by Alford (1975). The adult fly waits at flowers for foraging bees, and inserts a single egg through the intersegmental membrane into the abdomen of the host. Remarkably, the female fly has no hardened ovipositor for penetration of the host cuticle. This may explain why *Psithyrus* are rarely attacked (Schmid-Hempel *et al.* 1990), for they have a tougher exoskeleton than other *Bombus*. Bees are attacked from June to August.

Once inside the host the parasitoid egg rapidly hatches. The larvae consume haemolymph during their first two instars, but in the third and final instar switch to feeding on host tissues within the abdomen and, in some conopid species, they also feed upon

the contents of the thorax. This leads to the death of the host bee about 10–12 days after infection (Schmid-Hempel and Schmid-Hempel 1996b). Shortly afterwards the parasitoid pupates, remaining within the abdomen of the host. The adult fly emerges the following summer.

The behaviour of the host changes once infected. Workers of *B. terrestris* spend less time in their nest, and tend to stay outside the nest at night. They also actively seek out cold microclimates (Müller and Schmid-Hempel 1993a). This behaviour may have an adaptive explanation; by doing so they maintain a lower mean body temperature, which slows the development of the parasitoid and thus increases host longevity. Host workers continue to forage while parasitized, although they have a reduced capacity to carry nectar since the presence of the parasite constricts the volume of nectar that the honey stomach can contain (Schmid-Hempel and Schmid-Hempel 1991). Thus by keeping themselves cool at night, workers are prolonging their foraging life and so benefiting the colony. Conversely, in late stages of infection it seems that the parasitoid manipulates the behaviour of the host. Before death, parasitized bees tend to bury themselves, and the parasitoid is more likely to survive the winter when underground (Müller 1994). In addition to these dramatic behavioural changes, parasitism by conopids also alters the foraging behaviour of bumblebees. Infected *B. pascuorum* workers are less likely to forage at complex flowers (Schmid-Hempel and Schmid-Hempel 1990) and less likely to collect pollen as the conopid larvae develop inside them (Schmid-Hempel and Schmid-Hempel 1991).

The incidence of parasitization by conopids can be high but is very variable, ranging from 0% to 70% (de Meijere 1904; Cumber 1949c; Postner 1952; Schmid-Hempel *et al.* 1990; Schmid-Hempel and Müller 1991; Schmid-Hempel and Schmid-Hempel 1996a; Otterstatter 2004). Interestingly, the incidence of parasitization has been found to vary according to colony size; MacFarlane and Pengelly (1974) found that workers from small colonies were more likely to be parasitized. Since parasitization occurs at flowers, it is unclear why colony size should influence the prevalence of infection. One potential explanation is that in small colonies the proportion of workers who go out to forage, and thus expose themselves to parasitization by conopids, is higher, but this idea remains to be tested. Heavy infestation levels do impact on fitness of bumblebee nests, as they may result in the rearing of smaller queens (Müller and Schmid-Hempel 1992a,b) which are more likely to die in the winter (Holm 1972; Owen 1988), and also in a change in the sex ratio of sexual offspring due to a reduction in the number of new queens produced (Müller and Schmid-Hempel 1992b).

Host selection by conopids has been investigated by several studies. Larvae of the conopid *Sicus ferrugineus* were more frequent in larger workers of *B. pascuorum* and *B. terrestris/lucorum* (Müller *et al.* 1996; Schmid-Hempel and Schmid-Hempel 1996a). However, work in Canada showed that *Physocephala* conopids, which showed no preference for host size in Europe (Schmid-Hempel and Schmid-Hempel 1996a), have a more complex pattern of apparent size preference. In smaller species of bumblebee, these conopids were found in larger workers, whilst in larger species they were found in

smaller workers, resulting in a preference across all the bumblebee species available in the area for intermediate-sized hosts (Otterstatter 2004). This pattern reflects the fitness of the parasite, with parasite final size levelling off in intermediate-sized hosts—that is, there is no advantage to the parasite if it goes into even bigger bumblebees. Clearly, host preferences in conopids is complex, varying with both parasitoid and host species.

In addition to apparent selection on size, field data suggest that conopids may also discriminate between worker and male bumblebees, although results are contradictory. In a survey of the available literature, seven out of eight studies showed an apparent preference by conopids for worker bees (Ruiz-González and Brown 2006b). In Canada, males also seem to be parasitized at lower frequencies than workers (Otterstatter 2004). This preference may be a function of overlap between worker bumblebees and conopid flies in where they forage (Otterstatter 2004) versus the flight paths and foraging areas of males.

Only one parasitoid ever emerges from a host, so one would expect strong selective pressure on female conopids to avoid laying eggs in hosts that are already parasitized. However, hosts are frequently multiply parasitized (Clausen 1940; Schmid-Hempel and Schmid-Hempel 1989, 1996b). When this occurs there must be fierce competition resulting in the death of all but one parasitoid. Thus it seems likely that female conopids are unable to tell whether a bumblebee that they are ready to parasitize already contains another conopid's larva, despite the changes in bumblebee behaviour caused by the conopid (see earlier).

Finally, those few conopids that have been studied do not appear to be host-specific, although they do exhibit preferences for particular host species. For example in Switzerland, Schmid-Hempel and Schmid-Hempel (1996a) found that *Phyocephala rufipes* attacked *B. pascuorum*, *B. lapidarius* and, occasionally, *B. terrestris/lucorum*, while the sympatric conopid *S. ferrugineus* preferentially attacked *B. terrestris/lucorum* and *B. pascuorum* but was never found in *B. lapidarius*. In Canada, a *Phyocephala* conopid was found most frequently in *B. flavifrons* (Otterstatter 2004). These apparent preferences may relate to bumblebee size, rather than to their relative abundance in the bumblebee assemblage. Further host records are to be found in de Meijere (1912), Freeman (1966) and Schmid-Hempel (1994). Thus there is considerable potential for both intraspecific and interspecific competition within hosts, and the choice made by the female fly is vital to the fitness of her offspring.

### 5.2.2 Sarcophagidae (Diptera)

Various *Brachicoma* spp. are parasitoids of bee and wasp broods. Several species commonly attack bumblebees, notably *Brachicoma devia* in the United Kingdom and *Brachicoma sarcophagina* in North America (Alford 1975). The host range of *Brachicoma* spp. appears to be broad, spanning different families, but they do appear to exhibit preferences; for example, *B. sarcophagina* was most frequently recorded from the bees *B. bimaculatus* and *B. fervidus* (Townsend 1936). The adult fly must enter bumblebee

nests to deposit her offspring, and presumably has means of overcoming or avoiding the nest defences. She is viviparous, depositing young larvae directly on to bumblebee larvae. The fly larvae do not feed until their host spins a cocoon for pupation. They are ectoparasitoids, slowly consuming their host from the outside. A bumblebee larvae can support up to four parasitoids (Alford 1975). Once fully developed, the larvae drop to the floor of the nest and pupate among the nest debris. There may be several generations during the summer.

Other known bumblebee parasitoids within the Sarcophagidae include *Boettcharia litorosa*, *Helicobia morionella*, *Sarcophaga* spp. and *Senotainia tricuspis* (MacFarlane and Pengelly 1974, summarized in Schmid-Hempel 1998).

### 5.2.3 Braconidae (Hymenoptera)

*Syntretus splendidus* is a gregarious endoparasitoid of adult bumblebees, including queens, workers, males and the *Psithyrus* species *B. (P.) vestalis* (Pouvreau 1974; Alford 1975; Schmid-Hempel *et al.* 1990). Egg-laying has never been observed, but is thought to take place from March to June when bees are foraging on flowers as in conopids (Alford 1968; Goldblatt and Fell 1984; Rutrecht and Brown 2008a). The female may lay up to 70 eggs in queens, but usually fewer than 20 in workers (Alford 1968, 1973). A variety of host species are attacked, including *B. terrestris*, *B. lucorum* and *B. pascuorum* (Alford 1968). After hatching, the eggs develop through five larval instars within the thorax or abdomen of the host. In the fifth instar they emerge from the abdomen and burrow into the soil to pupate.

Parasitized bees continue to forage and behave normally, although the ovaries of queens degenerate so that egg-laying ceases. At best, infected queens rear a single generation of workers before dying, and these workers are significantly smaller than is usual (Alford 1968). After emergence of the parasitoids, the bee dies. The distribution and importance of braconid parasitoids of bumblebees is unknown. Most studies of *S. splendidus* have been carried out in the United Kingdom, but similar parasitoid larvae have been found in bumblebees in North America (Plath 1934) and Sweden (Hasselrot 1960), suggesting that they are widespread. Recent work in Ireland found larvae of *Syntretus* sp. in 7% of *B. pratorum* queens and these queens died from the infection without laying eggs 8 days after their collection in the field (Rutrecht and Brown 2008a). This suggests that the parasitoid can have a significant impact on the population of bumblebee species where queen emergence matches the flight time of the braconid parasitoid.

### 5.2.4 Mutilidae (Hymenoptera)

*Mutilla europa* is a parasitoid of bee larvae, attacking bumblebees, honeybees, and probably other bee species. This is a rare insect in the United Kingdom, and little is known of the details of its biology. The female is wingless and resembles a large hairy ant in appearance. She invades bee nests and lays her eggs in the pupal cocoons. The

larvae consume part or all of the host, and pupate inside a cocoon spun within the pupal cocoon of the host (Alford 1975).

### 5.3 Parasites and commensals

The parasites associated with social insects have been authoritatively reviewed by Schmid-Hempel (1998). Numerous organisms from diverse taxa are found associated with bumblebees and their nests. Some probably have no impact on their hosts (commensals) while others are major sources of mortality. With a few notable exceptions such as the nematode *Sphaerularia bombi* and the trypanosome *Crithidia bombi*, very little is known about the biology of these organisms. This is particularly true of the fungi, bacteria and viruses; few studies have examined their interactions with bumblebees (or indeed their associations with most other insects) and we have very little idea of their importance to bumblebee population dynamics.

#### 5.3.1 Viruses

Spectacularly little is known about the viruses of bumblebees. Viruses of honeybees are receiving increased attention since they are implicated in Colony Collapse Disorder (the sudden disappearance of the majority of honeybees in a colony, a phenomenon which affected many colonies in North America in 2007 and 2008). It seems certain that many viruses do infect bumblebees, but we do not know what impacts they may have. Entomopox-like viruses have been found in workers of the bumblebees *B. impatiens*, *B. pennsylvanicus* and *B. fervidus* in North America, although no adverse effects were found in infected individuals (Clark 1982). These viruses were most frequent in the salivary glands, and it seems likely that they are transmitted by ingestion of contaminated food. There is some evidence that honeybee viruses may also infect bumblebees, and that they can be readily transmitted between the two. Bailey and Gibbs (1964) detected inapparent infections of acute bee paralysis virus (ABPV) in various bumblebee species. Recently, Genersch *et al.* (2006) identified deformed wing virus (DWV) in about 10% of queens in a commercial *B. terrestris* rearing operation. In commercial bumblebee rearing, honeybees are often confined with the bumblebee queen to encourage her to nest, and this is presumed to be the source of cross-infection. The virus has also been detected in a wild nest of *B. pascuorum* that was robbing honey from nearby honeybee hives, so there is clearly the potential for the disease to spread into wild bumblebees. Infected individuals have deformed and non-functional wings, so depending on the prevalence of the virus within a colony, infection is likely to lead to its death. It seems probable that any systematic screening of bumblebee populations would rapidly reveal infection by other viruses.

#### 5.3.2 Prokaryotes (Bacteria and others)

It seems almost certain that many bacteria are associated with bumblebees and their nests, either as parasites or as commensals, but there have been very few studies. In

contrast, the bacteria *Melissococcus pluton* and *Paenibacillus larvae* which infect honeybees have been studied in considerable detail (Schmid-Hempel 1998). These organisms cause substantial mortality, demonstrating that bacterial diseases can be important in bees.

One particularly interesting group of prokaryotes associated with bumblebees are the Spiroplasmataceae. These bacteria-like organisms cause systemic infections in plants, and frequently occur on the surface of flowers. They have also been identified in various insects, including honeybees, the bumblebees *B. impatiens* and *B. pennsylvanicus* (Clark *et al.* 1985), and the solitary bees *Osmia cornifrons* and *Anthophora* sp. (Raju *et al.* 1981). In insects they occur in the gut and haemolymph. These organisms may primarily be sexually transmitted diseases of plants that employ bees as vectors to move between hosts (Durrer and Schmid-Hempel 1994). In honeybees infected with *Spiroplasma melliferum* death occurs after about 1 week (Clark 1977). Little is known of the pathological effects of these organisms on other bees.

### 5.3.3 Fungi

A range of generalist fungal pathogens including *Cordyceps*, *Paecilomyces* and *Beauveria* were recorded from UK bumblebees by Leatherdale (1970). Various other fungi that have been occasionally recorded from bumblebees include *Aspergillus candidus*, *Cephalosporium* sp., *Hirsutella* sp., *Paecilomyces farinosus* and *Verticillium lecanii* (summarized in Schmid-Hempel 1998). As far as is known, none of these fungi regularly causes significant mortality in bumblebees. The yeasts *Candida* and *Acrostalagmus* do appear to be widespread in bumblebees; they were found in about 30% of queens examined by Skou *et al.* (1963), and they appeared to trigger abnormally early emergence from hibernation. It is possible that these yeasts are important causes of overwintering mortality (Schmid-Hempel 1998).

### 5.3.4 Protozoa

Several protozoans infect bumblebees and two of these, the trypanosome *C. bombi* and the microsporidian *Nosema bombi*, have been the focus of considerable study.

*C. bombi* infects the gut of bumblebees and has been found throughout Europe and Canada (Schmid-Hempel 1998; Colla *et al.* 2006). Infection occurs via ingestion of parasite cells, and infected hosts later release hundreds of thousands of parasite cells in their faeces (Schmid-Hempel and Schmid-Hempel 1993). The prevalence of the parasite in spring queens varies between 0% and 50% (Shykoff and Schmid-Hempel 1991d; Brown, pers. obs.) and may rapidly approach 100% in workers and infect almost all colonies by the end of the season (Shykoff and Schmid-Hempel 1991d; Imhoof and Schmid-Hempel 1999). This rapid increase in prevalence through the season is due to the transmission of parasites via flowers during foraging (Durrer and Schmid-Hempel 1994) and rapid transmission within colonies (Otterstatter and Thompson 2007). While initially thought to have little impact on its bumblebee hosts, it significantly increases mortality rates in stressed workers (Brown *et al.* 2000). It also reduces the overall fitness of infected



populations by 40% through inhibiting colony founding by queens and reducing colony size and the production of new queens and males (Brown *et al.* 2003a; Yourth *et al.* 2008). Interestingly, when exposed to hosts from different regions with which it has not coevolved, *C. bombi* even causes mortality in unstressed workers (Imhoof and Schmid-Hempel 1998). This maladaptation may be related to strain-specific interactions, where parasite strains vary in their ability to infect different bumblebee families (Shykoff and Schmid-Hempel 1991a,b; Schmid-Hempel *et al.* 1999; Baer and Schmid-Hempel 2003; Mallon *et al.* 2003; Schmid-Hempel and Funk 2004; Yourth and Schmid-Hempel 2006), which is itself based on genetic variation in bumblebees (Wilfert *et al.* 2007).

In addition to reducing host fitness, *C. bombi* has intriguing effects on behaviour, memory and immune function in bumblebees. Parasitized bees forage more slowly, take longer to learn how to get nectar from novel flowers and are less capable of learning to associate flower colour with nectar rewards (Otterstatter *et al.* 2005; Gegear *et al.* 2005, 2006). Because infection by the trypanosome elicits an immune response in bumblebees (Brown *et al.* 2003a; Otterstatter and Thompson 2006), and activating immunity can impair learning in honeybees (Mallon *et al.* 2003) and bumblebees (Riddell and Mallon 2006; Alghamdi *et al.* 2008), these behavioural changes are probably mediated via the parasite's effect on bumblebee immune systems.

The microsporidian *N. bombi* appears to be less common than the trypanosome *C. bombi*; Skou *et al.* (1963) found that 18 out of 99 *Bombus* queens sampled in Denmark were infected, while Fisher (1989) found it in 10% of spring queens and 61% of mature colonies in New Zealand. While *N. bombi* is also transmitted by the oral-faecal route, it is less effective in infecting adults (Rutrecht *et al.* 2007) and this may explain its lower prevalence in wild populations. However, despite this lower prevalence, *N. bombi* appears to be effectively genetically identical across all its European hosts (Tay *et al.* 2005). In contrast to *C. bombi*, the microsporidian relies on infecting larvae, rather than adult workers (Eijnde and Vette 1993; Rutrecht *et al.* 2007; Rutrecht and Brown 2008b) to spread within colonies and unlike the trypanosome, *N. bombi* infects the entire animal, not just the gut (Fries *et al.* 2001). Historically, the impact of *N. bombi* on its bumblebee hosts was unclear, with some studies reporting negative (Fantham and Porter 1914; Skou *et al.* 1963; De Jonghe 1986; Eijnde and Vette 1993; MacFarlane *et al.* 1995; Schmid-Hempel and Loosli 1998; Whittington and Winston 2003), some neutral (Betts 1920; Fisher and Pomeroy 1989b; Shykoff and Schmid-Hempel 1991d; McIvor and Malone 1995; Whittington and Winston 2003) and some positive effects (Imhoof and Schmid-Hempel 1999). However, recent experimental infections have definitively demonstrated a significant impact of this parasite on its hosts. Infected colonies of *B. terrestris* have reduced worker survival and are of smaller size in the lab (Otti and Schmid-Hempel 2007), and of 14 infected colonies placed in the field none survived for reproduction (Otti and Schmid-Hempel 2008). It seems counterintuitive that this pathogen has such high pathogenicity; as far as is known it relies on infecting young queens for vertical transmission from one season to the next, yet infected *B. terrestris* nests die without reproducing. Perhaps the parasite relies on late-season horizontal transmission to

successful nests that are producing new queens, or alternatively it may be less virulent in other host species (Rutrecht and Brown, unpublished data).

We know least about a third protozoan parasite, the neogregarine *Apicystis bombi*. This parasite is associated with deterioration of the fat body and rapid queen death (MacFarlane *et al.* 1995; Rutrecht and Brown 2008a). How this parasite is transmitted and maintains itself in bumblebee populations is completely unknown, but the fact that it reappears in summer worker populations suggests either that not all infected queens are killed or that it has a reservoir in the natural environment (Rutrecht and Brown 2008a).

Recent evidence suggests that the breeding system of most bumblebee species makes them particularly susceptible to intra-colony epizootics of parasites such as protozoans. Queens of most bumblebee species mate only once, so that workers are all full siblings (Estoup *et al.* 1995; Schmid-Hempel and Schmid-Hempel 2000). Owing to the haplodiploid genetics of Hymenoptera, this means that all workers within a colony are 75% related to each other. Parasites and pathogens probably act with positive frequency dependence, so that rare host genotypes are favoured (Haldane 1949; Hamilton 1980). Thus, genetic variability within a colony of a social organism is likely to reduce the impact of parasites (Tooby 1982; Hamilton 1987; Sherman *et al.* 1988). Experimental tests with bumblebees support this hypothesis; infections of *C. bombi* spread more slowly among groups of unrelated workers than among related workers (Shykoﬀ and Schmid-Hempel 1991a,b). In an elegantly simple experiment, Liersch and Schmid-Hempel (1998) manipulated the genetic variability in colonies of *B. terrestris* by moving brood between nests; when placed under field conditions, colonies with artificially enhanced variability suffered from fewer parasites.

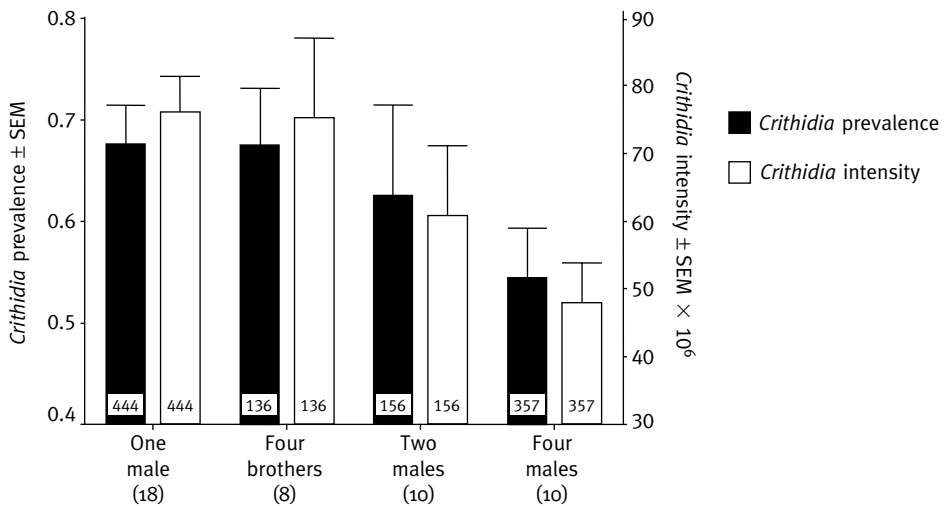
Genetic variability can be greatly increased if queens mate with several males, but most bumblebee queens do not do so. Why not? Mating takes up to an hour (Duvoisin *et al.* 1999) and during this period the mating pair cannot fly. They are presumably vulnerable to predation at this time, so it may pay a queen to mate only once. Also, males place a mating plug in the reproductive tract of the female which is at least partially effective in preventing further matings (see Chapter 4).

Newly developed techniques for artificial insemination of bumblebees (Baer and Schmid-Hempel 2000) make it possible to test the costs and benefits to queens of producing a genetically variable colony. In two experiments, Baer and Schmid-Hempel (1999, 2001) inseminated queens of *B. terrestris* with sperm from (i) either four unrelated males or four brothers (high and low genetic variability, respectively), or (ii) either one, two or four unrelated males or four brothers. Once colonies were established they were placed out in the field, and their fitness and the prevalence of infection with multiple parasites or, in the second experiment, just *C. bombi*, was subsequently compared. In the first experiment, they found that low diversity colonies had higher parasite prevalence and lower fitness than genetically diverse colonies, suggesting that females should mate multiply. However, the second experiment revealed a more complex picture. While colonies with greater genetic variation had lower prevalence and intensity of infection

(Fig. 5.4), colony fitness, as measured by the number of males and queens produced, was highest in the least and most diverse colonies and was lowest in the intermediate-variability colonies. This U-shaped fitness function has not been adequately explained, but may be due to conflict between workers of different patriline within the nest (see Chapter 3). This suggests that selection for resistance to parasites does favour multiple matings, but that other factors, including an immediate reduction in fitness for low levels of multiple mating and the evolution of mating plugs in males, constrain the evolution of polyandry.

### 5.3.5 Nematodes

One of the best-known parasites of bumblebees is the nematode worm *S. bombi*. This parasite is unusual in that it only attacks queens (and female *Psithyrus*), a strategy that inevitably restricts it to a very small proportion of the host population. The life cycle is described and illustrated in detail by Alford (1975). A mated nematode female enters either through the gut or the cuticle of a queen while she is hibernating in the soil, and takes up residence in the haemocoel. The uterus of the nematode may evert whilst the queen is still hibernating, or after she leaves hibernation, but within a week post-hibernation it is at its maximum size (up to 2 cm long), dwarfing the rest of the nematode's body (Kelly and Brown, unpublished data). Hosts are often multiply infected with



**Figure 5.4.** Intensity (the average number of cells found in the gut of workers per colony) and prevalence (the proportion of parasitized workers in a colony) of *C. bombi* in colonies of *B. terrestris*. The foundress queens had been artificially inseminated with sperm from one, two or four unrelated males, or four brothers. Both intensity and prevalence of infection differ significantly between treatments ( $p < 0.0001$  and  $p = 0.025$ , respectively). From Baer and Schmid-Hempel (2001).

several nematodes (Alford 1969; Poinar and van der Laan 1972), and infection rates can be high; Schmid-Hempel *et al.* (1990) report an average of 12%, but on occasion far higher rates have been recorded (Alford 1975). The female nematode releases eggs into the haemocoel, which rapidly hatch, producing up to 100,000 offspring. The juveniles migrate to the gut and are egested with the faeces. They reach adulthood and mate in the soil, and so complete the cycle.

One of the more intriguing aspects of this parasite is its ability to influence the behaviour of its host. In a healthy queen, hormones are released from the corpora allata in the spring, stimulating the development of the ovaries. In a parasitized queen this does not occur. Rather than attempting to found a nest and lay eggs, the queen investigates overwintering sites and so contaminates them with parasites (Lundberg and Svensson 1975). Any queens remaining on the wing by May or June are generally infected, since healthy queens will by this stage have founded a nest. Infected queens become increasingly sluggish and eventually die in spring or early summer. While most infected queens never manage to reproduce, queens of *B. hortorum* have been found who are parasitized by the nematode but are still raising a new colony (Alford 1969; Röseler 2002). Even more surprisingly, Röseler (2002) reared successful colonies from parasitized queens of *B. hypnorum*. This suggests that bumblebee queens are capable of resisting the parasite, but how frequently this occurs or whether it is only some bumblebee species that can do it remains unknown. Occasionally the parasite passes through two generations in a single season for young queens have been found in late summer containing well-developed adult nematodes (Alford 1975).

It seems that infected queens do not travel far. In New Zealand, *S. bombi* was presumably introduced accidentally with the first bumblebee release in 1885. By the early 1970s the parasite had spread by only about 40 km, about 0.5 km per year, while the bumblebees had colonized the whole of New Zealand within a few years of their release (MacFarlane and Griffin 1990).

### 5.3.6 Mites (Acarina)

At least 15 genera of mites are associated with bumblebees (Alford 1975; Eickwort 1994; Schmid-Hempel 1998). The most familiar of these are mites of the genus *Parasitellus* (Mesostigmata: Parasitidae), which are very often to be seen attached to the bodies of adult bumblebees, particularly queens. These mites are only ever found in close association with bumblebees (Richards and Richards 1976; Schousboe 1987; Schwarz *et al.* 1996). However, they do not feed directly upon bumblebees, but are phoretic, using the adult bees for transport between nests. This is a common phenomenon; mites have poor locomotory abilities, but with their small size they can easily attach themselves to larger organisms and so gain a free ride (Evans 1992). *Parasitellus* species are thought to feed upon wax, pollen and other small arthropods that are found in bumblebee nests (Richards and Richards 1976). Only the deutonymph stage is phoretic, colonizing new nests by transferring from workers to flowers, and then awaiting the arrival of another

worker (Schwarz and Huck 1997). The prevalence of *Parasitellus* spp. is generally high. Schousboe (1987) found that 15–28% of spring queens of *B. terrestris/lucorum* were infested in Denmark. Schwarz *et al.* (1996) recorded infestation levels of 22% on spring queens of *B. pascuorum* and 46–49% on *B. terrestris*, *B. lucorum* and *B. lapidarius* in Switzerland. Comparable estimates from Corbet and Morris (1999) were 57% for *B. terrestris*, 83% for *B. pascuorum* and 100% for *B. hortorum* in England. With this level of prevalence at the beginning of the season, it is not surprising that the vast majority of bumblebee nests become infested by the end of their growth (Huck *et al.* 1998).

Because these mites do not feed upon the bees themselves, it is debatable whether they have a negative impact. However, infestation levels can be high; Huck *et al.* (1998) report up to 165 deutonymphs on a single *B. lapidarius* queen. It seems inevitable that loads of this magnitude must hamper a queen's ability to fly, and so her ability to find food, a mate and a hibernation site.

A diversity of other mites are found on or in bumblebees, including the tracheal mite *Locustacarus buchneri* (Skou *et al.* 1963), *Scutacarus* spp. (Schousboe 1986), *Pneumolaelaps* spp., *Hypoaspis* spp. (Hunter and Husband 1973) and *Kuzinia* spp. (Goldblatt 1984). It seems probable that there are many more as yet unknown. The tracheal mite shows interesting patterns of host specialization, being significantly more common in some host species than others (reviewed in Otterstatter and Whidden 2004). However, there is no obvious explanation for these patterns and they await further investigation. *L. buchneri* is truly parasitic, feeding directly on the haemolymph of its host, and is therefore likely to reduce host fitness (Husband and Sinha 1970), perhaps by reducing the lifespan of individual infected hosts (Otterstatter and Whidden 2004), although a recent study suggested that they were associated with higher fitness in colonies of *B. pratorum* (Rutrecht and Brown 2008a). In addition to fitness impacts, tracheal mites are associated with changes in foraging behaviour, with infected workers showing higher flower constancy than their uninfected sisters (Otterstatter *et al.* 2005). However, most mites are not parasitic. For example, *Scutacarus acarorum* feeds on fungi (Schousboe 1986), and *Kuzinia laevis* on pollen and fungi (Chmielewski 1969). They are all probably phoretic to varying degrees, and a range of species can be found on flowers visited by bumblebees (Schwarz and Huck 1997). One very small species, *S. acarorum*, is actually phoretic on larger mites such as *Parasitellus*, even while their hosts are phoretic on bumblebees (Schwarz and Huck 1997), inevitably bringing to mind “A flea hath smaller fleas that on him prey; and these have smaller fleas to bite ‘em, and so proceed ad infinitum” (Jonathan Swift 1733).

Because bumblebee nests are short-lived, mites must attach themselves to new queens at the end of the season (Stebbing 1965; Richards and Richards 1976). They then overwinter with the queen in her underground hibernaculum, and infest the nest that she founds in the spring. In choice tests, deutonymphs of *Parasitellus fucorum* exhibited a strong preference for queens over males, and readily transferred from males to queens, which clearly makes sense since males do not go in to nests (Huck *et al.* 1998). In mature nests of *B. terrestris*, the vast majority of deutonymphs are attached

to new queens (D.G., unpublished data). Similarly, the phoretic instars of *Parasitellus*, *Pneumolaelaps* and *Scutacarus* are all found more frequently on queens than on workers (Hunter and Husband 1973; Richards and Richards 1976; Schousboe 1986, 1987).

### 5.3.7 Other commensals

If a bumblebee comb is lifted, a wriggling mass of insect larvae is usually revealed. These organisms scavenge upon detritus, dead brood, wax, pollen and adult bee faeces. Many of these organisms also occur elsewhere (e.g. in bird's nests or in the faeces of mammals). The majority have little or no adverse effects on their hosts, and may even be helpful in disposing of waste. In general, the most abundant of these scavengers are dipteran larvae (maggots). One of the most frequent denizens of bumblebee nests is *Fannia canicularis* (Muscidae). *Volucella bombylans* (Syrphidae) also deserves particular mention for this fly is an obligate bumblebee nest commensal and the adult fly is a splendid and convincing bumblebee mimic (Evans and Waldbauer 1982). It is also polymorphic, with one morph mimicking bees with yellow stripes and a white tail (such as *B. hortorum*) and another mimicking black bumblebees with a red tail (such as *B. lapidarius*). If attacked by the bees when attempting to enter a nest, the female fly immediately lays her eggs (even doing so after her death), which generally go unnoticed by her assailants (Sladen 1912).

Other nest scavengers include several species of lepidopteran larvae including *Endrosis sarcitrella* (Oecophoridae), *Vitula edmandsii* and *Ephestia kühniella* (Pyralidae) and an as yet unidentified member of the Tineidae (Smith 1851; Davidson 1894; Frison 1926; Alford 1975; Whitfield and Cameron 1993; Whitfield *et al.* 2001). In contrast with *A. sociella*, it seems that most of these species inflict little or no damage on the nest. Finally, all stages of the life cycle of the coleopteran *Antherophagus nigricornis* can be found in bumblebee nests (Alford 1975). This beetle is phoretic; the young adult beetle climbs on to a flower, and then hitches a ride to a nest by clinging to the tongue, antennae or leg of a visiting bumblebee (von Frisch 1952). The adult beetle and its offspring feed on nest debris.

These nest commensals themselves support a range of parasitoids including ichneumonid and braconid wasps which may often be found in bumblebee nests (reviewed in Alford 1975; see also Whitfield and Cameron 1993; Whitfield *et al.* 2001).

## 5.4 The immune system of bumblebees

Bumblebees do have a defence against internal parasites and pathogens; as in most insects, they have an immune response (Gupta 1986). While significantly less complex than the vertebrate immune response that we, as humans, possess, recent research suggests that it is not as simple as was first assumed. The immune response has two main branches. The constitutive branch involves phagocytosis by haemocytes, melanization through the phenoloxidase pathway and encapsulation of foreign particles such as

bacteria, fungi and possibly parasitoid eggs. The inducible branch involves the production of potent molecules, the antibacterial peptides, which are involved in the attack of bacteria and fungi.

In bumblebees, foreign bodies (presumably including parasitoid eggs) are rapidly encapsulated (Schmid-Hempel 1998; Allander and Schmid-Hempel 2000; Moret and Schmid-Hempel 2000). Encapsulation may kill a parasitoid egg, but we do not know how often, if ever, bumblebees are successful in doing this. Activation of the immune response is known to be costly. Moret and Schmid-Hempel (2000) stimulated the immune response of workers of *B. terrestris* by implanting non-pathogenic and non-toxic latex beads or lipopolysaccharides (molecules that are normally found on the surface of bacteria). When maintained on a starvation diet, worker mortality was substantially increased by this procedure, and it was concluded that it was the cost of immunity that directly caused mortality. Interestingly, bumblebees have been shown to increase their food consumption when their immune response is stimulated, presumably in an attempt to compensate for the cost of immunity (Tyler *et al.* 2006).

In *B. terrestris*, the encapsulation response is very variable between individuals and between colonies (Schmid-Hempel 1994; König and Schmid-Hempel 1995; Schmid-Hempel and Schmid-Hempel 1998; Baer and Schmid-Hempel 2006). This may in part reflect environmental effects; colonies with reduced resources are likely to exhibit a weaker immune response. Similarly, workers that are active foragers have a weaker immune response than workers who do not have to fly, presumably indicating a trade-off in the allocation of resources to behaviour and immunity (König and Schmid-Hempel 1995; Doums and Schmid-Hempel 2000). Furthermore, in both *B. terrestris* and *B. lucorum* the encapsulation response declines as workers age (Doums *et al.* 2002). Male immune response also seems to vary through the season, with *B. terrestris* males from late-reproducing colonies having a lower encapsulation response than those produced earlier, perhaps because they have a shorter expected reproductive lifespan (Baer and Schmid-Hempel 2006).

In addition to environmental affects, there is likely to be genetic variability in immune response between bumblebee populations as a result of variation in their past exposure to pathogens. Wilfert *et al.* (2007) found that the genetic architecture behind immunity was complex and interactive, as would be expected if parasites were exerting selective pressure on host immunity. Surprisingly, however, Gerloff *et al.* (2003) found that highly inbred workers resulting from brother–sister matings did not have a reduced immune response in *B. terrestris*, although males had a lower immune response than workers, and diploid males had a lower immune response than haploid males. As yet we know very little about variation in immune response within and between bumblebee species since, as with so many aspects of bumblebee ecology, almost all published work focuses on *B. terrestris*.

Bumblebees have been one of the major research organisms for understanding the evolutionary ecology of the insect immune response. Since the first edition of this

book, a series of elegant studies have demonstrated previously unimagined complexity. Human mothers can transfer specific immune protection to their offspring either across the placenta or via breast feeding. Moret and Schmid-Hempel (2001) showed that bumblebee colonies can do something very similar. By challenging the immune system of workers, they showed that males produced by such challenged colonies had higher levels of constitutive immune defences (as measured by phenoloxidase activity; the production of melanin) than males from unchallenged colonies. This suggests that bumblebee colonies in areas with a high parasite threat can prepare their male offspring to enhance their survival. A further study by Sadd and Schmid-Hempel (2007) showed that this trans-generational immune priming occurs through unknown factors in the egg, that it occurs in worker offspring as well as males, and that eggs themselves exhibit higher antibacterial activity if their mother faced an immune challenge. The bumblebee immune system can also remember past challenges and respond appropriately when challenged up to several weeks later by the same bacterial threat (Sadd and Schmid-Hempel 2006). Bumblebees are clearly at the forefront of changing our understanding of innate immunity in insects.

Finally, as we saw previously, activation of the immune response can have significant effects on behaviour and learning in bumblebees (Riddell and Mallon 2006; Alghamdi *et al.* 2008). Furthermore, bumblebee colonies may alter their life history, bringing forward the production of sexuals, if their immune system is put under pressure (Moret and Schmid-Hempel 2004). Trying to understand the mechanism behind these links is a highly active area of current research.

## 5.5 Social parasitism

The success of social insects is largely due to their ability to accrue resources efficiently through division of labour, and to store these resources within the nest. A number of organisms have evolved methods for diverting the efforts of social insects to their own ends, so that the parasites benefit from the resources gathered, and are often directly cared for by their hosts. This is known as social parasitism. Very often social parasites are closely related to their hosts, for they are thus better equipped with the chemical armoury necessary to subvert the efforts of their host to their own ends. Bumblebees suffer from two sorts of social parasites; other non-*Psithyrus* bumblebees (either of their own or a different species) and cuckoo bees (subgenus *Psithyrus*). These are considered in turn, although in many respects the details are similar.

### 5.5.1 Nest usurpation

Bumblebee queens vary greatly in their time of emergence from hibernation, even within species, perhaps as a result of their choice of overwintering site or their body condition. Late-emerging queens, when searching for nest sites, will often find that



suitable sites are already occupied. In this situation they may attempt to take over an established nest for themselves (Alford 1975). Species that tend to emerge late, such as *B. rufocinctus*, are particularly prone to this behaviour (Hobbs 1965b). In years when queens are abundant, nest usurpation may become very frequent (Bohart 1970). Sladen (1912) describes one nest of *B. terrestris* which contained 20 dead queens, presumably the foundress queen and successive usurpers. The process of usurpation is described in detail by Alford (1975). The foundress and intruder may avoid each other for some time, but a fight to the death eventually ensues. The fights are usually brief, being concluded when one queen successfully stings the other. If the intruder is successful she will continue to care for the brood in the normal manner. Usurpation becomes rarer as colonies grow in size, and is never observed once the second batch of brood has emerged.

There are very few data as to how frequently nest usurpation is successful, although the fact that the strategy persists suggests that it must sometimes succeed. However, Paxton *et al.* (2001) used microsatellite analysis of workers genotypes to demonstrate the presence of workers that were unrelated to the queen in 6 out of 11 nests of *B. hypnorum*. They concluded that these workers were probably the offspring of a previous queen that was usurped. The alternative explanation is that these workers had drifted between nests, but this seems unlikely since the individual bees were all small, of a size normally associated with the queen's first brood.

Usurpation only occurs within species of the same subgenus (Hobbs 1965b). Thus, for example, *B. terrestris* will often attempt to usurp its sister species, *B. lucorum*, which tends to emerge slightly earlier. It is easy to see how this behaviour could eventually evolve into obligate usurpation. In arctic North America, *B. hyperboreus* frequently usurps *B. polaris* (Milliron and Oliver 1966; Richards 1973). Because the season is short, the usurping queen does not rear any workers of her own, but rears only reproductives. Since no worker *B. hyperboreus* are reared, the life cycle then becomes identical to that of *Psithyrus* (Section 5.5.3). Outside of the subgenus *Psithyrus*, there is one *Bombus* species suspected of having adopting an obligate parasitic lifestyle. No workers of *B. inexpectatus* have ever been recorded, and it is thought that this species may be an obligate parasite of its close relative *B. ruderarius* (Yarrow 1970).

### 5.5.2 Social parasitism by drifting workers

Fascinatingly, it has emerged that worker *B. terrestris* sometimes enter unrelated *B. terrestris* nests and lay eggs, thus avoiding the possible costs associated with trying to reproduce within the natal nest. These workers exhibit higher levels of aggression and lay more eggs than do reproductively active workers that have remained within their own nest (Birmingham *et al.* 2004; Lopez-Vaamonde *et al.* 2004). However, it is not yet clear whether this is an artefact of using artificially reared nests. Both studies used nests reared in captivity, which may smell more similar to one another than is usual in the wild, encouraging and enabling workers to enter the 'wrong' nest. These nests were also

housed in similar or identical nest chambers, and placed close to one another, making accidental movement between nests far for likely; wild nests are unlikely to be close to one another, and when they are very likely to have markedly different nest entrances. Nonetheless, the fact that these drifting workers exhibited higher levels of aggression and reproduction suggests that they may have detected that they were no longer in their natal nest. Clearly, this phenomenon merits further investigation in more natural settings, where it would be straightforward to use microsatellite markers to identify unrelated bees, and dissection could reveal whether these bees possessed unusual levels of ovarian development.

### 5.5.3 Cuckoo bees (*Psithyrus*)

Cuckoo bees (subgenus *Psithyrus* spp.) were for many years placed in a separate genus to the 'true' bumblebees (Williams 1994). In all probability they evolved from social *Bombus* via nest usurpation as described earlier. Recent authors agree that they have a monophyletic ancestry (Plowright and Stephen 1973; Pekkarinen *et al.* 1979; Ito 1985; Pamilo *et al.* 1987; Williams 1985a, 1994; Cameron *et al.* 2007). *Psithyrus* do not have pollen baskets and so they now have an obligate dependency on social bumblebees.

Female *Psithyrus* emerge from hibernation later than their hosts, and spend some time foraging on flowers while their ovaries develop. They then search for nests of their host species, probably at least in part using scent (Frison 1930). The female *Psithyrus* will enter a bumblebee nest and attempt to dominate or kill the foundress. *Psithyrus* females have a more powerful sting and mandibles than their hosts, and generally have a thicker exoskeleton. They are thus at a distinct advantage in conflicts with the foundress queen, and if they attack a colony before the second batch of workers have been produced they usually prevail. For example, Frehn and Schwammberger (2001) placed *B. (P.) vestalis* queens into three young *B. terrestris* nests resulting in the death of all three host queens within 6 days. Sometimes the host queen will retreat and become subservient to her usurper (Hobbs *et al.* 1962; Hobbs 1965a). She behaves much like a worker; if the nest is disturbed she engages in active nest defence, rather than hiding within the comb as she would normally do.

Although bumblebee queens are unable to repel *Psithyrus*, a large group of workers may do so. When *Psithyrus* attempt to invade large nests they are usually fiercely attacked by a number of workers and may be killed. Interestingly, most *Psithyrus* species are able to parasitize host species from more than one subgenera (Sakagami 1976), and they are notably less specific than *Bombus* species which are only able to usurp nests of their own species or very close relatives (Alford 1975). Perhaps their physical strength means that they do not need to closely match the chemistry of their hosts to successfully invade. In the United Kingdom at least, *Psithyrus* often resemble their hosts in coloration. Most authors agree that this is probably not to aid entry in to the nest, but that the *Psithyrus* and their hosts are members of Müllerian mimicry groups (Alford 1975; Prys-Jones and Corbet 1991).

If her takeover attempt is successful, the *Psithyrus* female will lay eggs which will be reared by the bumblebee workers as their own (Weislo 1981; Fisher 1987). This form of social parasitism is known as inquilinism (Hölldobler and Wilson 1990). Since *Psithyrus* do not have a worker caste, all of the offspring are males or future breeding females. The invading *Psithyrus* may eat host eggs and young larvae, but older ones are allowed to develop to add to the work force. Nests that have been invaded produce few or no host queens or males, although workers do lay eggs and a few of the resulting male offspring may survive (Frehn and Schwammberger 2001). The *Psithyrus* queen presumably attempts to prevent this; she chases and mauls the workers, particularly those with active ovaries (Fisher 1988; Frehn and Schwammberger 2001).

Nests may be easier to appropriate when they are small, but then a smaller workforce will be available for rearing the offspring of the *Psithyrus* female (Fisher 1984). In nests with few workers, few *Psithyrus* are reared and they tend to be smaller in size than usual (Alford 1975). Thus there is likely to be a trade-off between the ease with which nests can be taken over and the benefits to be accrued from doing so. Müller and Schmid-Hempel (1992b) found that female *B. (P.) bohemicus* preferentially attacked the largest nests of *B. lucorum*. Little information is available on the frequency with which bumblebee nests repel invasion. *Psithyrus* may target large nests simply because they are easier to find (presumably they produce a stronger odour).

Bumblebee queens may also face a trade-off with regard to the optimum time at which to leave hibernation and found a nest. Müller and Schmid-Hempel (1992b) found that early-founded nests of *B. lucorum* were most frequently attacked by *B. (P.) bohemicus*, but have a higher expected reproductive output if they are not taken over by *Psithyrus*. Similarly, Carvell *et al.* (2008) found that artificial *B. terrestris* colonies were more likely to be invaded by *B. (P.) vestalis* when placed out in the field earlier in the season. Thus, we might expect queens to nest early in areas where *Psithyrus* are scarce, but later when they are common.

The frequency of invasion of bumblebee nests by *Psithyrus* is highly variable both between localities and years. Alford (1975) considered attacks by *Psithyrus* to be generally rare, but high infestation levels have been recorded. Awram (1970) found that more than 50% of nests of *B. pratorum* were taken over by *B. (P.) sylvestris*, while Sladen (1912) reports rates of 20–40% for invasion of *B. lapidarius* nests by *B. (P.) rupestris* (both studies were carried out in England). More recently, Müller and Schmid-Hempel (1992b) recorded rates of attack of *B. lucorum* by *B. (P.) bohemicus* approaching 30% in Switzerland, although these attacks were not necessarily successful. To my knowledge, the highest rates of attack recorded are from Carvell *et al.*'s (2008) study using artificial nests of *B. terrestris terrestris* (a non-native subspecies) placed in the field in the United Kingdom, where 38 out of 48 colonies (79%) were invaded by at least one *B. (P.) vestalis*, with a total of 129 cuckoo females invading the 48 nests. However, these data must be treated with some caution as the artificial nature of the nest boxes may have rendered them more easily detected or invaded by cuckoos. In this study, it was also found that invasion rates were significantly higher when host colonies were adjacent to oilseed

rape fields (92%) compared to those next to wheat fields (67%), suggesting that proximity to floral resources can have indirect negative effects on bumblebee colony performance through attracting natural enemies.

In most other respects the life cycle of *Psithyrus* is rather similar to that of their hosts. Mating occurs in mid to late summer, and only females hibernate. Males are far more frequently seen than females, and they are very commonly observed feeding sluggishly on flower heads of thistles (*Cirsium* and *Carduus* spp.) and knapweeds (*Centaurea* spp.) in July and August.

*This page intentionally left blank*

# 6

---

## Foraging Economics

*Dave Goulson and Juliet L. Osborne*

*Time is honey*  
*Bernd Heinrich (1996)*

Insect foraging behaviour is an area in which knowledge has advanced rapidly in recent years, and much of this research has focussed on bumblebees. There are a number of reasons why bumblebees are excellent organisms for studies of foraging behaviour: they are abundant in the northern hemisphere where most researchers are based; they are conspicuous, docile and easily observed without causing interference; and they forage ceaselessly, even under cool, cloudy conditions when other insects are inactive (a particular advantage if you happen to live in Scotland!). Furthermore, studies of pollinator behaviour are of particular interest because the majority of flowering plants rely on insects to mediate pollen transfer. Thus, it is the behaviour of insects which determines which flowers will set seed and which will not, and which governs the pattern of transfer of gametes among plants (of topical relevance to the risks associated with the use of genetically modified crops). Aside from their economic and ecological importance as pollinators, bumblebees have become popular vehicles for examining the assumptions and predictions of foraging models and the interplay between learning, memory constraints and foraging efficiency in a complex and unpredictable environment.

Bees and a number of other insect groups, including butterflies and moths (Lepidoptera), some flies (Diptera) and beetles (Coleoptera), depend for their sustenance on pollen or nectar rewards provided by flowers. Both nectar and pollen have much to recommend them as food for insects. Nectar provides sugars and water necessary to sustain an active adult insect, while pollen is a rich source of protein. In general, they are not heavily protected by toxins or physical defences, as are most plant tissues. Proteins are particularly important during growth of immature insects, but it is generally only adult winged insects that specialize in visiting flowers. Immature stages do not have the mobility necessary to gather such carefully rationed and sparsely scattered resources (unless they are very small and can survive on a handful of flowers). Of course bees have overcome this problem; the larvae feed upon pollen and nectar collected by the adults.

Even for insects capable of flight, efficient collection of floral rewards is problematic. The distribution of rewards is unpredictable in time and space; individual plants and plant species open their flowers at different times of the day and flower at different

times of the year (Waser 1982b; Zimmerman and Pyke 1986; Real and Rathcke 1988). Rewards per flower vary greatly between plants of a single species and between flowers on a single plant due to genetic and environmental influences on reward production rates and also in response to the pattern of depletion of rewards by foragers (e.g. Pleasants and Zimmerman 1979, 1983; Zimmerman 1981a,b; Brink 1982; Thomson *et al.* 1982; Pleasants and Chaplin 1983; Cruden *et al.* 1984; Zimmerman and Pyke 1986; Real and Rathcke 1988; Mangel 1990; Waser and Mitchell 1990; Gilbert *et al.* 1991). At any one time many flowers may be empty (Wetherwax 1986; Real and Rathcke 1988; Cresswell 1990; Waser and Mitchell 1990). To add to the difficulties, many plant species hide their floral rewards within complex flowers so that only insects with an appropriate morphology can enter them; for example, flowers of broom, *Cytisus scoparius*, produce an abundance of pollen, but it can only be accessed by heavy insects such as bumblebees that have sufficient weight to depress the keel of the flower, so revealing the stamens. Very often, the nectaries are located at the bottom of a narrow tube so that efficient nectar extraction necessitates a proboscis which in length roughly matches or exceeds the depth of the tube (e.g. Inouye 1978, 1980a; Pyke 1982). Thus many of the flowers that a forager encounters may have rewards which are at least partially inaccessible, or no reward at all.

Even if the forager possesses a suitable morphology, learning to handle flowers with complex structure takes time (Kugler 1943; Weaver 1957, 1965; Macior 1966; Heinrich 1976b, 1984; Laverty 1980, 1994a; Waser 1983; Schmid-Hempel 1984; Lewis 1986). It seems that insects are also unable to retain and swiftly recall effective handling skills while foraging among several plant species with different flower structures (Heinrich *et al.* 1977; Lewis 1986; Woodward and Laverty 1992). Thus insects must make economic decisions while often faced with a bewildering array of flowers of varying abundance, structure, colour and reward, incomplete knowledge as to which flowers contain rewards and as to how to extract these rewards, and limitations on their ability to simultaneously remember handling skills for a range of different flowers (Wells and Wells 1986).

Making wrong decisions is particularly costly for bumblebees because, for them, flight is energetically very costly. Many of the details of bumblebee flight have been revealed by a series of ingenious experiments performed by Charles Ellington and coworkers. They persuaded bumblebees to fly in place against an air stream of variable velocity in a wind tunnel, using moving visual cues to convince the bees that they were making forward progress. They were thus able to film bees flying at up to  $4.5 \text{ ms}^{-1}$  with a stationary camera. To summarize their results very briefly, bumblebees beat their wings at about 160–200 Hz in flight, with larger bees tending to have slightly lower frequencies than smaller bees (Dudley and Ellington 1990; Hedenström *et al.* 2001). The frequency and amplitude of wing beats does not appear to change whether hovering or moving forwards up to a speed of about  $4.5 \text{ ms}^{-1}$  (Dudley and Ellington 1990).

To maintain such high wing beat frequencies requires considerable energy expenditure. Using thermal balance analysis, Heinrich (1975a) calculated that flying

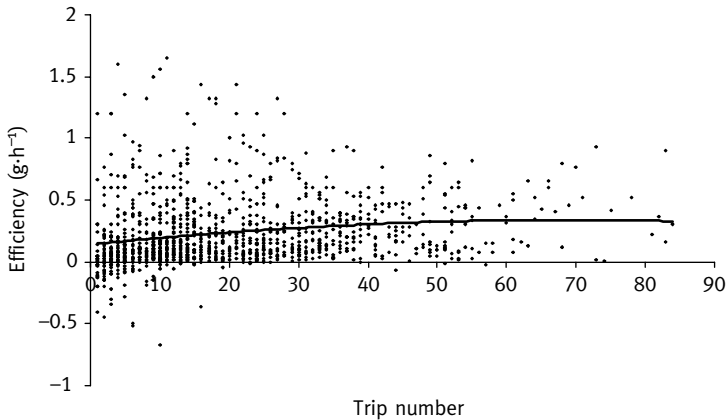
bumblebees consume about 80–85 ml O<sub>2</sub>/gram/h, or roughly 0.04 watts per worker. This agrees reasonably well with analyses of oxygen use of bees flying in a sealed wind tunnel, which suggest consumption levels between 40 and 70 ml O<sub>2</sub>/gram/h (Ellington *et al.* 1990). Interestingly, as with wing beat frequency, the metabolic rate of bumblebees does not seem to vary with flight speed, at least within the range 0–4.0 ms<sup>-1</sup>. More recently, Ellington's group pioneered the use of doubly labelled water to quantify the metabolic rate of flying bumblebees (Wolf *et al.* 1996). This has the advantage that it can be used for free flying bees under field conditions (Wolf *et al.* 1999). This approach revealed great variation in the metabolic costs of individual *B. terrestris* flying in windy conditions, which are as yet unexplained. Predictably, the average metabolic costs of flying in windy conditions were higher than when flying within the shelter of a greenhouse. To obtain sufficient oxygen for respiration during flight, bumblebees cannot rely on diffusion of oxygen through the trachea. Instead they actively pump air in and out of internal body sacs by contracting and extending the abdomen (Heinrich 1979b; Komai 2001).

The estimates for the metabolic costs of flight suggest that flying bumblebees have one of the highest metabolic rates recorded in any organism, being 75% higher than that of hummingbirds. To illustrate the magnitude of their metabolic rate, Heinrich compares a flying bumblebee to a jogging human male (Heinrich 1996). The human burns the energy in a Mars bar in roughly 1 h. A bumblebee of equivalent mass (a disturbing prospect) would burn the same energy in just 30 s.

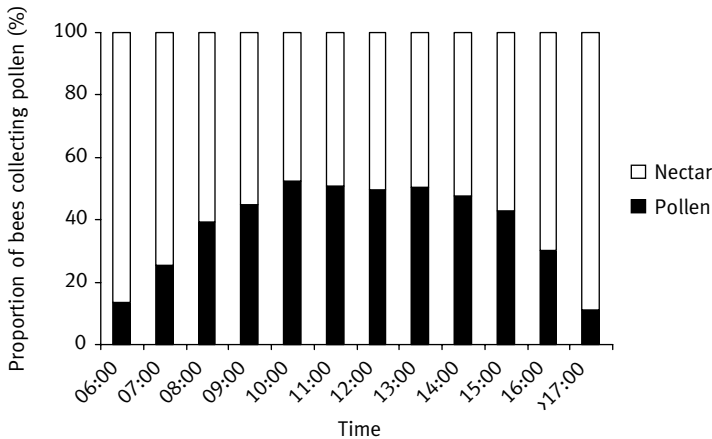
Thus for bumblebees, profitable foraging is a challenge. The rewards they must gather are sparsely and to a large extent unpredictably distributed, yet to gather them they must expend considerable energy in flight. If the time taken to locate and handle each flower is too long, or the reward too small, then foraging will result in a net loss of resources. A queen that makes poor decisions will quickly starve, while an inefficient worker will drain the resources gathered by her nestmates; naïve bees commonly return to the nest lighter than when they left on their first few foraging trips (Peat and Goulson 2005) (Fig. 6.1). It is perhaps not surprising that bumblebees have evolved an array of behaviours to improve (if not maximize) foraging efficiency.

Almost everything we know about foraging economics in bumblebees relates to nectar collection. Nectar quantity and calorific content is readily measured, whereas pollen is primarily a source of protein, and its protein content is both time consuming to measure and does not directly relate to the resource expended to collect it (energy). Pollen is harder to collect than nectar, requiring more experience, and tending to be collected by older bees (Raine and Chittka 2007a). Bees tend not to collect pollen when vegetation is wet from rain or dew, or when humidity is high, presumably because the pollen becomes sticky if contaminated with water droplets (Peat and Goulson 2005). Bees, therefore, tend to collect pollen primarily in the middle of the day when it is warmest (Fig. 6.2). Hence, it is high time that attempts were made to study the pollen economy of bumblebee colonies, for it seems quite probable that pollen is more likely to limit bumblebee colony growth than nectar.





**Figure 6.1** The effect of experience, measured as the number of previous foraging trips recorded for each bee, on foraging efficiency of *B. terrestris* workers when collecting nectar, measured as weight gained during the foraging trip. On the first few trips bees often return to the nest lighter than when they left, and on average it takes about 30 trips before efficiency reaches a plateau. From Peat and Goulson (2005).



**Figure 6.2** Proportions of pollen versus nectar collecting visits according to time of day of departure of *B. terrestris* workers from the nest. From Peat and Goulson (2005).

## 6.1 Foraging range

All bee species, be they solitary or social, provision their broods by central place foraging, which means they gather pollen and nectar from flowers in the surrounding area and bring it back to a central nest. The foraging range of bees is thus a fundamental aspect of their ecology, for it determines the area of the habitat that an individual or a colony

can exploit. Understanding the spatial relationship between nest and food resources allows us to make predictions about colony survival and distribution (Nakamura and Toquenaga 2002; Williams and Kremen 2007). Also, if we are to study the effects of habitat management on bee reproduction (i.e. nest growth and success), the appropriate scale of experimental plots depends on the area over which the occupants of each nest forage (whether it is a single bee or a large group of workers). Similarly, if we are to manage habitats to conserve particular bee species, their foraging range influences the distribution of forage that is considered optimal; a species with a large foraging range may be able to cope in a landscape with a few large patches of forage that are widely dispersed, whereas a species with a shorter range needs forage patches to be close together. Bees often use different habitat for nesting and foraging; clearly, the two habitats must be within foraging range of one another if bees are to thrive. Even for species with long foraging ranges, the value of forage patches within foraging range must be lower if they are further from the nest, all else being equal, due to the cost of travel. Matters are further complicated by the ephemeral nature of flower patches; social species such as bumblebees have nests that may persist for many months, and these must be within foraging range of suitable flowers throughout its life. Because bumblebees store rather little food in the nest, even a week without any flowers within foraging range is likely to be disastrous for the colony.

Bee foraging ranges are also important in the consideration of insect-mediated crop pollination. The distance a bee flies will determine which fields are visited within the vicinity of the nest, and also the distances over which pollen might be carried to effect gene flow within and between fields (Damgaard *et al.* 2008). This is particularly relevant when crops are grown for high seed purity, or when genetically modified crops are grown and the transfer of pollen between neighbouring fields or farms is undesirable (Cresswell *et al.* 2002; Rieger *et al.* 2002; Damgaard and Kjellsson 2005; Weekes *et al.* 2005).

Flight ranges vary considerably among bee species, and also among studies. By far the most intensively studied species is the honey bee, *Apis mellifera*. Quantifying the foraging range of honey bees is relatively easy because the 'waggle dance' of a returning forager describes the distance and direction of the food source (von Frisch 1967; Seeley 1985a). Honey bees have a foraging range of 1-6 km, very rarely up to 20 km when local resources are exceedingly scarce (Vissher and Seeley 1982; Seeley 1985b; Schneider and McNally 1992, 1993; Waddington *et al.* 1994; Schwarz and Hurst 1997). Honey bees are clearly not 'doorstep foragers'. Little is known of the foraging range of most other bee species, but those estimates that are available suggest that honey bees are not typical, and that most bees forage over much shorter distances. This is perhaps not surprising given that honeybees are large size relative to most bee species, and perhaps more importantly they have numerous workers, often more than 10,000 per colony (which presumably necessitates exploitation of resources available over a large area). Other social bees that have been studied to date travel substantial but shorter distances; for example, the stingless bee *Melipona fasciata* travels up to 2.4 km (Roubik and Aluja 1983)

and members of the Trigonini up to 1 km (Roubik *et al.* 1986). Solitary bee species are generally thought to travel only a few hundred metres, but only a tiny number of species have been studied (Gathmann and Tscharrntke 2002). Greenleaf *et al.* (2007) review the records of foraging range for 62 bee species, and find a positive relationship with body size, but data for the majority of bee species are lacking (Schwarz and Hurst 1997).

It has long been assumed that bumblebees (and for that matter other bee species) forage as close to their nest as possible, for, all else being equal, this would seem to be the most efficient strategy (Free and Butler 1959; Crosswhite and Crosswhite 1970; Heinrich 1976b; Teräs 1976; Bowers 1985a; Free 1993). Indeed, optimality models predict (rather obviously) that choosing the closest foraging sites is the best strategy, unless other constraints are in operation (Heinrich 1979a). Of course the same arguments ought to apply to honey bees, yet clearly they do sometimes travel great distances, perhaps driven by a paucity of forage near the nest. Remarkably, despite the wealth of literature on bumblebee foraging behaviour, few studies have succeeded in providing measures of bumblebee foraging range (Bronstein 1995; Osborne *et al.* 1999; Cresswell *et al.* 2000). It is unexpectedly hard to quantify, and particularly to understand its relationship to the quantity and quality of forage available.

### 6.1.1 Measuring foraging range

#### 6.1.1.1 *Marking experiments and direct observation*

The simplest (or at least most obvious) approach to studying foraging range in bumblebees or any other central place forager is to mark the bees at the nest, and then search the flowers in the surrounding area to see where the marked bees are foraging. Bumblebee nests can be frustratingly hard to find, so some researchers have resorted to marking the bees as they forage. Bowers (1985a) marked *B. flavifrons* while foraging in meadow clearings surrounded by forest in Utah. Subsequent recaptures were all in the same meadows in which the bees had been marked, leading to the conclusion that bees did not move between meadows. However, the locations of the actual nests were not identified, so this tells us nothing about foraging range. The bees might have been nesting in the meadow or the surrounding forests nearby, or they could have been travelling from other meadows elsewhere. One would expect individual bees to return to the same site repeatedly, having found it to be rewarding, for this is a well-known feature of bumblebee behaviour (see Thomson *et al.* 1997; Osborne and Williams 2001). It does not mean that their nests were situated nearby.

It is far more informative to mark the bees at their nests if they can be located, and then search for them to discover where they go to forage. Unfortunately, this is also fraught with difficulties. Where forage is abundant close to the nest (e.g. if the nest is in or adjacent to a flowering crop), a small proportion of marked bees have been observed foraging, and these tend to be close to the nest (Saville 1993; Schaffer and Wratten 1994). Where the rest of the marked bees are going is harder to discover. Studies of nests situated in more typical fragmented habitat with small, scattered sources of forage have

found very few marked bees on flowers, even when many hundreds of bees were marked at the nest (Kwak *et al.* 1991a; Dramstad 1996; Saville *et al.* 1997). For example, Dramstad (1996) found that few *B. terrestris/lucorum* workers were to be seen on patches of flowers located even within 50 m of their nest, and searches at distances of up to 300 m located very few marked bees. Dramstad concluded that these bees do not forage close to their nests, but exactly where they do forage was not clear. Schaffer (1996) suggested that the leptokurtic distribution observed in earlier studies was an artefact of the experimental design. Observer effort was always biased towards searching areas close to the nest for the simple reason that the area to be searched increases as the square of the distance from the nest. To properly evaluate the distribution of marked bees within even a moderate distance of the nest such as 1 km would require 3.1 km<sup>2</sup> to be thoroughly searched; a formidable task. Suppose that there were 50 workers foraging at any one time (which would be quite a large and active nest), this would translate to an average of one marked bee per 6.2 ha or 62,000 m<sup>2</sup>. Wolf and Moritz (2008) overcame this problem by placing nests of *B. terrestris* in an intensively farmed agricultural 'desert' landscape in Germany, where the only flowers within 3 km of the nests were along a single linear track which could be monitored relatively easily. They found that the majority of workers foraged near to their nest (mean distance 267 m, maximum 800 m). However, this is a very odd situation; ordinarily one would expect the amount of forage available to increase as the square of the distance from the nest. In more typical, patchy landscapes the mark-reobservation method seems to be of little use without a huge team of observers to search for bees.

#### 6.1.1.2 *Modelling foraging range*

If we cannot easily directly measure the foraging range of bumblebees, perhaps we can calculate how far they ought to be able to fly? The economics of bumblebee foraging have been the subject of a substantial body of research, initiated by Bernd Heinrich in the 1970s (reviewed in Heinrich 1979b). Detailed information is available on the speed and energetic cost of bumblebee flight, on the amount of forage that they can carry, the time it takes them to handle flowers of different species, and the energetic rewards that they obtain per flower. Cresswell *et al.* (2000) combined these data to estimate the maximum distance that a bumblebee could travel to reach a patch of nectar-rich flowers and return with a net profit. The most accurate estimates of flight speeds are provided by recent studies using harmonic radar (see following text), which measured a mean airspeed of 7.1 ms<sup>-1</sup> for *B. terrestris* (Riley *et al.* 1999). The energetic costs of flight have been estimated from oxygen consumption rates to be 1.2 kJ•h<sup>-1</sup> (Ellington *et al.* 1990). Estimates of the volume of the honey stomach (which determines the maximum volume of nectar that a bee can carry) vary from 60 to 120 µl, and vary greatly according to the size of the worker (Allen *et al.* 1978; Heinrich 1979; Goulson *et al.* 2002b). Nectar concentrations vary greatly between flower species, and also with time of day, but commonly fall within the range 40–60% sugars (about 1–1.5 M sucrose or equivalent) (Cresswell *et al.* 2000). The metabolism of nectar sugars yields 16.7 kJ•g<sup>-1</sup> (Heinrich 1979). Let us

assume that a worker leaves the nest with an empty honey stomach, and occasionally stops to feed at flowers to fuel the outward flight. If it returns with any nectar, it has thus made a profit. The limit to the distance from which the bee can return with a net profit is simply given by the time taken to burn up all of the sugars in the honey stomach on the return flight. For a 40% nectar solution and a honey stomach capacity of 80  $\mu\text{l}$ , the maximum range is about 10 km (Cresswell *et al.* 2000). If the nectar is more concentrated, or if the bees concentrated the nectar within their honey stomach as they foraged, then the range could be larger.

Cresswell's model makes it clear that travel to flower patches constitutes a relatively small portion of a forager's time and energy budget. Bees should choose the forage patch closest to the nest, given a choice of equally rewarding patches, but because flight is swift relative to the time spent within patches of flowers, the more distant site does not have to be much more rewarding to be the better option. For example, if given the choice between a patch of flowers immediately adjacent to the nest, and a more distant patch in which average nectar rewards are twice as high, it may be worth flying up to 4 km further to reach the more distant patch. If this model is approximately correct in its assumptions, then it may explain why bumblebees often do not seem to visit patches of apparently suitable forage close to their nests (Dramstad 1996). Even in the most fragmented and impoverished habitat there is likely to be a considerably better patch located within a radius of, say, 5 km (an area of 78 km<sup>2</sup>).

The model is concerned only with nectar collection, and so tells us nothing about the economics of trips to gather pollen, or trips where both nectar and pollen are collected. Very little information is available on the rate at which bees are able to collect pollen, or on the relative values of pollen from different sources (Cook *et al.* 2003). Pollen is the only source of protein for bumblebees, and is vital for larval growth and development of eggs in the queen, so this represents a substantial knowledge gap. It has arisen simply because it is much easier to measure nectar volume and concentration than it is to quantify the amount and quality of pollen available per flower, so researchers tend to focus on the former. If pollen is in short supply near to the nest, it is conceivable that workers could engage in flights of more than 10 km to obtain it. Such flights would result in a net loss of energy, but could (theoretically) be fuelled by visits to nearer nectar sources on both the outward and return journeys.

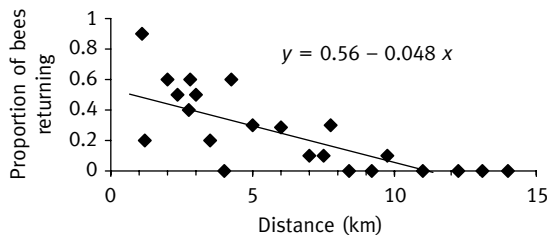
### 6.1.1.3 *Homing experiments*

An entertaining and relatively easy approach to studying foraging range and navigational abilities is to carry out homing experiments. In the late 1800s, the famous entomologist Jean-Henri Fabre demonstrated that the solitary sphecoid wasp *Cerceris tuberculata* and the gregarious bee *Chalicodoma muraria* could return to their nests when transported away from them several kilometres in darkened boxes (Fabre 1882). Similar experiments have since been performed on a range of solitary and social hymenopterans (reviewed by Wehner 1981; Southwick and Buchmann 1995; Chmurzynski *et al.* 1998; Capaldi and Dyer 1999; Greenleaf *et al.* 2007). Most of these studies have examined homing from

distances ranging from 100 m to 3–4 km, and all have found that at least a proportion of the released insects return to their nests. The current record-holder among the Hymenoptera is the Euglossine bee *Euplusia surinamensis* (now *Eufriesea surinamensis*; Roubik and Hanson 2004), which has been found to successfully return home from 23 km (Janzen 1971), a prodigious feat indeed for a small insect.

Homing experiments have been carried out on one bumblebee species, *B. terrestris* (Goulson and Stout 2001). The maximum distance from which a bee successfully returned to its nest was 9.8 km, with a clear decline in the probability of a bee returning as the distance over which it was displaced increased (Fig. 6.3). Unexpectedly, no relationship was apparent between the displacement distance and the time to return to the nest. Times from release to recapture varied between 6 h (from 2 km) to 9 days (from 3.5 km). Notably, one bee that returned to its nest after being displaced by 4.3 km was observed on a subsequent occasion gathering nectar at the release site, which contained a large patch of nectar-rich flowers.

What does this tell us about the foraging range of bumblebees? Does this suggest that *B. terrestris* forage over distances up to 9.8 km from their nests? Probably not. Prolonged homing times have been found in studies of other species. For example, of 374 *Anthophora abrupta* females displaced up to 3.2 km from their nest, homing times varied from 20 min to 50 h (Rau 1929). This may provide a clue as to how Hymenoptera locate their nests. *B. terrestris* flies at a mean speed of  $7.1 \text{ ms}^{-1}$  when tagged with a harmonic radar transponder (Osborne *et al.* 1999; Riley *et al.* 1999), and so could theoretically return from up to 15 km within a little over 30 min. Pigeons are well known for their prodigious homing abilities, and they do so swiftly, flying more or less directly from the release site to their loft. Their homing abilities have been the subject of intensive studies, and it is thought that they possess some sort of coordinate system which enables them to determine their location relative to home, perhaps based on olfactory or magnetic stimuli (Wiltschko and Wiltschko 1988; Wallraff 1990; Able 1994). They may also be able to detect information as to the direction of transport during the outward journey,



**Figure 6.3** The proportion of marked *B. terrestris* workers returning to their nest after artificial displacement over distances up to 14 km. In total, 220 bees were displaced in batches of 10, so that each point marked is based on 10 bees. There was a clear negative relationship between the proportion of bees returning and the distance of the release site (linear regression,  $r^2 = 0.55$ ,  $p < 0.001$ ). After Goulson and Stout (2001). With permission.

and simply reverse their path (Wallraff 1980; Wallraff *et al.* 1980). It seems highly unlikely that Hymenoptera possess either of these abilities. If they did, we would expect them to return swiftly to their nests. In reality, over moderate to long displacement distances they usually return very slowly, often taking days rather than hours (and many do not return at all). This is many times longer than one would expect if they flew directly home. Recent studies proposed a third mechanism: displaced insects are thought to use a systematic search for familiar landmarks, and then use these to locate their nest (reviewed in Witte *et al.* 1989). Desert ants (*Cataglyphis* spp.) engage in systematic searches when displaced to unfamiliar terrain (Wehner 1996). Honey bees use visual landmarks to aid navigation between their nest and forage (Wehner 1981; Dyer 1996), and use a sun compass to relate the positions of landmarks and the nest (Wehner 1994). Honey bee homing is better when prominent horizon landmarks are present (Southwick and Buchmann 1995). Searching for familiar landmarks could lead to protracted homing times and so explain why, from more distant sites, many bees fail to return.

Directly tracking honey bee flight paths with radar provides insights as to how bees explore unfamiliar landscapes. When honeybees are displaced to an unfamiliar location and begin searching for their colony—or when searching for a feeder in a known location—they generally adopt an optimal scale-free search strategy (Reynolds *et al.* 2007a,b). The patterns of these flights can be described mathematically using a Levy distribution, which has been used to characterize search patterns of many animals. In simple terms, the bees tend to fly in a loop away from the release point and back, before taking another loop in a different direction, and gradually these loops may get larger over time (looping Levy flight patterns; Reynolds *et al.* 2007a,b). The flights may result in them finding the goal they were searching for, or a familiar landmark allowing them to orientate on the goal. It seems probable that the homing mechanism used by Hymenoptera is a systematic search of the area surrounding the release site using an optimal, scale-free strategy of expanding loops, until a familiar landmark is recognized. If this is so, then we might expect all bees released within an area that they have previously explored to successfully return to the nest, and to do so rapidly, for they will soon recognize a familiar landmark. Of course, individual bees are likely to vary in their ability to home according to their age and foraging experience, and also according to the particular directions that they have previously explored, which will determine the number and distribution of familiar landmarks. Rau (1929) found that homing success in *A. abrupta* was strongly related to age, with older (and presumably more experienced) bees being much more likely to return to the nest. Such variability may obscure relationships between displacement distance and success in homing.

It seems improbable that a bee released 9.8 km from its nest could find familiar landmarks unless its home range was several kilometres in radius (Goulson and Stout 2001). Since one marked bee which returned to its nest from 4.3 km was subsequently seen foraging at the site where it was released, bumblebees are clearly capable of remembering the location of forage at such distances and successfully navigating to and from these patches. Whether bumblebees locate forage at such distances from their nests

naturally remains to be determined, but it seems likely that they will do so if forage nearer to the nest is lacking. Since many bumblebees successfully returned from considerable distances (>5 km), it seems reasonable to conclude that *B. terrestris* naturally forage over several kilometres. However, we must be cautious when interpreting homing experiments, because we cannot directly observe the bees during most of their journey home. We do not know the size of the area that a bumblebee can search for familiar landmarks (if indeed that is what they do), and so we can only speculate as to the likely foraging area.

#### 6.1.1.4 Radar tracking

Perhaps the most innovative (and certainly the most expensive) approach yet deployed to measure forage range in bumblebees is the use of harmonic radar. This system for tracking insect movements was developed by the Natural Resources Institute in conjunction with Rothamsted Research Institute, UK (Riley *et al.* 1996, 1998; Osborne *et al.* 1997, 1999). The technique involves attaching a 16-mm vertical aerial-like transponder to the thorax of the bumblebee (the system has also been used with other large insects such as honeybees and butterflies). The transponder captures the energy in radar emissions sent out from a base unit and re-emits the energy at a higher frequency, providing a harmonic of the original signal that can be tracked as the bee flies (Riley and Smith 2002). The transponder weighs 12 mg, and so is very light in comparison with the weight of a typical bumblebee forager (6–7% of the insects' body mass), and is much lighter than the normal foraging load which can reach 90% of the body mass (Goulson *et al.* 2002b; Peat and Goulson 2005). As far as can be ascertained the transponder does not seem to interfere greatly with the behaviour of the bumblebee, although bees with transponders do take longer time to complete foraging trips than usual, perhaps because the transponder impedes their handling of flowers (Osborne *et al.* 1999). On one occasion, a flower became impaled on the transponder but the bee still managed to fly home to the nest, albeit slowly.

These studies have provided some fascinating insights into the flight paths of workers of the bumblebee *B. terrestris*. For example, they have revealed that bumblebees can compensate for cross winds and manage to fly directly between the nest and patches of forage by flying at an angle to their intended course (Riley *et al.* 1999). Unfortunately, this technique has a major limitation with respect to determining foraging range, for bees can only be detected up to about 1 km at most, and then only if they remain within a direct line of sight of the radar equipment. Osborne *et al.* (1999) found that very few foragers flew less than 200 m from their nest, even though there were patches of suitable forage just 50–100 m from the nest. In separate studies in June and August, Osborne *et al.* (1999) recorded mean maximum distances from the nest of 339 m (range 96–631 m) and 201 m (range 70–556 m), respectively (Fig. 6.4). However, many of these bees flew beyond the range of the radar, being obscured from the radar's view behind hedges or other landscape features, so these do not represent the actual foraging ranges (13 out of 35 tagged bees flew beyond radar range in June, and 14 out of 30 in August). This study





**Figure 6.4** A *B. terrestris* forager fitted with a transponder for use in harmonic radar studies. Photograph provided courtesy of Andrew Martin, Institute of Arable Crops Research, Rothamsted.

confirms that bumblebees do not necessarily forage on the closest available patches, but that a small majority of them do remain within 500–700 m of the nest. Therefore, although the harmonic radar approach is an elegant method to measure forage distances of bumblebees, and is unique in providing detailed information on the paths followed by foraging bees, it cannot tell us what the full distribution of foraging ranges is, or what the limit to foraging range might be.

#### 6.1.1.5 *Mass-marking and pollen analysis*

Recently, the distribution of bumblebee foragers away from their colonies has been quantified using a combination of mass-marking of bees as they leave the nest and analysis of pollen loads as they return (Osborne *et al.* 2008a). Unusually, this information on foraging range was also analyzed in the context of the spatial distribution of foraging habitats in the agricultural landscape in which the experiment took place, as determined from remote-sensed data. Experimental colonies were placed at 250 m intervals along a 1.5 km transect across UK farmland. A novel device was placed on the entrance to the colony (Martin *et al.* 2006) and this marked each exiting forager with powder dye

(different colours for each position on the transect). There was a borage field at one end of the transect and the numbers of marked bees foraging on the borage were recorded by repeated searching of the borage field for marked bees (Fig. 6.5).

A second device was designed to capture returning foragers as they entered the nest, so that their pollen loads could be sampled and analyzed (Martin *et al.* 2006). The proportion of pollen foragers returning to each colony with borage pollen was then recorded. Sixty-three per cent of pollen foragers at colonies next to the borage field collected borage pollen (and were therefore assumed to have foraged on the one field as no other borage was growing in the area) (Fig. 6.5). The respective percentage declined, in an approximately linear fashion, to 17% of borage pollen foragers at 1.5 km (Osborne *et al.* 2008a). Once colony activity, the area surveyed and the percentage contribution of borage to the forage landscape were taken into account, the relationship between the number of marked bees seen in the borage field and the distance from their colony was a shallow curve with distance (Fig. 7.3). Whilst neither measurement can tell us the maximal foraging range, the distributions are comparable with predictions made by Dukas and Edelman-Keshet (1998) for solitary foragers provisioning a nest, based on maximization of energy intake.



**Figure 6.5** Harmonic radar tracks of the bumblebee, *B. terrestris*, flying away from or returning to the nest. Rings are at 200 and 400 m from the radar. Shaded areas are patches of forage. Thick lines are hedges. Each symbol denotes an individual bee. Shown are 35 outward tracks by nine individuals. (Adapted from Osborne *et al.* (1999).

### 6.1.2 Do bumblebees forage close to their nests?

A recurring feature of studies of bumblebee foraging range is that a relatively small proportion of bees seem to forage close to the nest (but see Wolf and Moritz 2008). One suggestion as to why this may be so is that it minimizes intracolony competition (Dramstad 1996). Colonies of some species such as *B. terrestris* grow to contain up to 400 workers, and a work force of this size would quickly deplete resources close to the nest. Heinrich (1976a) found that bumblebees could remove 94% of the standing crop of nectar within an area. Since it is the cumulative foraging success of all foragers that determines colony success, one would predict that there is a trade-off between travel time and competition. Patches that are near the nest should always receive more visits than those that are further away, but the difference need only be slight if travel is rapid and cheap compared to the time and energy spent within forage patches (Dukas and Edelman-Keshet 1998; Cresswell *et al.* 2000). Given that each individual bee may visit hundreds, sometimes even thousands, of flowers in a foraging bout (e.g. Cresswell *et al.* 2002), one might expect only a very few bees to visit the nearest patches if the patches are small. This might explain the very low numbers of observed visits to patches close to the nest described by Dramstad (1996) and Osborne *et al.* (1999).

An alternative potential explanation for the apparent tendency of bumblebees to forage far from their nest relates to predation. It has been suggested that colonial food provisioners such as bumblebees may avoid foraging close to their nests so as to avoid attracting predators or parasites to the nest (Dramstad 1996). Bumblebee nests are attacked by a range of organisms including queens of their own species and cuckoo bumblebees (subgenus *Psithyrus*) (reviewed in Alford 1975). Dramstad (1996) suggests that a high concentration of workers close to the nest might attract *Psithyrus* queens and other enemies. It is not known how *Psithyrus* females locate the nests of their hosts. If foragers remained close to their nests then the chemical cues deposited on flowers to aid foraging (Goulson *et al.* 1998b; see also Chapter 12) could potentially provide a 'scent magnet' to cuckoo bees (Dramstad 1996). However, cuckoo bees are probably only able to invade fairly small nests, as are conspecific usurper queens, and hence both cuckoo females and usurper queens are active early in the season. Hence if this were a factor driving workers to avoid foraging close to their nest it should only be important when nests are small, but most of the published studies are in summer when nests are large and unlikely to be attacked by cuckoos.

Alternatively, if foragers were all concentrated in the area close to the nest then they might attract aggregations of true predators such as birds. Gentry (1978) found that aggregations of pollinators on the flowers of tropical trees attracted large numbers of bee-eating birds. Many researchers have considered predation on foraging bumblebees to be rare and of minimal ecological importance (Brian 1965a; Pyke 1978d; Zimmerman 1982), but others suggest predation rates are significant (Rodd *et al.* 1980; Goldblatt and Fell 1987). There are also likely to be big differences between regions; for

example, the United Kingdom has rather few specialist bee-eating birds (although see Chapter 5), but they are common in southern Europe (Alford 1975).

The difficulty with these hypotheses concerning the risk of attack by predators or inquilines is that they are hard to test since the available evidence suggests that bumblebees do not forage close to their nests. It is not easy to demonstrate that this is a result of past predation pressure. A comparison of the foraging ranges of species with and without these enemies could in theory provide an insight, if such species exist, but our sketchy knowledge of both the foraging ranges and natural enemies of different bumblebee species prevents a meaningful comparison at present. It is probably fair to say that there is actually very little evidence that the *density* of foragers close to the nest is generally lower than elsewhere (but see Dramstad *et al.* 2003). The most likely explanation for the low number of bees close to their nest is simply that flight is relatively cheap and intracolony competition would be high if many workers stayed close to their nests. Consequently, the most economic strategy for a colony is to distribute its foragers widely in space.

### 6.1.3 Differences between bumblebee species

There is growing evidence that bumblebee species differ markedly in foraging range and that this correlates with colony size (Table 6.1). Experiments with bees marked at the nest (Kreyer *et al.* 2004) and anecdotal observations suggest that species such as *B. pascuorum*, *B. sylvarum*, *B. ruderarius* and *B. muscorum* are 'doorstep foragers', mostly remaining within 500 m of their nests whilst *B. lapidarius* forages further afield (mostly <1,500 m), and *B. terrestris* regularly forage over more than 2 km away from their nests (Walther-Hellwig and Frankl 2000). Although these experiments suffer from a reduced intensity of sampling at greater distances from the nest, and also from rather small sample sizes, this cannot explain the differences that were found between species. These differences appear to correspond to the known nest sizes of the bee species: *B. terrestris* and *B. lapidarius* nests grow to a large size (100–400 workers), while those of *B. pascuorum*, *B. sylvarum*, *B. ruderarius* and *B. muscorum* (all commonly known as carder bees, and belonging to the subgenus *Thoracobombus*) are generally small (20–100 workers) (Alford 1975). This obviously makes sense as a large colony needs to range over a larger area to find sufficient food, all else being equal.

Recent attempts to compare the foraging range of bumblebees have adopted a very different approach, but largely confirm the findings of Walther-Hellwig and Frankl (2000). Darvill *et al.* (2004) and Knight *et al.* (2005) used molecular (microsatellite) markers to identify sister pairs along a transect of samples of foragers. This approach is aided by the haplodiploid genetics of bumblebees and the monogamous nature of queens, so that all workers from a nest should be 75% related to one another. The distribution of sisters along the transect can be used to estimate foraging range. This approach has advantages, in that the bees are from wild nests and are foraging naturally. The disadvantage, however, is that the actual sites of the nests are not known, and also that sister

**Table 6.1** Summary of bumblebee (*Bombus* sp.) foraging range data available to date. Thorax widths are from D.G. (unpublished data). Colony sizes are from Benton (2006).

		<i>B. terrestris</i>	<i>B. lapidarius</i>	<i>B. pascuorum</i>	<i>B. pratorum</i>
Worker thorax width range (foragers)		3.9–6.8 mm	3.4–5.8 mm	3.3–5.2 mm	3.2–4.6 mm
Average colony size (no. of workers)		Large (<400)	Large (<300)	Medium (<200)	Small (<100)
Method	Study	Foraging range			
Pollen and marking	Osborne <i>et al.</i> (2008a)	>1,500 m	—	—	—
Genetics	Knight <i>et al.</i> (2005)	758 m	450 m	449 m	674 m*
Genetics	Darvill <i>et al.</i> (2004)	>312 m	—	<312 m	—
Mark-recapture	Walther-Hellwig and Frankl, (2000)	1,750 m	1,500 m	500 m	—
Visit response to landscape**	Westphal <i>et al.</i> (2006)	3,000 m	2,750 m	1,000 m	250 m
Mark-recapture	Wolf and Moritz (2008)	800 m	—	—	—

\*Knight *et al.* (2005) suggest that their results for *B. pratorum* should be treated with caution due to anomalies in the genetic data.

\*\*Westphal *et al.* (2006) used statistical estimation of how well flower visitation response correlated with landscape structure at different scales.

foragers at the outer limits of their foraging range are at very low density. Thus, the tail of the forager distribution is unlikely to be detected (of course this criticism applies to other approaches too). Nonetheless, this method provides a powerful test for differences between species in their foraging range. The maximum detected foraging range was greatest for *B. terrestris* (758 m), least for *B. pascuorum* (449 m) and *B. lapidarius* (450 m), and intermediate for *B. pratorum* (674 m) (although the authors note that the data for *B. lapidarius* may be unreliable). Since the area of forage available to nests increases as the square of foraging range, these differences correspond to a three-fold variation in area exploited by bumblebee nests of different species.

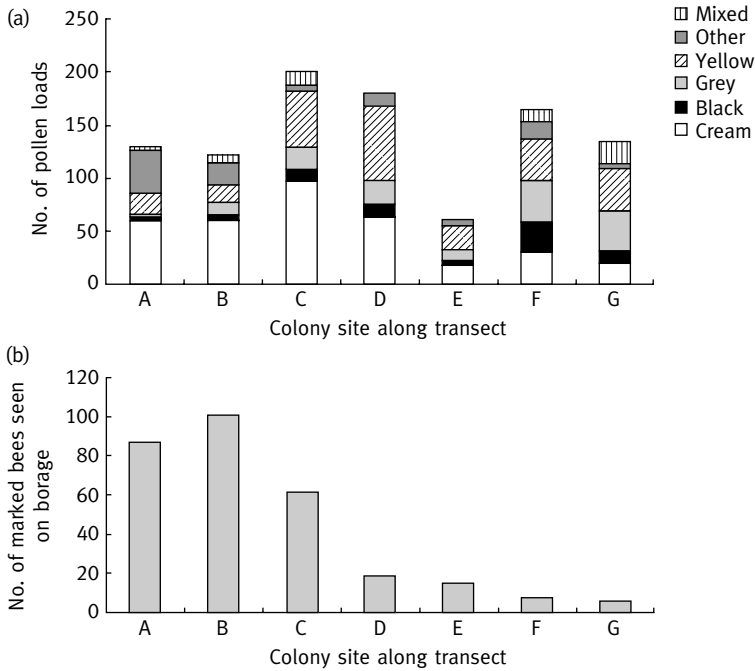
Westphal *et al.* (2006) examined the spatial scales at which the density of mass-flowering crops in the surrounding area affects recruitment of the same four bumblebee species. Interpretation of this approach is difficult, but the authors found that abundance of different bee species was best described by the density of mass-flowering crops at different radii from a focal point: 3,000 m for *B. terrestris*, 2,750 m for *B. lapidarius*, 1,000 m for *B. pascuorum* and 250 m for *B. pratorum*. The foraging range is best interpreted as half these figures, since for example in the case of *B. terrestris*, a nest up to 1,500 m from the focal point with a foraging radius of 1,500 m will be foraging at the focal point and up to 1,500 m in the opposite direction, at 3,000 m from the focal point. These estimates compare well with those of Walther-Hellwig and Frankl (2000), and are broadly comparable but generally larger than those obtained by Darvill *et al.* (2004) and Knight *et al.*

(2005) using molecular methods. The difference is likely to be due to the low probability of detecting the tail of the foraging range using the molecular approach.

Three quite different approaches to measuring or inferring foraging range have reached broadly similar conclusions: there are large differences in foraging range between species, with *B. terrestris* having a long foraging range and *B. pascuorum* foraging much closer to the nest (Table 6.1). There are almost certainly differences between species in the way that they navigate, which perhaps correlate with their foraging range. Try standing still in a flowery meadow or flowering crop on a fine day in the summer; every few minutes you will be circled by a worker bee; typically the bee flies around at a height of ~2 m in two or three small circles of perhaps 2–5 m radius before departing. Catching the bees reveals that only some species do this: *B. pascuorum*, *B. pratorum* and *B. hortorum* may be abundant in the area but almost never circle humans; the majority of the circling bees are *B. lapidarius*, *B. soroensis* (when present) and *B. terrestris* (Goulson *et al.* 2004). Exactly what this tells us is debatable, but it seems probable that the bees are investigating and memorizing a novel landmark; it seems reasonable to suppose that bees foraging over longer distances have to pay more attention to navigation than those which always remain close to their nests.

#### 6.1.4 Management implications

If there are fundamental differences in the spatial foraging behaviour of bumblebee species, then this has clear implications for management of bumblebees for pollination or conservation purposes. In their foraging range experiment, Osborne *et al.* (2008a) used remote-sensed data and extensive ground-truthing to map the distribution of habitats with good nectar and pollen sources in the landscape surrounding experimental colonies. Examination of the variation in foraging habitat availability around colonies with respect to foraging range was most revealing. Using a radius of 500 m (likely to be typical for a doorstep forager such as *B. pascuorum*), there was great variation in forage availability (Fig. 6.6). However, for larger foraging ranges the variation declines markedly, so that for foraging ranges exceeding 1 km (typical for *B. terrestris*), there was very little variation in forage availability to nests placed at different points in the landscape. The authors hypothesized that the scale of *B. terrestris* foraging (>1.5 km) would be large enough to buffer effects of forage patch and flowering crop heterogeneity in this landscape; almost all nests are likely to be within foraging range of at least some suitable habitat. In contrast, nests of bee species with shorter foraging ranges are likely to be more vulnerable to this spatial variation, with many nests experiencing low availability of forage than they could reach (Osborne *et al.* 2008a) (Fig. 6.7). The location of colonies in the landscape could thus have serious consequences for the survival and reproduction of these ‘doorstep’ foragers. We do not as yet know whether nest-searching queens use cues to locate nest sites that are likely to have nearby forage later in the season. If they choose their nest sites on the availability of a suitable mouse hole or tussock of grass, and have no means of assessing likely future forage in the vicinity (as seems

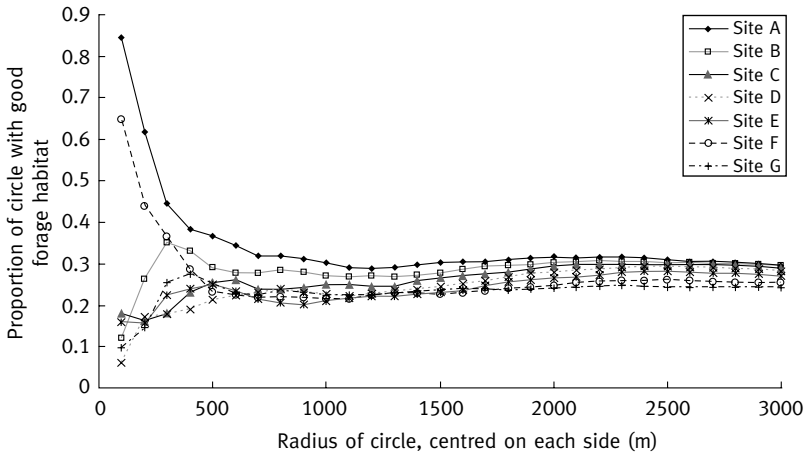


**Figure 6.6** (a) Total pollen loads returning to *B. terrestris* nests located along a 1.5-km transect, separated by colour of load. Cream loads were 99% borage, yellow loads were primarily oilseed rape, *Brassica napus*; grey pollen was primarily bramble *Rubus* spp.; and black pollen was primarily poppy *Papaver rhoeas* L. A field of borage was located at site A. Colony locations were spaced at approximately 250 m intervals along the transect. (b) Total marked bees seen on the borage, arriving from each colony site. From Osborne *et al.* (2008a).

probable), then it may be that many nests of doorstep foragers are doomed from the outset. This said, *B. pascuorum* remains one of the commonest bumblebee species in much of Europe, so clearly foraging range alone is not a good predictor of which species will survive in fragmented landscapes.

In terms of pollen flow between flowers, these studies of foraging range provide some indication of the likely distance over which we might expect gene flow in bumblebee-pollinated flowers (including GM crops). Clearly some foragers travel well over 1 km from their nest, and it is likely that the tail of this distribution might extend to at least 2–3 km. It is improbable that a single bee would travel such distances in opposite directions from the nest, since individual bees show high fidelity to forage patches once they have discovered them (see Chapter 7). However, contact with other individuals in the nest could readily lead to occasional spread of pollen over twice the foraging range (i.e. up to 6 km).

To summarize, studies using a diversity of approaches including direct observation, harmonic radar, theoretical modelling of energetics and molecular markers have



**Figure 6.7** Forage landscape for colonies at each site A–G, estimated by calculating the proportion of the landscape containing good forage habitats at different radial distances from each site. After Osborne *et al.* (2008a). With permission.

provided a range of measures as to how bumblebee foragers distribute themselves around their nests. However, only a small number of species have been studied (predominantly *B. terrestris*), and it is apparent that there is considerable variation between species. The ecological/evolutionary explanation for these differences remains unclear. Greenleaf *et al.* (2007) show that, across a range of bees (mainly solitary species), body size is a reliable predictor of foraging range, and the evidence that is available for bumblebees would appear to support this (see Table 6.1; the mean sizes of these species are *B. terrestris* > *B. lapidarius* > *B. pascuorum* > *B. pratorum*). However, further comparative studies are required to establish whether this is a general relationship, and if it is, this then begs the question why does size vary between bumblebee species? We also have little idea at present how flexible bumblebees are with regard to foraging range. Estimates for *B. terrestris* vary from >312 m (mixed farmland, southern United Kingdom) to 3,000 m (intensively farmed arable land, Germany) (Table 6.1), but whether this represents a response to differing floral resource density and distribution or differences between experimental approaches is unclear. Given the enormous elasticity of foraging ranges shown by honeybees, it seems probable that bumblebees might be rather adaptable and, if forced, able to considerably extend their foraging range, although this must come at a cost in terms of energetic expenditure and a higher loss of workers through navigational errors. The mass-marking approach of Martin *et al.* (2006) probably represents the most cost-effective technique for studying bumblebee foraging range, and comparative studies of bee species in a range of landscapes differing in forage availability using this approach would be invaluable in resolving these issues.



*This page intentionally left blank*

## Exploitation of Patchy Resources

Within the foraging range of a bee, there will probably be many different patches of flowers, varying in size and in the plant species of which they are composed. Patches of a particular plant species may vary in the rewards that they provide, according to local microclimate, soil quality or genetic differences. Each individual bee has to choose which patch(es) to exploit. One might naively predict that, all else being equal, large patches should be favoured over small ones, since this would minimize travelling time between flowers. However, if all bees adopted this strategy, then large patches would become overrun with bees, and flowers in small patches would contain much more nectar because they would never be visited. Whatever size of patch a bee chooses, it must then decide how long to stay. The longer it stays in a patch, the more depleted the resources will become, unless the patch is so large that it produces rewards faster than the bee can gather them. At some point, the bee would probably be better served by going to find another patch.

One approach to understanding forager behaviour when exploiting patchy resources which has proved to be fruitful is the use of optimality models. Although optimality models have in the past received much criticism (e.g. Pierce and Ollason 1987), the criticisms largely stem from a failure to understand the point of a modelling approach. Optimality models do not aim to provide a precise and definitive explanation for a particular foraging behaviour, but instead are best viewed as a way of structuring thinking. For example, we might predict that birds lay an appropriate number of eggs in a nest to maximize the number of young they can fledge, that is, we test the assumption that they are maximizing offspring production per brood. It turns out that many birds are not maximizing offspring production per brood, but tend to produce slightly fewer offspring than they could to increase their own survival. Hence we can learn from the failure of a simple optimality model to accurately predict behaviour. Hence models remain a valuable starting point for generating hypotheses to explain behaviour, and also provide a means of testing our understanding of behaviour.

Optimal foraging models generally assume that foragers maximize their rate of resource acquisition (Charnov 1976). Pyke (1978a) argues that this is a reasonable assumption for workers of social insects such as bumblebees since they are freed from many of the constraints which are likely to affect the behaviour of other foragers (such as looking for mates or avoiding predators, although as we have seen in Chapter 5 the latter may well not be true). Hence optimality models have frequently been applied to

bumblebees (e.g. Pyke 1978a,b, 1983; Hodges 1981, 1985a; Zimmerman 1982, 1983; Best and Bierzychudek 1982; Cibula and Zimmerman 1987; Dreisig 1995; Goulson 1999, 2000b). The assumption of maximized rate of resource acquisition is less reasonable for insects such as butterflies which intersperse nectaring with all sorts of other activities such as searching for mates or oviposition sites, and so regularly indulge in longer flights than do most foraging bumblebees (Schmitt 1980; Waser 1982a; Goulson *et al.* 1997a).

Two optimal foraging models are particularly relevant to bumblebee foraging among patches of flowers, the ideal free distribution (Fretwell and Lucas 1970) and the marginal value theorem (Charnov 1976). I shall examine the predictions of these two models in turn.

## 7.1 The ideal free distribution

Flowers typically exhibit a patchy distribution at a number of levels; flowers are often clustered into inflorescences, several flowers or inflorescences may be clustered on each plant, and the plants themselves are likely to be patchily distributed. According to the ideal free distribution model, the evolutionary stable strategy for foragers exploiting a patchy resource is to equalize the rate of gain of reward in all patches by matching the proportion of foragers in each patch to the rate of reward production in the patch (Fretwell and Lucas 1970). Applying the ideal free distribution model, we predict that the ratio of foragers to flowers should be independent of patch size (assuming that reward production per flower does not vary with patch size). If we incorporate travel time between patches, we would expect the proportion of foragers to flowers to increase with patch size, so that foragers in small patches receive a higher reward per time within the patch but spend more time moving between patches; overall, the rate of reward received by all foragers is equal. For social organisms, the distribution of foragers among patches may also be influenced by the location of nests; if we take into account travel time from the nest then we would predict a higher proportion of foragers close to nests (Dukas and Edelman-Keshet 1998). However, since travel time is often likely to be negligible compared to time spent within patches (Dreisig 1995), the ratio of foragers to flowers should generally remain more or less independent of patch size and nest locations.

So do bumblebees achieve an ideal free distribution? An ideal free distribution can be achieved by non-random searching or by non-random choice of patches (i.e. a preference for large patches) (Dreisig 1995). Both are exhibited by bumblebees when visiting flowers.

### 7.1.1 Search patterns within patches

Foragers that adopt a non-random search pattern can achieve a higher reward per time than individuals that are searching randomly, so that non-random searching should predominate where it is possible (although if all foragers have non-random

search strategies then rewards per unit time are the same as when all foraging is random (Possingham 1989)). At least two forms of non-random spatial searching have been identified in bumblebees visiting flowers: traplining along established routes and systematic searching (which does not require a prior knowledge of the area).

Traplines of various lengths have been identified in butterflies (Gilbert 1975) and in a variety of bees, including euglossines (Janzen 1971; Ackerman *et al.* 1982), flower bees (*Anthophora* spp.) (Kadmon 1992), honeybees (Ribbands 1949), but most frequently in bumblebees (Manning 1956; Heinrich 1976b; Thomson *et al.* 1982, 1987, 1997; Corbet *et al.* 1984; Williams and Thomson 1998; Ohashi *et al.* 2008). Bumblebees seem to show very strong fidelity to sites at which they have previously found a reward, visiting the same patches over and over again on successive days or weeks (Bowers 1985a; Dramstad 1996; Saville *et al.* 1997; Osborne *et al.* 1999; Osborne and Williams 2001; Cartar 2004). Bees possess impressive navigational abilities and are able to remember the relative positions of landmarks and rewarding flower patches (Southwick and Buchmann 1995; Menzel *et al.* 1996, 1997) which is no doubt valuable when following traplines. For example, honeybees are able to integrate movement vectors; after a series of movements between patches they are able to plot a direct route home, thus avoiding the need to backtrack (Menzel *et al.* 1998). It seems likely that bumblebees also have this ability. Traplining along a regular route enables the forager to learn which flowers or patches are most rewarding, and also to avoid visiting flowers that she has recently depleted (Cartar 2004). Ohashi *et al.* (2008) demonstrate that traplining *B. impatiens* become faster and more accurate in following their trapline with experience. Visiting the same group of flowers at regular intervals may discourage competitors since any new forager attempting to exploit the same flowers may not know which flowers have been most recently depleted and so will initially receive a lower rate of reward than the resident forager (Corbet *et al.* 1984; Possingham 1989; Ohashi *et al.* 2008). This strategy also enables the bee to build up knowledge of the relative rewards produced by different patches, and to modify its foraging route accordingly over time; Makino and Sakai (2007) found that foraging *B. ignitus* initially preferred large patches of artificial flowers but over time they learned to avoid less rewarding patches (regardless of size).

Even without prior knowledge of the distribution of rewarding flowers, foragers can improve their efficiency compared to a strategy of random searching by using a systematic spatial search pattern so that they avoid encountering areas where they themselves have recently depleted rewards (Bell 1991). For example, various bee species and also Lepidoptera are able to remember their direction of arrival at a flower, and tend to continue in the same direction when they leave (reviewed in Waddington and Heinrich 1981; Pyke 1983, 1984; Schmid-Hempel 1984, 1985, 1986; Cheverton *et al.* 1985; Dreisig 1985; Ginsberg 1985, 1986; Ott *et al.* 1985; Plowright and Galen 1985; Schmid-Hempel and Schmid-Hempel 1986; Soltz 1986; Kipp 1987; Kipp *et al.* 1989; for exceptions see Zimmerman 1979, 1982). Bumblebees are even able to accomplish this correctly when the flower is rotated while they are feeding on it, provided that there are landmarks

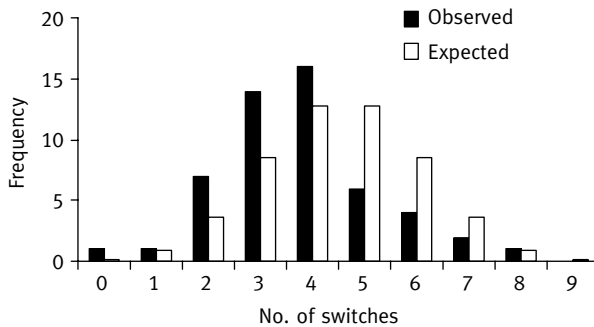
available by which they can keep track of their orientation relative to their direction of arrival (Pyke and Cartar 1992). They also may be able to use the earth's magnetic field to orientate themselves (Chittka *et al.* 1999b).

Superimposed on the general tendency for foragers to exhibit directionality, they may also adjust their turning rates and movement distances according to the size of rewards so that they quickly leave areas with few flowers or unrewarding flowers, and remain for longer in patches which provide a high reward or where flowers are dense (Pyke 1978a; Heinrich 1979a; Pleasants and Zimmerman 1979; Thomson *et al.* 1982; Rathcke 1983; Real 1983; Cibula and Zimmerman 1987; Kato 1988; Cresswell 1997; Burns and Thomson 2006). Short flights and frequent turns entails the risk of revisiting flowers, but this is presumably more than offset by the benefits of remaining within a patch containing many or highly rewarding flowers, and in any case the system is self-regulating since if revisitation becomes frequent then movement patterns will alter accordingly (Zimmerman 1982). Bumblebees tend to remain longer in patches with 'landmarks' (features protruding above the herb layer), perhaps because the landmarks facilitate a systematic search (Plowright and Galen 1985). If bumblebees do encounter flowers that they have already emptied, they have a further trick up their sleeve. They are able to distinguish and avoid entering flowers that have recently been visited by detecting the scent of previous visitors, although they still incur a small time penalty due to the time it takes to detect the scent (Núñez 1967; Wetherwax 1986; Giurfa and Núñez 1992b; Giurfa 1993; Giurfa *et al.* 1994; Goulson *et al.* 1998b; Stout *et al.* 1998) (see Chapter 10).

Systematic search patterns are also evident in the movements of bees between flowers on the same inflorescence. Many plants present flowers in a vertical raceme, which bees almost invariably exploit by starting at the bottom and working upwards (Heinrich 1975b, 1979a; Pyke 1978a) (Plate 7). In some plants, the lower flowers in the raceme produce more nectar, so that bees forage upwards until low rewards stimulate departure (Pyke 1978b). It makes sense for bees to start at the most rewarding point and depart when rewards become too low to be worthwhile. However, bumblebees continue to forage upwards when the distribution of nectar is artificially reversed so that the top-most flowers are most rewarding (Waddington and Heinrich 1979). Some flowers such as *Linaria vulgaris* provide most nectar at the top of inflorescences, but bumblebees usually forage upwards on these too (Corbet *et al.* 1981). Rather than relating to the distribution of nectar, upwards foraging may simply be a result of the position which bees generally adopt when foraging on flowers (facing forwards and upwards); climbing or flying backwards is presumably more awkward and hence slower than going forwards. Corbet *et al.* (1981) noted that *B. terrestris* robbed *L. vulgaris*, and that to do this some individuals perched on the inflorescence facing downwards. These individuals tended to start at the top and work downwards. Whatever the distribution of nectar and the direction taken by the bee, a simple foraging rule in which each individual bee always moves in the same direction ensures that they rarely encounter flowers that they have just visited, at least within a single inflorescence.

Simple systematic search patterns are also possible on other types of inflorescence. Many plants provide rings of open flowers around a central stem (e.g. *Trifolium* spp. or *Monarda* spp.). When visiting inflorescences of this sort, bees simply circle around them until they re-encounter the first floret that they landed on. Interestingly, individual bumblebees exhibit a strong tendency to rotate around the flower in a particular direction. Kells and Goulson (2001) studied the direction of rotation of workers of four UK bumblebee species, *B. lapidarius*, *B. terrestris*, *B. lucorum* and *B. pascuorum*, when foraging on inflorescences of *Onobrychis viciifolia*. Individuals of all four species tended to rotate in the same direction in successive visits to inflorescences (Fig. 7.1). Overall, bees rotated around inflorescences in the same direction as on their previous visit on 68.6% of visits (all bee species combined, SE = 9.34). Presumably, a bee which exhibited random rotation would receive the same rate of reward, and hence just as much reinforcement of its behaviour, as a bee with a fixed direction of rotation. Ecologically, the direction of rotation would seem to be trivial, since it has no consequence for either the bee or the plant. The direction in which a naïve bee turns on the first inflorescence it encounters may be random, but the bee may then simply repeat this behaviour because it has proved to be successful.

For three of the four species, approximately equal numbers of individuals tended to rotate either clockwise or anticlockwise, but intriguingly *B. pascuorum* exhibited a significant tendency to rotate in an anticlockwise direction (Kells and Goulson 2001). It is tempting to dismiss this as a spurious result, but parallels can be found in higher



**Figure 7.1** The frequency distribution of switches between anticlockwise and clockwise rotations around flowers, compared to that which would be expected if the direction of foraging was random on each visit to an inflorescence. Each bee was observed on 10 consecutive inflorescences. Data have been combined for four bumblebee species, *B. lapidarius*, *B. terrestris*, *B. lucorum* and *B. pascuorum*, when foraging on inflorescences of *Onobrychis viciifolia*. The proportion of switches between clockwise and anticlockwise visits did not differ between the four bee species ( $\chi^2 = 4.86$ , d.f. = 3,  $p > 0.05$ ). Overall, bees tended to forage on consecutive inflorescences by rotating in the same direction. The number of switches between directions was significantly lower than the number of times a bee continued to forage by rotating in the same direction ( $t = 3.34$ , d.f. = 51,  $p < 0.001$ ). From Kells and Goulson (2001).

organisms. In behaviours which require body rotation, children exhibit a tendency to turn in one direction or another, and just as in *B. pascuorum*, most children tend to rotate anticlockwise. This tendency becomes more pronounced with age (Day and Day 1997). Preferred directions are correlated with handedness (Yangzen *et al.* 1996). Similar rotational preferences have been found in other mammals including capuchin monkeys (Westergaard and Suomi 1996) and mice (Nielsen *et al.* 1997), but apparently they do not occur in goats (Ganskopp 1995)! The origins and significance of these preferences remain to be explained.

### 7.1.2 Non-random choice of patches

The distribution of foragers among patches depends on the relationships between recruitment rate and patch size, and also how long foragers spend in patches of varying size once they get there. In general, insect foragers preferentially visit large patches (plants with many flowers) (reviewed in Goulson 1999; more recently, Ohashi and Yahara 1998, 2002; Vrieling *et al.* 1999; Makino and Sakai 2004, 2007; Mitchell *et al.* 2004; Grindeland *et al.* 2005; Miyake and Sakai 2005; Makino *et al.* 2007), although the relationship between recruitment and patch size is often less than proportional (Schmid-Hempel and Speiser 1988; Klinkhamer *et al.* 1989; Dreisig 1995; Goulson *et al.* 1998a).

Several studies have found that this combination of higher recruitment to large patches and systematic searching results in a visitation rate per flower which is independent of plant size (i.e. foragers achieve an ideal free distribution) (Heinrich 1976b; Pleasants 1981; Schmitt 1983; Bell 1985; Geber 1985; Schmid-Hempel and Speiser 1988; Thomson 1988; Dreisig 1995; Robertson and Macnair 1995; Kunin 1997). When nectar production rates varied greatly between plants, Dreisig (1995) found that foraging bumblebees achieved an ideal free distribution by preferentially visiting individual *Anchusa officinalis* which had high rates of nectar production, the result of which was that all bees received an approximately equal rate of reward. However, an ideal free distribution has not been found in all studies. For example, Klinkhamer and de Jong (1990) found that visits per flower by bumblebees declined with plant size in *Echium vulgare* (see also Grindeland *et al.* 2005), while Klinkhamer *et al.* (1989) describe the reverse in *Cynoglossum officinale*.

It appears that, more often than not, bumblebees achieve an approximately ideal free distribution, but how do they do this? Factors governing recruitment rates to patches have received little attention. Greater recruitment to large patches is presumably at least partly because large patches are more easily detected or because they are more likely to be encountered, and does not necessarily imply an active preference by the forager. The general finding that increases in recruitment are less than proportional to increases in patch size is less easily explained. It may be because foragers searching for flowers tend to search in two dimensions (they tend to fly at an approximately uniform height) so that the probability of encountering a patch is a function of its diameter rather than its area (Goulson 1999). Since the number of flowers in a patch is likely to be

proportional to its area, this could result in a decelerating relationship between flower number and recruitment. At present, there is insufficient information available to determine whether recruitment patterns are the result of passive encounter rates or active choice by foragers.

## 7.2 The marginal value theorem

Studies of the response of pollinators to varying patch sizes have found that not only are more foragers attracted to larger patches, but also that they spend longer time in them, and visit more flowers while they are there, as one would intuitively expect (reviewed in Goulson 1999, 2000b). More interestingly, studies of a diverse range of plant-pollinator systems have also found that the pollinators visit a smaller proportion of the available flowers in larger patches (Beattie 1976; Heinrich 1979a; Zimmerman 1981b; Schmitt 1983; Geber 1985; Morse 1986a; Andersson 1988; Schmid-Hempel and Speiser 1988; Thomson 1988; Klinkhamer *et al.* 1989; Klinkhamer and de Jong 1990; Pleasants and Zimmerman 1990; Dreisig 1995; Harder and Barrett 1995; Robertson and Macnair 1995; Brody and Mitchell 1997; Goulson *et al.* 1998a; Ohashi and Yahara 1998; Cresswell and Osborne 2004), although the opposite was found for bumblebees visiting patches of *Nepeta cat-aria* (Sih and Baltus 1987). The explanation for this general pattern is not obvious.

The marginal value theorem is an optimality model for investigating the behaviour of foragers exploiting patchy resources (Charnov 1976). The theorem states that a forager should leave a patch when the rate of food intake in the patch falls to the average for the habitat as a whole. This can be used to predict the optimal duration of stay of a forager in a patch, if the shape of the pay-off curve for staying within a patch and the mean travel time between patches are known. Can the marginal value theorem explain why pollinators visit a decreasing proportion of flowers in a patch as patch size increases? Several researchers have applied the marginal value theorem to bees foraging on flowers held in vertical racemes (Pyke 1978c, 1981, 1984; Hodges 1981; Zimmerman 1981c; Best and Bierzychudek 1982; Pleasants 1989). The aim of these studies was to predict when the insect should move to a new inflorescence, and to examine what departure rules might be used to achieve the most efficient strategy. However, this is a special case. Vertical racemes are easy to search systematically (insects typically start at the bottom and work upwards; Heinrich 1975b, 1979a), and usually have a predictable, declining reward in successively higher florets (Pyke 1978b). More commonly, a pollinator has to search among loose aggregations of flowers or inflorescences with no clear spatial structuring. Here the search strategy employed by the pollinator will largely determine the shape of the pay-off curve that it gains from visiting a patch of flowers. If we can ascertain the shape of the pay-off curve in different patch sizes, then it will be possible to predict the optimal duration of stay (sometimes known as the 'give up time'; Charnov 1976).

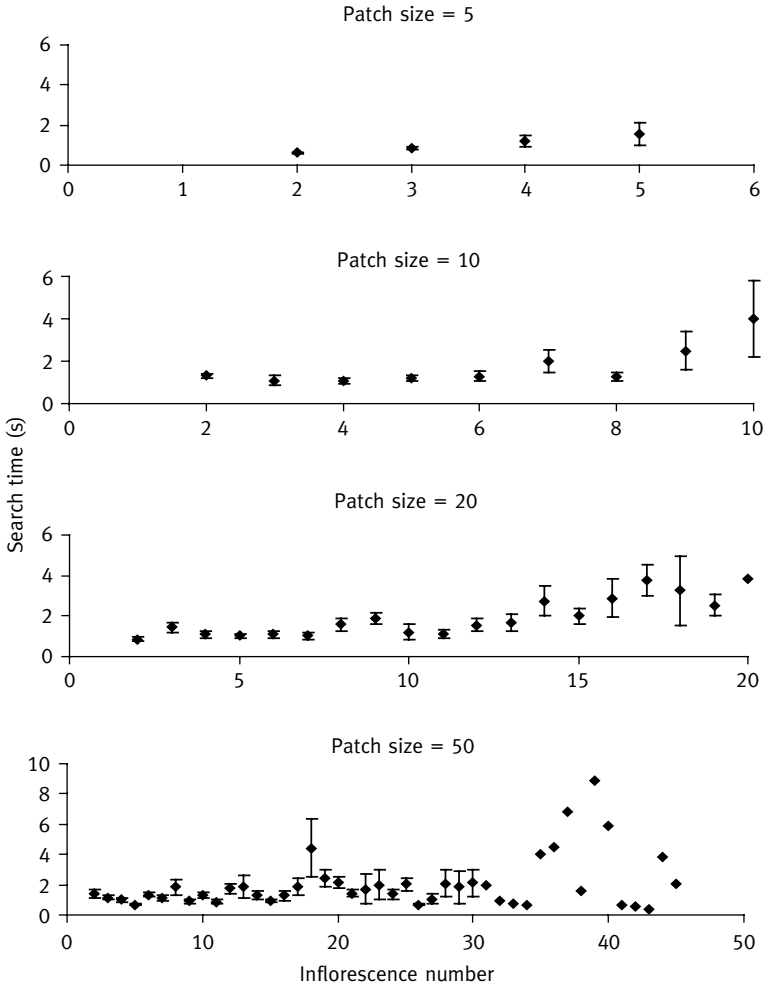
The shape of the pay-off curve will depend on whether the forager searches randomly, or has a systematic strategy. As we have seen, bumblebees use systematic search



patterns, which include directionality, and turning more frequently when in particularly rewarding or dense patches of flowers. However, it seems probable that a forager will be unable to carry out a systematic search of all the flowers on a large plant without making mistakes, and re-encountering flowers that it has depleted. Thus, we would expect the rate of reward acquisition to begin to decline after a period of time spent within the patch. If travel time between patches is short, then an insect should depart soon after this decline begins (Goulson 1999). Two models have been developed applying the marginal value theorem to bumblebees exploiting patches within which flowers were haphazardly arranged (Goulson 1999; Ohashi and Yahara 1999). Both models predict that bumblebees should visit a greater proportion of flowers in small patches. However, the relevant parameters were not quantified, so only qualitative predictions were possible. No information was available on the proportion of flowers on a patch an insect can visit before it begins to make mistakes (revisit flowers), and how this proportion changes with patch size.

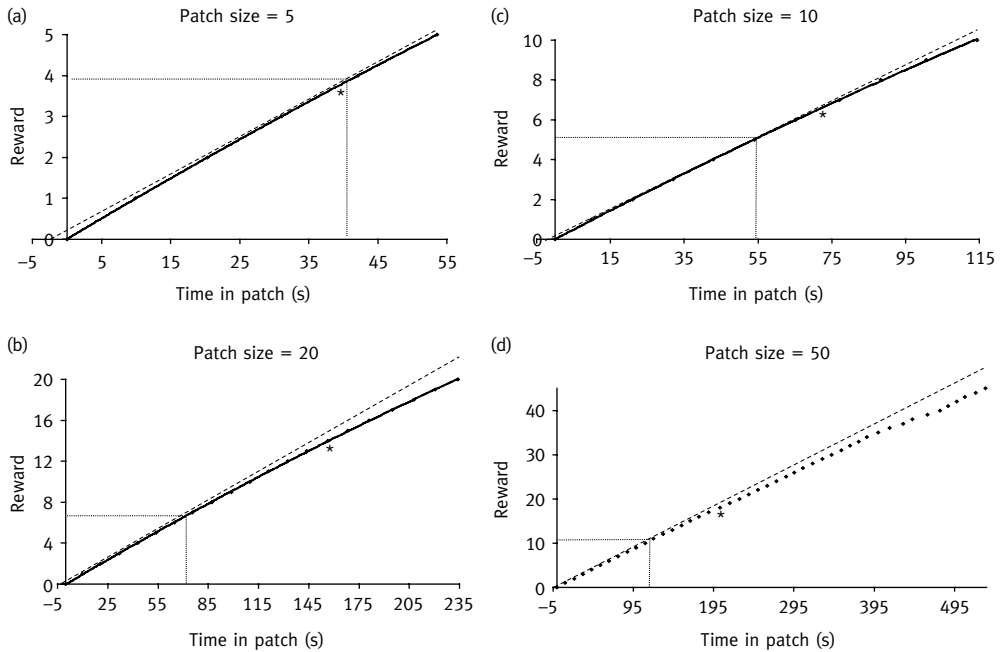
I attempted to quantify the pay-off curve for workers of the bumblebee *B. lapidarius* foraging in artificially created patches of varying size of white clover, *Trifolium repens* (Goulson 2000b). By quantifying travel time between patches, handling time per inflorescence, and search time for each successive inflorescence located, it was possible to construct pay-off curves for different patch sizes, and predict the optimal duration of stay within patches. Search time within patches increased as the proportion of inflorescences visited increased, demonstrating that foraging bumblebees cannot systematically visit all of the flowers within a patch without making mistakes (Fig. 7.2). For all four patch sizes that were examined, pay-off curves were very closely described by quadratic equations, with each linear and quadratic term significantly improving the fit of the line (Fig. 7.3). Since handling times were not affected by patch size or duration of stay, it is the increase in search time for successive inflorescences that results in the typical pay-off curve with a declining slope (Charnov 1976). The optimum duration of stay in each patch is given by the point of contact between the curve and a tangential straight line plotted through coordinate  $-(\text{travel time between patches}), 0'$  (following Charnov 1976). The optimum duration of stay increased with patch size, but was less than proportional so that to achieve a maximal rate of reward per time bees should visit a smaller proportion of inflorescences in larger patches.

For the smallest patch size, the predicted optimum duration of stay was close to the observed value, but as patch size increases, observed and predicted values diverged, with bees staying for shorter periods than predicted. However, even in the largest patch size where the discrepancy between observed duration of stay and the predicted optimum was greatest, the bees were still achieving a rate of reward acquisition very close to the optimum due to the shape of the pay-off curve (Fig. 7.3). So although bees were apparently behaving in a suboptimal way in larger patches (assuming that calculation of the pay-off curves is accurate and that the assumptions of the model are met), they are only very slightly suboptimal.



**Figure 7.2** Search times for successive inflorescences within patches containing 5, 10, 20 or 50 inflorescences of *T. repens* ( $\pm$  SE). Values shown were calculated by taking the means for five bumblebees that visited each patch, and using these means from five replicate patches to calculate a grand mean and standard error. The bees arrival at the first inflorescence in a patch was deemed to be the time of arrival in the patch, so there is no search time for the first inflorescence. Data from Goulson (2000b).

Both observed and predicted durations of stay within patches result in a declining proportion of inflorescences being visited as patch size increases. It appears that visiting a declining proportion is optimal, but why? The answer must lie in the changing patterns in the time it takes to find unexploited inflorescences. In small patches, use of a systematic search pattern could enable pollinators to visit all of the inflorescences without mistakes, and thus without an increase in search time (the pay-off curve would



**Figure 7.3** (a–d) Pay-off curves for the bumblebee, *B. lapidarius*, visiting patches containing 5, 10, 20 or 50 inflorescences of *T. repens*. Curves are constructed from measured search times, which increase as the proportion of inflorescences within the patch that have already been visited increases. Handling time is independent of patch size with a mean of  $9.79 \pm 0.35$  s per inflorescence; this value is used for constructing curves. As handling time is independent of patch size, the assumption that reward per inflorescence is equal across patch sizes appears to be valid, since inflorescence handling time is closely correlated to reward received (Harder 1986; Kato 1988). Reward is thus measured as the number of inflorescences handled. The mean travel time between patches was  $2.29 \pm 0.63$  s. The optimum duration of stay and number of inflorescences handled in each patch size is marked (dotted lines). H = observed duration of stay within patches. Data from Goulson (2000b).

be a straight line) (Goulson 1999). Similarly, Ohashi and Yahara (1999) suggest that pollinators are able to memorize and avoid the last few flowers that they visited, so that when the number of flowers in the patch is less than or equal to the number that can be memorized, the pollinator should visit every flower in the patch. It seems that, if pollinators can memorize the positions of flowers that they have visited, they can do so for only a very few (less than four). Even in patches containing just five inflorescences, search time exhibited a marked increase with the fifth inflorescence taking on average 2.5 times as long to locate as the second (Goulson 2000b).

Presumably searching for the remaining unvisited inflorescences is simpler in a small patch than in a large one. In this respect, pollinators visiting flowers represents a rather different situation to that for which the marginal value theorem was originally

developed (predators searching for prey) because the flowers remain after they have been visited. By doing so, they render locating the remaining unvisited flowers more difficult. The explanation as to why search times overall are longer in bigger patches may be illustrated by a simple numerical example. Consider a bee foraging in a patch of 5 inflorescences, of which it has already visited 3 of them. If it visits the next inflorescence at random, it has a  $2/5$  chance of locating one of the unvisited ones on its first attempt. However, the simple movement rules of bees render it unlikely that it will visit the inflorescence it has just left, so it actually has a chance of  $2/4$  of locating an unvisited flower on the first attempt. In contrast, consider a bee in a patch of 50 flowers, of which it has visited 30 (the same proportion). When it departs from the 30th flower it has a  $20/49$  chance of choosing an unvisited flower on its first attempt, a value substantially less than  $2/4$ . Finding the fourth flower of five, and so achieving an 80% visitation rate (as most bees did; Goulson 200b), is substantially easier than locating the 31st, 32nd, ..., 40th flower in a patch of 50 (and very few bees did so). This argument does not require the pollinator to memorize the positions of flowers that it has recently visited, only that it does not immediately visit the flower that it just departed from.

Another way of considering this is to examine what cues stimulate departure from a patch. It is clear that the size of rewards recently received and the density of flowers influence the probability of departure. In both bumblebees and solitary bees, low rewards promote departure from an inflorescence (Cresswell 1990; Kadmon and Shmida 1992). Similarly in bumblebees and honeybees, low rewards trigger longer flights and so often result in departure from the plant or patch (Heinrich *et al.* 1977; Pyke 1978a; Thomson *et al.* 1982; Zimmerman 1983; Plowright and Galen 1985; Kato 1988; Dukas and Real 1993b; Giurfa and Núñez 1992a). This has a clear analogy in the triggering of switching between plant species by receipt of low rewards (Greggers and Menzel 1993; Chittka *et al.* 1997; Goulson *et al.* 1997a) (see Chapter 8).

There is some disagreement as to the departure rules used by foragers. For some time, it was thought that departure from a patch was triggered by the reward from a single flower falling below a threshold (Pyke 1978a; Best and Bierzychudek 1982; Hodges 1981, 1985a,b; Pleasants 1989). It subsequently became apparent that a simple threshold departure rule was not strictly accurate, at least for bumblebees, but rather that the probability of departure increases with decreasing reward (Cresswell 1990; Dukas and Real 1993b). However, any strategy based on only the last visit to a flower seems intuitively likely to be suboptimal given the high heterogeneity of rewards that is usually found within patches, since it is likely to result in premature departure from highly rewarding patches. In fact studies have demonstrated that both bumblebees and other bee species are able to integrate information over several flower visits (not just the last one) in making decisions about departure from a patch (Hartling and Plowright 1978; Waddington 1980; Cibula and Zimmerman 1987; Kadmon and Shmida 1992; Dukas and Real 1993b,c; Taneyhill and Thomson 2007).

Let us return to the data on pay-off curves for *B. lapidarius* feeding on patches of clover. Suppose that a bee departs from a patch if it encounters two inflorescences in a row

that it has already visited (and which are thus more or less empty). If we assume that the bee is equally likely to encounter any inflorescence (excluding the one that it just left), then it is simple to calculate the probability that this inflorescence has already been visited, and to square this to obtain the probability of this happening twice and the bee departing from the patch. We can thus calculate the probability of a bee departing after one visit, two visits, and so on, and use this to calculate the expected mean number of inflorescences visited per patch for bees using this departure rule. For the patch sizes of 5, 10, 20 and 50 flowers used by Goulson (2000b), we would predict mean numbers of inflorescences visited per patch to be 3.95, 6.06, 9.88 and 18.48, respectively. These values are remarkably close to those that were observed (Fig. 7.3). Whether this is coincidence is hard to say without explicitly studying the departure rules used, but nonetheless this example illustrates an important point; that is, a simple departure rule can result in pollinators visiting more inflorescences per patch but a declining proportion of inflorescences per patch, exactly as is observed in nature.

Fascinatingly, Biernaskie *et al.* (2002) provide evidence that the departure rules used by bees can be manipulated by the plant to improve pollination. As we have seen, large floral displays attract more pollinators, but are likely to result in a long residence time within the display and hence high levels of selfing. Ideally, a plant would benefit if it could attract lots of pollinators but persuade them to leave quickly. By manipulating the variance in reward between florets in artificial inflorescences (but keeping the mean reward per patch constant), they demonstrated that *B. flavifrons* visit fewer flowers per inflorescence when rewards are more variable. This presumably reflects suboptimal decision making by the bee, since the expected patch residency—pay-off curve is identical in both inflorescence types. There is no doubt that rewards per floret do vary greatly within many natural inflorescences, but whether this is the result of selection to minimize selfing remains to be established.

To summarize, floral resources are patchily distributed. All else being equal, selection will favour foraging strategies that maximize the rate of resource acquisition. Bumblebee workers are less likely to be constrained in their foraging behaviour than most other insects. Bumblebees use systematic searches within flower patches, but these break down as the number of flowers already visited within the patch increases. Thus the search time increases with duration of stay within a patch. Application of the marginal value theorem to experimentally obtained pay-off curves predicts that bees should visit more flowers in large patches, but should visit a declining proportion of flowers as patch size increases. This is broadly in agreement with a large body of evidence from field studies. A simple departure rule based on two successive encounters with inflorescences that have already been visited closely predicts observed behaviour in the bumblebee *B. lapidarius*.

---

## Choice of Flower Species

Although current plant-pollinator mutualisms represent the result of approximately 100 million years of co-evolution, extreme specialization is unusual (reviewed in Waser *et al.* 1996). There are a small number of plant species which depend on a single or very few pollinator species throughout their range; examples include the Yucca (*Yucca* sp.) (Bogler *et al.* 1995), Figs (*Ficus* sp.) (e.g. Wiebes 1979), various orchids such as *Ophrys speculum* (Orchidaceae) (Nilsson 1992), and a guild of red-flowered plants found in the Fynbos of South Africa which are pollinated by the butterfly *Aeropetes tulbaghia* (Marloth 1895; Johnson and Bond 1992). Examples in which an insect depends exclusively on one plant species for all of its nectar or pollen requirements appear to be even more scarce (Waser *et al.* 1996), and at present include a handful of species of bee (Westrich 1989). Interestingly, three bumblebee species are known that are each almost entirely dependent on one species or genera of flowers, at least in some populations or parts of their range; *B. consobrinus* on *Aconitum septentrionale*, *B. gerstaeckeri* on *Aconitum* spp. and *B. brodmannicus* on *Cerinth* spp. (Løken 1973; Rasmont 1988; Konovalova 2007). All three are alpine species with short colony duration, which presumably allows them to specialize.

The vast majority of insects, including most bumblebees, have flexible floral preferences and visit a range of flowers of different plant species according to availability. Similarly, the majority of plants are visited by several or many insect species (Waser *et al.* 1996), although not all may be effective pollinators. Some of the insects that visit flowers exhibit little in the way of specialized adaptations for feeding on nectar or pollen, and are thus only able to exploit simple flowers. For example, the inflorescences of many umbellifers (Apiaceae) effectively form a platform upon which a range of polyphagous beetles and flies can graze pollen without requiring specialized morphological adaptations or particular handling skills. However, most flower-visiting insects are specialists in that nectar, pollen or both represent their major food source, and in that they possess appropriate morphological adaptations (typically elongated sucking mouthparts and/or hairs or baskets to trap pollen; e.g. Thorpe 1979; Gilbert 1981). This group, which includes bumblebees, are able to tackle a broad range of flower species, and are responsible for the pollination of many (perhaps most) insect-pollinated plants.

Bumblebees are usually faced with a choice of flower species. Each will differ in abundance, distribution, the likely rewards that it provides, and the ease with which

the flowers can be handled. The best strategy for a worker to pursue is not clear. Should she visit flowers at random, or specialize in one or more particular types. If the latter, which types?

## 8.1 Learning and flower constancy

Insects foraging for nectar or pollen have long been known to exhibit a learned fidelity to flowers of a particular plant species which has previously provided a reward. In doing so, they ignore many other suitable and rewarding flowers which they pass, but of course they also avoid visiting unsuitable flowers. This behaviour was first described by Aristotle in the honeybee in about 350 BC (Grant 1950), and subsequently attracted the attention of Darwin (1876).

Naïve bees have innate flower colour preferences, notably for the wavelengths 400–420 nm and 510–520 nm, but their preferences quickly change with experience (Lunau 1990; Gumbert 2000). They exhibit rapid sensory learning, and can use scent, colour, shape or a combination of all three to identify flower species which previously provided a reward (Koltermann 1969; Menzel and Erber 1978). When multiple cues are available (such as colour *and* scent), bees can use both to achieve a higher level of accuracy in decision-making (Gegebar and Laverty 2005; Kulahci *et al.* 2008). When colour cues differ greatly from surrounding colours, learning is fast and decision-making is accurate, but when colour cues differ only subtly errors are more frequent and bees take longer time to make decisions (Dyer and Chittka 2004). Foragers can learn to selectively attend to particular cues that are associated with reward, and ignore others that are not (Dukas and Waser 1994). The learning process takes as little as three to five consecutive rewards, and once learned, a preference may persist for minutes, hours or even for days (Menzel 1967; Heinrich *et al.* 1977; Dukas and Real 1991; Keasar *et al.* 1996; Chittka 1998). In honeybees, the learned fidelity can be strong, so that 93–100% of all visits in a single foraging bout are to the favoured plant species (Grant 1950; Free 1963). Learned fidelity of this sort became known as flower constancy (a term perhaps first coined by Plateau 1901 and defined by Waser 1986) and has been identified in the foraging regimes of other pollinators, including bumblebees. The preference shown by an individual insect is not fixed, and varies between individual foragers of the same species (Heinrich 1979c; Barth 1985).

Flower constancy is of crucial importance to plant reproductive biology (Levin 1978). From the point of view of the plant, constancy in its pollinators is of great benefit since it minimizes pollen wastage and stigma clogging with pollen from other species. Flower constancy influences the outcome of interspecific competition for pollination services (Waser 1982b; Rathcke 1983; Kunin 1993), and may also reduce inter-morph pollen transfer in polymorphic flowers and reduce hybridization between related species (Grant 1949, 1952; Jones 1978; Goulson 1994; Goulson and Jerrim 1997). It has been implicated as a contributory factor in sympatric speciation (Free 1963), although current opinion is that flower constancy alone is unlikely to provide sufficient isolation for speciation to occur (Grant 1992, 1993, 1994; Waser 1998; Chittka *et al.* 1999a).

Flower constancy is also intriguing from a behavioural viewpoint because in some circumstances it seems to be a suboptimal pattern of foraging (Woodward and Lavery 1992). By adopting this strategy the insects are bypassing other rewarding flowers. If they were not flower constant but visited with equal preference all flower species which provided a reward (assuming they knew which ones they were) then they could reduce travelling time. This apparent inefficiency is even more striking when, in two-choice experiments, some honeybees remained constant to an artificial flower morph which provides a consistently lower reward than the alternative (Wells and Wells 1983, 1986; Wells *et al.* 1992).

Studies of flower constancy have continued to focus primarily on Hymenoptera, principally bumblebees and honeybees, but in the past 10 years it has become clear that flower constancy is more widespread. It has recently been identified in butterflies (Lewis 1989; Goulson and Cory 1993; Goulson *et al.* 1997a) and hoverflies (Syrphidae: Diptera) (Goulson and Wright 1998), and circumstantial evidence from analysis of gut contents in pollen feeding beetles suggests that they may also exhibit constancy (De Los Mozos Pascual and Domingo 1991). It thus seems probable that flower constancy is a general phenomenon amongst foragers which gather nectar and/or pollen, although there is still disagreement as to why it occurs (e.g. Oster and Heinrich 1976; Real 1981; Barth 1985; Waser 1986; Woodward and Lavery 1992, Goulson 2000a; Raine and Chittka 2007b). Because bumblebees are docile and easily observed in the field, they have become a popular vehicle for testing the alternative hypotheses that have been put forward.

### 8.1.1 Explanations for flower constancy

Several explanations for flower constancy have been proposed; perhaps the most favoured theory is based on an idea proposed by Darwin (1895) :

That insects should visit the flowers of the same species for as long as they can is of great significance to the plant, as it favours cross fertilization of distinct individuals of the same species; but no one will suppose that insects act in this matter for the good of the plant. The cause probably lies in insects being thus enabled to work quicker; they have just learned how to stand in the best position on the flower, and how far and in what direction to insert their proboscides. (p. 419)

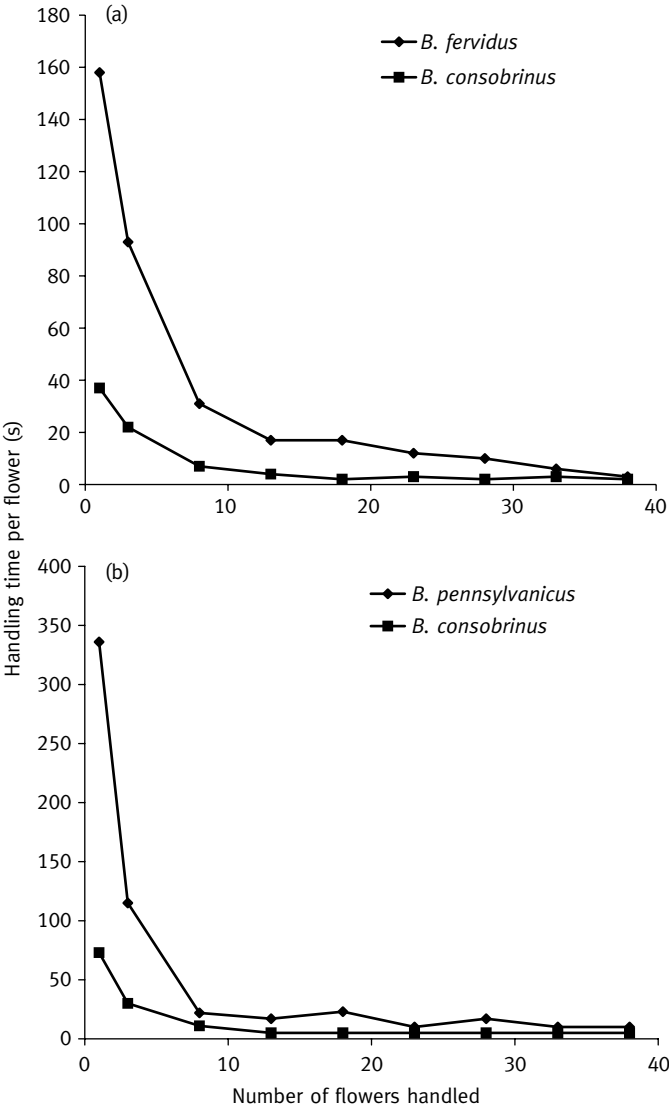
This idea has since been elaborated upon and has become known as Darwin's interference hypothesis (Lewis 1986; Waser 1986; Woodward and Lavery 1992). Essentially what Darwin suggested is that insects may be constant because they are quicker at repeating the same task (handling a particular type of flower) than they would be if they switched between different tasks. More recently, this has been interpreted as arguing that constancy is a result of learning and memory constraints; foragers may be limited by their ability to learn, retain and/or retrieve motor skills for handling flowers of several plant species (Proctor and Yeo 1973; Waser 1983, 1986; Lewis 1986, 1989, 1993; Woodward and Lavery 1992). Learning to extract rewards efficiently from within the structure of a flower takes a number of visits to that flower species, resulting in a decline in handling



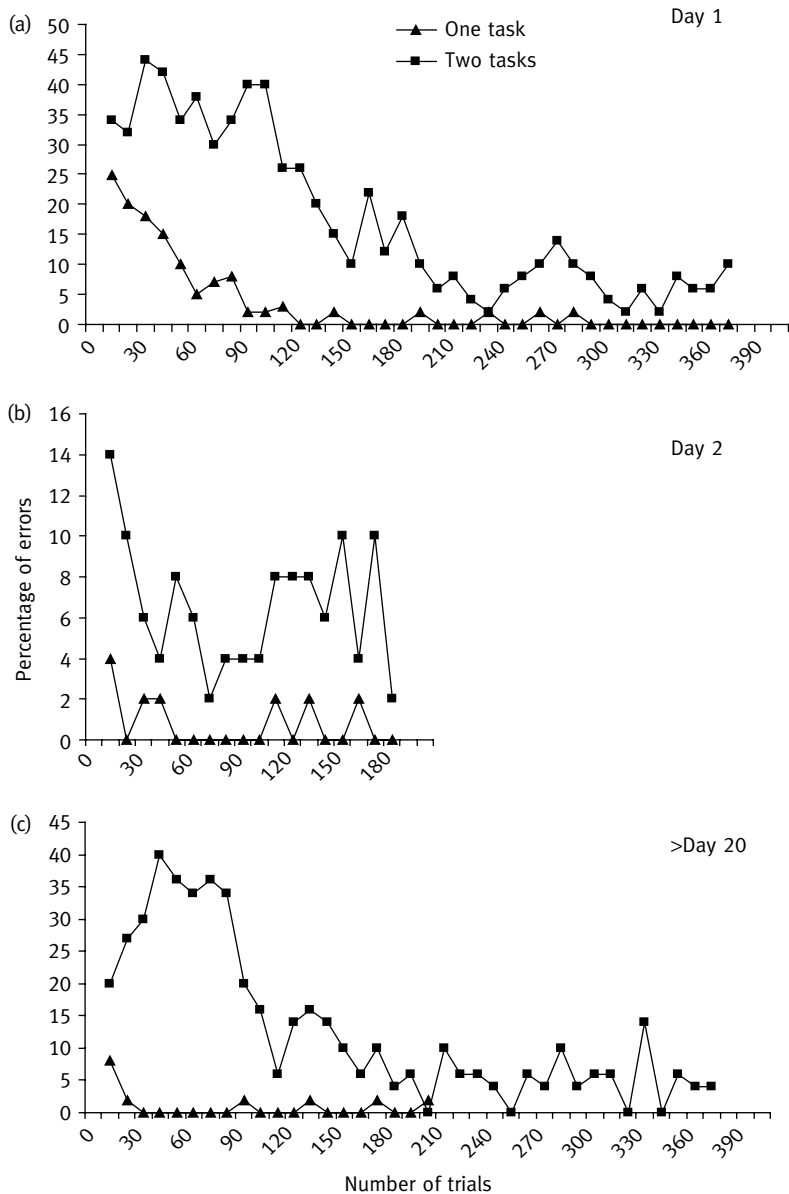
time on successive visits (Lavery 1980; Lewis 1986; Lavery and Plowright 1988; Keasar *et al.* 1996) (Fig. 8.1). Switching between species of flower differing in floral morphology often temporarily increases handling time as Darwin predicted, particularly when the morphology is complex (Heinrich *et al.* 1977; Lewis 1986; Woodward and Lavery 1992; Chittka and Thomson 1997; but also see Raine and Chittka 2007b).

It has been argued that memories of handling skills for one flower type are replaced if new skills are learned, that is, insects have a limited memory (Lewis 1986). However, considerable research on insect memory has been carried out in recent years and most researchers now agree that memory capacity is not the limiting factor; bees (and probably related insects) appear to have an accurate and large long-term memory (Chittka 1998; Menzel 1999). In honeybees and bumblebees, learned handling skills may be retained in long-term memory for weeks even when they are not being used (Menzel *et al.* 1993; Chittka 1998). For example, *B. impatiens* trained to locate rewards within a simple maze retained the ability for at least 20 days although there was no reinforcement within this period (Chittka 1998; Fig. 8.2). It appears that bees can learn to suppress associations between sensory inputs and learnt handling skills if they become inappropriate, but that the memories are retained (Chittka 1998). Hence learned motor (handling) skills are probably not lost as new skills are learned, but there is evidence that errors are likely to be made in retrieving the correct memory in the appropriate context if a bee switches between tasks frequently (Greggers and Menzel 1993; Chittka *et al.* 1995, 1997; Chittka 1998). After the initial learning process, a flower constant forager maintains a low handling time (but requires longer flight times to locate flowers), while a labile forager may incur a penalty of an increased handling time following switches between flower species (but benefits from a higher density of available resources and so a reduced flight time). Thus Darwin's interference hypothesis requires the trade-off between handling and flight times to favour constancy.

Attempts to quantify this trade-off suggest that this may not be so. Studies of bumblebees and butterflies have found that increases in handling time following switching vary greatly between plant species but are generally too small (0–2 s) to outweigh savings in travelling time (Woodward and Lavery 1992; Lavery 1994a; Gegear and Lavery 1995; Goulson *et al.* 1997b; Raine and Chittka 2007b). Also, if forced to switch between tasks, bumblebees may eventually be able to eliminate interference effects (Dukas 1995), although probably only when foraging on no more than two types of flower with simple structures (Gegear and Lavery 1998). Indeed bees do switch between simple flowers of different species with minimal interference effects (Lavery and Plowright 1988; Chittka and Thomson 1997; Gegear and Lavery 1998; Raine and Chittka 2007b). However, switching between three simple flower types or between two complex flower types does induce substantial handling penalties (Gegear and Lavery 1998). It seems that not only do bumblebees become more adept in handling flowers with practice, but also that the skills they learn are transferable between flower species; experience with other species of broadly similar flower morphology may actually increase learning rates (Lavery 1994b).



**Figure 8.1** Standardized handling times of naïve worker bumblebees visiting flowers of (a) *Aconitum napellus* and (b) *A. variegatum*. Beginning with the first flower visit, means are calculated over five visits. All three bee species show marked improvement as they learn to handle flowers. *B. consobrinus* is the only known example of a specialist bumblebee, feeding primarily on *Aconitum* spp. Even naïve bees of this species are markedly better at handling *Aconitum* flowers than the generalist bee species *B. fervidus* and *B. pennsylvanicus*. From Laverty and Plowright (1988).



**Figure 8.2** Percentage of errors made by the bumblebee, *B. impatiens*, trained to locate rewards within a simple maze. The entrance to the maze was either yellow or blue, and the reward obtained by turning either left or right. Bees trained to a single task (triangles) were provided either with mazes with yellow entrances where food was obtained by turning left, or with blue entrances where food was obtained by turning right. Bees trained to two tasks (squares) experienced both maze types in alternation. Bees experienced (a) 400 trials on day 1, (b) 200 on day 2 and (c) a further 400 after more than 20 days (after Chittka 1998). It is clear that overnight retention of memories is good. However, even after at least 20 days without practice on these artificial flowers, performance was substantially better than that of naïve bees, demonstrating that memories can be retained for long periods.

There is an alternative hypothesis that has gained some favour; that insects might use a search image when looking for flowers (Waser 1986; Goulson 2000a). Tinbergen (1960) introduced the search image as an explanation for prey selection patterns of great tits (*Parus major*) foraging under natural conditions in woodland. He noted that individual birds tended to collect sequences of the same prey species, and that they exhibited positive frequency-dependent selection. Although an intuitively appealing concept, search images have proved difficult to demonstrate convincingly, and it remains unclear how frequently they occur in natural situations (Guilford and Dawkins 1987; Allen 1989). Also, the cognitive mechanisms which give rise to the use of a search image are poorly understood. Almost all definitions of search images specify that they apply to cryptic prey (although Tinbergen himself did not explicitly state this). For example, 'as a result of initial chance encounters with cryptic prey, the predator "learns to see," and selectively attends to those cues that enable it to distinguish the prey from the background' (Lawrence and Allen 1983). This assumption now appears to be valid: experiments using pigeons have found that search image effects are only evident when prey are cryptic (Bond 1983; Bond and Riley 1991; Reid and Shettleworth 1992). Adoption of a search image for a particular prey's visual characteristics enhances its detectability and interferes with incoming perceptual information regarding alternative prey types (Bond 1983).

It has become apparent that the search image concept has much in common with a phenomenon known to psychologists as selective attention, by which predators learn to detect cryptic prey by selectively attending to particular visual features of the prey which best distinguish them from the background (Langley 1996). Both bumblebees and honeybees are able to use selective attention when distinguishing among flower types (Dukas and Waser 1994). Psychological studies of humans and various animals have demonstrated that the brain has a limited capacity for processing information simultaneously, that is, it has a limited attention (Blough 1979; Corbetta *et al.* 1990; Eysenck and Keane 1990; Posner and Peterson 1990). An analogous situation has been described in bees; honeybees have a fragile and probably limited short-term memory which is prone to rapid decay and to replacement by new memories (Menzel 1979; Menzel *et al.* 1993; Chittka *et al.* 1999a). Dukas and Ellner (1993) predicted that if predators have a limited attention and prey are cryptic then they should devote all their attention to a single prey type, but that if prey are conspicuous then predators should divide their attention among prey types. Thus, search images may result from both a limited ability to process information simultaneously and from selective attention to cues associated with particular prey types.

The obvious flaw in the argument for the use of search images by insects is that plants pollinated by animals have evolved brightly coloured flowers specifically to attract the attention of their pollinators. It thus seems implausible to argue that flowers may actually be cryptic. However, studies of pollinator fidelity (either in the laboratory or field) almost invariably focus on situations where the pollinator is presented with several flower choices at high densities. When viewed against a backdrop of other floral

displays (either of the same or different plant species) all of which are vying for the attention of pollinators then any particular flower may be effectively cryptic since it represents a random sample of the background (Endler 1981). Many flowers which commonly occur together have colours which are extremely similar to insect colour vision systems, and to the human eye (Kevan 1978; 1983; Chittka *et al.* 1994; Waser *et al.* 1996). When an insect flies through a meadow containing several flower species, individual flowers appear in the insect's field of view in very rapid succession; making some conservative assumptions about flight speed, flower density and size, and the insect's visual resolution, Chittka *et al.* (1999a) estimate that a bee encounters a new flower every 0.14 s. Even if the bee had previously encountered all of the flower species, it seems unlikely that in such a short time period the bee would be able to retrieve memories necessary to recognize the flower, recall the likely rewards and the motor skills required to access them, and then make an economic decision as to whether to visit the flower or not.

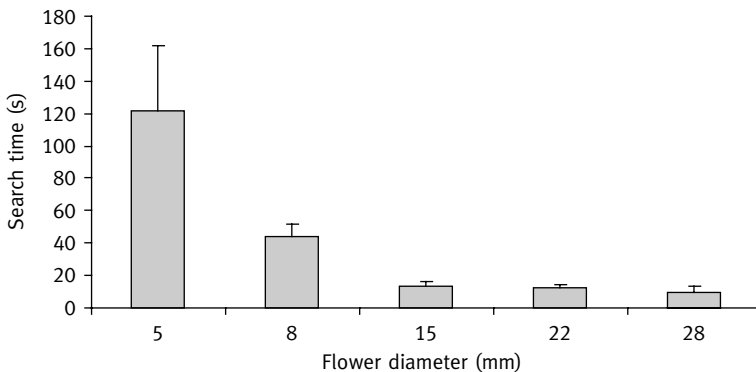
The suggestion that search images may be involved in flower constancy is not a new one. Levin (1978) was (to my knowledge) the first to argue that pollinators may develop a search image when foraging for flowers. He proposed that frequency-dependent selection by pollinators among colour morphs of the same plant species is best explained by use of a search image (constancy to particular colour morphs when all have identical structure cannot be explained by Darwin's interference hypothesis). This is supported by evidence that constancy declines as flower density (and thus crypsis) declines (Kunin 1993; Goulson *et al.* 1997a), in accordance with the predictions of Dukas and Ellner (1993), although this relationship would also be expected if flower constancy resulted from a trade-off between flight time and handling time. Dukas and Real (1993a) demonstrated that bumblebee foraging efficiency is limited in part by their ability to recognize rewarding flower types. Bees made fewer errors in identification when visiting only one rewarding flower type, even when the flower types differed markedly in colour (although Chittka *et al.* (1999a) argue that the experimental design was flawed). It seems that constraints on recognition (rather than handling) may favour constancy. Several studies have demonstrated that pollinators switch readily between plant species which have similarly coloured flowers (Waser 1986; Kunin 1993; Laverty 1994b; Chittka *et al.* 1997), even when these flowers have very different structures (Wilson and Stine 1996). Conversely, pollinators rarely switch between flowers of similar structure but of different colour (Wilson and Stine 1996). Darwin's interference hypothesis predicts precisely the reverse, but this is consistent with the hypothesis that search images are used by foragers.

### 8.1.2 Can flowers be cryptic?

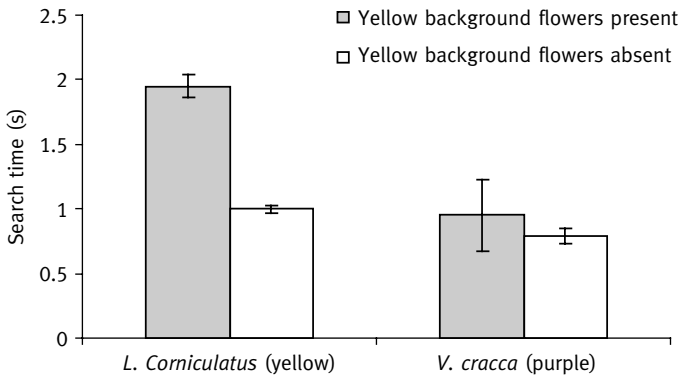
So are flowers really hard to find, despite their bright colours? There is some evidence to suggest that they are. Spaethe *et al.* (2001) demonstrated that the time taken by *B. terrestris* workers to locate artificial flowers against a green background was very strongly

correlated with flower size; flowers of 4 mm diameter took approximately 10 times as long to find as flowers of 28 mm diameter (Fig. 8.3). This suggests that time taken to locate flowers may be a major component of total foraging time. Any mechanism which improved the efficiency with which flowers were located would be of great benefit. Interestingly, Spaethe *et al.* (2001) also found that search times depend greatly on the colour of the flower, suggesting that the foraging efficiency (and thus optimal floral preference) of bees depends not only on floral rewards, flower density and handling times, but also on variation in search times due to flower colour.

These experiments were conducted against a uniform green background, against which the flowers tested were not, strictly speaking, cryptic (they did not resemble a random sample of the background). Nevertheless, small flowers were still hard to find. Flower location is likely to be even more difficult when the desired flower species is viewed against a background of similar coloured flowers of other species. To examine this, I quantified the flight times of wild bumblebees, *B. pascuorum*, foraging among grids of flowers of *Lotus corniculatus* or *Vicia cracca*, two species which are favoured by *B. pascuorum* (Goulson 2000a). Flowers of *L. corniculatus* are yellow and those of *V. cracca* are purple. These grids were presented either with or without a background of yellow flowers of species not generally visited by *B. pascuorum*. The background of yellow flowers greatly increased flight times when foraging on the yellow-flowered *L. corniculatus*, but had no effect when foraging on *V. cracca* (Fig. 8.4). Bees took on average twice as long to locate *L. corniculatus* flowers when they were presented against a background of other yellow flowers compared to when they were on their own. This is hardly surprising since the apperancy of flowers is simply a function of the degree of contrast they make with their background (Lunau *et al.* 1996). Frequently, bees were observed to approach to within 1–2 cm of yellow flowers other than *L. corniculatus* but then rejected them after close inspection. Small flowers of different species but with similar colour



**Figure 8.3** Search times for *B. terrestris* when locating artificial blue flowers of varying sizes, viewed against a green background. From Spaethe *et al.* (2001).



**Figure 8.4** Flight times (mean (s)  $\pm$  SE) of *B. pascuorum* when moving between inflorescences of *L. corniculatus* or *V. cracca* arranged in a regular grid with 1 m spacing, with and without a natural background of yellow flowers. Flowers of *L. corniculatus* are yellow and those of *V. cracca* are purple. Times are grand means of individual means from each bee, based on five bees per grid and four replicate grids. When searching for the yellow *L. corniculatus*, flight times were much shorter without a background of yellow flowers ( $F_{1,12} = 19.6, p < 0.001$ ). From Goulson (2000a).

are likely to be indistinguishable to a bee until it is at very close range. In fact, *L. corniculatus* inflorescences are hard for human observers to find when mixed with other yellow flowers (Plate 8). Of course, bee vision is markedly different to our own, and it is likely that some of the flower species present were, to a bee, markedly different in colour or brightness to *L. corniculatus*. However, the results suggest that at least some of the species had a similar spectral reflectance since their presence appeared to increase bee foraging time.

The weight of evidence suggests that bumblebees looking for flowers use search images, that is, they have a limited ability to process visual information from many floral displays simultaneously, and so selectively attend to particular visual features of their preferred flowers. It is likely that other insects also do so, although experimental evidence is lacking. Of course, if bumblebees are using a search image this does not rule out the possibility that Darwin's interference hypothesis may also be valid since the two hypotheses are not mutually exclusive (Wilson and Stine 1996). In fact, the two mechanisms may be synergistic. A perceptual mechanism which renders fidelity a more efficient means of finding flowers (i.e. minimizes search time) could act in conjunction with selection for minimized handling times to promote constancy. Carefully executed experimental tests are required to establish the relative importance of these two processes in promoting flower constancy. To do this successfully, it would probably be necessary to use arrays of artificial flowers in which both colour and structural complexity could be varied independently. Thus it would be possible to manipulate both apparency (difference in flower size and reflectance spectrum compared to the background) and handling time, and examine the conditions which promote constancy.

## 8.2 Infidelity in flower choice

Although flower constancy occurs in a diverse range of insects, it is important to emphasize that constancy is usually far from absolute, and that the terms ‘constancy’ and ‘fidelity’ are slightly misleading in this context. Foragers will sample other flowers (sometimes known as minoring in bumblebees), and may also change their preference over time in response to a sequence of low rewards or reduced availability of their preferred flower. Minors may be included as a compromise required to track changing rewards through time, that is, to check whether something else has come into flower that may be more rewarding (Heinrich 1979c). Bumblebees in particular frequently visit flowers of several species during a single foraging bout, and are markedly less constant than honeybees (Bennett 1884; Brittain and Newton 1933; Grant 1950; Free 1970; Thomson 1981; Waddington 1983a). For example, Gegear and Laverty (2004) compared the foraging behaviour of honeybees and bumblebees (*B. impatiens*) in mixed arrays of equally rewarding blue and yellow flowers following sequential training on each colour in isolation. They found marked differences between the two species, with honeybees being flower constant in the mixed arrays while bumblebees readily visited both colour.

If the favoured flower ceases to be rewarding, it seems that bees can rapidly replace learned preferences with new ones (Menzel 1969, 1990; Meineke 1978). They may change their foraging preference in response to rewards received or according to changing frequencies of encounter with different flowers. They appear to follow simple rules. When flowers are scarce, theory predicts that foragers should abandon specialization in favour of generalization (e.g. Levins and MacArthur 1969; Schoener 1969; Colwell 1973; Kunin and Iwasa 1996). Empirical studies have confirmed that, even given the memory constraints previously discussed which favour constancy, this does indeed occur in insects visiting flowers. Bumblebees, honeybees and hoverflies all abandon constancy when their preferred flower is scarce (Kunin 1993; Chittka *et al.* 1997). For example, Raine and Chittka (2007b) show that bumblebees are most likely to land on a flower if it is of the same type as the last one that they visited, but that this choosiness rapidly declines over time following the visit if a flower of that type is not encountered. Similarly, Fontaine *et al.* (2008) found that *B. terrestris* foragers tended to exhibit a broader diet breadth when experiencing high intraspecific competition for food.

The mechanism driving both increased switching when preferred flowers are scarce and diet breadth extension when rewards are low is probably essentially the same; bees exhibit fidelity so long as they are being rewarded, but it quickly breaks down if they are not. In honeybees, low rewards from individual flowers promotes switching between different coloured artificial feeders in laboratory studies (Greggers and Menzel 1993). Feeding time is known to be an indicator of the reward received in bumblebees and honeybees, and probably also in other insects feeding on nectar (Pyke 1978a; Schmid-Hempel 1984; Bertsch 1987; Greggers and Menzel 1993), enabling examination of the relationship between reward and subsequent behaviour under natural conditions.



Both bumblebees and butterflies exhibit higher rates of switching following low feeding times on individual flowers (Chittka *et al.* 1997; Goulson *et al.* 1997b). There is evidence that bees develop an expectation of the level of reward that they can expect from a given flower type, and once the actual reward falls below the expected value a switch to a different flower type is triggered. Wiegmann *et al.* (2003) trained *B. impatiens* to artificial red flowers containing either 0.5 or 0.2 M sucrose solution, and then offered these bees an array containing mixed yellow and red flowers all containing 0.2 M sucrose solution. Those bees previously fed on the higher concentration of sugar solution were far more likely to experiment with visiting the novel yellow flower. Hence, it is the relative rather than the absolute reward that seems to be important.

Switching away from a flower species after receiving a lower-than-expected reward may explain apparently risk-averse behaviour which has been recorded in bumblebees and wasps. In experiments where nectar levels were manipulated, these insects preferred floral types which provided a less variable reward over types which provided a more variable reward with the same mean reward per flower (Real 1981; Waddington *et al.* 1981; Real *et al.* 1982; Harder and Real 1987).

Whatever the mechanism involved in switching, having a flexible preference for particular flowers enables bumblebees to adapt their strategy according to changing spatial and temporal patterns of availability of reward in different flower species.

### 8.3 Variation in learning ability

One might expect strong selective pressure on foraging bees to maximize their learning ability, since learning clearly plays a vitally important role in enabling them to forage profitably in a complex and changing floral market. Hence, one would predict that there should be little genetic variation between individuals or colonies of a species for learning ability, for strong directional selection should eliminate such variation. However, there is clear evidence that there is in fact great variation between colonies in their learning ability, at least in *B. terrestris* (Raine *et al.* 2006b). In honeybees, artificial selection can quickly exaggerate these differences, demonstrating a genetic basis (reviewed in Raine *et al.* 2006a). This suggests that there must be a trade-off associated with rapid learning. Perhaps the most likely is that there are disadvantages to learning too much as it interferes with efficient memory retrieval (Chittka 1998). A foraging bumblebee will live for several weeks, during which time it will encounter large numbers of flowers of various types, many of which it will sample. For those that it visits, it might store information on their location, the reward they provided, and on how best to handle that flower type. Thus it might accumulate a lot of information in its long-term memory. The downside to this is that retrieval of information from long-term memory becomes slower and less accurate the more information is stored (Chittka *et al.* 1997; Chittka and Thomson 1997). Hence it may not be adaptive to store all possible information about flowers that have been encountered in long-term memory. Instead, it might be best if bees selectively store only what appears to be the most valuable information,

for example, on how to handle only the most rewarding or the most common flowers; those individuals that 'know too much' might find themselves disadvantaged since they cannot quickly or accurately recall the correct memory for every circumstance.

## 8.4 Coping with deceptive unrewarding flowers

Among the many challenges facing foraging bumblebees is that presented by plant species that produce floral displays that are attractive to bees but offer no reward (so called 'food-deceptive' plants). This is particularly common in orchids. As we have seen, bumblebee can readily learn to detect and avoid unrewarding flowers, so this is a potentially risky strategy on the part of the plant. Many orchids flower early in the year and are probably relying on naïve bees that have just emerged from hibernation for their pollination (a queen may have gained some foraging experience the previous summer, but none of the flowers that she encountered then are available in the spring so she is essentially starting again from scratch). It is likely that, within any population of deceptive orchids, those that flower first are more likely to be pollinated, since bees will not have had time to learn to avoid them (Tremblay 2005). This would place selective pressure for progressively earlier flowering, until balanced by the declining abundance of bees in early spring, and may explain why orchids tend to flower earlier than most other insect-pollinated plant species in temperate climates.

There are conflicting pressures that may lead deceptive flowers to time their flowering phenology to coincide with or swiftly follow that of rewarding flowers, particularly those of similar colour or morphology. Johnson *et al.* (2003) demonstrate that the bumblebee-pollinated deceptive orchid *Anacamptis morio* receives a better pollination service where it flowers alongside the highly rewarding and similarly coloured *Allium schoenoprasum* in Swedish meadows, presumably because the rewarding flower acts as a magnet, drawing foraging bumblebees into the area. Similarly, Gumbert and Kunze (2001) studied pollination of Greek populations of the deceptive orchid *Orchis boryi* and found the plants were more likely to be pollinated if they grew alongside rewarding plants of similar colour, and received few visits when surrounded by rewarding flowers of a markedly different colour. To benefit from the presence of a rewarding flower, deceptive species do not have to flower at the same time. For example, using experiments on foraging *B. terrestris* visiting artificial flowers which were either rewarding or non-rewarding, Internicola *et al.* (2008) showed that bumblebees made more visits to deceptive flowers if they flowered after a rewarding species and were similar to it in morphology.

Deceptive plants necessarily tend to be rare, since if they are frequently encountered than the majority of the bee population will rapidly learn to avoid them. As noted earlier, bees probably tend not to store information in their long-term memory about flowers that they only encounter infrequently since long-term memory becomes inefficient when it contains too much information; it may be this constraint on bee learning that allows deceptive flowers to exist.

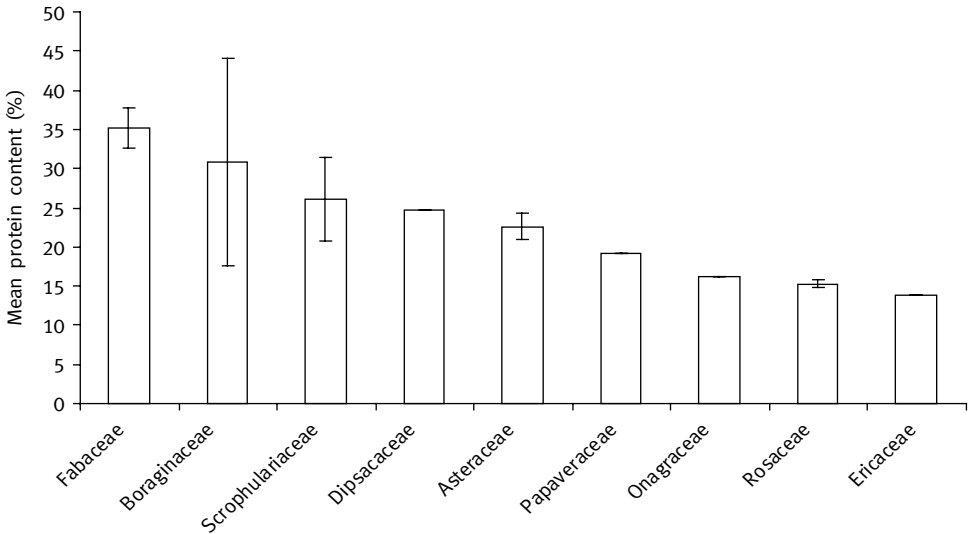
## 8.5 The influence of pollen quality on flower choice

The vast majority of studies of foraging choices made by flower-visiting insects have focussed on the influence of nectar quality or quantity; almost nothing is known about how pollen availability or quality influence floral choices. The reason for this bias is a practical one. It is very easy to quantify nectar volume and sugar concentration using only a microcapillary tube and a hand-held refractometer, and conversely it is rather difficult to manually extract and quantify pollen mass, and it is very expensive and time consuming to measure pollen quality. Within zoophilous plants there is considerable variation in the quality of pollen offered (Roulston *et al.* 2000), but we know little about how this affects pollinator foraging behaviour. That there ought to be strong selection pressure on bees to choose high-quality pollen is demonstrated by the studies of Génissel *et al.* (2002) and Tasei and Aupinel (2008) using *B. terrestris* microcolonies (small colonies created from brood and workers). They found that growth and reproduction was very strongly influenced by the species of pollen with which they were fed; for example, colonies fed on *Taraxacum* pollen failed to rear any offspring. A number of studies suggest that in natural situations bumblebees are choosy with regard to pollen, and that they tend to collect pollen from a narrower range of plants than those from which they collect nectar (Goulson *et al.* 2005, 2008a,b). It also seems that species vary greatly in their niche breadth with regard to pollen collection, with some species such as *B. terrestris* and *B. pratorum* having a broad diet, and others such as *B. hortorum*, *B. subterraneus* and *B. humilis* having narrow diets consisting largely of pollen from Fabaceae (Rasmont and Mersch 1988; Goulson *et al.* 2005, 2008b; Kleijn and Raemakers 2008). Notably, many plant species that are both abundant and frequently visited by bumblebees (such as many Asteraceae and Lamiaceae) are rarely used as sources of pollen, even though the pollen appears to be abundant (Table 8.1). For example, bees

**Table 8.1** Percentage visitation by bumblebees (all species combined) to the main plant families exploited by bumblebees in the United Kingdom.

Plant family	Pollen (%)	Nectar (%)
Asteraceae	2.2	21.9
Boraginaceae	4.1	21.4
Ericaceae	13.5	3.1
Fabaceae	61.6	36.8
Lamiaceae	2.5	3.5
Rosaceae	4.1	1.5
Scrophulariaceae	5.8	3.2

Based on >3,000 visitation records from across the United Kingdom (from Goulson *et al.* 2005). Note that Asteraceae are favoured by nectar-collecting bees but little visited for pollen, while Fabaceae are of great importance as a source of nectar and overwhelmingly favoured as a source of pollen.

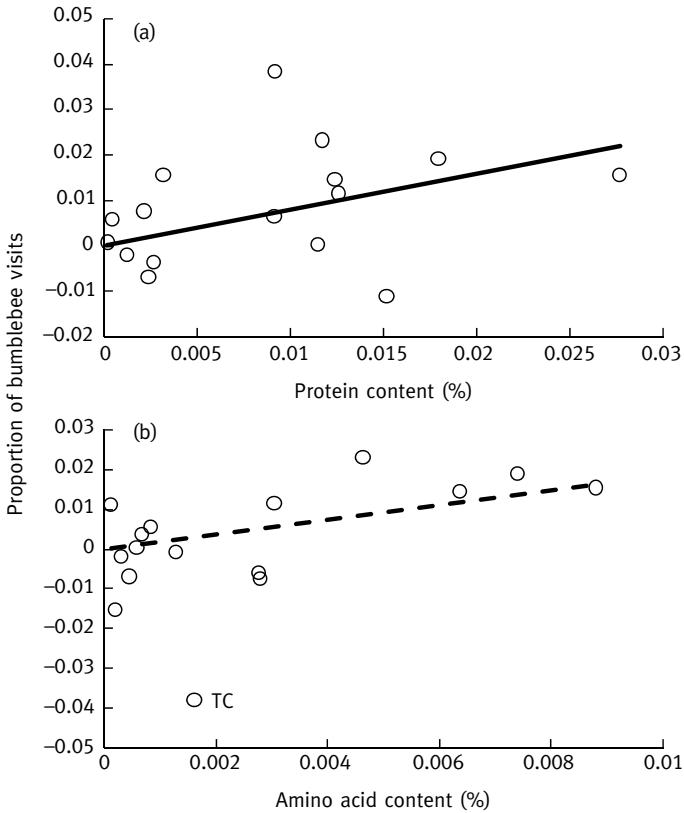


**Figure 8.5** Protein content of pollens collected from plants frequently visited by bumblebees for nectar or pollen. From Hanley *et al.* (2008).

**Table 8.2** Mean percentage amino acid composition of proteins in pollen of Fabaceae versus Asteraceae (Hanley *et al.* 2008)

	Asteraceae	Fabaceae
Aspartic acid + Asparagine	9	11
<b>Threonine</b>	<b>4</b>	<b>5</b>
Serine	5	7
Glutamic acid + Glutamine	9	10
Glycine	7	8
Alanine	7	8
<b>Valine</b>	<b>5</b>	<b>7</b>
<b>Methionine</b>	<b>2</b>	<b>2</b>
<b>Isoleucine</b>	<b>4</b>	<b>5</b>
<b>Leucine</b>	<b>6</b>	<b>10</b>
Tyrosine	2	3
<b>Phenylalanine</b>	<b>3</b>	<b>4</b>
Histidine	3	2
<b>Lysine</b>	<b>6</b>	<b>7</b>
Arginine	3	4
Proline	18	5

Essential amino acids are shown in boldface. Note the generally higher levels of essential amino acids in Fabaceae compared to Asteraceae.



**Figure 8.6** The relationships between (a) the proportion of bumblebee visits and protein content, and (b) the proportion of visits and the essential amino acid content. All data arcsine transformed. From Hanley *et al.* (2008).

collecting nectar on *Cirsium* and *Centaurea* often become covered in pollen but they appear reluctant to groom it into their corbiculae.

Analysis of pollen protein and amino acid composition provides a clear explanation as to why Fabaceae pollen is favoured by many bumblebee species; it is both richer in protein and the protein present contains a higher proportion of essential amino acids, when compared to less favoured families such as the Asteraceae (Fig. 8.5 and Table 8.2; Hanley *et al.* 2008). There is an ongoing debate as to whether bees are able to directly assess pollen protein content and so choose more rewarding flowers (see Roulston *et al.* 2000; Minkley and Roulston 2006). Although there is some evidence suggesting that direct assessment does occur (Rasheed and Harder 1997; Robertson *et al.* 1999), the mechanism remains unclear.

Protein-rich pollen is one way in which plants can promote the fidelity and reliability of bumblebees; Hanley *et al.* (2008) demonstrate that protein content of pollen

and bumblebee visitation rates are positively correlated (Fig. 8.6). Whether pollen protein levels are influenced by selective pressures based on bee foraging choices, or whether protein content of pollen is driven by other factors (such as the amount of protein needed to grow the pollen tube) has not yet been satisfactorily resolved. It is perhaps worth noting that those bumblebee species that appear to be particularly specialized in collecting pollen from Fabaceae tend to have long tongues (Fig. 13.5) and visit deep-flowered Fabaceae such as red clover (*Trifolium repens*) and tufted vetch (*V. cracca*). Why should tongue length correlate with pollen diet breadth, when the tongue is not used for collecting pollen? The answer may be that deep flowers tend to have long styles and hence their pollen grains need to produce long pollen tubes, which presumably requires them to have more protein. Hence deep flowers might be expected, on average, to have higher quality pollen. An alternative is that deep flowers exclude most insect visitors, but can expect higher fidelity from those insects that do visit them, so perhaps they can afford to provide higher quality pollen to reward their visitors and further promote fidelity.

*This page intentionally left blank*

# 9

---

## Intraspecific Floral Choices

Within plant species, individual flowers exhibit considerable variation in the rate at which they produce rewards. There can also be substantial variation between flowers on the same plant. This variation may be due to micro-environmental influences, genetic variation, age of the plant or age of the flower. If foragers can distinguish between more and less rewarding flowers of their preferred species, then they can enhance their foraging success. The time it takes for a bumblebee forager to handle a flower varies greatly according to floral morphology, from less than 1 s for simple flowers to up to 10 s for complex flowers (e.g. Heinrich 1979b; Pyke 1979; Hodges 1981; Best and Bierzychudek 1982; Osborne 1994; Cresswell 1999). If the flower contains little or no reward then this time is wasted, so there is strong selection pressure on bees to evolve means of choosing the more rewarding flowers.

There is abundant evidence that bumblebees use a variety of cues to indicate which flowers are most likely to provide a high reward, and thus to improve their foraging efficiency.

### 9.1 Direct detection of rewards

Both bumblebees and honeybees are often seen to hover in front of a flower, sometimes briefly touching the corolla, and then depart without probing into the flower structure. These rejected flowers contain, on average, less nectar than flowers which are probed (Heinrich 1979a; Corbet *et al.* 1984; Wetherwax 1986; Kato 1988; Duffield *et al.* 1993). Several mechanisms may be in operation. Where the flower structure is open and the anthers are clearly visible, bumblebees are able to visually assess pollen content of open flowers (Zimmerman 1982; Cresswell and Robertson 1994). It has been suggested that they may be able to determine the nectar content of some flower species in the same way (Thorpe *et al.* 1975, 1976; Kevan 1976), although in most flowers the nectar is not directly visible from outside the flower. It has also been proposed that bees may be able to assess nectar volumes from the scent of the nectar itself or from the scent of fermentation products from yeasts in the nectar (Crane 1975; Heinrich 1979a; Williams *et al.* 1981). They could plausibly detect nectar volumes from humidity gradients surrounding the flower (Corbet *et al.* 1979), although evaporation from the generally tiny nectar surface is likely to be obscured by moisture transpiring from the surrounding floral and leaf surfaces. Apart from visual detection of pollen availability, no other mechanisms of direct detection of floral rewards have been demonstrated.



## 9.2 Flower size

Where direct assessment of the reward contained within a flower is not possible, bees may use other cues to indicate which flowers are most rewarding. Bumblebees generally prefer to visit the largest flowers available (usually measured as corolla width) (e.g. Galen and Newport 1987; Galen 1989; Cresswell and Galen 1991; Eckhart 1991; Cresswell and Galen 1991; Ohara and Higashi 1994; Shykoff *et al.* 1997), although Cresswell and Robertson (1994) found no relationship between size and visitation rate. Higher visitation rates may simply be because large flowers are more apparent, but there is some evidence that flower size is correlated with the production of pollen or nectar, so that selection of large flowers may be reinforced by learning (Teuber and Barnes 1979; Brink and Wet 1980; Stanton and Preston 1988; Cresswell and Galen 1991; Duffield *et al.* 1993; Gomez *et al.* 2008).

## 9.3 Flower age

Bees can learn to be selective with regard to the age of the flowers that they choose to visit. Rates of nectar production may vary with flower age (Boetius 1948; Manning 1956), but there is no general pattern to changes in nectar production with age. In some plants, nectar production increases with flower age (Pyke 1978b; Brink and Wet 1980; Corbet and Willmer 1980; Best and Bierzychudek 1982; Robertson and Wyatt 1990), while in others nectar production is independent of flower age (Bertsch 1983; Pleasants 1983; Marden 1984; Zimmerman and Pyke 1986). Perhaps most frequently, nectar production declines over time (Voss *et al.* 1980) or reaches an early peak and then declines (Carpenter 1976; Bond and Brown 1979; Frost and Frost 1981; Bertin 1982; Pleasants and Chaplin 1983; Southwick and Southwick 1983; Cruzan *et al.* 1988). It has been argued that this is a sensible strategy for bee-pollinated plants as bees show patch fidelity and will continue to visit a formerly rewarding patch for some time after it ceases to provide a reward; hence, a plant could save nectar by ceasing to produce it when its flowers are nearing the end of their life without necessarily reducing insect visitation (Makino and Sakai 2007).

It has long been known that bumblebees, honeybees, solitary bees, hoverflies and butterflies are able to discriminate between age classes of some flowers using visual cues, and so preferentially select the more rewarding flowers (Lex 1954; Müller 1883; Ludwig 1885, 1887; Kugler 1936, 1950; Lex 1954; Jones and Buchmann 1974; Kevan 1978; Thomson *et al.* 1982; Weiss 1995a). Discrimination among flowers according to their age may be facilitated by clear visual cues given by the plant itself, particularly by colour changes which variously occur in part or all of the flower (Schaal and Leverich 1980; Kevan 1983; Gori 1983, 1989; Delph and Lively 1989; Weiss 1995a; Nuttman and Willmer 2003). Such changes have been described in 78 families of plant so far (reviewed in Weiss 1995b; Weiss and Lamont 1997). For example, flowers of *Pulmonaria* spp. change from red to blue, enabling bumblebees and flower bees (*Anthophora pilipes*) to select the more

rewarding red flowers (Müller 1883; Oberrath *et al.* 1995). These age-dependent preferences can be flexible; honeybees select 3-day-old capitula of *Carduus acanthoides* in the early morning, and switch to 2-day-old capitula later in the day. This accurately targets the time of maximum nectar production in capitula which is from midway through their second day until early on their third (Giurfa and Núñez 1992a). Although these colour changes are often triggered by pollination and so benefit the plant by directing pollinators to flowers which are as yet unpollinated (Gori 1983; Weiss 1995b), this is not always so. It is unclear why unpollinated older flowers of some species give clear signals that they are producing little reward (Oberrath *et al.* 1995).

## 9.4 Flower sex

The reproductive success of male flowers (in monoecious and dioecious species) or male phase flowers (in dichogamous species where male and female functions are temporally separated within the same flower) is likely to be more variable than that of female flowers, since a male flower could in theory fertilize numerous female flowers. Thus we may expect male flowers to invest more time in attracting pollinators. However, if males produce more nectar than females and the sexes can readily be distinguished then we might expect foragers to prefer to visit male flowers, which would clearly be counterproductive from the plants' perspective. Higher levels of nectar production in male flowers coupled with pollinator preferences for male flowers have been found in a number of systems (Bell *et al.* 1984; Devlin and Stephenson 1985; Delph and Lively 1992; Shykoff and Bucheli 1995). For example, in viper's bugloss (*Echium vulgare*), the protandrous flowers produce more nectar and receive higher rates of visitation during their male phase than during their female phase (Klinkhamer and de Jong 1990). However, male flowers are not always more rewarding (reviewed in Willson and Ågren 1989). For example in *Digitalis purpurea*, nectar rewards are higher during the female phase: in this species female phase flowers are at the bottom of vertical racemes and bumblebees forage upwards, so that this arrangement prevents selfing (Best and Bierzychudek 1982).

Foragers differ in their requirements; some gather nectar, some pollen, while others may gather both. Those which are collecting pollen clearly benefit from avoiding female flowers, and appear to be able to do so. For example, honeybees which are collecting nectar prefer inflorescences of *Lavandula stoechas* with a high proportion of female flowers (which produce more nectar than male flowers), while individuals which are collecting both nectar and pollen choose inflorescences with a greater proportion of male flowers (Gonzalez *et al.* 1995). Similar preferences for pollen or nectar producing flowers according to requirements have been recorded elsewhere, in bumblebees (Alexander 1990; Cresswell and Robertson 1994), honeybees (Kay 1982; Greco *et al.* 1996) and solitary bees (Eckhart 1991). Clearly, bees are able to distinguish between sexes or sexual phases of the flowers of at least some plant species, and are able to learn which provide the greatest reward.

From the point of view of the plant, forager preferences for flowers of a particular sex clearly threaten efficient pollination; if, for example, male flowers invest more in attracting visitors so that female flowers are ignored then pollination will be poor. Hence neither sex will benefit if sexual differences are too marked. Similarly, we might predict that monoecious and dioecious plant species should not evolve to offer pollen as a reward to pollinators as many plants do. As discussed in Chapter 3, individual worker bees tend to specialize in either collecting pollen or nectar, and a pollen specialist would be expected to avoid female flowers and hence provide no pollination service.

## 9.5 Flower symmetry

All flowers exhibit either radial or bilateral symmetry, although this symmetry is never perfect if measured carefully enough (Neal *et al.* 1998). Recently, it has become clear that insects may use floral symmetry in floral recognition and in discrimination between more or less rewarding flowers. Both honeybees and bumblebees show an innate preference for symmetrical shapes, which can be reinforced by learning (Giurfa *et al.* 1996; Rodriguez *et al.* 2004). Symmetrical artificial flowers placed in the field attracted more foraging Hymenoptera, Diptera and Coleoptera than less symmetrical flowers (Møller and Sorci 1998). There is a fascinating parallel between the use of fluctuating asymmetry (small random departures from perfect bilateral symmetry) as an indicator of mate quality in animals (reviews in Møller 1993; Møller and Pomiankowski 1993; Watson and Thornhill 1994; Markow 1995; Møller and Thornhill 1998) and these preference by pollinators which also exert sexual selection pressure, but in this situation upon plants. So why might foragers prefer symmetrical flowers? In mate choice in animals, symmetry is thought to be an indicator of genetic quality, so it makes sense to discriminate. But bees are not mating with flowers, just extracting rewards from them. The answer seems to be that, at least in some systems where pollinators exhibit a preference for symmetrical flowers, floral symmetry is a good indicator of floral reward (Møller 1995; Møller and Eriksson 1995). For example, foraging *B. hortorum* show a strong preference for unblemished (and hence more symmetrical) flowers of *Tropaeolum majus*, and such flowers contained on average 48% more nectar (Goulson *et al.* 2007). Blemishes presumably accumulate over time and hence are a useful indicator of flower age, and as discussed in Section 10.3, nectar production often declines with flower age. Handling times of bumblebees have also been found to be lower on symmetrical artificial flowers than on asymmetrical flowers (West and Lavery 1998). Thus, there are at least two potential benefits of preferentially visiting symmetrical flowers. If these preferences are widespread, then they should exert strong stabilizing selection upon plants for floral symmetry.

However, it is worth noting that not all studies have found pollinator preferences for symmetrical flowers or a positive relationship between floral symmetry and reward, and more studies are needed before any firm conclusion can be reached (Møller and Eriksson 1995). Studies of fluctuating asymmetry in animals have often suffered from a

range of methodological flaws which researchers of floral symmetry would do well to learn from (reviews in Palmer 1994, 1996; Markow 1995).

## 9.6 Floral scent

Most work on discrimination among flowers by pollinators has concentrated on visual cues such as size, shape or colour, since these are easily recorded. However, many pollinators undoubtedly also use scents produced by flowers as an important source of sensory information, particularly at close range (reviewed in Von Frisch 1967; Williams 1982; Waddington 1983b). The use of modern analytical techniques has revealed that many flowers exhibit intraspecific variation in floral scent quality or quantity (Tollsten and Bergstrom 1993; Knudsen 1994; Olesen and Knudsen 1994; Tollsten and Ovstedal 1994). To my knowledge, only two studies have tried to examine whether pollinators discriminate among flowers of the same species using scent. Pellmyr (1986) found that floral scent variation in *Cimicifuga simplex* determined whether bees or butterflies were attracted, while Galen and Newport (1988) found that flowers of *Polemonium viscosum* produce either 'skunky' scented flowers which are preferred by flies, or sweet scented flowers which are preferred by bumblebees. It is possible, perhaps likely, that floral scent variation is far more widespread than is currently appreciated, but that it has been largely overlooked due to our own particular sensory biases.

## 9.7 Thermal rewards

As discussed in Chapter 2, one of the challenges facing a foraging bee is to maintain an adequate body temperature for flight. The very act of flying generates lots of heat, but while sitting on flowers, particularly large inflorescences from which it may take a long time to extract the rewards, there is a risk that the body temperature of the insect will fall below  $\sim 30^{\circ}\text{C}$ ; below this temperature the bee will be unable to take off again. This can be prevented by generating heat through shivering or other metabolic means, but this is energetically costly. This cost may be reduced if bees preferentially forage on warmer flowers, and it appears that they are capable of doing so. Dyer *et al.* (2006) found that foraging *B. terrestris* prefer warmer flowers, and that they can learn to associate colour with warmth and so selectively visit the warmest flowers. One might argue that bumblebees are large and well-insulated insects, that they generate most of their heat internally, and that they typically spend very little time on each flower so that floral temperature ought to be of little importance. However, foraging bees spend a large proportion of their time on flowers because they visit many hundreds in a foraging bout. Also, the nectar they imbibe will be the same temperature as the flower, so by choosing warm flowers the bees are also choosing a warm drink, which may be very welcome on a cold day.

Although this work demonstrates that bees can discriminate upon the basis of floral temperature, it remains to be established how important temperature is compared to

other factors. Whitney *et al.* (2008) demonstrated that floral temperature and reward are processed independently, and that foraging *B. terrestris* preferred flowers with a higher sucrose concentration even if the more rewarding flowers were several degrees cooler, suggesting that floral rewards are more important than thermal rewards (although of course this might not be true at lower ambient temperatures).

## 9.8 Motivation and choosiness

It is clear that bumblebees can use a broad range of cues to indicate which are the more rewarding flowers of those available. Interestingly, their choosiness can also vary according to levels of energy reserves in the colony. Cartar and Dill (1990) experimentally manipulated the reserves of nectar stored in honey pots within nests, either by draining the pots or filling them with sucrose solution. In colonies with depleted stores of nectar, bees tended to be less selective; they visited smaller inflorescences, they probed flowers at a higher rate and they tended to fly between inflorescences rather than walk. The net result was that the rate at which they gathered nectar increased. So why do bumblebees not always behave in this way? Gathering rewards more quickly should enable the colony to grow faster and ultimately produce more reproductives. Presumably there is a cost to this enhanced level of activity. The lifespan of honeybees appears to be limited by energy expenditure, so that the more active an individual is, the shorter its life expectancy (Wolf and Schmid-Hempel 1989). Similarly, in the bumblebee *B. terrestris*, more active individuals exhibit a weaker encapsulation response (the defence response to parasitoid eggs) (König and Schmid-Hempel 1995). In bumblebees, the foraging behaviour that results in the higher rate of reward also entails higher activity levels (more flight, and more rapid probing). Cartar (1992b) found that bumblebees with increased natural wing wear (which presumably accumulates during flight) had elevated levels of mortality, and also that artificial wing-clipping increased mortality. Surprisingly, realistic levels of artificial wing damage do not appear to increase the metabolic cost of flight in bumblebees, or to have significant influence on their flight performance when foraging, but wing wear may make them more susceptible to predation (Hedenström *et al.* 2001; Haas and Cartar 2008). Thus, the cost of gaining high rewards may be a shortened life expectancy; when colony reserves are low, workers may sacrifice longevity for short-term replenishment of nectar stores.

# 10

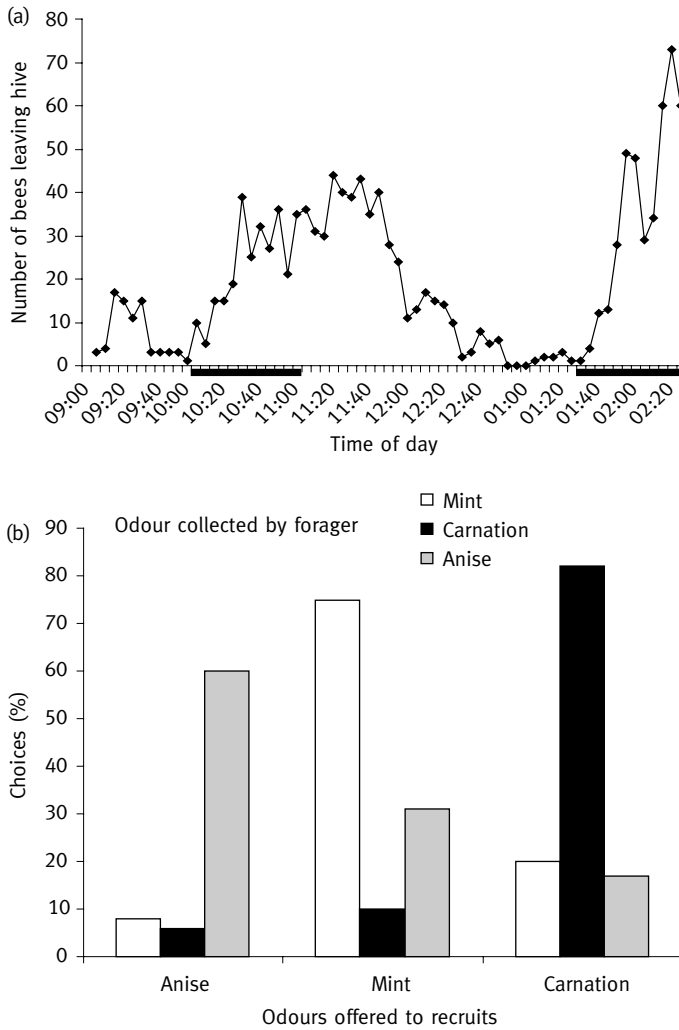
---

## Foraging Cues Gained from Other Bees

### 10.1 Communication in the nest

The waggle dance of the honey bee has been frequently described and much studied, and is one of the most complex systems known in insect communication; indeed, far more information is conveyed than can be managed by most vertebrates. In contrast, it has long been assumed that foraging in bumblebees is essentially a solitary endeavour—that workers do not communicate with each other about good sources of forage, so that each individual has to learn for itself which flowers provide reward. Indeed, it has been known for many years that bumblebees (of a range of species) are unable to recruit nestmates to specific places (Jacobs-Jessen 1959; Esch 1967; von Frisch 1967; Kerr 1969). Nevertheless, it has become apparent that bumblebee foragers do communicate, and that recruitment does occur, but not to specific locations. In an elegantly simple experiment, Dornhaus and Chittka (1999, 2001) demonstrated that, on their return to the nest, successful foragers of *B. terrestris* stimulate other workers to forage, and communicate to them the scent of the food source that they have located (Fig. 10.1). The returning forager runs around on the surface of the nest in an excited manner, frequently bumping into nest mates and buzzing her wings (very similar behaviour occurs in some stingless bees). She also releases a pheromone from tergites 5–7 (Dornhaus *et al.* 2003). The combination of pheromone and behavioural signalling stimulates workers to leave the nest and search for the source of the floral scent. Workers in the nest also respond differentially according to the quality (sugar content) of the incoming nectar, and are more likely to go foraging themselves when the incoming nectar is sugar-rich (Dornhaus and Chittka 2005).

Both the behaviour of the returning forager and the response of workers in the nest are variable, depending on nest resources. In *B. terrestris*, when the colony nectar pots are full, the returning successful forager performs fewer runs on the nest surface (Dornhaus and Chittka 2005), and fewer workers respond (Molet *et al.* 2008). Similarly, Pelletier and McNeil (2004) found that *B. impatiens* colonies which were given supplementary food foraged less. This is intriguing. It suggests that there are times when colonies may have enough food, and that at these times workers choose not to forage for more even if a sister has found a good supply, presumably because foraging is a dangerous or expensive activity (see also Section 9.8). To put this in another way, the decision as to whether to



**Figure 10.1** Recruitment of *B. terrestris* foragers to a newly discovered food source. (a) The number of bees leaving the nest to forage increases when a successful forager returns. The number leaving increases dramatically when an incoming forager returns with food (horizontal black bars). (b) The newly recruited foragers tend to choose a food source with the same odour as that brought back by the successful forager. From Dornhaus and Chittka (1999).

forage is presumably based on a trade off between the rewards to be gained by foraging and the costs, in terms of reduced life expectancy. The fact that, when colony reserves are great, bees choose not to respond to the exhortations of a returning forager suggests that the value of gathering further rewards are devalued in these circumstances (the cost of foraging exceeds the benefit). In turn, this argues that there is a non-linear

relationship between colony food reserves and colony reproductive success. This begs the question as to what other factors limit colony growth? Perhaps the simplest explanation may be that at times of food superabundance the reproductive capacity of the queen is saturated so that gathering further food does not translate into further colony growth. Alternatively, it may be that at these times nest growth is limited by pollen supply, and hence that adding further nectar to the reserves is of little value.

The communication system of bumblebees clearly is less complex than that of honey bees, for the new recruits do not appear to be given any positional information as to the location of the food source. It appears that there is a pheromone signal released by returning forager consisting of the terpenes eucalyptol, ocimene and farnesol (Granero *et al.* 2005), and these compounds have been shown to stimulate foragers to leave the nest (Dornhaus *et al.* 2003; Granero *et al.* 2005). Granero *et al.* (2005) hypothesize that the evolutionary origins of the bumblebee alert system and the honey bee waggle dance are separate since honey bees use terpenes primarily to mark food sources, rather than alert foragers.

Why do bumblebees not communicate positional information? Dornhaus and Chittka (1999) argue that conveying the location of food sources may be less important to bumblebees than to honey bees; honey bees evolved in tropical ecosystems where they rely heavily on flowering trees, a highly clumped resource which may be several kilometres from the nest and so would be difficult to locate. In the temperate habitats in which bumblebees probably evolved, the herbaceous plants which are their main food source are generally more scattered. There is nothing to be gained in recruiting more workers to a specific small patch that one bee can adequately exploit single-handedly. However, communication as to the types of flowers that are providing rewards will allow the colony to rapidly recruit to feeding on a rewarding plant species when it comes to flower, and so keep track of the changing seasonal availability of different species (aided by the minor behaviour of individual foragers discussed in Chapter 8). A second possibility is that bumblebees forage over shorter distances than do honey bees—perhaps as a result of their smaller colony size—thus rendering communication as to the precise location of forage less important (if forage is near the nest, it will not take long for a forager to find it even without any clues as to its location). Alternatively, it has been hypothesized that the honey bee's dance language evolved not in the context of foraging but as a means to communicate the location of new nest sites. Since honey bees need to guide an entire swarm (including the valuable queen) to a new site, they need to accurately convey the location (Beekman and Bin Lew 2008). The annual life cycle of bumblebees renders this unnecessary.

There is a cost to conveying location information. Honey bee recruits can take over an hour to decide where to forage when presented with just two returned foragers advertising different locations. They also take a long time to find the food source that is being advertised, for the location information is not precise (Wenner and Wells 1990). It may be that, in bumblebees, the costs of conveying this information outweigh any gains.



## 10.2 Visual responses to other bees on flowers

Bees may use the presence of other bees on a flower as a clue as to whether it is likely to be rewarding. In cage situations, Kawaguchi *et al.* (2006) found that naïve foraging *B. terrestris* were more likely to land on flowers to which a dead conspecific had been pinned. This response remained (although it was weaker) if the dead bee was wrapped in plastic, which the authors argue suggests that this is both a visual and olfactory response. However, it may simply be that a bee wrapped in plastic looks less like a bee, reducing the strength of a purely visual response.

However they detect it, presumably the bees are using the presence of a conspecific as a likely indication that the flower type is worth investigating further. The response of flower-searching bumblebees to the presence of conspecifics on flowers is seemingly context-dependent. In field situations, Kawaguchi *et al.* (2007) found that when a nectar-foraging *Bombus diversus* encounters a familiar inflorescence, the probability of landing is reduced if a conspecific is already present. However, if the inflorescence is of a type that the bee has not encountered before, the presence of a conspecific *increases* the probability of landing. This switch in behaviour makes sense; if a bee has experience of a flower type and knows it to be rewarding, then avoiding inflorescences that are already being exploited by another bee and preferentially landing on those with no bee is likely to reduce competition for floral resources. Conversely if a bee is among unfamiliar flowers, many of which may prove to have no reward or be poorly matched to its morphology, then using the behaviour of conspecifics as a clue to which flowers to explore is a sensible strategy.

The strategy of attraction to inflorescences of a novel plant species upon which a conspecific is foraging is only likely to be worthwhile if the inflorescence is large. If florets are presented individually, then there would be nowhere for the second bee to land, and in any case the resources in the floret are likely to have been extracted by the first bee. Amazingly, it seems that bees can learn from simply observing other bees visiting flowers, even when they are themselves not able to forage at the time. Worden and Papaj (2005) demonstrate that *B. impatiens* kept in an observation box in which there were no flowers that were able to learn from observing experienced conspecifics foraging in an adjacent arena, and adjust their subsequent foraging behaviour accordingly. Although this has not been confirmed in a natural situation, it seems probable that foraging bees do take cues from observations of what conspecifics are doing even when they are not able to simply land on the same flower on which the conspecific is feeding.

## 10.3 Scent marking of flowers

It has long been observed that bumblebees (*Bombus* spp.) can distinguish between more and less rewarding flowers of the same plant species without actually sampling the reward available. Typically, the bee hovers briefly next to a flower with its antennae extended and nearly touching the corolla, and then either proceeds to land and



**Figure 10.2** A worker of *B. hortorum* inspects a flower of *Echium vulgare*. The bee hovers close to the flower with her antennae extended, almost touching the flower corolla. She then either lands and probes for nectar or rejects the flower. Rejected flowers have less nectar than those that are accepted. The cue used to discriminate between flowers is a scent mark deposited by the feet of bees that visited the flower previously; flowers that have been recently emptied have a stronger scent mark than those that have not been visited for a long while. Photograph by Ben Darvill, with permission.

attempt to feed, or instead rejects the flower without landing and moves on (Fig. 10.2). In some circumstances, the bee may be directly assessing the reward level, or perhaps examining correlates of reward such as flower size and symmetry (Brink and Wet 1980; Stanton and Preston 1988; Cresswell and Galen 1991; Møller 1995; Møller and Eriksson 1995). However, there is now strong evidence that perhaps the most important cue used by bees to decide whether to probe or reject a flower are chemical clues left by bees on previous visits (Cameron 1981; Marden 1984; Kato 1988; Schmitt and Bertsch 1990; Goulson *et al.* 1998a; Stout *et al.* 1998).

Bumblebees, honeybees, sweat bees (Halictidae), carpenter bees (*Xylocopa* sp.), stingless bees (*Trigona* sp.) and flower bees (*Anthophora* sp.) have all been found to leave repellent marks on flowers that they visit and conspecifics are able to use these to discriminate between visited and unvisited flowers (Núñez 1967; Frankie and Vinson 1977; Cameron 1981; Wetherwax 1986; Giurfa and Núñez 1992b; Giurfa 1993; Giurfa *et al.* 1994; Goulson *et al.* 1998a, 2001; Stout *et al.* 1998; Williams 1998; Gilbert *et al.* 2001; Gawleta *et al.* 2005; Yokoi and Fujisaki 2007; Yokoi *et al.* 2007). This behaviour presumably increases foraging efficiency by reducing the time spent landing on and handling flowers that have recently been emptied by another bee, and thus contain little or no reward (Kato 1988; Schmitt and Bertsch 1990; Goulson *et al.* 1998a).

In honeybees, the chemical cue which causes repellency is thought to be secreted from the mandibular glands (Vallet *et al.*, 1991), while Nasanov secretions induce an attractant effect (von Frisch 1923; Free and Williams 1972; Free *et al.* 1982a,b). A Dufour's

gland secretion is probably responsible for carpenter bees (*Xylocopa virginica texana*, Anthophoridae) avoiding recently visited flowers (Frankie and Vinson, 1977). In bumblebees, the scent marks appear to consist of a chemical cue found on the tarsi, and are probably produced at least in part by the tarsal glands (Schmitt *et al.* 1991). The tarsi of queen, worker and male bumblebees all contain a substantial secretory gland described in detail by Pouvreau (1991). However, these compounds also occur in considerable quantities elsewhere on the body, and may be the result of a blend of secretions from several different glands (Goulson *et al.* 2000). For *B. terrestris*, the components of both tarsal glands and the deposited scent marks have been identified and are similar (Schmitt 1990; Schmitt *et al.* 1991). Tarsal glands produce primarily straight chain alkanes and alkenes of between 21 and 29 carbon atoms, with compounds with odd numbers of carbons predominating. The alkenes are thought to be mostly (*Z*)-9 and (*Z*)-11 configurations (Schmitt 1990; Schmitt *et al.* 1991). These compounds are common cuticular hydrocarbons found in a broad range of insects, not just bees, and they probably have the primary function of reducing water loss (Lockey 1980; Blum 1981, 1987).

Although broadly similar compounds are found on the cuticles of diverse insects, there are notable differences between species in the precise composition, even among congeners. Comparisons of the hydrocarbons on the tarsi of three sympatric European *Bombus* species, *B. lapidarius*, *B. pascuorum* and *B. terrestris*, have revealed clear differences (Goulson *et al.* 2000). For example, while tricosane was found in significant quantities in all three species, tricosene was only found in abundance in *B. lapidarius*. Pentacosenes were major constituents of the extracts of *B. lapidarius* and *B. pascuorum*, but were virtually absent in *B. terrestris* (Table 10.1). Differences between species have been described previously in the composition of labial gland secretions of male bumblebees (where they presumably help in mate recognition) (Bergstrom *et al.* 1981) and also in Dufour's gland secretions of bumblebees (Tengö *et al.* 1991). Oldham *et al.* (1994) analysed cuticular hydrocarbons in *B. lapidarius*, *B. pascuorum* and *B. terrestris*, and also compared *B. terrestris terrestris* from mainland Europe with the UK race, *B. terrestris audax*. Although they did not examine tarsal glands, they concluded that the mixture of cuticular hydrocarbons was constant across different body parts, but that the species and the two *B. terrestris* subspecies differed in the relative quantities of different compounds. The composition of tarsal extracts described by Goulson *et al.* (2000) closely follows that for cuticular hydrocarbons found over the rest of the body (Oldham *et al.* 1994). It seems likely that, during grooming and movement, these compounds are distributed across the surface of the body and limbs. During foraging many parts of the bumblebee body may come into contact with the corolla depending on the shape of the flower, not just the tarsi. Thus it seems probable that scent marks are not exclusively placed by the feet.

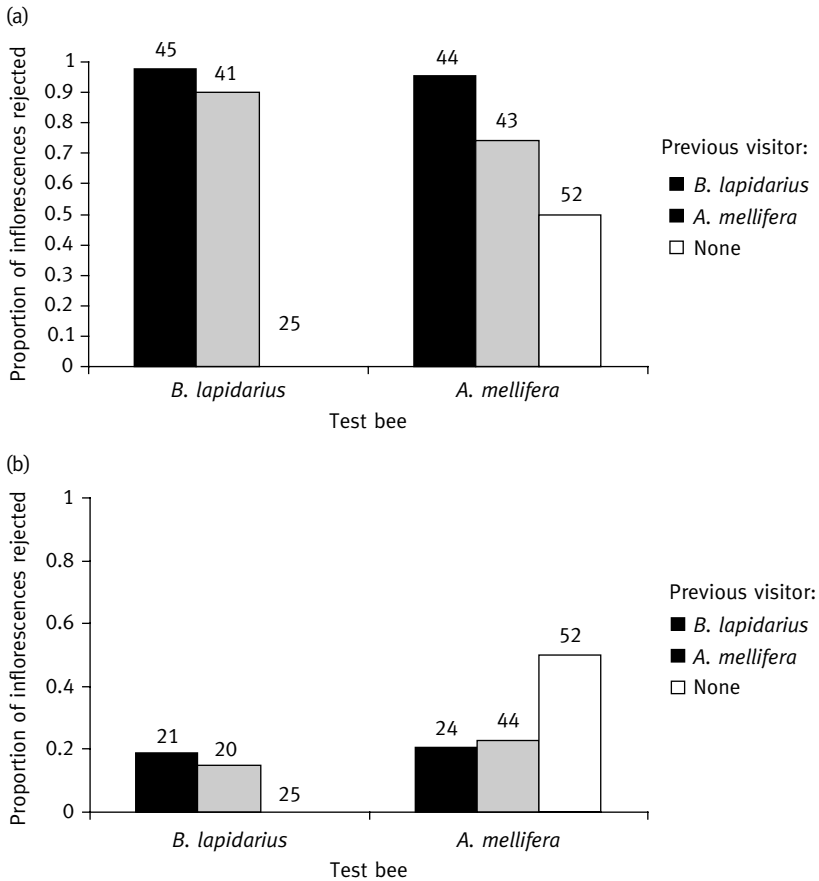
In bumblebees, despite differences in the composition of scent mark deposited by different species, it appears that marks deposited by other species are readily detected. For example, interspecific tests between *B. terrestris*, *B. hortorum*, *B. pascuorum* and *B. pratorum* reveal that each is repelled by scent marks deposited by the other species

**Table 10.1** Amounts of each compounds present in tarsal washes (ng/tarsus  $\pm$  SE) of three bumblebee species, based on four replicate samples per species.

Compound	MW	<i>B. terrestris</i>	<i>B. pascuorum</i>	<i>B. lapidarius</i>
Heneicosane	296	12.5 $\pm$ 2.41	—	+
Tricosenes	322	9.38 $\pm$ 6.63	5.90 $\pm$ 0.95	70.5 $\pm$ 15.1
Tricosane	324	110 $\pm$ 13.4	99.3 $\pm$ 1.21	94.8 $\pm$ 8.63
Methyl-tricosane	324	—	—	+
Tetracosenes	336	—	12.5 $\pm$ 6.03	+
Tetracosane	338	—	+	+
Pentacosenes	350	+	174 $\pm$ 12.3	155 $\pm$ 11.5
Pentacosane	352	114 $\pm$ 17.9	106 $\pm$ 5.98	170 $\pm$ 6.06
Heptacosenes	378	—	64.5 $\pm$ 13.2	+
Heptacosane	380	174.5 $\pm$ 28.6	35.5 $\pm$ 5.60	+
Nonacosenes	406	102.9 $\pm$ 26.1	+	+
Al		514 $\pm$ 68.7	491 $\pm$ 30.5	490 $\pm$ 32.4

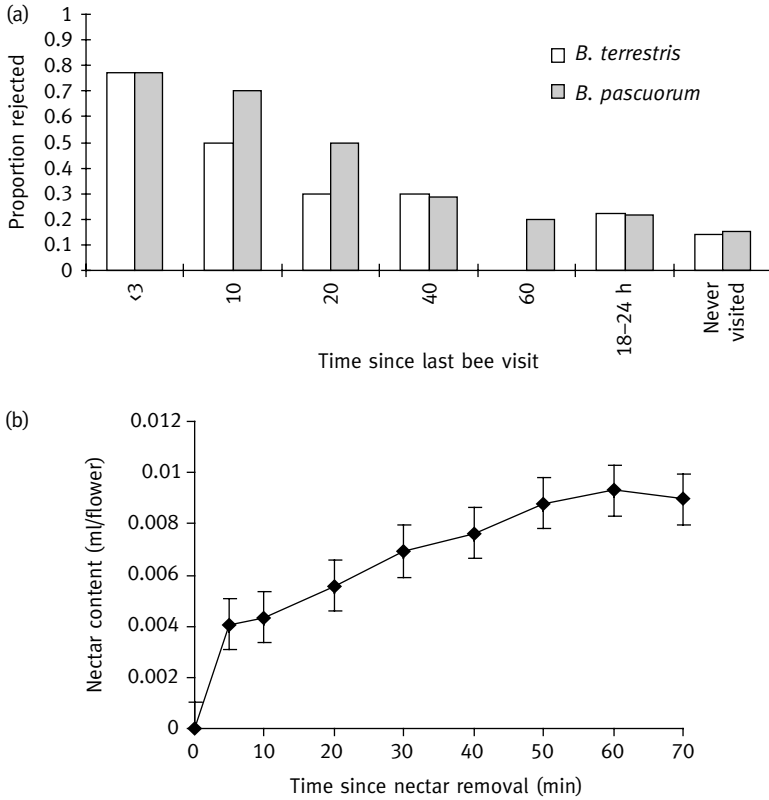
MW, molecular weight; +, trace. Samples were prepared by cutting the tarsi and approximately half of the tibia from five individuals of one species and combining them in 0.5 ml of pentane. The samples were analysed with a VG-Analytical 70-250 SE mass spectrometer coupled to a Hewlett Packard 5790 gas chromatograph. The column was a BP1 of dimension 25 m  $\times$  0.33 mm with a film thickness of 0.25  $\mu$ m, and the carrier gas was helium. Temperature programming was as follows: 60°C for 3 min; heating 20°C min<sup>-1</sup>; 300°C for 10 min; 280°C for 12 min. Nonadecane was used as an internal standard to quantify the amounts of compounds present. After Goulson *et al.* (2000).

(Goulson *et al.* 1998b; Stout *et al.* 1998). Also, tarsal extracts obtained by putting *B. terrestris* legs in organic solvents, when artificially applied to flowers mimic the repellency of natural scent marks, and induce repellency in a range of *Bombus* species (Stout *et al.* 1998; Goulson *et al.* 2000). Even applications of a range of pure synthetic chemical constituents of scent marks (rather than the mixtures that naturally occur) produce more or less the same repellent response. It seems that *Bombus* species exhibit a generalized response to flowers that are contaminated with any of the common hydrocarbons found on the cuticles of bumblebees, be they conspecifics or heterospecifics. This makes sense, for many flower species are commonly visited by a range of *Bombus* species with overlapping resource use (Goulson *et al.* 2005). The advantage to be gained from detecting empty flowers would be small if only those flowers visited by conspecifics could be detected. Since these compounds are common to most insects, not just *Bombus* sp., it seems likely that bumblebees may be able to detect and reject flowers which have been visited by other insects. Recent studies suggest that *Bombus* species are able to detect scent marks deposited by honeybees (Fig. 10.3) and by the solitary bee *Anthidium manicatum*, and vice versa (Stout and Goulson 2001; Gawleta *et al.* 2005; but see Williams 1998 for conflicting evidence). Bumblebees also seem to be capable of avoiding flowers previously visited by hoverflies (Diptera, Syrphidae) (Reader *et al.* 2005). Given the impressive learning abilities of bees and the generality of hydrocarbons on insect cuticles, it seems probable that bumblebees are able to learn to avoid flowers that have been visited by any other insect.



**Figure 10.3** The proportion of flowers rejected by *B. lapidarius* and *Apis mellifera* workers: (a) less than 3 min after the first visitor and (b) 24 h after the first visitor. The frequency of rejection of flowers that had no previous visitors is also shown. Numbers above the bars represent sample sizes. Responses are recorded as acceptance if bees landed and probed for nectar, or as rejection if the bees approached the flower, but departed without landing or feeding. After Stout and Goulson (2001).

The repellent effect of scent marks wanes over time. Thus when visiting comfrey, *Symphytum officinale*, foraging *B. terrestris* rejected nearly all flowers that had been visited in the previous 3 min, but by 40 min the rejection response had disappeared (Fig. 10.4a) (Stout *et al.* 1998). This broadly matches the rate of accumulation of nectar in *S. officinale*; 40–60 min after being emptied, flowers have refilled (Fig. 10.4b) (Stout *et al.* 1998). However, different flower species vary greatly in the rate at which they secrete nectar, so a fixed repellent response of 40 min duration would not be appropriate for all flower species. For flowers that replenished nectar more rapidly than *S. officinale*, this would result in bees rejecting many flowers that were full of nectar, and conversely, if



**Figure 10.4** (a) The proportion of flowers of *Symphytum officinale* rejected by foraging *B. terrestris* and *B. pascuorum*, according to the time that had elapsed since the previous visit to the flower. (b) The rate of accumulation of nectar in flowers of *S. officinale* after they have been emptied. From Stout *et al.* (1998).

the secretion rate was slower, many of the acceptable flowers would contain little nectar. Also, if visitation rates are high or flowers are scarce, we would predict that bees should be less choosy (i.e. have a lower threshold for acceptance of a flower) and hence be more likely to accept flowers which were visited quite recently.

It seems probable that bees learn to use an appropriate concentration of scent mark as the threshold for rejection depending on the circumstances (Stout *et al.* 1998; Stout and Goulson 2002). Given that most individual bees are flower constant (i.e. they tend to visit the same flower species over and over again), they have the opportunity to learn an appropriate threshold concentration of scent mark for their preferred flower species. It is known that bumblebees do sample available floral rewards and modify their behaviour accordingly (Dukas and Real 1993a,b). If bumblebees can gain information on the time that has elapsed since a scent mark was deposited from its strength or composition (as suggested by Schmitt *et al.* 1991; Stout *et al.* 1998), then it would be possible for

them to learn what concentration of scent corresponds to an appropriate threshold for acceptance of a flower. There is evidence that this does indeed occur. Williams (1998) found that repellency was of very short duration (about 2 min) when *Bombus* species were foraging on *Borago officinalis*, which has an unusually high rate of nectar secretion. Conversely, Stout and Goulson (2002) found that repellent scent marks deposited by *B. lapidarius* on *Lotus corniculatus* flowers lasted for 24 h; *L. corniculatus* has a low nectar secretion rate and was extremely abundant at the study site so that bees could afford to select only the most rewarding flowers.

Until very recently it was assumed that the mechanism by which rejection responses waned over time was evaporation of the scent mark, or at least evaporation of the more volatile components (Goulson 2003). A mark that evaporated at a predictable rate would enable a bee to estimate the time since the mark was deposited from its strength. However, recent work by Eltz (2006) draws this assumption into question. He demonstrates that scent marks left behind by foraging bumblebees do not wane to any appreciable extent within 2 h of deposition, and that a flower may contain detectable traces of scent marks left behind by the sequence of insects that have visited it over a number of days. In fact, the main hydrocarbons involved in scent marks are large and have low volatility (they would be of little use as cuticular waterproofing if they were not), so this result is not surprising. However, this finding raises questions as to how bees are able to judge the time since a scent mark was deposited over time scales of less than 1 h, which they are clearly able to do. The most probable explanation at present is that the hydrocarbons are slowly adsorbed into the hydrophobic surface of the corolla, so that although still detectable by solvent extraction and gas chromatography, they are not available for detection by the bee in the headspace volatiles surrounding the flower. Although plausible, this explanation remains to be tested. It is also not consistent with the findings of Saleh *et al.* (2006) that scent marks on complex artificial plastic flowers remain repellent to bumblebees for longer than marks on simple artificial flowers. Presumably in this circumstance, the scent marks cannot readily be adsorbed into the plastic surface; if they are not evaporating either, how can bees judge their age? This is a fascinating aspect of scent marking that deserves further investigation.

### 10.3.1 Repellent versus attractant marks

There is a notable anomaly in studies of scent marking in bumblebees which requires an explanation. The first studies to describe deposition of scent marks on flowers by foraging bumblebees found that the marks were attractant rather than repellent, and were used to mark rewarding flowers (Schmitt and Bertsch 1990; Schmitt *et al.* 1991). Similar results have been found in honeybees (Ferguson and Free 1979). All subsequent studies of scent marking in bumblebees have only found repellent effects, whether using natural marks, tarsal extracts or synthetic compounds (Goulson *et al.* 1998; Stout *et al.* 1998; Williams 1998). It has previously been suggested that fresh scent marks might be initially repellent, but that as they evaporate (or are adsorbed into the flower) they may

become attractants (Stout *et al.* 1998). However, attempts to test this hypothesis suggest that this is not so. When applying dilution series of tarsal extracts to flowers, even when the lowest concentrations contained less than one molecule per flower (homeopathy for plants?), there was no evidence for an attractant response at any concentration (Goulson *et al.* 2000).

An alternative possibility is that the more volatile or easily adsorbed components produce repellency, and the less volatile ones attraction. However, when a range of pure synthetic compounds present in natural extracts were bioassayed, all induced repellency (Goulson *et al.* 2000). Thus this explanation seems unlikely. It is possible that the changing composition of a scent mark over time as some compounds are adsorbed more quickly than others could result in attractive marks. However, bumblebees tend to reject flowers of *S. officinale* for about 40 min following a visit, but flowers visited 1, 4 or 24 h previously have acceptance rates equal to flowers that have never been visited (Stout *et al.* 1998). At no point were flowers that had previously been visited found to be more attractive than controls. Generally, unvisited (and unmarked) flowers receive very high rates of acceptance, so there was little scope for a scent mark to increase attractiveness of flowers (Goulson *et al.* 1998, 2000; Stout *et al.* 1998). Overall, it seems unlikely that attractant marks are in operation when bumblebees forage at natural flowers.

Examination of the experimental design used by Schmitt *et al.* (1991) suggests another explanation (Goulson 2003). Their study used artificial flowers that were either always rewarding (regardless of whether they had been visited or not) or were never rewarding. In this (unnatural) circumstance, bees would inevitably spend longer feeding on the rewarding flowers, so that rewarding flowers would become liberally covered in cuticular hydrocarbons. Given that, as we have seen, bees are readily able to learn associations between sensory cues and rewards, it is likely that they may have learned to preferentially visit the marked flowers, since these were the rewarding ones. Witjes and Eltz (2007) set out to test whether bumblebees would behave differently when presented with artificial flowers with realistic, small and slowly replenishing rewards. In this situation, *B. terrestris* workers were repelled by scent marks, behaving much as they do on real flowers. Similarly, Saleh and Chittka (2006) found that bumblebees were attracted to scent marks left on artificial flowers when the flowers continuously contained a reward, but were repelled by the scent marks when the flowers were completely emptied by only one visit. Hence it is clear that bumblebees are able to adjust their response to scent marks according to experience and the context in which they are presented.

### 10.3.2 The evolution of scent marking

The value of using scent marks is presumably that it allows the bee to save time that she would otherwise spend in handling flowers that contain little or no reward. The time saving to be gained thus depends on the handling time of the flower in question. When visiting complex flowers one might predict that bees should be more sensitive to scent marks, whereas when visiting simple flowers where the reward can be swiftly accessed



and assessed directly, using scent marks would be of little advantage. Saleh *et al.* (2006) tested this hypothesis in a laboratory situation using bumblebees foraging on artificial flowers that were either simple or complex. As predicted, bees were more than twice as likely to reject scent-marked flowers that were complex compared to simple flowers.

Since bumblebees do not forage randomly they rarely encounter inflorescences which they themselves have just visited, so that the evolutionary benefit gained by leaving scent marks is not immediately apparent. Presumably they help in avoiding errors in systematic foraging (Goulson 1999, 2000). In social bees such as bumblebees, the depositors of scent marks may also benefit through improving the foraging efficiency of siblings. However, bumblebee colonies are rather small (compared to honeybees), so that the majority of beneficiaries of marks left by bumblebees are often probably not siblings. Genetic studies of patterns of relatedness between foragers have demonstrated that the worker bumblebees foraging on any one patch of flowers contain representatives of numerous nests, and that rather few of them are sisters (Darvill *et al.* 2004; Knight *et al.* 2005). Competition between bumblebee species is thought to occur in some communities (Inouye 1978; Pyke 1982), and thus scent marking may benefit both siblings and probable competitors. It seems probable that the action of scent marking did not initially evolve as a benefit to the marker or her siblings. Indeed, there is no evidence that repellent scent marks are deliberately deposited. As we have seen, they are composed of alkanes and alkenes which commonly occur on the cuticles of diverse insect species (Lockey 1980; Blum 1981, 1987), and which are bound to be left behind in tiny amounts if any part of the body comes into contact with flower parts. Indeed, Saleh *et al.* (2007) recently demonstrated that the same compounds are left behind on any substrate bumblebees walk on, including for example the entrance to their nest. If surfaces which bees have walked over are moved and placed by artificial flowers the flowers become repellent, strongly indicating that scent marking is passive, that is, scent marks should be regarded as cues that are accidentally deposited rather than as signals (Wilms and Eltz 2008). Most insects are able to detect and recognize conspecifics by scent, and this ability is highly advanced in social insects that commonly have complex chemical recognition and communication systems. It seems likely that the ability to detect the scent of other insects evolved long before flowers or indeed bees existed. Thus the only step required for a system of repellent scent marking to evolve is for foragers to learn to associate the scent of another insect on a flower with a low reward. Thus scent marking should not be regarded as a form of communication, since the information carrying cue is likely to be accidental.

There is some evidence that scent marks may not just be a means of avoiding landing on empty flowers. *B. terrestris* exhibit a stronger avoidance response to flowers visited by the aggressive, territorial solitary wool carder bee *A. manicatum* than they do to flowers visited by conspecifics (Gawleta *et al.* 2005). Similarly, in *Anthophora plumipes* bees appear to respond to scent marks as territorial markers as well as indicators of low reward, with dominant females responding differently to scent marks left by those of low rank (Gilbert *et al.* 2001).

It has only relatively recently become apparent that the use of scent marks by bees when choosing which flowers they are going to visit is not confined to honeybees. As yet we do not know how widespread this phenomenon is. As mentioned previously, scent marking has recently been described in the neotropical stingless bee *Trigona fulviventris* (Goulson *et al.* 2001), in the solitary bees *A. manicatum* (Gawleta *et al.* 2005) and *A. plumipes* (Gilbert *et al.* 2001) and in the sweat bee *Halictus aerarius* (Yokoi and Fujisaki 2007; Yokoi *et al.* 2007). Clearly this behaviour is not confined to social species. Are all bees able to use scent marks, and are scent marks used in all circumstances? Do naïve bumblebees respond to scent marks, or is it something that they learn from experience? Are they used by flower-visiting insects other than Hymenoptera, such as hoverflies or butterflies? Since the compounds used are widespread, it is likely that interspecific interactions could occur between distantly related taxa, but this has not yet been investigated.

*This page intentionally left blank*

---

## Competition and Niche Differentiation in Bumblebee Communities

There are about 250 species of bumblebee worldwide, mostly distributed through the temperate, alpine and arctic regions of the northern hemisphere (Williams 1989a). In most communities, several different species of bumblebee occur sympatrically (Ranta and Vepsäläinen 1981; Williams 1989b). All *Bombus* species occupy a broadly similar niche. They are all large (relative to other bees), hairy and facultatively endothermic; they exhibit remarkably little morphological variation; they all nearly have an annual cycle and are active at similar, overlapping, times of the year; and they all feed almost exclusively on nectar and pollen throughout their lives. One might expect fierce inter-specific competition to shape bumblebee communities (Brian 1954; Heinrich 1976a). How then do many species manage to coexist?

Although *Bombus* species are all superficially similar in shape, they differ markedly in one characteristic; the length of their tongues. Some species, notably *B. hortorum* and *B. ruderatus*, have very long tongues (approximately 14 mm) compared to others such as *B. terrestris* (approximately 8.5 mm). The former also have a noticeably longer head. In combination, this enables the longer-tongued species to reach the nectaries in deep, narrow flowers that exclude access by other bumblebees. As a consequence, *B. hortorum* tends to visit flowers with deeper corollas (mean 8.8 mm) compared to *B. terrestris* (mean 6.3 mm) (Prys-Jones 1982). *Delphinium* provide a familiar garden example of a flower in which the nectar is hidden in a narrow tubular spur beneath the flower, and in the United Kingdom *Delphinium* are a favourite with *B. hortorum* but are rarely visited by the other bumblebee species found in gardens, all of which have relatively short tongues. In contrast, species such as *B. terrestris* feed on shallow flowers (e.g. bramble, *Rubus fruticosus*). Similar patterns are evident in other parts of the world: for example in Japan, *B. diversus* has a long tongue, narrow head and body, and prefers deep flowers while *B. hypocrita* and *B. ignitus* are short-tongued, fat-bodied and prefer shallow flowers (Inoue and Yokoyama 2006). Thus variation in tongue length between species leads to differences in the floral preferences of bumblebees (Stapel 1933; Brian 1957; Hobbs *et al.* 1961; Hobbs 1962; Holm 1966; Macior 1968; Ranta and Lundberg 1980; Harder 1985; Graham and Jones 1996).

Resource partitioning with respect to tongue length is thought to be an important factor in allowing a number of bumblebee species with otherwise very similar biology

to coexist (Heinrich 1976a; Teräs 1976; Inouye 1978, 1980a; Pyke 1982; Barrow and Pickard 1984; Harder 1985; Johnson 1986; Graham and Jones 1996). Inouye (1976) noted that sympatric bumblebee species in valleys near Crested Butte, Colorado, differed in mean tongue length by a constant factor of 1.2–1.4, and inferred that this pattern was the result of competition. To test whether this was so, one pair of species was examined in more detail (Inouye 1978). *B. appositus* is a long-tongued species that preferentially foraged on *Delphinium barbeyi*, while *B. flavifrons* has a medium length tongue and preferentially foraged on *Aconitum columbianum*. In three separate experiments, foragers of one species were caught and removed, and the behaviour of the other species recorded. On each occasion, the remaining species increased its visitation rate to the plant that it did not normally visit (although this difference was only statistically significant for one experiment). This was interpreted as an example of competitive release, whereby each bee species is restricted to one preferred flower species by intraspecific competition. Subsequent studies at the same site indicated that *B. appositus* chose *D. barbeyi* because they obtained a higher rate of reward than if they visited *A. columbianum*. However, in the absence of their competitor, *B. flavifrons* gained equal rates of rewards on both flower species, again suggesting that in nature they are confined to *A. columbianum* through the effects of competition (Graham and Jones 1996).

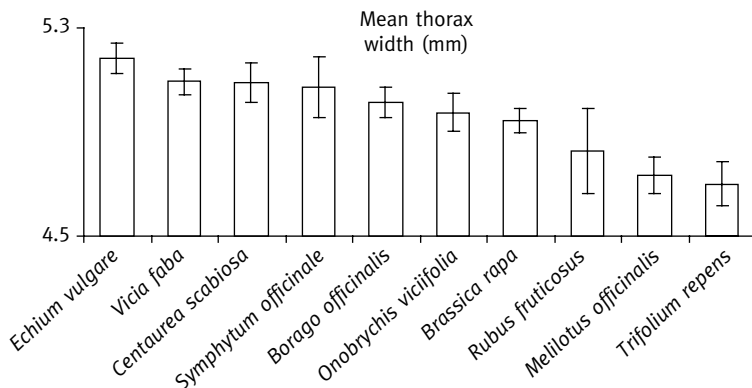
In a famous study, Pyke (1982) examined the distributions of seven bumblebee species in the same locality. He found that the seven species could each be assigned to one of four groups according to tongue length: long, medium and short tongued, and a short-tongued species that was also a nectar robber. Each group tended to feed upon different flower species with corolla depths appropriate to their mouthparts, with the nectar robbing species feeding primarily on bird-pollinated flowers that no other bumblebees were able to visit. The bumblebee community at any particular site tended to consist of at most four species, and never more than one from each group, although the actual species differed between sites. This he interpreted as evidence for powerful competition within groups leading to competitive exclusion of all but one species.

It is not immediately obvious why bees with long tongues should generally avoid flowers with shallow corollas. Indeed, one might imagine that long-tongued species would generally be at an advantage because they would be able to feed on both shallow and deep flowers (Ranta and Lundberg 1980). Field observations have demonstrated that long-tongued species can feed on shallow flowers, even though they usually choose not to (Heinrich 1976a; Ranta and Lundberg 1980). Yet there are generally more short-tongued than long-tongued species in any given area, and long-tongued species are usually less abundant (Anasiewicz 1971; Teräs 1976; Anasiewicz and Warakomska 1977; Ranta and Lundberg 1980). It is species with medium and long tongues that have declined most in Europe, while species with unusually short tongues (e.g. *B. terrestris*, *B. lucorum* and *B. pratorum*) are still widespread and abundant. Kugler (1940) suggested that a long tongue might be a hindrance when feeding on shallow flowers. This explanation was confirmed by studies in Canada: Plowright and Plowright (1997) found that bees with long tongues fed more slowly on shallow flowers than bees with shorter

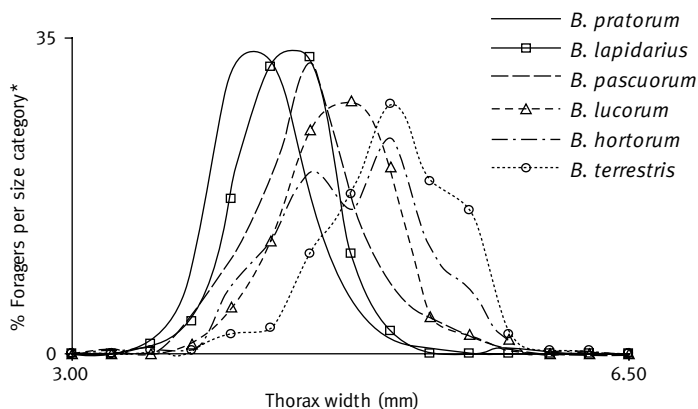
tongues. Presumably a long tongue is rather unwieldy in these circumstances. To make a human analogy, knickerbocker glory desserts are served in a very deep glass with a special long-handled, small-headed spoon. Without this spoon it would be impossible to eat much of the dessert. But this spoon would probably not be very efficient as a means of eating a bowl of soup, for which a short-handled and broad-headed soup spoon would be far more appropriate and would enable the soup to be consumed more quickly. Thus short-tongued bumblebees may exclude longer-tongued species from shallow flowers by being superior competitors. This would explain the neat partitioning of floral resources described by Pyke (1982); bees are at their most efficient when feeding on flowers with a corolla depth that matches the length of their tongue.

Superficially, convincing though the studies of Pyke and Inouye in Colorado are as evidence that competition is an important factor influencing bumblebee communities, more recent studies in Europe have failed to find such clear patterns. North and Central European bumblebee communities can be more diverse than those in North America, commonly consisting of up to 16 species, with considerable overlap in tongue lengths (Ranta *et al.* 1980; Ranta and Vepsäläinen 1981). Several short-tongued species are ubiquitous and coexist at most sites. In the United Kingdom, six bumblebee species are abundant, widespread and generally occur together. Yet four of them have short tongues of very similar length (Williams 1989b; Goulson *et al.* 1998a). Several studies of local assemblages of bumblebees have failed to find any pattern in the tongue lengths of species in relation to their co-occurrence (Ranta 1982, 1983; Ranta and Tiainen 1982; Williams 1985b, 1988; Goulson *et al.* 2008b). Ranta and Vepsäläinen (1981) attribute coexistence of species with similar tongue lengths in Europe to spatiotemporal heterogeneity in nest distribution and floral resources (see also Tepedino and Stanton 1981; Ranta 1982, 1983). They argue that the strength and direction of competitive interactions between colonies of different species will fluctuate greatly over the season (as the availability of different flower species varies) and also from nest to nest, because flower distributions are patchy. Thus competition will not drive species to local extinction.

This explanation is plausible enough, but begs the question as to why this does not occur in Colorado too. It could be that floral resources are not limiting in Europe (and are in Colorado), but this seems unlikely, especially since the common short-tongued species in Europe often co-occur in habitats of rather low quality such as intensively farmed areas. A more promising explanation is that there are niche dimensions other than tongue length that may vary between species, but which have received comparatively little attention. Harder (1985) examined flower choice by bumblebees in Ontario and concluded that although tongue length was an important factor, the relationship between tongue length and flower choice varied over time, and was influenced by numerous factors such as flower abundance and species richness, and also by body size and wing length of individual bees. Within species, different sized workers tend to feed on different flower species (Cumber 1949a; Heinrich 1976a; Morse 1978b; Inouye 1980a; Barrow and Pickard 1984; Johnson 1986; Peat *et al.* 2005b) (Fig. 11.1). This may be in part because size relates to tongue length, but is also probably because smaller bees have

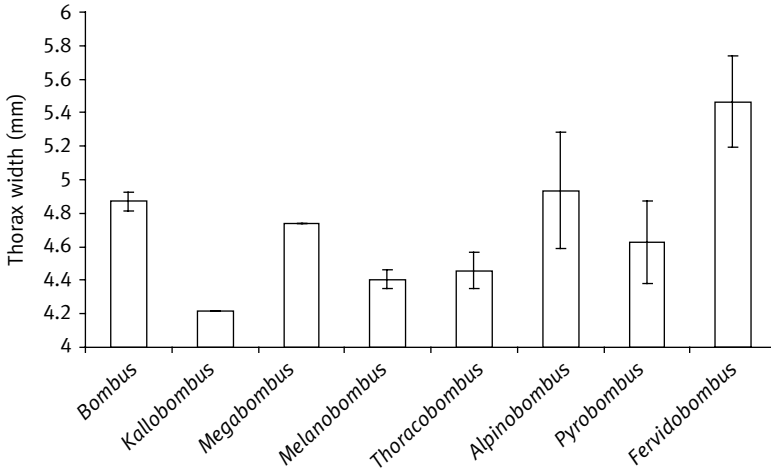


**Figure 11.1** The mean thorax width of foraging *B. terrestris* workers visiting flowers of each of 10 different plant species (ISE). Differences were significant ( $F_{9,247} = 5.53$ ,  $p < 0.001$ ). From Peat *et al.* (2005b).



**Figure 11.2** Size variation amongst foraging workers in six common and sympatric UK *Bombus* species. Size categories were defined by 0.25 mm divisions. From Peat *et al.* (2005a).

lower metabolic costs during foraging and so can profitably forage on flowers that provide lower rewards per flower (Corbet *et al.* 1995). There are substantial size differences found *between* bumblebee species (Fig. 11.2) and also on an average between bumblebee subgenera, which are likely to influence foraging preferences (Fig. 11.3). Morse (1977) examined competition between *B. ternarius* and *B. terricola* when feeding on goldenrod, *Solidago canadensis*, in coastal Maine, USA. He found that competition led to the smaller species, *B. ternarius*, being excluded from proximal parts of the inflorescences where the larger florets occur. *B. ternarius* continued to visit the smaller distal florets, so that resources became neatly partitioned according to the size of both the bee and the floret.



**Figure 11.3** Mean thorax width of foraging workers of representatives of eight bumblebee subgenera ( $\pm$ SE). From Peat *et al.* (2005a).

Morphological variation between species, such as in size or tongue length, is easily recorded and is likely to influence foraging niche, but is only part of the picture. It is now clear that bumblebee species also differ with respect to their physiology. Teräs (1985) found that in Finland, long-tongued bumblebee species such as *B. hortorum* tended to visit flower species that had deep corollas, but also preferred those that were sparsely distributed. Similarly, both Sowig (1989) and Carvell (2002) found that *B. hortorum*, *B. humilis* and other longer-tongued species tend to visit flowers that occur in small patches, while short-tongued bumblebees including *B. terrestris* and *B. lucorum* favoured plants that provided large patches of flowers. Why should some species prefer clustered flowers and others scattered flowers? It seems that these preferences may reflect differences between bumblebee species in their abilities to generate heat internally (Newsholme *et al.* 1972; Prys-Jones 1986). Bumblebees must attain a high body temperature to take off, and they are able to generate heat in their thorax (Heinrich 1975a). The exact mechanism of thermogenesis is a bone of contention; Heinrich (1979b) maintains that it is produced through shivering, while other researchers claim that heat can be produced through substrate cycling (discussed in detail in Chapter 2).

Fructose biphosphatase is a key enzyme involved in substrate cycling (if this process occurs, see Chapter 2), and has unusually high activity in the flight muscles of bumblebees (Newsholme *et al.* 1972; Prys-Jones and Corbet 1991) (Table 11.1). In non-flying bumblebees, the rate of substrate cycling is inversely related to ambient temperature, enabling the bees to maintain an internal temperature that is independent of ambient conditions even when they are not active (Clark *et al.* 1973; Clark 1976). Although all bumblebees that have been examined have this enzyme, the amount varies greatly between species (Newsholme *et al.* 1972; Prys-Jones 1986). Bumblebee species with high



**Table 11.1.** Activity of fructose biphosphatase in the flight muscles of different bee species, and their tendency to visit plants that present massed flowers.

Species	Fructose biphosphatase activity ( $\mu\text{mol}\cdot\text{min}^{-1}\text{g}^{-1}$ muscle, mean $\pm$ SE)	Proportion of visits to massed flower arrangements
<i>B. lapidarius</i>	131 $\pm$ 7 (8)	0.54 (210)
<i>B. lucorum</i>	80 $\pm$ 16 (5)	0.39 (84)
<i>B. pratorum</i>	73 $\pm$ 10 (13)	0.19 (177)
<i>B. terrestris</i>	59 $\pm$ 13 (7)	0.38 (188)
<i>B. pascuorum</i>	45 $\pm$ 6 (20)	0.18 (254)
<i>B. hortorum</i>	23 $\pm$ 1 (11)	0.07 (159)

The two variables are strongly correlated:  $r = 0.88$ , d.f. = 5,  $p < 0.02$ . From Prys-Jones and Corbet (1991).

enzyme activity can more readily generate heat, and thus need to fly less frequently to maintain a high body temperature. While feeding on a flower, the body temperature of a bumblebee will tend to fall. If feeding on large inflorescences, the temperature may fall below the threshold for flight,  $\sim 30^\circ\text{C}$  (Heinrich 1993). *B. lapidarius* has a relatively high level of fructose biphosphatase activity, can maintain a high temperature while feeding for long periods on a large inflorescence, and so can take off at any time (Prys-Jones 1986). In contrast, *B. hortorum* has a low enzyme activity; if it were to spend a long period feeding on a single inflorescence it would cool and then be unable to take off without a period of shivering of the flight muscles. But because they preferentially forage on scattered flowers, necessitating frequent flights, they do not need high levels of fructose biphosphatase activity to keep warm (and they also minimize competition with species such as *B. lapidarius*). There appears to be a clear relationship between the preference of bee species for plants with massed flower arrangements and their fructose biphosphatase levels (Table 11.1).

Interestingly, despite its greater potential for thermogenesis through substrate cycling, *B. lapidarius* has a higher minimum air temperature threshold for activity than other common European species such as *B. terrestris* and *B. hortorum* (Reinig 1972; Corbet *et al.* 1993). We do not know what physiological or metabolic factors determine differences in the temperature range over which bumblebees are active (other than size). The latitudinal ranges of bumblebee species vary greatly; for example, *B. distinguendus* is a northern European species while its close relative *B. subterraneus* has a more southerly distribution. Presumably, these species are adapted to activity under different temperature regimes; *B. subterraneus* does have a noticeably more sparse coat. Peat *et al.* (2005a) compared hair length of 10 bumblebee species and found that those from more southerly latitudes tended to have shorter hair on their thorax than species from more northerly regions (Fig. 2.1). Niche differentiation resulting from differences in optimal temperature among bumblebee species has received surprisingly little attention. Williams (1986, 1989a,b) argues that the patterns of abundance of bumblebee species in the United Kingdom are best explained by their climatic optima, rather than

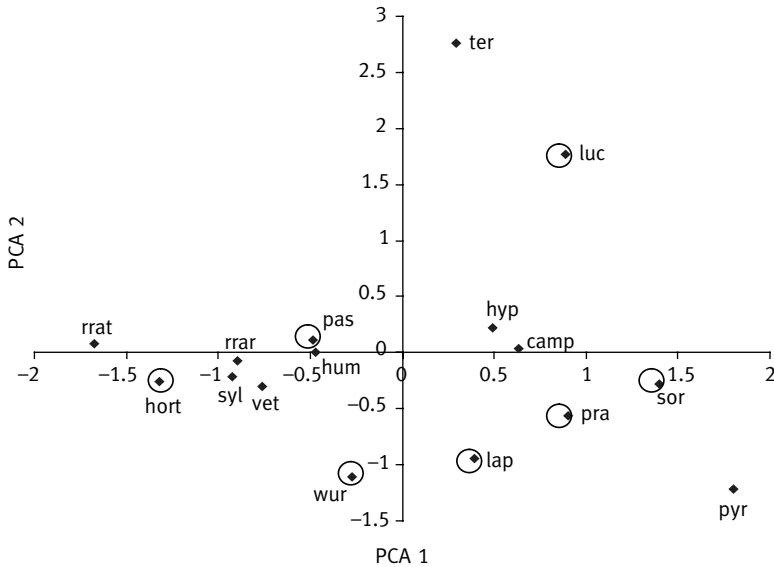
by competition. Species which are near the edge of their range tend to be less abundant and confined only to the highest quality sites.

In addition to factors affecting floral choices, bumblebee species differ subtly in many other ways; they use different nest sites (Alford 1975; Svensson *et al.* 2000), queens emerge at different times (Prys-Jones 1982; Inoue and Yokoyama 2006) and they reach peak worker abundance at different times of year (Goodwin 1995). The successional emergence of queens from hibernation must inevitably reduce interspecific competition, and this may be particularly important at a time when flowers are scarce. Differences in the timing of peak worker foraging may serve the same purpose. For example, *B. pratorum* is one of several ubiquitous short-tongued bumblebee species in the United Kingdom, but it differs from its potential competitors by having a very short colony duration. Worker abundance peaks in May or early June, and reproductives are produced from April onwards (Alford 1975; Goodwin 1995). In contrast, most of the other UK species do not reach peak abundance until July. Species also differ in their proclivity for collecting pollen versus nectar. For example, *B. lucorum* and *B. terrestris* appear to collect significantly more pollen, and proportionally less nectar, than *B. pascuorum* (Brian 1957).

Factors other than tongue length have received little scrutiny, yet one of the most convincing demonstrations of competition between North American bumblebees strongly suggests that factors other than tongue length are important. Bowers (1985b) experimentally produced sympatric and allopatric populations of *B. flavifrons* and *B. rufocinctus* in subalpine meadows of Utah. In the absence of competition, both



**Figure 11.4.** The mountains of southern Poland have an exceptionally high diversity of bumblebee species, with up to 16 species co-occurring in single sites. This is largely attributable to the high density and diversity of forage provided by the extensive farming system, with low inputs, small fields and traditional crop rotations still in use.



**Figure 11.5** The proportion of visits to different plant families by bumblebee species coexisting in southern Poland (nectar- and pollen-collecting visits combined), subjected to principal components analysis. The first two components are plotted here, and account for 25.1% and 17.4% of variation in forage use, respectively. Component one is strongly negatively correlated with visits to Fabaceae, and positively correlated with visits to Dipsacaceae and Onagraceae. Component two is positively correlated with visits to Apiaceae and Lamiaceae, and negatively correlated with visits to Ranunculaceae (*Aconitum* spp.). The seven most abundant species are circled. Cam, *campestris*; hort, *hortorum*; hum, *humilis*; hyp, *hypnorum*; lap, *lapidarius*; luc, *lucorum*; pas, *pascuorum*; pra, *pratorum*; pyr, *pyrenaicus*; rrat, *runderatus*; rrar, *runderarius*; sor, *soroensis*; syl, *sylvarum*; ter, *terrestris*; vet, *veteranus*; wur, *wurflenii*. From Goulson *et al.* (2008b).

species fed on a similar range of flowers. When sympatric, *B. rufocinctus* were excluded from their preferred flower species and the body weights of foragers were smaller, indicating that they had received less food during development. No effects of competition were detected in *B. flavifrons*. These two species are indistinguishable with regard to tongue length or size, so their floral choices and the asymmetry of competition between them must be due to other factors. The only obvious difference is in phenology; *B. flavifrons* emerges from hibernation several weeks before *B. rufocinctus*, so that by the time workers of *B. rufocinctus* appear, workers of *B. flavifrons* are already numerous. This may provide *B. flavifrons* with a competitive advantage; for example, *B. flavifrons* workers will have already worked out how to handle the most rewarding flower species and have learned the locations of the most rewarding patches, making it harder for young and hence naïve *B. rufocinctus* foragers to compete.

The mountains of southern Poland have one of the most diverse bumblebee communities that has been studied with regard to competition, with 23 species occurring in

the region and up to 16 coexisting within single sites (Goulson *et al.* 2008b) (Fig. 11.4). As elsewhere in Europe, species with similar-length tongues frequently coexist, and overlap in tongue length does not appear to affect the likelihood of two species co-occurring. However, the most abundant species (which co-occurred at most sites) occupied distinct dietary niche space (Fig. 11.5). Very little of this differentiation is attributable to tongue length: for example, *B. lucorum* and *B. pratorum* both have short tongues but differ considerably in their floral preferences. Whatever factors underlie these differences in floral preference (e.g. differences in body size or thermoregulatory abilities) these data go a long way to explaining how superficially similar species can coexist.

*This page intentionally left blank*

---

## Bumblebees as Pollinators

*I hate myself, I hate clover, and I hate bees*

Charles Darwin, from a letter to John Lubbock (1862)

Darwin was fascinated by pollination and by bees, and particularly by bumblebees (or humble-bees, as he knew them). His prodigious correspondence is littered with descriptions of his observations on the interactions between bees and flowers; the quote above follows his inaccurate prediction that nectar-robbing honeybees on clover might have shorter tongues than those visiting the flowers legitimately. A great deal of what we know today about pollination is based on Darwin's somewhat obsessive studies of the plants and insects in his garden in Kent.

Pollination is defined as the transfer of pollen from the anthers of one flower to the stigma of the same or a different flower. In the majority of plants, pollination is necessary for seed set. Plants may employ a variety of vectors to transport pollen, including wind, water, birds and bats, but a significant majority are pollinated by insects. Unlike any other insect group, adult bees feed their offspring on pollen. To gather sufficient resources for its offspring, a bee has to maintain a high work rate (compared to, say, a butterfly, which stops at flowers only to feed itself). Because of this work rate they make excellent pollinators, and a great many plants are adapted primarily for bee pollination. The efficiency of a social lifestyle means that social bees tend to be far more numerous than their solitary counterparts, and throughout much of their range (notably in the temperature zone of the northern hemisphere) bumblebees are the most abundant native pollinators, both of crops and of wild flowers. As a consequence, many plants are adapted primarily or sometimes exclusively for pollination by bumblebees.

Plants adapted for pollination by bees tend to show a number of characteristics, a 'pollination syndrome'. Those pollinated by bumblebees are often large and brightly coloured (especially blue/purple or yellow). They are frequently bilaterally symmetrical (rather than radially), and provide large nectar rewards, often located in a deep spur (Corbet *et al.* 1991). That said, there are a great many exceptions, and the pollination syndrome of a flower can only be taken as an indication of the likely pollinator (Waser *et al.* 1996). Albert Einstein is commonly attributed as saying '*If the bee disappears from the surface of the earth, man would have no more than four years to live*'. In fact, there is no evidence that the famous physicist said anything of the sort, and it seems unlikely that he would have ever ventured to make such a bold statement about a subject on which, so far as we know, he had no expertise or interest. It is also almost certainly an

overstatement of the facts. Nonetheless, there can be no doubt but that if bees were to somehow disappear entirely, the economic and ecological impacts would be devastating, as we shall see.

## 12.1 Pollination of crops

A broad variety of crops depend on insect pollinators. Some, such as alfalfa (*Medicago sativa*) and clovers (*Trifolium* spp.), set no seed unless they are cross-pollinated (pollen is transferred from flowers on one plant to another). Self-fertile crops such as oil-seed rape (*Brassica napus*), brown mustard (*Brassica juncea*) and tomato (*Lycopersicon esculentum*) are capable of self-pollination, but insect visits are needed to move pollen from the anthers to the stigma. In oilseed rape, adequate pollination further benefits the grower by ensuring an early and uniform ripening of seeds; otherwise, seed ripening is staggered and some seeds are shed before harvest (Williams *et al.* 1987). Some crops, notably sunflower (*Helianthus annuus*), are partially self-fertile, but produce better quality seed when cross-pollinated. Even fully self-fertile crops can benefit from cross-pollination through improved quality of the offspring; for example, field beans (*Vicia faba*) will set seed in the absence of pollinators, but the offspring produced will themselves set few or no seed without insect visitors (Stoddard and Bond 1987). In fruits such as strawberry (*Fragaria x ananassa*), melon (*Cucumis melo*) and kiwifruit (*Actinidia deliciosa*), fruit size is related to the number of seeds produced (and hence to the number of ovules fertilized). Adequate pollination ensures maximum fruit size. Thus, for example, in glasshouse conditions, providing captive *B. terrestris* colonies doubles the number of marketable fruit produced by strawberries (Dimou *et al.* 2008).

Remarkably, we are ignorant of the pollination requirements of a great number of crops despite the fundamental and well-appreciated relationship between pollination and yield (Corbet *et al.* 1991). In Europe, a region better studied than most, about 250 plant species are grown as crops. Of these, about 150 are thought to be insect pollinated, but for most we do not know which insects pollinate them, or whether yields are being limited by inadequate pollination (Corbet *et al.* 1991; Williams 1995). The current drive to diversify arable production is leading to the introduction of yet more crops, many of which require insect pollination (e.g. lupin, *Lupinus* spp.), yet whether we have sufficient appropriate insects to pollinate them is unknown.

It is exceedingly hard to estimate the total value of bee pollination (see Gill 1991), but various estimates have been produced and all agree that the economic contribution made by bees is vast. The most recent estimates for the United States suggest a value of US\$14.6 billion for honeybees alone (Morse and Calderone 2000; see also Levin 1983; Robinson *et al.* 1989; Southwick and Southwick 1992; Ghazoul 2005). Gill (1991) estimated the value to be US\$103 million for Australia, while Winston and Scott (1984) put the value for Canada at US\$1 billion. A comparable estimate for the EC suggests that insect pollination was worth US\$6.6 billion in 1989, of which US\$5.5 billion was ascribed

to honeybees (Borneck and Merle 1989). More than a third of all human food is thought to depend on insect pollination (McGregor 1976).

### 12.1.1 Honeybees versus bumblebees

The honeybee, *Apis mellifera*, is overwhelmingly the most widely managed pollinator of crops, and many farmers are entirely unaware that there are other insects that are capable of pollination. The economic value of pollination is often credited entirely to honeybees (Parker *et al.* 1987), and is often used to justify public subsidizing of honeybee keeping. Even the scientific literature is frequently blinkered in this respect (discussed by Richards 1993; Batra 1995). For example, honeybees were promoted for pollination of alfalfa up until the 1980s even though Henslow noted in 1867 that honeybees were incapable of tripping the flowers (Olmstead and Wooten 1987; Robinson *et al.* 1989; Batra 1995). In 1909, it was discovered that other species of bee, notably those belonging to the Megachilidae, did trip the mechanism and provide efficient pollination (Brand and Westgate 1909), but through a combination of inertia and poor advice to farmers it was not until the 1970s that use of Megachilidae for alfalfa pollination became widespread.

There is now growing appreciation that there are alternatives to the honeybee, and that in some situations the alternatives may be better (Westerkamp 1991). Honeybees do have a number of advantages as pollinators: they form vast colonies that can pollinate large areas of crops; there is a substantial body of expertise in the management of these colonies; and they provide honey. However, they also have disadvantages. First, honeybees are fair weather foragers (Willmer *et al.* 1994). In cold conditions, and when it is raining, they will not forage. In an unpredictable climate such as that of the United Kingdom this can be important, particularly when growing crops such as apples that flower early in the year when a spell of poor weather is likely. Second, honeybees are not able to adequately pollinate some crops. They have short tongues, and so are not keen to visit crops with deep flowers such as red clover (*Trifolium pratense*). In some plants, such as the Solanaceae (which includes tomatoes and potatoes) the pollen is presented in poricidal anthers. These are essentially similar to an inverted salt cellar; to obtain the pollen an insect has to shake the anthers (known as buzz pollination). Honeybees are not able to do this, and thus cannot efficiently pollinate these crops (Rick 1950). Finally, reliance on a single species for pollination of crops is an inherently risky strategy. This has been made all too clear during the recent epidemic of the mite *Varroa destructor*, which all but exterminated wild honeybees through vast parts of their range, and causes substantial loss of managed hives. Most recently, in North America 'Colony Collapse Disorder', a somewhat mysterious phenomenon probably attributable to viral diseases, has devastated commercial hives and threatens yields of bee-pollinated crops such as almonds.

In contrast, bumblebees are hardy and will forage in very cold conditions and even when it is raining (Corbet *et al.* 1993). In North America, bumblebee queens have been



seen foraging when the air temperature was below freezing, while in the Scandinavian summer they will forage for 24 h each day. Because of their greater cold tolerance, bumblebees begin foraging earlier in the day than honeybees; for example on curcubit crops, *B. impatiens* began foraging 15–40 min before honeybees (Stanghellini *et al.* 2002). Under the same conditions, bumblebees tend to forage faster than honeybees, and so pollinate more flowers per bee (Poulsen 1973; Free 1993; Stanghellini *et al.* 2002; Fuchs and Muller 2004). Thus they provide a reliable pollination service despite the vagaries of the weather. Because different bumblebee species differ in their tongue lengths, between them they can pollinate a range of crops. For example, short-tongued bumblebee such as *B. terrestris* are important pollinators of oilseed rape, particularly in poor weather when honeybees are inactive (Delbrassinne and Rasmont 1988). Species with medium or long tongues (*B. pascuorum* or *B. hortorum*) are needed to pollinate crops with deep flowers such as field beans and red clover (Fussell and Corbet 1991) (Fig. 12.1).

Bumblebees are capable of buzz pollination, and make excellent pollinators of Solanaceae such as tomatoes (Van den Eijnde *et al.* 1991). The anthers of these flowers only release pollen when vibrated, which bumblebees achieve by placing their thorax close to the anthers and contracting their flight muscles at a frequency of about 400 Hz (King 1993). Members of the Ericaceae such as cranberries and blueberries (*Vaccinium* spp.), and also kiwifruit (*A. deliciosa*) also benefit from buzz pollination (Buchmann 1985), and so are more effectively pollinated by bumblebees than by honeybees (Kevan *et al.* 1984; Mohr and Kevan 1987; Cane and Payne 1988; MacKenzie 1994).



**Figure 12.1** *B. ruderatus* queen pollinating field beans. *B. ruderatus* is one of many long-tongued species that have declined in recent years, threatening the pollination service for deep-flowered crops such as this. Photograph by Ben Darvill.

In general, adequate pollination requires an approximate match between the size and shape of the flower and that of the pollinator. For some plants, honeybees are ineffective at pollen transfer (Westerkamp 1991; Wilson and Thomson 1991). Thus, for example, on cranberry (*Vaccinium* spp.), alfalfa (*M. sativa*) and Delicious apples (*Pyrus malus*), honeybees gather nectar while making little or no contact with the reproductive structures, and thus are poor pollinators (Gray 1925; Roberts and Struckmeyer 1942; Farrar and Bain 1946; McGregor 1976; Robinson 1979). Similarly, bumblebees have been demonstrated to be better pollinators than honeybees for watermelon (*Citrullus lanatus*), cucumber (*Cucumis sativus*) (Stanghellini *et al.* 1997, 1998) and for apples (Thomson and Goodell 2001). Bumblebees are hairier than honeybees, which may contribute to their efficacy in transferring pollen; for example when visiting raspberry flowers, bumblebees deposited significantly more pollen on the stigmas than did honeybees (Willmer *et al.* 1994).

In Europe and North America, bumblebees are among the most important wild pollinators of crops (Corbet 1987; Plowright and Lavery 1987; Corbet *et al.* 1991). At least 25 major crops grown within the EC are visited and pollinated by bumblebees, including field beans, red clover, alfalfa, oilseed rape and various hard and soft fruits (Corbet *et al.* 1991) (Table 12.1). There are almost certainly more crops that benefit from bumblebee pollination, but as noted earlier, the pollination requirements of most crops have not been investigated.

### 12.1.2 Approaches to enhancing bumblebee pollination

There are two alternative approaches to using bumblebees as pollinators; they can be bred for the purpose, and the captive colonies placed in the crop, or the grower can exploit natural populations of bees. The former approach is perhaps best suited to high-value crops grown intensively in glasshouses (Plowright and Lavery 1987). Until recently, pollination of glasshouse tomatoes was carried out by hand using a vibrating wand, no doubt a very tedious job and costly in terms of labour (Cribb 1990). Honeybees have been used for tomato pollination but they provide an erratic yield, and from preference will not visit tomato flowers (Spangler and Moffett 1977; Banda and Paxton 1991). In contrast, bumblebees are highly effective pollinators, and give increased yield compared to honeybees or hand pollination (Banda and Paxton 1991). Some even claim that bumblebee-pollinated fruit taste and smell better than those produced by hand pollination (Heinrich 1996).

The efficacy of bumblebees as tomato pollinators was discovered in the 1980s in the Netherlands. Several companies began commercial rearing of *B. terrestris*, and within 3 years 95% of tomato growers in the Netherlands had switched to bumblebee pollination. *B. terrestris* is now the standard pollinators for glasshouse tomatoes in Europe; in 1990 over 500 Ha of glasshouse tomatoes were pollinated by bumblebees in the Netherlands alone (Van den Eijnde *et al.* 1991). They are also widely used for aubergines and cucurbits (e.g. Fisher and Pomeroy 1989a). More recently, use of *B. terrestris* for glasshouse pollination has spread to North Africa, New Zealand, Japan, Korea

**Table 12.1** Crops known to benefit from bumblebee pollination.

Crop		Need for pollination	Other probable pollinators
Actinidiaceae			
<i>Actinidia deliciosa</i>	Kiwifruit	***	H
Brassicaceae			
<i>Brassica napus</i>	Rape	*	H, S
<i>Brassica campestris</i>	Turnip rape	**	H, S
Asteraceae			
<i>Helianthus annuus</i>	Sunflower	***	H, S
Ericaceae			
<i>Vaccinium macrocarpon</i>	Cranberry	***	H
<i>Vaccinium angustifolium</i>	Lowbush blueberry	***	H
<i>Vaccinium ashei</i>	Rabbiteye blueberry	***	H
<i>Vaccinium corymbosum</i>	Highbush blueberry	***	H
Grossularidaceae			
<i>Ribes grossularia</i>	Gooseberry	*	H
<i>Ribes</i> spp.	Currants	**	H
Malvaceae			
<i>Gossypium</i> spp.	Cotton	*	H, S
Fabaceae			
<i>Phaseolus multifloris</i>	Runner bean	**	H
<i>Phaseolus lunatus</i>	Lima bean	*	H
<i>Vicia faba</i>	Field or broad bean	**	H, S
<i>Vicia villosa</i>	Vetch	**	H, S
<i>Medicago sativa</i>	Lucerne or alfalfa	***	H, S
<i>Melilotus</i> spp.	Sweet clover	***	H, S
<i>Trifolium</i> spp.	Clovers	***	H, S
<i>Glycine max</i>	Soya bean	*	H
<i>Lupinus</i> spp.	Lupins	**	-
Rosaceae			
<i>Prunus avium</i>	Sweet cherry	***	H
<i>Prunus cerasus</i>	Sour cherry	***	H
<i>Prunus communis</i>	Pear	***	H
<i>Prunus domestica</i>	Plum	**	H
<i>Pyrus malus</i>	Apple	***	H, S
<i>Rubus fruticosus</i>	Blackberry	**	H, S
<i>Rubus ideaus</i>	Raspberry	*	H
Rutaceae			
<i>Citrus</i> spp.	Orange, lemon, etc.	*	H, S
Solanaceae			
<i>Solanum melongena</i>	Aubergine	*	H
<i>Lycopersicon esculentum</i>	Tomato	*	H, S
<i>Capsicum</i> spp.	Pepper	*	H
Curcubitaceae			
<i>Cucumis melo</i>	Muskmelon	**	H
<i>Cucumis sativus</i>	Cucumber	***	H
<i>Citrullus lanatus</i>	Watermelon	***	H
<i>Cucurbita</i> spp.	Squash, pumpkin, gourd	***	H, S

H, honeybees; S, solitary bees. \*\*\*Insect pollination essential and \*insect pollination improves yield to some degree. Data derived primarily from Corbet *et al.* (1991) and Delaplane and Mayer (2000).

and Russia (and probably many other countries, but the companies that rear them are reluctant to reveal which). The global trade in bumblebee colonies probably exceeds 1 million nests per year, but precise figures are not available. Every year Japan alone imports about 40,000 colonies (Asada and Ono 2000). Colonies are contained within a shoe-box sized artificial nest box, and are readily delivered by courier. They are simply placed within the glasshouse and the colony entrance opened. The workers quickly acclimatize themselves to their new surroundings and within a matter of minutes begin their pollination duties.

North American growers were quick to realize the value of bumblebees for tomato pollination, but import of *B. terrestris* to Canada and the United States was wisely banned because of perceived risks of escape into the wild or accidental introduction of disease. In the early 1990s, commercial rearing of the native *B. impatiens* was developed. This has proved to be similarly successful for pollination of glasshouse crops, notably tomato, muskmelons and sweet peppers (Fisher and Pomeroy 1989a; Kevan *et al.* 1990; Meisels and Chiasson 1997). Recent studies by Morandin *et al.* (2001) suggest that 7–15 colonies of *B. impatiens* per hectare (equivalent to about 2,000 bee trips per hectare per day) are sufficient for tomato pollination in glasshouses.

Rearing of bumblebee colonies is necessarily expensive, and it has been argued that for most field crops it is uneconomical (Plowright and Lavery 1987). However, trials have taken place in various crops in Europe, North America and New Zealand (Van Heemert *et al.* 1990; Ptáček 1991; Whidden 1996). Desjardins and De Oliveira (2006) created a density gradient of *B. impatiens* by placing a large number of colonies (72) at one end of a lowbush blueberry crop, and found that fruit set and fruit size were both improved up to 150 m into the crop. Stubbs and Drummond (2001) demonstrated that only 5 colonies of *B. impatiens* per hectare of lowbush blueberry produced yields equal to using 7.5 honeybee colonies per hectare, despite presumably having far fewer workers per colony. Costs of hire of bumblebee and honeybee colonies vary from year to year, but were similar at the time of their study, suggesting that use of bumblebees may be more economical than honeybees in this crop. Fuchs and Muller (2004) compared the efficiency of bumblebees (*B. terrestris*) with honeybees for pollination of open-field Styrian oil pumpkin (*Cucurbita pepo pepo* var. *styriaca*) in Austria. They conclude that although bumblebees visited flowers five times faster than honeybees (on an individual basis), and continued foraging in worse weather than honeybees, five bumblebee colonies were needed per hectare which made pollination by bumblebees more expensive than using honeybees. For most field crops, exploiting natural populations of bumblebees is likely to be a better option than using commercial bumblebee colonies. This is an approach that has been championed particularly in Europe (Corbet *et al.* 1991; Fuchs and Muller 2004).

As discussed in Chapter 13, modern farming practices have led to a decline in the abundance of bumblebees both in Europe and North America (Peters 1972; Williams 1982, 1986; Rasmont 1988, 1995; Kosior 1995; Banaszak 1996; Buchmann and Nabhan 1996; Westrich 1996; Westrich *et al.* 1998). Boyle and Philogène (1983) counted only five

bumblebees in a 3-year census of orchard pollinators in Ontario. Bumblebees are abundant in other parts of Ontario, but are thought to have been driven from the fruit-growing regions by intensive use of pesticides. These crops now rely solely in pollination by honeybees. Similarly, native populations of bumblebees are rarely adequate to pollinate cranberries in North America (Marucci and Moulter 1977; Winston and Graf 1982; Kevan *et al.* 1990). Cranberry farmers are forced to rent honeybees colonies to effect pollination (Robinson *et al.* 1989), but as with tomatoes, honeybees do not favour cranberry flowers and from preference will forage elsewhere (Marucci and Moulter 1977; Kevan *et al.* 1990). Even when they do visit cranberries they provide a far less effective pollination service than bumblebees (MacKenzie 1994).

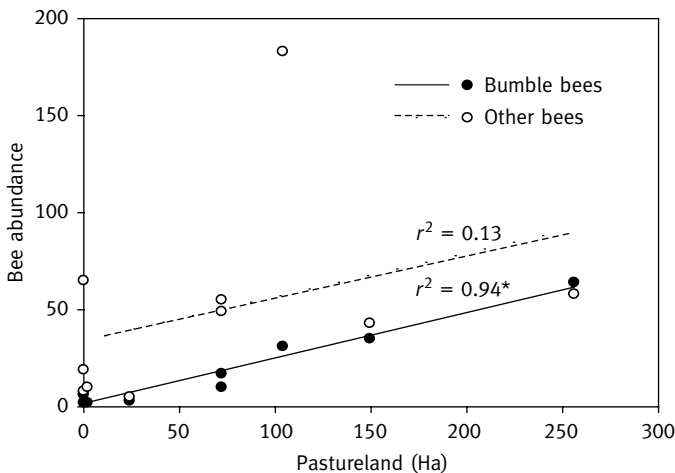
If field sizes are large then there may simply not be enough bumblebees to go around (regardless of the pesticide regime adopted) (Fussell *et al.* 1991). Farms with large field sizes necessarily have a low proportion of hedgerows or other field margins, and since these are the places that provide nest sites and floral resources for bees when crops are not flowering, then farms with large fields will have relatively few bumblebees. Yield of crops may be limited if there are insufficient bees to visit all of the flowers. For example in fields exceeding 12 Ha in size the yield of field beans was reduced through inadequate pollination by long-tongued bumblebees (Free and Williams 1976). Similarly, Clifford and Anderson (1980) estimated that if field sizes exceeded 5 Ha then yield of red clover in New Zealand declined through a shortage of bumblebees.

At present, the area of entomophilous crops in the EC and United States is increasing, and some researchers have predicted that we will soon be facing a serious shortage of both wild and managed bees (Borneck and Merle 1989; Torchio 1990). If pollination is inadequate then farmers may be tempted to switch to growing crops that do not require insect pollination (Osborne *et al.* 1991). For example, red clover is now rarely grown for seed production in Europe because yields are poor, probably because of a lack of appropriate pollinators. Ironically, most seed is imported from New Zealand where long-tongued bumblebees (originally from the United Kingdom) are the main pollinators (Osborne *et al.* 1991). The introduction of novel crops may also be limited by pollinator availability. A diversity of new crops have been introduced in Europe in recent years, as yet grown only on a small scale. Many are insect pollinated; for example, lupins (*Lupinus* spp.), borage (*Borago officinalis*), camelina (*Camelina sativa*), cosmea (*Cosmea maritima*), cuphea (*Cuphea* spp.) and niger (*Guizotia abyssinica*) (Corbet *et al.* 1991). The potential of these crops may never be realized if yields are limited by a paucity of suitable insects to pollinate them.

There are ways in which farmers can encourage natural populations of bumblebees. Schemes such as uncropped field margins and conservation headlands were not designed specifically to increase numbers of wild bees, but probably do so. Appropriate management of uncropped areas to encourage wild pollinators may prove to be a cost-effective means of maximizing crop yield (Prescott and Allen 1986). Depending on the crops that they grow, farmers may wish to encourage particular species. For example, if they grow field beans in the United Kingdom then they require healthy populations

of *B. pascuorum* and *B. hortorum*. Field beans are robbed by *B. terrestris* and *B. lucorum*, which gain access to the nectar by biting through the rear of the flower, and by doing so do not come into contact with reproductive parts of the flower. To encourage long-tongued species but discourage nectar robbers, the farmer might sow wildflower strips containing deep flowers such as white deadnettle (*Lamium album*) and red clover (*T. pratense*) (Fussell and Corbet 1992a). Of course the crops themselves provide vast areas of forage, but only for short periods. However, planting a succession of crops that flowered at different times could greatly enhance pollinator abundance while simultaneously maximizing yields. In Alberta, Canada, Morandin *et al.* (2007) demonstrated that bumblebee abundance and seed set in oilseed rape fields was very strongly correlated with the area of pastureland nearby; 94% of variation in bee abundance was explained by the area of pasture within 800 m (Fig. 12.2). Similarly, in Sweden, Rundlöf *et al.* (2008) found that bumblebees were significantly less abundant in homogenous farmed landscapes when compared to more heterogeneous areas and those with a higher proportion of pasture. Hence, farms that provide a mosaic of crop and non-crop areas may obtain better yields than farms with large monocultures of crops.

In addition to providing extra-floral resources, there has been interest in providing artificial nests sites to encourage queens to nest close to target crops (Fye and Medler 1954; Hobbs *et al.* 1960, 1962; Wojtowski and Majewski 1964; Hobbs 1967b; Palmer 1968; Donovan and Weir 1978; Barron *et al.* 2000). We have little idea whether nest sites are generally in short supply, but it seems likely that they may be in areas with intensive farming regimes. In New Zealand, red clover is grown for seed on a large scale, and provision of artificial nesting boxes for bumblebees has been shown to increase yields



**Figure 12.2** The relationship between the number of bumblebees, and other wild bees, and the amount of pastureland within 800 m radius of oilseed rape fields in Alberta, Canada. From Morandin *et al.* (2007).

(Donovan and Wier 1978; MacFarlane *et al.* 1983). Artificial nests placed in intensively managed agroecosystems in New Zealand had a very low take-up rate (2%), compared to those placed in less disturbed sites with a higher availability of flowers (Barron *et al.* 2000). Planting food sources for foraging queens is thought to encourage them to nest nearby (Teräs 1985; Williams 1989b), and in combination with provision of nest sites may be a good strategy to enhance pollinator availability for pollination of crops later in the year (Woodward 1990). Nest boxes also appear to be more successful when left in place for a number of years (Barron *et al.* 2000). Previously occupied boxes are more likely to be re-occupied, perhaps because queens return to their maternal site to found their nest (Donovan and Wier 1978; Pomeroy 1981). Alternatively, they may search for suitable nest sites using olfactory cues to locate sites which have shown themselves to be suitable for bumblebee nest development.

Occupancy of artificial nest boxes appears to be much lower in the United Kingdom than in New Zealand (Fussell and Corbet 1992c). This may be because natural nest sites are scarcer in New Zealand, due to the limited number of small burrowing mammals, or because bumblebee populations are higher due to a paucity of natural enemies in New Zealand. Provision of nest boxes has not to my knowledge been adopted as an economically viable practice in any country other than New Zealand, and even there, their use is not widespread.

Management of farmland with the specific aim of enhancing wild bee populations is in its infancy, and at present is largely based on educated guesswork. Large-scale experimental trials are urgently needed to establish which methods are most cost effective, and must take in to account the costs of lost crop area and establishment and management of bee resources, versus the financial benefits gained through improved yields. Enhancing populations of wild bees is likely to be most successful if it is carried out at a landscape scale, which would require cooperation and coordination at a regional level (Richards 1993). One interesting facet of managing pollinators at the landscape scale is that the strategy is open to cheating by individual farmers. Bees are highly mobile, so that the benefits of deploying measures to boost their populations (e.g. wildflower strips) are received by all farmers within ~1–2 km, not just by the farmer that has invested in them. Hence one can easily envisage a situation in which the optimal strategy for any individual farmer is to invest nothing in pollinator conservation but instead parasitize his neighbours' efforts.

A particular area of environmental concern relating to the use of bumblebees for pollination is their introduction to areas to which they are not native. Four species of bumblebee were introduced to New Zealand in ~1885 for the pollination of red clover, and this led to an immediate and substantial increase in yield of seed (Hopkins 1914). Bumblebee populations in New Zealand remain high, probably in part because they are free from most of their natural enemies (Donovan and Wier 1978). The efficacy of bumblebees as pollinators of glasshouse tomatoes is likely to have provided the motivation behind the recent arrival of *B. terrestris* in Tasmania (they were probably smuggled into the country from New Zealand). Interestingly, the original introduction of *B. terrestris* to New Zealand was misguided since this species has a short tongue and shows little

interest in red clover (the other three species that were introduced have longer tongues and are effective pollinators of clover). However, *B. terrestris* has become valued for pollination of alfalfa (Gurr 1955). *B. ruderatus* has since been introduced to Chile for clover pollination. *B. terrestris* has also been introduced to Chile and has accidentally escaped from glasshouses and become established in Japan. Applications have been lodged to introduce it to mainland Australia, South Africa and Argentina, all motivated by the desire to use it for tomato pollination. Bumblebees are so effective as tomato pollinators that tomato growers in regions where bumblebees are not available suffer a considerable economic disadvantage on the world market. The merits and pitfalls of introducing bumblebees beyond their natural range are discussed in Chapter 14.

## 12.2 Pollination of wild flowers

Because of their ability to remain active at low temperatures, bumblebees are reliable pollinators in unpredictable climates. They also have large foraging ranges, compared to smaller solitary species, and thus are better able to pollinate plants which exist as small, fragmented populations, a situation which generally prevails in Europe (Gathmann *et al.* 1994; Steffan-Dewenter and Tschardtke 1999). Many wild flowers in the temperate, arctic and alpine zones of the northern hemisphere are pollinated mainly or entirely by bumblebees, and sometimes by particular species of bumblebee. For example, high-altitude populations of *Polemonium viscosum* possess a suite of adaptive features that have coevolved with their bumblebee pollinators (Galen 1989). Unfortunately, the pollination requirements of the vast majority of wild flower species have never been studied. For most we can only make an educated guess based on the pollination syndrome of the flower, and this approach is not particularly reliable. Some plant families are thought to be very largely dependent on bees for pollination. These include the Boraginaceae, Ericaceae, Iridaceae, Lamiaceae, Malvaceae, Orchidaceae, Fabaceae, Scrophulariaceae, Solanaceae and Violaceae (Corbet *et al.* 1991).

The decline in bumblebee abundance in Western Europe, North America and elsewhere (see Chapter 13) must have resulted in reduced pollination services for some plants. The consequences of this depend on whether the plant species in question are limited in their seed set by pollination, and if so, whether their populations are limited by recruitment of seedlings. The relative importance of pollen versus resource limitation in determining seed set remains contentious (e.g. Bierzychudek 1981; Stevenson 1981; Wilson *et al.* 1994), but pollen is certainly limiting in some species, including ones pollinated by bumblebees (Galen 1985; Snow and Whigham 1989; Zimmerman and Aide 1989; Primack and Hall 1990; Johnston 1991). A recent review suggests that pollen limitation may be common (Burd 1994). This issue is complex, for even if pollen is limiting in any particular year, fruit production may ultimately be resource limited. For example, *Lathyrus vernus* is exclusively pollinated by bumblebees in Sweden. Supplementing pollen increased seed set, indicating pollen limitation of seed set (Ehrlén 1992). However, plants paid for this in the subsequent year, for plants that had



received supplementary pollen became markedly smaller and produced fewer flowers (Ehrlén and Eriksson 1995). Overall pollen supplementation did not affect their lifetime reproductive success.

These issues aside, it seems intuitively likely that a reduced pollination service will adversely affect some plant populations, and given the large number of plants that are probably pollinated by bumblebees these effects are likely to be widespread. A decline in pollination services can have more subtle effects than reduced seed output; it may also lead to reduced outcrossing and thus to inbreeding. For example, *Phyteuma nigrum* is an endangered plant in The Netherlands which exists mainly as small, isolated populations. These fail to attract adequate numbers of bees and receive little or no outcross pollen from other populations (Kwak *et al.* 1991a,b). Both reduced seed set and increased inbreeding may lead to declines in the abundance of plant species, which can be very detrimental when plants are already scarce and threatened directly by the same changes in land use that threaten the bees (Senft 1990; Jennersten *et al.* 1992; Lavery 1992; Oostermeijer *et al.* 1992; Kwak *et al.* 1996; Young *et al.* 1996; Fischer and Matthies 1997; Steffan-Dewenter and Tschardtke 1997). Unfortunately, for most wild flowers we do not know their pollination requirements, let alone whether they are pollinator limited, so it is impossible to predict which species are most at risk. It is likely that many rare plants are receiving a less reliable pollination service than they once did, but this will generally go unnoticed since no one is studying them (Corbet *et al.* 1991). If perennial plants fail to set seed it may be many years before effects are seen. Alteration of the relative reproductive success of plant species according to their pollination system may lead to profound changes in plant community structure, and in turn this will have knock-on effects for the associated animal community. Rare habitats such as Mediterranean garigue and Atlantic heathland are dominated by bee-pollinated plants, and so may be particularly susceptible to changes in bee abundance (Osborne *et al.* 1991). However, very few long-term studies are carried out in any habitats, and it will be extremely difficult to separate effects of pollinator abundance from those of other changes in the environment, such as climate change. At present, there are simply too few data available to draw any broad scale conclusions as to whether changes in bumblebee abundance are having widespread impacts on natural plant communities.

### 12.2.1 Nectar robbing

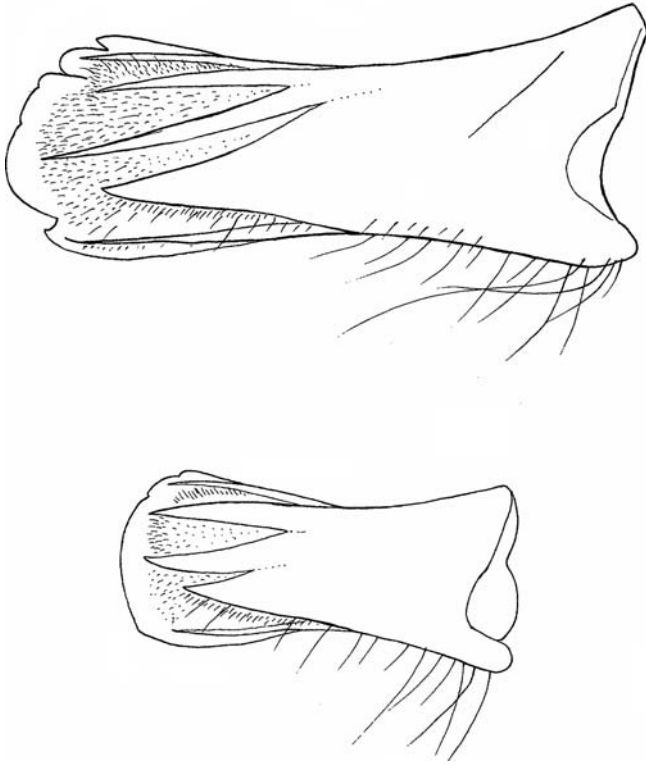
The relationship between plants and their pollinators is mutualistic since both plant and pollinator benefit from the association. However, mutualistic relationships are susceptible to cheating; if one partner evolves the ability to obtain the reward from its mutualist without providing anything in return then it will flourish (at least until the partner evolves counter-measures) (Boucher *et al.* 1982). In the case of insects and flowers, there is probably little direct pressure on insects to minimize the pollination service that they provide, since carrying a few pollen grains between flowers is not a costly

activity; the fitness of an insect is likely to be largely independent of whether it provides an adequate pollination service to the flowers that it visits. However, if they are able, insects will readily gather rewards from flowers without effecting pollination.

A great many (perhaps the majority) of insect visits to flowers do not result in pollination. This commonly happens if there is a mismatch between the morphology of the insect and that of the flower (because the flower is adapted for pollination by a different insect species). For example if the insect is small, it may be able to enter a flower and gather nectar without contacting either the stamens or the stigma. Ants are common 'nectar thieves' of this sort. In Colorado the ant *Formica neorubifibarbus gelida* takes nectar from flowers that are adapted for bumblebee visitation (Galen 1983). Insects may extract nectar by pushing in between the petals at the base of the flower corollas and by-passing the reproductive structures of the flower ('base foragers'). Both bumblebees and honeybees sometimes forage in this way (Free and Williams 1973). Finally, some animals make holes in sympetalous flower corollas (where the petals are fused into a tube) to allow direct access to the nectaries ('nectar robbers') (Inouye 1980b). Nectar robbers are either primary robbers (individuals which actually make holes in the flower corolla by piercing or biting) or secondary robbers (individuals which use the holes made by primary nectar robbers). If flowers have previously been robbed, primary nectar robbers may re-use holes and act as secondary robbers.

Bumblebees are common nectar robbers of many flower species in both Europe and North America, and have been recorded robbing over 300 different plant species (Lovell 1918; Inouye 1983) (Plate 10). For example in the United Kingdom, *B. terrestris* and *B. lucorum* are common primary robbers whilst *B. lapidarius*, *B. pratorum* and *B. pascuorum* sometimes secondarily rob (Free 1962). All of these robbing species have relatively short tongue lengths (with the exception of *B. pascuorum* which has an intermediate tongue length) and are thus unable to reach nectar in flowers with a deep corolla by foraging legitimately. The species with the longest tongue that is found in the United Kingdom, *B. hortorum*, is rarely seen to rob nectar from flowers (Brian 1957), and in general long-tongued bumblebees show no interest in robbing flowers even when they are unable to handle them legitimately (Inouye 1983). Some of the nectar-robbing species have adaptations for the purpose; *B. mastrucatus* and *B. occidentalis* both have mandibles with distinct teeth, unlike most bumblebees (Løken 1949) (see also Fig. 12.3). Interestingly, nectar robbing can be a contagious behaviour; Leadbeater and Chittka (2008) show that *B. terrestris* workers that encounter robbed flowers are more likely to become robbers themselves, so that the behaviour can spread from one individual to many.

Intuitively, nectar robbing is a process that we would expect to be costly to the plant. Darwin (1872) had a particular interest in nectar robbing and wrote that 'all plants must suffer in some degree when bees obtain their nectar in a felonious manner by biting holes through the corolla'. There is concern that nectar robbing by bumblebees may reduce the yields of some crops. For example in Europe, *B. terrestris* and *B. lucorum* commonly rob field beans, *V. faba* (Poulsen 1973). In British Columbia, *B. occidentalis* robs nectar from high bush blueberries, *Vaccinium corymbosum*. In this region,



**Figure 12.3** Mandibles of *B. terrestris*, a nectar-robbing species, and those of *B. pascuorum*, a species that does not rob flowers (although it sometimes secondarily robs flowers using holes made by *B. terrestris*). Note the teeth on the mandible of *B. terrestris*.

honeybee hives are stationed close to the crop to provide pollination, but the honeybees preferentially behave as secondary nectar robbers where holes have been provided by bumblebees (Eaton and Stewart 1969). Similarly, it has been argued that nectar robbing of wildflowers by *B. terrestris* in areas where the bee is not native (e.g. in New Zealand and Tasmania) may reduce seed set of some plants and so adversely alter the composition of native plant communities (Stout and Goulson 2000). However, there is no hard evidence for such effects.

The impact of nectar robbing on plant fecundity has been assessed in various tropical and temperate plant species (reviewed in Maloof and Inouye 2000). Nectar robbers do sometimes have a detrimental effect on seed set in the plants they visit. Robbers reduce the amount of reward available to pollinators which may result in decreased visitation rates by pollinators (McDade and Kinsman 1980) and a reduction in seed set (Roubik 1982b; Roubik *et al.* 1985; Irwin and Brody 1999; Irwin 2003). Robbers can also damage floral tissues and thus prevent seed production (Galen 1983). Surprisingly, however,

nectar robbery has often been found to have no adverse effects on plant fecundity (Newton and Hill 1983; Kwak 1988; Scott *et al.* 1993; Arizmendi *et al.* 1995; Morris 1996). In some instances this is because the 'nectar robbers' are still effective pollinators, despite their unconventional means of accessing the nectaries (Koeman-Kwak 1973; Higashi *et al.* 1988). For example, Koeman-Kwak (1973) found that nectar robbing *B. terrestris*, *B. lucorum* and *B. jonellus* still transferred pollen between flowers of *Pedicularis palustris* (the use of the term nectar-robber is clearly misleading in such examples, and Higashi *et al.* (1988) suggest the use of the term 'robber-like pollinators'). Similarly, Palmer-Jones *et al.* (1966) found that red clover, *T. pratense*, set more seed in the presence of nectar-robbing *B. terrestris* than when no bumblebees were present (although it set far more when long-tongued bumblebees were present). The same is true of the bean *Phaseolus coccineus* (Kendall and Smith 1976). Some nectar robbers may be pollinators because in addition to robbing nectar, they also collect pollen in the conventional manner (Kwak 1988; Scott *et al.* 1993; Morris 1996). For example when foraging on *Linaria vulgaris*, *B. terrestris* take nectar from the rear of the flowers by robbing, but some individuals then visit the front of the flowers to gather pollen (Stout *et al.* 2000). Similar observations have been made by Meidell (1944) and Macior (1966). Finally, nectar robbing may have no impact on fecundity if pollinators are present in sufficient abundance and are not deterred by robbers (Newton and Hill 1983; Arizmendi *et al.* 1995). For example, Stout *et al.* (2000) found that although flowers of *L. vulgaris* were very frequently robbed by *B. terrestris*, they were still visited with adequate frequency by their main pollinator, *B. pascuorum*, so that pollen did not limit seed set.

It has even been suggested that some plants may actually benefit from the activity of nectar robbers since legitimate foragers are forced to visit more flowers per foraging bout and to make more long-distance flights hence increasing genetic variability through outcrossing (Zimmerman and Cook 1985; Cushman and Beattie 1991; Maloof and Inouye 2000; Richardson 2004). Although experimental evidence for this hypothesis is largely lacking, Zimmerman and Cook (1985) did induce a greater frequency of long-distance movement of pollinators by artificially robbing flowers. Similarly, Maloof (2000, 2001) found that pollinating *B. appositus* moved further between flowers when visiting patches of *Corydalis caseana* that had been previously robbed by *B. occidentalis* than in unrobbed patches. Richardson (2004) demonstrated that male reproductive success of desert willow (*Chilopsis linearis*) was sometimes increased by nectar robbing, while female reproductive success was unaffected. Overall, if plants actually gained fitness through having lower rewards in their flowers, it is hard to explain why they would have evolved to produce higher rewards in the first place.

Nectar robbing may have complex and unpredictable effects on other insects and hence on plant reproduction. Newman and Thomson (2005) studied pollination of the invasive weed *L. vulgaris* in the Rocky Mountains, where the flowers are regularly robbed by *B. occidentalis*. Robbing created extra-floral nectaries which attracted ants, and ants appear to act as a deterrent to seed-predating beetles, although the overall effect of robbing on seed set was not calculated. In a recent review of 18 studies assessing the

effects of nectar robbers on plant fecundity, 6 had a negative effect, 6 had no effect, and 6 actually increased seed set (Maloof and Inouye 2000). A subsequent meta-analysis concluded (perhaps unsurprisingly) that nectar robbing is more likely to have a negative effect on plant reproduction when the plant species requires cross-pollination and is generally pollen limited (Burkle *et al.* 2007). However, it is clear that few broad generalizations can be made. Many factors, including the breeding biology of the plant, the foraging strategy of the robber, the abundance and efficiency of the pollinator and indirect effects upon insect herbivores affect the impact that nectar robbing is likely to have on any particular plant-pollinator system.

---

## Conservation

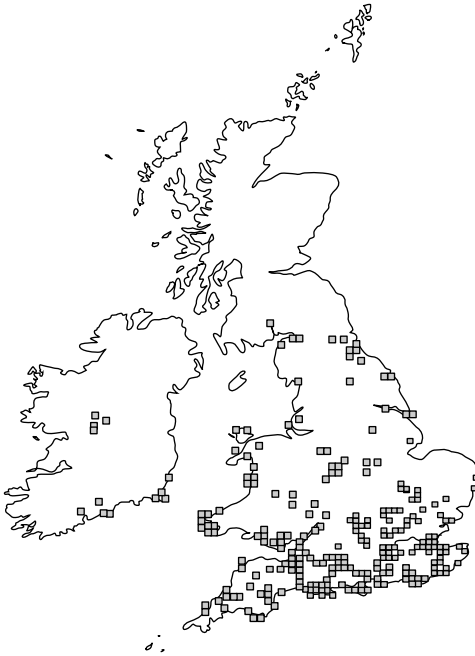
*Dave Goulson and Ben Darvill*

The available evidence suggests that many bumblebee species have declined dramatically in recent decades, both in the United Kingdom, in continental Europe and in North America (Peters 1972; Williams 1982, 1986; Rasmont 1988, 1995; Kosior 1995; Banaszak 1996; Buchmann and Nabhan 1996; Westrich 1996; Westrich *et al.* 1998; Sarospataki *et al.* 2005; Goulson *et al.* 2008a). Unfortunately, detailed information on the abundance and distribution of most species is not available, and so it is difficult to accurately estimate the extent of this decline. The most comprehensive records available are from the United Kingdom, where detailed surveys of the distribution of bumblebee species have been carried out under the Bumblebee Distribution Maps Scheme (Alford 1980). Between 1970 and 1974, data were collected on the bumblebee fauna of 2,317 10-km grid squares, comprising most of the British Isles. This can be compared with a considerable body of 'pre 1960' records (see Williams 1982). This comparison, which is already 30 years out of date, revealed a dramatic decline in the distributions of many bumblebee species (Williams 1982). More recent data, albeit for a restricted group of species, are available from the studies of the Bumblebee Working Group (see Edwards 1998, 1999, 2000, 2001) and the Bees, Wasps and Ants Recording Society (BWARS). These data suggest that the declines documented by Williams (1982) have continued.

The United Kingdom is accredited with 27 species of *Bombus*, including the recent arrival *B. hypnorum* and the recent discovery that *B. cryptarum* is present. One of these bumblebee species, *B. pomorum*, has not been recorded since about 1864 and was only ever known from a few specimens. The local extinction of this species should perhaps not be regarded as too serious a loss, since it may never have been a long-term resident of the United Kingdom. The second species to become extinct in the United Kingdom was *B. cullumanus*, a chalk-grassland species of southern England that was probably always local and scarce; this species was last recorded in about 1941 (BMNH collection). More recently, declines appear to have accelerated, particularly in the agricultural lowlands of the south. Post-1960 populations of *B. subterraneus* were scattered across southern England from Cornwall to Kent and East Anglia. However, recent searches in its known haunts have failed to find any specimens, and it has not now been seen since 1988. The species was declared extinct in 2000. *B. sylvarum*, another species that once occurred throughout southern United Kingdom is now exceedingly scarce and confined to a handful of sites (Fig. 13.1). *B. distinguendus* has disappeared entirely from England and is only known from the far north of mainland Scotland, the Orkney Islands and the Hebrides (Fig. 13.2). A further six species, *B. muscorum*, *B. humilis*, *B. soroensis*,

1900 – 2000

*B. sylvarum*

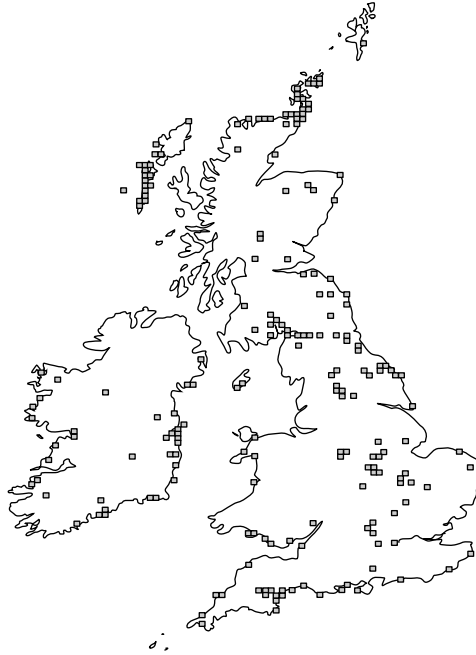


2000 – 2008



**Figure 13.1** Historical distribution of *B. sylvarum* (all records from 1900 to 2000), and present day distribution. Extensive searches have been undertaken for this species in recent years, so the recent map is almost certainly more or less accurate. Data collected mainly by the Bees, Wasps and Ants Recording Society, and mapped by the National Biodiversity Network.

1900 – 2000

*B. distinguendus*

2000 – 2008



**Figure 13.2** Historical distribution of *B. distinguendus* (all records from 1900 to 2000), and present day distribution. Extensive searches have been undertaken for this species in recent years, so the recent map is almost certainly more or less accurate. Data collected mainly by the Bees, Wasps and Ants Recording Society, and mapped by the National Biodiversity Network.



*B. ruderarius*, *B. monticola* and *B. ruderatus* have disappeared from substantial portions of their historical range. Seven of the 27 UK bumblebee species have been accorded Biodiversity Action Plan (BAP) status in recognition of their plight (the formal designation for endangered species), a higher proportion than any other invertebrate group. The future of these species in the United Kingdom is precarious. If the United Kingdom is representative of the situation elsewhere, then bumblebees are facing a crisis.

Declines in bumblebee species may not be immediately apparent to the casual observer because some bumblebee species remain abundant. In the United Kingdom, six species are widespread and numerous, particularly in gardens, so that it is easy to get the impression that bumblebees are faring well. Many rare and declining species are similar in appearance to the more common ones, so that their absence is easily overlooked.

It seems that similar declines are occurring in Europe. In a review of changing distribution of bumblebees of 11 central and western European countries, Kosior *et al.* (2007) describe extinctions of 13 species in at least one country between 1950 and 2000. Four species (*B. armeniacus*, *B. cullumanus*, *B. serratissima* and *B. sidemii*) went extinct throughout the entire region. In Hungary, Sarospataki *et al.* (2005) conclude that 10 out of the 21 extant species are declining and should be classified as 'endangered' or 'critically endangered'.

There are few equivalent baseline data for bumblebees in North America and there is debate as to whether or not they are suffering similar long-term declines. For example, Golick and Ellis (2006) found little variation in the Nebraska bumblebee fauna between 1962 and 2000, while Grixti and Packer (2006) describe a significant increase in bee diversity between 1968 and 2003 at a site in Ontario. However, it could be argued that the major loss of flower-rich prairie habitat in North America occurred before this time, and hence that there may have been associated declines in bee abundance that were never documented. In perhaps the most detailed North American study to date, Grixti *et al.* (2009) examined changes in the bumblebee fauna of Illinois by surveying sites for which previous records were available dating back to 1900. They revealed substantial declines in species diversity, particularly in the period 1940–1960, with the extirpation of four species during the twentieth century (*B. borealis*, *B. ternarius*, *B. terricola* and *B. variabilis*).

Although large-scale studies of past and present bumblebee distributions in North America are largely lacking, there is a strong evidence for precipitous declines of some North American bumblebee species in the past 10 years, notably within the subgenus *Bombus*. *B. franklini* is endemic to a small area in the west of the United States, and has declined rapidly since 1998. Recent searches found none at many former strongholds, and it is now thought to be extinct at many or all of them (Thorp 2005). *B. occidentalis* is native to the west of North America and was once the commonest bumblebee here, but since the late 1990s it has declined dramatically, and is now extremely rare (Thorp 2005; Thorp and Shepherd 2005; Rao and Stephen 2007). *B. affinis* and *B. terricola*, both eastern North American species, are suffering similar declines (Thorp and Shepherd

2005; Colla and Packer 2008). These two species were recorded by Williams as the commonest bumblebee species in southern Ontario in 1983, but widespread sampling of eastern North America (including southern Ontario) from 2002 to 2008 resulted in just two records of *B. terricola* and none of *B. affinis* (Williams and Osborne 2009). *B. ash-toni*, a social parasite of *B. affinis* and *B. terricola*, also appears to be suffering losses, presumably in response to decline of its hosts (Winter *et al.* 2006).

Elsewhere in the world, few data are available. There is some evidence of loss of species richness from lowland areas of Sechuan in China (Xie *et al.* 2008; Williams *et al.* 2009). In Japan, rapid declines since the mid-1990s are again affecting particularly the subgenus *Bombus* (Matsumura *et al.* 2004; Inoue *et al.* 2008).

## 13.1 Causes of declining bumblebee numbers

### 13.1.1 Loss of habitat

That changes in farming practices are largely to blame for the loss of many bumblebee species is beyond doubt (Williams 1986; Osborne and Corbet 1994; Goulson *et al.* 2006). In the United Kingdom, there is now a 'central impoverished region' covering much of the midlands and the south-east of England in which only the six most common *Bombus* species are regularly found (Williams 1982, 1986). This region closely corresponds with the 'predominantly planned countryside' of Rackham (1976), and consists almost entirely of intensively farmed arable land and improved pasture, with extensive urban areas. The same can be said of Western Europe where bee declines have been far greater in the agricultural lowlands than in Mediterranean and mountainous regions where agricultural practices are generally less intensive (Rasmont 1995).

In Europe, agricultural intensification has been underway for 250 years, but it accelerated during the latter half of the twentieth century. In the United Kingdom, the Second World War led to a drive for self-sufficiency. The main thrust of the 1947 Agriculture Act was to increase farming productivity by improving yields on farmed land and by bringing unfarmed areas into production. This approach was subsequently adopted by much of Europe under the Common Agricultural Policy. Permanent unimproved grassland was once highly valued for grazing and hay production. The development of cheap artificial fertilizers and new fast-growing grass varieties meant that farmers could improve productivity by ploughing up ancient grasslands or simply by applying fertilizers to them, and this they were encouraged to do (Stapledon 1935; Waller 1962). Hay meadows gave way to monocultures of grasses, notably rye grass, *Lolium perenne*, which are directly grazed or cut for silage. Between 1932 and 1984 over 90% of unimproved lowland grassland was lost in the United Kingdom (Fuller 1987; Howard *et al.*, 2003).

Development grants were also introduced to grub out hedgerows, to plough and re-seed pasture and to drain marshy areas. This led to a steady decline in the area of unfarmed land and of unimproved and semi-improved farmland. In the drive for increased production many farmers took to ploughing right up to field boundaries,

and to cutting hedges very low to the ground (Marshall and Smith 1987). With the loss of hedgerows and unimproved herb-rich grassland (including neutral grasslands, wet meadows and calcareous downland) we have inevitably lost botanical diversity. The process has been further accelerated by increasing use of herbicides, which directly impact on flowers, and by increasing use of fertilizers which allow a few rapid growing plant species to outcompete and exclude slower growing species. The widespread availability of selective herbicides now makes it possible to grow cereal crops whilst almost entirely eliminating broad-leaved weeds within the crop, reducing food availability for bees (Houghton *et al.* 2003; Hawes *et al.* 2003). When there is no buffer zone between the crop and the hedge, pesticides and fertilizers can penetrate into the hedge bottom, degrading the flora.

In North America, agricultural intensification has caused similar loss and fragmentation of natural and semi-natural habitat and an associated loss in biodiversity, at least in some regions (Wilcove *et al.* 1998). For example in Iowa, 85% of the land area was once prairie grassland which provides good bumblebee habitat, but less than 0.1% now remains. The remainder of the land is largely covered with monocultures of crops or by urban areas (Hines and Hendrix 2005). Illinois once had vast areas of prairie grasslands; Grixti *et al.* (2009) describe a rapid decline in the diversity of the Illinois bumblebee fauna in the period 1940–1960, coinciding with the main period of agricultural intensification. It seems certain that loss of habitat in other states led to similar bumblebee declines elsewhere in North America during the twentieth century, but they were not documented.

Bees are, of course, entirely dependent on flowers, because they feed more or less exclusively on pollen and nectar. Declines in British and European flora as a result of agricultural intensification are well documented, and have occurred over a similar time-scale to the contractions of bumblebee distributions (Ingelög 1988; Høiland 1993; Rich and Woodruff, 1996). Studies in Poland, Finland and the United Kingdom have all demonstrated a direct correlation between the floral diversity of an area and the number of bee species (Banaszak 1983; Kells *et al.* 2001; Bäckman and Tiainen 2002). Loss of floral abundance and diversity is widely considered to be the major cause of loss of bee diversity in agricultural landscapes (Banaszak 1983, 1992; Gathmann *et al.* 1994; O'Toole 1994). In studies of the Canadian species *B. impatiens* and *B. ternarius*, Pelletier and McNiel (2003) found that directly supplementing food in the nest enhanced colony reproduction (by 51% following provision of nectar and 86% following provision of pollen), suggesting that reproduction may be limited by availability of floral resources (although it must be noted that this effect is also subject to a number of alternative explanations such as reduced exposure of workers to predation and disease).

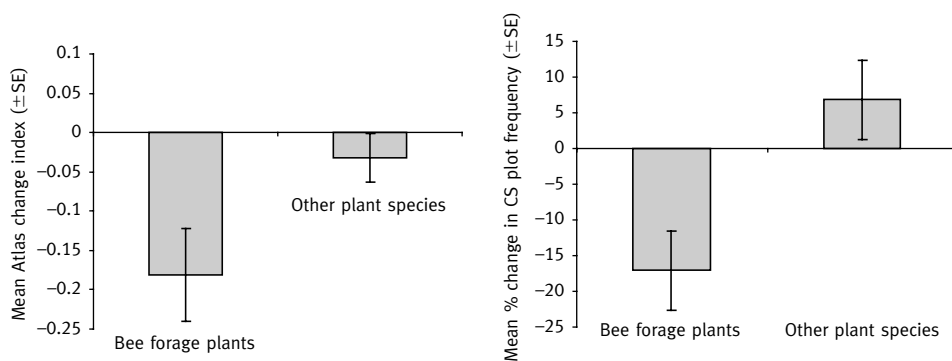
On farmland, the crops themselves may provide an abundance of food during their brief flowering periods. Leguminous crops (notably clovers, *Trifolium* spp.) used to be an important part of crop rotations in much of Europe, and these are highly preferred food sources, particularly for long-tongued bumblebees. Since the introduction of cheap artificial fertilizers, rotations involving legumes have been almost entirely abandoned, and it has been argued that this is one of the primary factors driving the decline

of long-tongued bumblebees (Rasmont 1988; Rasmont and Mersch 1988; Edwards 1999, 2000). There is some evidence that flowering crops such as oilseed rape contribute to supporting bumblebee populations in arable landscapes (Westphal *et al.* 2003; Herrmann *et al.* 2007) (although Carvell *et al.* (2008) found that *B. terrestris* nests adjacent to oilseed rape were more likely to be invaded by cuckoo bumblebees). However, for bumblebees to thrive they require a continuous succession of flowers from April to July, and flowering crops alone are unlikely to provide this. Bumblebees do not store large quantities of honey in the way that honeybees do, and they store little pollen, so they are vulnerable to discontinuities in the food supply (Shelly *et al.* 1991; Williams and Christian 1991). The nest establishment phase in spring when the queen has to single-handedly gather sufficient forage to feed her first batch of offspring may be the time when availability of flowers is most vital, but few crops flower this early (Bohart and Knowelton 1953; Alford 1975). Thus unless farms contain areas of wildflowers, they will not support bumblebees.

Uncropped areas of farmland, such as hedgerows, roadside verges, shelterbelts, borders of streams and ponds, green lanes and unimproved grasslands can provide flowers throughout the season, and tend to support far greater numbers of foraging bumblebees than cultivated areas (Banaszak 1983; Barrow 1983; Croxton *et al.* 2002; Mänd *et al.* 2002). However, these areas will only be adequate if there are enough of them, and if they have not been degraded by drift of herbicides and fertilizers. Even where flower-rich field margins and road verges remain, they are often regularly cut so that most of the flowers are destroyed. When uncropped areas are scarce or in poor condition, there will be less food available for bees, and there may be gaps in the succession of flowering plants during which bumblebee colonies will starve and die.

Bumblebee colonies frequently die out without producing new males or queens. For example of 80 nests of *B. pascuorum* followed by Cumber (1953) only 23 produced any new queens (a further nine produced only males). Extinction of colonies can occur for a variety of reasons, but is more likely when floral resources are scarce (Bowers 1985a). And in turn, if bees decline, then the plants that they pollinate set less seed, so that there is even less food for the bees (Corbet 1987; Osborne *et al.* 1991; Rathke and Jules 1993; Osborne and Corbet 1994). This kind of positive feedback has been rather dramatically described as an 'extinction vortex', in which mutually dependent species drive each other to extinction. We do not as yet know whether this process is really occurring, but a recent study in the United Kingdom found that of 97 preferred bumblebee forage species, 71% have suffered range restrictions and 76% have declined in abundance over the past 80 years, exceeding declines of non-forage species (Carvell *et al.* 2006a) (Fig. 13.3).

Although substantial data sets are available on forage use by different bumblebee species (e.g. Goulson *et al.* 2005), the habitat preferences of most bumblebee species have not been quantified in detail (Goulson *et al.* 2006). The rare UK species now persist in isolated and peripheral areas, notably in south-west England, in south and west Wales, and in remote regions of Scotland, areas that have been less affected by the drives for increased agricultural productivity. Some of the strongest remaining bumblebee communities are in military training areas such as Salisbury Plain and Castlemartin Range



**Figure 13.3** Changes in (a) range size of bumblebee forage plants ( $n = 97$ ) vs all other native non-forage plant species ( $n = 671$ ) from 1930–1969 to 1987–1999 measured by the Atlas change index for 10 km squares, and (b) abundance of bumblebee forage plants ( $n = 68$ ) vs all other native non-forage species ( $n = 257$ ) from 1978 to 1998 measured as relative percentage change in frequency of occupied Countryside Survey plots within 1 km squares. From Carvell *et al.* (2006a).

in Pembrokeshire (Edwards 1998, 1999; Carvell 2000, 2002). These areas are still farmed, but the grasslands have not been improved and traditional grazing regimes have been retained. Other strongholds are areas of coastal marsh (e.g. Dungeness in Kent and the Thames corridor, both in south-east England), areas which are particularly unsuited to agricultural activities.

Interestingly, the data we have suggest that most bumblebee species are generally not strongly associated with particular habitats; for example, *B. sylvarum* is probably the second rarest extant bee species in the United Kingdom, with about seven surviving populations, yet these are found in such diverse habitats as the Somerset levels (fenland) and the dry calcareous grasslands of Salisbury Plain, two habitats that have few plant species in common (Goulson *et al.* 2006). *B. distinguendus* is now extremely rare and found only in a few areas of machair (flower-rich coastal grassland), dunes and steep clifftop grasslands in the far north and west of Scotland. Yet it is clearly not a machair or coastal specialist; its former distribution spans 75, 50-km cells (Williams 2005) and covers the entire country south to Cornwall, with numerous inland records from, for example, Oxfordshire, Warwickshire and Berkshire, counties not known for their coastal habitat. Similarly, *B. subterraneus* now appears to be restricted to the vicinity of lakes in New Zealand, particularly shingle-covered lake margins where there is plenty of its favoured foodplant, *Trifolium pratense* (Goulson and Hanley 2004). The last known population in the United Kingdom (which became extinct in about 1988) was on the coastal shingle and marshes at Dungeness. Yet in the past this species was not confined to shingle (a very rare habitat in Europe), for in the United Kingdom it was once distributed throughout the south, the Midlands and East Anglia on various other habitats including saltmarshes, sand dunes, calcareous grasslands and neutral unimproved meadows (Alford 1980; Goulson *et al.* 2006).

It is notable that almost all of the sites with high bumblebee species richness in the United Kingdom are now coastal, and it is unclear why this should be. Coastal populations of rare bees occupy very varied habitats (marshes, dunes, calcareous grassland, shingle). What feature do these habitats have in common that allow them to support these rare bumblebee species? It seems probable that they all have a higher floral density and diversity than the intensively farmed countryside that comprises most of the British landscape. A particular change likely to have had a major impact on bumblebees is the switch from hay to silage production (Rasmont 1988). Fabaceae are among the favoured food sources of almost all UK bumblebee species (Goulson *et al.* 2005), and hay meadows are rich in Fabaceae such as *Trifolium* and *Lotus*. Large tracts of the farmed lowlands of the United Kingdom probably once supported high densities of wildflowers in hay meadows, unimproved pasture and hedgerows, so that currently rare bumblebee species were once widespread. The contraction of rare bumblebee populations to coastal sites may simply be because coastal habitats such as dunes, shingle and marshes are relatively infertile and unproductive for agriculture (hence suiting nitrogen-fixing legumes), and so have been more likely to escape the negative effects of intensive farming. That there is not some factor present only in coastal sites that is essential to these rare bee species is demonstrated by both the large former ranges of these species and by the survival of many rare species on Salisbury Plain (Goulson and Darvill 2004), the largest tract of England to have escaped intensive cultivation through its status as a military training area.

In addition to reducing the availability of food, modern farming practices are likely to have had other impacts on bees. Bumblebees need suitable nesting sites, the precise requirements for which vary between species. The carder bees such as *B. pascuorum* tend to nest in dense grassy tussocks, while other species such as *B. terrestris* nest underground in cavities. Both groups often use abandoned rodent nests. Studies of solitary bees show that underground-nesting species have declined disproportionately in Europe, suggesting that a lack of undisturbed nest sites may be a major factor driving declines in bee numbers (Westrich 1989). Certainly, the loss of hedgerows and of unimproved pastures is likely to have reduced the availability of nest sites for both above and below-ground nesting bumblebee species (Banaszak 1983; von Hagen 1994). Those species that nest above ground frequently have their nests destroyed by farm machinery, particularly by cutting for hay or silage. The scarcity of weeds and field-margin flowers on modern intensive farms means that there are fewer seeds for voles and mice to eat, and lower populations of these mammals will lead to fewer nest sites for both below and above-ground nesting bumblebee species.

In California, even on organically managed farms, the presence of bumblebees, in this case *B. vosnesenskii* and *B. californicus*, depends on proximity to areas of natural habitat in which the bees can nest (Kremen *et al.* 2002). A study in Sweden found that field boundaries within 100 m of a semi-natural grassland area contained a greater abundance and diversity of foraging bumblebees than similar sites >1 km from such habitat. However, foraging bumblebee abundance was found to be significantly lower in the

semi-natural grasslands themselves suggesting that these sites were used primarily for nesting (Ockinger and Smith 2007). Similarly, Greenleaf and Kremen (2006) found that tomato fields in northern California obtain high visitation rates from *B. vosnesenskii* only when they were positioned within 300 m of a patch of natural habitat and if at least 40% of the land within a 2,100 m radius of the farm was natural habitat. There is some evidence for a paucity of suitable nest sites in urban areas. Bumblebee abundance in urban parks in San Francisco has been found to be positively correlated with the number of rodent holes (McFrederick and LeBuhn 2006) suggesting that nest sites may be a limiting factor.

Bumblebees also need suitable hibernation sites where young queens can remain undisturbed through the autumn and winter (although for most of the less common species we have no idea where these sites are). For the more common bumblebee species for which some data are available, it seems that hibernation sites are quite different from the sites used for nesting; most species hibernate in soil on north-west facing slopes or in the shade of trees. It is possible that undisturbed sites of this sort are not as easy to find as they once were.

### 13.1.2 Pesticides

The second half of the twentieth century saw the widespread introduction of organic insecticides, compounds that were initially developed during the Second World War. Little is known as to how much effect these compounds have on wild bees in natural situations. Pesticide risk assessments are routinely carried out for honeybees, but the results from these are probably not directly applicable to bumblebees because they have different floral preferences, and are active at different times of the day (Thompson and Hunt 1999). For example, pyrethroids are commonly applied to flowering oilseed rape in the early morning or evening to avoid honeybees. Pyrethroids are repellent to most insects, so that sprayed crops are avoided by honeybees. However, spraying in the early morning or evening is likely to result in direct contact with foraging bumblebees since these are precisely the times when bumblebees are most active. This problem is exacerbated by the higher toxicity of pyrethroids at low temperatures (Inglesfield 1989).

Stimulated by the growing use of bumblebees in glasshouses for crop pollination, laboratory and field bioassays appropriate to bumblebees have been developed (van der Steen 1994, 2001), but these are not widely used so that few toxicological data are available (reviewed in Thompson 2001). Almost all tests conducted so far have been on *B. terrestris*. From these studies, it seems that toxicity to *B. terrestris* and honeybees tends to be similar.

There are three possible routes of exposure for bumblebees to agrochemicals; through direct contact with sprays (such as when sprays are applied to flowering crops or drift onto flowering weeds where bees are foraging); through contact with contaminated foliage; and through uptake of chemicals in nectar. The latter is most likely with systemic insecticides. Tests with dimethoate and carbofuran suggest that they are selectively

transported into the nectar, where they can reach high concentrations (Davis and Shuel 1988). Given the large volume of nectar consumed by bumblebees and their offspring, this could prove to be the most important route of exposure.

When colonies are large it is likely that they can support some loss of workers. However, in the spring when queens are foraging, and subsequently when nests are small and contain just a few workers, mortality may have a more significant effect (Thompson 2001). Thus spring applications of pesticides are of particular concern.

Despite risk assessments, widespread poisoning of honeybees has been reported in fields of oilseed rape in the United Kingdom and elsewhere (Free and Ferguson 1986). Such effects are readily noticed in domestic hives where dead bees are ejected and form piles by the nest. It seems probable that pesticides have similar effects on bumblebees, but they are unlikely to be noticed in most situations (particularly if they occur early in the year before workers are present or when nests are small). Probably for this reason there are few records of mortality in wild bumblebees caused by pesticides. In Canada, the use of the insecticide fenitrothion in forests led to a decline in yield of nearby *Vaccinium* crops due to a reduction in abundance of bumblebee pollinators (Ernst *et al.* 1989). In the United Kingdom, bumblebee deaths have been reported following applications of dimethoate and alphacypermethrin to flowering oilseed rape, and of  $\lambda$ -cyhalothrin to field beans (Thompson and Hunt 1999; Thompson 2001). Most insecticides are broadly toxic against both honeybees and bumblebees (reviewed in Thompson and Hunt 1999), and their inappropriate use will inevitably lead to bee mortality.

Confirmed incidents of honeybee poisoning appear to have declined considerably in the United Kingdom and Germany since the 1990s (Brasse 2003; Barnett *et al.* 2007). However, in 2008 there was a devastating incident in Germany where at least 12,000 honeybee colonies were killed by Clothianidin following mistakes made in the dressing of maize seed (Rosenkrantz and Wallner 2008). This is very likely to have had major effects on wild bees such as bumblebees but despite the high media profile of this incident no attempt was made to record impacts on bees other than honeybees.

A growing appreciation of the damaging effects of broad-spectrum pesticides has led to the development of a new generation of more target-specific compounds. EU, United States and Canadian law now demand that oral and acute toxicity tests are carried out on honeybees before the registration of any new pesticide (Morandin *et al.* 2005; Mommaerts *et al.* 2006). However, there is no obligation to study sub-lethal effects on any bees, or to look at specific effects on bumblebees. Some of these substances cause no mortality in bumblebees if used appropriately (Sechser and Freuler 2003; Morandin and Winston 2003; Franklin *et al.* 2004), but there is evidence that supplementary trials for non-lethal effects are necessary. For example, spinosad is a commonly used insect neurotoxin which, based on studies of honeybees, has been deemed harmless to bees. However, it has recently been shown that bumblebee larvae fed with pollen containing this pesticide give rise to workers with reduced foraging efficiency (Morandin *et al.* 2005). Mommaerts *et al.* (2006) screened eight chitin synthesis inhibitors currently registered as pesticides and found that although no lethal effect could be found on adults,



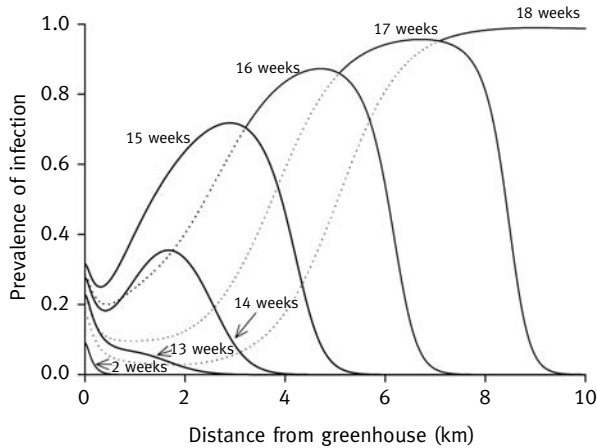
the use of these pesticides has strong effects on colony growth and the development of larvae. Diflubenzuron and teflubenzuron were found to be the most harmful to bumblebees, greatly reducing reproductive output at concentrations far below the recommended field concentrations.

In summary, it is likely that some pesticides currently in use do impact on bumblebee populations, but hard data are largely lacking and the extent and significance of this impact is unknown.

### 13.1.3 Impacts of non-native bees and commercial beekeeping

The subject of impacts of non-native bumblebees on native fauna (including native bumblebees) is dealt with in some detail in the following chapter. In brief, since the late 1980s a small number of bumblebee species (primarily *B. terrestris* and *B. impatiens*) have been commercially reared for pollination of glasshouse crops such as tomatoes. The trade in *B. terrestris* is mainly in the subspecies *B. t. dalmatinus* from south east Europe and *B. t. terrestris* from western Europe, or hybrids between the two. At present, an unknown number of colonies that probably approaches one million or more are shipped to at least 60 countries around the globe. These threaten native bumblebee species in the regions to which they are introduced in a number of ways: competitive displacement; introgression (where related species occur); accidental introduction of non-native pathogens; by acting as a reservoir for pathogens which spill over into wild populations (Goulson 2003).

Even when commercially reared bumblebees are native to the region in which they are being deployed, their use has the potential to be damaging to wild bee populations. For example in North America, the importation and use of non-native bumblebee species has been banned, and now only native species such as *B. occidentalis* and *B. impatiens* are used. *B. occidentalis* production has been ravaged by outbreaks of *Nosema bombi* so that much of the industry now relies on *B. impatiens*. It seems that commercially reared nests are regularly infested with parasites such as *Crithidia bombi* and *Locustacarus buchneri*, which spread from the commercial glasshouses into wild bee populations nearby, a phenomenon often known as 'pathogen spillover' (Colla *et al.* 2006; Otterstatter and Thomson 2008; Yoneda *et al.* 2008). For example, Yoneda *et al.* (2008) calculate that a single *B. terrestris* colony can generate >10,000 *L. buchneri* mites. A combination of field observations and modelling suggest that waves of infection of *C. bombi* travel outwards through the wild bee populations from glasshouses, that the wave of infection can spread at ~2 km per week, and that up to 100% of wild bees within the spreading radius of the pathogen can be infected by it (Otterstatter and Thomson 2008) (Fig. 13.4). Such figures provide the only coherent explanation for the rapid demise of several wild bumblebee species in North America in the past 10 years; transport of a pathogen with commercial bees to multiple sites across the continent, followed by waves of infection spreading outwards from these sites through wild bee species, some of which appear to be especially susceptible. It is notable that the most striking declines are within the subgenus *Bombus* (*B. terricola*, *B. affinis*, *B. franklini*



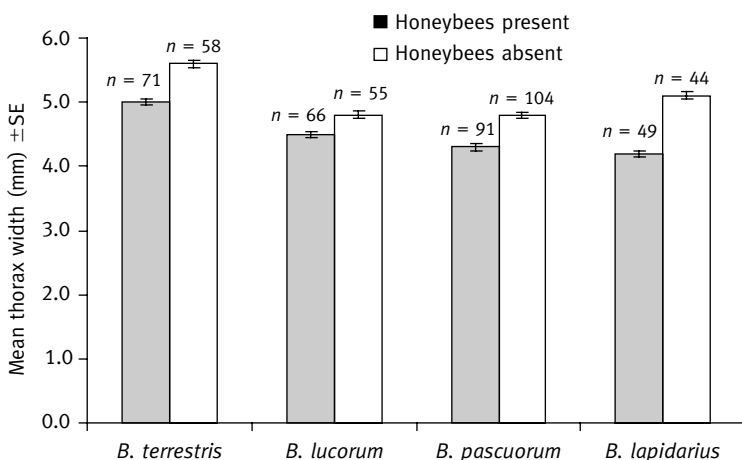
**Figure 13.4** Predicted long-term dynamics of pathogen spillover into wild bumblebee populations near glasshouses. From Otterstatter and Thomson (2008). Models for *Crithidia bombi* suggest that a wave of infection can spread from commercial glasshouse colonies through wild bee populations at a rate of 2 km per week. Predictions are partially supported by experimental observations.

and *B. occidentalis*) (Thorp 2005; Thorp and Shepherd 2005; Rao and Stephen 2007), suggesting that this subgenus has little resistance to the pathogen involved. The origins of the putative pathogen are unknown, but it is likely to be a non-native strain accidentally imported from Europe (see Chapter 14).

In addition to non-native bumblebee species, native pollinator communities in many parts of the globe also have to contend with other introduced bee species, most notably honeybees (*Apis mellifera*). These natives of Europe, Africa and the Middle East have been introduced by man to almost every country in the world. Honeybees are highly polylectic, usually visit a hundred or more different species of plant within any one geographic region (e.g. Butz Huryn 1997; Coffey and Breen 1997). In total they have been recorded visiting nearly 40,000 different plant species (Crane 1990b). There is thus the potential for them to compete with a large number of other flower-visiting organisms. It is well documented that honeybees can displace native organisms from preferred forage sources through disturbance and suppression of resource levels, but few studies have found evidence for impacts at the population level (Goulson 2003).

In Europe, honeybees are widely viewed as native. However, in northern Europe, it is unlikely that honeybees would be able to persist without human intervention, or would occur at low density. Feeding of colonies in the winter, and general care and maintenance of domesticated colonies almost certainly results in far higher densities of honeybees than would occur naturally (Goulson 2004). Thus, regardless of whether honeybees are native in northern Europe or not, there is the potential for them to have human-mediated negative impacts on populations of other flower-visiting insects.

Recent studies suggest that honeybees can have negative effects on bumblebees in Europe. In studies in agroecosystems in Germany, Walther-Hellwig *et al.* (2006) found that short-tongued bumblebees avoided areas of forage close to honeybee hives, while carder (*Thoracobombus*) bumblebees switched to foraging later in the day and were displaced from their preferred foodplant. Similarly, in studies of heathland bee communities in the United Kingdom, Forup and Memmott (2005) found that bumblebees were less abundant in places where honeybees were common (although competition between honeybees and bumblebees is not the only possible interpretation of their data). Perhaps more convincing as a demonstration of competition, Goulson and Sparrow (2009) found that workers of four common bumblebee species were significantly smaller in sites where honeybees were present, compared to where they were absent (Fig. 13.5). Worker size is highly variable in bumblebees, notably more so than in other social bee species (see Chapter 3). Smaller workers tend to carry out within-nest tasks while the larger ones collect pollen and nectar. Only when forage is scarce or if the large workers are lost from the colony do the smaller ones leave the nest to forage. Thus, the smaller size of bumblebees at sites where honeybees were present might reflect depression of resource levels, forcing smaller bees to forage and so reducing the average worker size. Alternatively and perhaps more likely, worker size may be smaller in areas where honeybees are present due to reduced food availability as larvae; adult size in bumblebees is determined by the amount they are fed during the larval stage (Sutcliffe and Plowright 1988; Ribeiro 1994). Either explanation suggests a direct and significant impact of honeybees on bumblebees. Large workers collect more food per unit time than do their smaller sisters (Goulson *et al.* 2002b; Peat and Goulson 2005), in part because large workers have higher visual acuity and so are more efficient at locating floral resources (Spaethe and Weidenmuller 2002), and perhaps also



**Figure 13.5** Mean thorax widths ( $\pm$ SE) of workers of four bumblebee species in sites in Scotland with and without honeybees ( $F_{1,507} = 190$ ,  $p < 0.001$ ). From Goulson and Sparrow (2009).

because they are better able to forage in cool weather (Peat *et al.* 2005b). Hence a nest with smaller workers is likely to have a reduced food supply and so produce fewer or smaller reproductives.

Probably the most telling evidence for competition between honeybees and bumblebees comes from outside the native range of honeybees, in North America. Here, Thomson (2004) experimentally introduced honeybees and found that proximity to hives significantly reduced the foraging rates and reproductive success of *B. occidentalis* colonies. Thomson (2006) also found a strong overlap between the foraging preferences of the two species, which peaked at the end of the season when floral resources were scarce, corresponding with a negative relationship between honeybee and bumblebee abundance.

There is increasing evidence that the spread of natural enemies of bumblebee colonies is being aided by honeybees. Honeybees can act as vectors for the bumblebee specific *C. bombi* via flowers (Ruiz- González and Brown 2006a). The African honeybee parasite *Aethina tumida* (small hive beetle) recently invaded North America, Egypt, Australia and Europe, and attacks *B. impatiens* colonies where it causes considerable damage (Spiewok and Neumann 2006; Hoffmann *et al.* 2008). It seems highly likely that it also attacks other wild bumblebee species that are not readily cultured and studied. Deformed wing virus, a viral honeybee pathogen, has been found in commercial colonies of *B. terrestris*, transmitted between the two species as a result of the practice of placing honeybees with queens to induce colony founding (Genersch *et al.* 2006). However, it has also been found in a wild colony of *B. pascuorum* which had been robbing a managed honeybee hive (Genersch *et al.* 2006). This virus appears to have higher virulence to bumblebees than to honeybees and the findings raise important questions about transmission and cross-infectivity between bumblebees and honeybees. Given the current issues surrounding honeybee health (particularly the outbreak of Colony Collapse Disorder in North America in 2007 and 2008), improving our understanding of disease transmission between wild and domesticated bees should be a priority.

If honeybees do impact on bumblebees as various studies suggest, then care should be taken when positioning hives, both within and outside the natural range of honeybees. For example, it would seem sensible to avoid positioning large numbers of hives near or in sites where rare bumblebee species survive. At present, there is no central register of honeybee hive locations in most countries, including the United Kingdom, and there are no controls on where hives are placed. It is thus extremely difficult to monitor or manage this potential threat to native bee species.

#### 13.1.4 Population structure and habitat fragmentation

Of course bumblebees are not the only wildlife to have declined in the previous past century. Many butterflies have decreased in abundance, particularly those associated with chalk and limestone grassland. For example, the number of known British populations of the adonis blue butterfly, *Lysandra bellargus*, approximately halved every 12 years

between 1950 and 1980 (Thomas 1983). Similarly, birds such as the skylark, lapwing and grey partridge have suffered catastrophic declines; in the past 20 years of the twentieth century they went from being among the most abundant farmland birds in the United Kingdom to being relative rarities. There are many other examples. However, it seems that bumblebees have been particularly hard hit as a group, with a disproportionate number of endangered species (e.g. 7 out of 27 UK species are listed on the Biodiversity Action Plan). Why should this be?

A clue can be gleaned from studying the pattern of decline. As a consequence of the various factors discussed earlier, populations of a number of bumblebee species have become increasingly small, fragmented and separated from one another by large distances. In the United Kingdom, where distributions are best known, declines appear to have followed a characteristic pattern. The last bumblebee species to disappear from the United Kingdom (*B. subterraneus*) was once widespread across southern England, but declined rapidly in the years after the Second World War. By the 1980s, the few remaining populations were small and isolated, surviving on habitat islands (nature reserves) that had escaped agricultural intensification. However, these populations subsequently disappeared despite the apparent suitability and protected status of the remaining habitat. The species was last recorded at Dungeness National Nature Reserve in 1988. Several other UK species such as *B. distinguendus* and *B. sylvarum* are in the late stages of a similar process, and are likely to go extinct in the near future. Why do isolated populations go extinct? Understanding the consequences of the fragmentation of remnant populations of bumblebees is of great importance to conservationists, given the current distributions of many rare species.

Small populations of all taxa are inherently more vulnerable to local extinctions due to environmental and demographic stochasticity (Frankham *et al.* 2002). If these populations form part of a broader metapopulation then regional extinctions can be balanced by subsequent recolonization, but if fragmentation is severe then extinct patches may never be repopulated. There are a number of reasons why bumblebees may be particularly badly affected by habitat fragmentation. It is the effective population size ( $N_e$ ), rather than the census population size ( $N_c$ ) which determines the rate of genetic drift in a population, and  $N_e$  may be several orders of magnitude lower than  $N_c$ . In bumblebees, as in many other social insects,  $N_e$  depends on the number of successful colonies. The  $N_e$  contributed by an individual colony depends on the number of egg-laying queens and the number of males they have mated with, but (unlike many other hymenopterans) bumblebee colonies are all founded by a single queen, and the vast majority of species are monoandrous (Estoup *et al.* 1995; Schmid-Hempel and Schmid-Hempel 2000). Hence most bumblebee nests are the product of a single mated pair. Furthermore, as a consequence of haplodiploidy (see Chapter 3), their  $N_e$  is equal to the number of successful nests  $\times 1.5$ , not  $\times 2$  as would be the case for a diplo-diploid organism, since males have half of the 'usual' amount of DNA. Hence a species that may appear to be abundant, in terms of workers, may have a very small effective population size.

Estimates of nest density for the common species in the United Kingdom suggest that they range from  $\sim 0.2\text{--}2\text{ Ha}^{-1}$ , averaged across habitats (Darvill *et al.* 2004; Knight *et al.* 2005; Osborne *et al.* 2008b). It is likely that nest densities for the rarer species are generally considerably lower. It is perhaps informative to do some crude 'back of an envelope' calculations. Let us suppose that the minimum viable population size for bumblebees is 100 breeding individuals ( $100/1.5 = 66.7$  nests surviving to reproductive age). If there are 0.2 successful nests/Ha (an optimistic estimate for rare species), then 333 Ha of suitable habitat would be required. Edwards (1999) suggested that a healthy bumblebee population requires at least  $10\text{ km}^2$  (1,000 Ha) of suitable habitat (this is an educated guess since we have very poor data on the nest densities or foraging ranges of bumblebees). It is notable that no surviving populations of *B. sylvarum* or *B. distinguendus* in the United Kingdom are known from areas smaller than this. Nature reserves have preserved some fine examples of natural and semi-natural habitats, but in densely populated countries such as the United Kingdom most of these reserves are tiny fragments of the original area, often of just a few hectares. Very few are large enough to support a viable population of bumblebees.

Contrast these figures with those for a solitary insect such as the adonis blue butterfly (*L. bellargus*). Healthy population of this species can persist on quite a small area of land for many decades; for example, a south-facing downland of just a few hectares near Folkestone in south-east England has supported a population of many thousands of adonis blues (all of which are potentially reproductively active) for at least 100 years, even though this population is very isolated (most surviving adonis blue populations are in Dorset and Wiltshire, more than 200 km to the west). It seems therefore that population sizes of bumblebees are very low compared to many solitary insect species, and due to their generally monogamous nature may be low even relative to other social insects. Small populations are inherently susceptible to chance extinction, and are also susceptible to the loss of genetic diversity. It is thus not surprising that only a few generalist species, those able to eke out a living in an impoverished agricultural landscape, have survived in most regions.

In addition to population size, a key factor influencing the viability of metapopulations in the long term is dispersal ability. In general, organisms with low dispersal are more prone to inbreeding and local extinction, and less able to colonize suitable unoccupied habitats. Until recently, very little was known about the dispersal abilities of bumblebees. Only young mated queens are able to found new populations, and on rare occasions they have been observed to travel considerable distances after hibernation. For example in Scandinavia, bumblebee queens have been recorded moving in streams along the coastline in spring; Mikkola (1978, 1984) recorded up to 900 queens of *B. lucorum* passing through a coastal strip 150 m wide within 1 h (although it is not clear where they were coming from or going to). On a rather smaller scale, Bowers (1985a) found movements of up to 1 km of nest-searching queens in the spring using mark-recapture, and this is almost certainly an underestimate since this method is not appropriate

for detecting rare long-distance movements. Dispersal of males has received very little attention, but could play a vital role in maintaining gene flow between population fragments. There is weak anecdotal evidence of occasional long-distance movement by male bumblebees; for example in 2007, a male *B. monticola* was caught in Hertfordshire, United Kingdom, more than 200 km from any suitable habitat for this montane species (B. Darvill, pers. comm.).

Another source of information on the dispersal abilities of bumblebees comes from monitoring their spread when introduced to areas where they are not native. When bumblebees were first introduced to New Zealand, they spread by up to 140 km per year (Hopkins 1914), suggesting a potential for very rapid movement. However, we cannot be certain that their dispersal was not artificially aided. They also successfully colonized islands up to 30 km off shore (Macfarlane and Griffin 1990), but conversely they are absent from islands at distances ranging from 16 to 55 km from the mainland (MacFarlane and Gurr 1995). In Tasmania, to which *B. terrestris* was introduced in 1992 (near Hobart), spread was initially slower, estimated at about 10 km per year (Stout and Goulson 2000), but it has since spread as far as the north coast (~200 km) (Hingston 2006).

It seems that sea barriers of over 10 km wide are sufficient to restrict gene flow and allow the evolution of subspecies. Subspecies of *B. terrestris* and *B. lucorum* have developed where populations are separated by straits of 10 km (Elbe/Corsica), 12 km (Italy/Sardinia), 16 km (Spain/North Africa) and 32 km (Great Britain/Europe) (Rasmont 1983). In Japan, incipient speciation is evident in populations of *B. diversus* separated by straits of 19 and 43 km width (Ito 1987). Conversely, bumblebee queens (notably *B. terrestris*) are occasionally caught at lightships at sea, up to 30 km offshore, suggesting that major trips across water barriers do occur.

Dispersal of small organisms such as insects is exceptionally hard to observe directly under normal circumstances, and can provide us with little information on the frequency or magnitude of movements. An alternative approach is to use neutral genetic markers to quantify patterns of relatedness within and between populations. If all populations within a region are genetically homogenous, the implication is that movement of individuals between populations is frequent. Populations can only diverge (via genetic drift or founder effects) if gene flow is negligible. During the 1970s and 1980s, studies using allozymes were popular in this respect; these are polymorphic enzymes that can be separated using gel electrophoresis. However, it seems that *Bombus* exhibit unusually little variation in their allozymes compared to other insects, rendering this approach of little value (Pamilo *et al.* 1984; Scholl *et al.* 1990; Owen *et al.* 1992; Estoup *et al.* 1996). With hindsight this may not be surprising since many of the most polymorphic allozymes have since been found to be temperature sensitive (morphs have different optimal temperatures for activity) and subject to selection: since active bumblebees maintain a near-constant internal temperature, temperature-dependent selection is unlikely to operate.

More recently, the development of an array of molecular techniques have made it possible to directly assess variation in DNA sequences between individuals, and this approach has revealed considerable variation within bumblebee species. Mitochondrial DNA sequences and microsatellites have both proved to be variable and informative (Estoup *et al.* 1996; Pirounakis *et al.* 1998; Widmer and Schmid-Hempel 1999). Initial studies focused largely on two abundant and widespread European species, *B. terrestris* and *B. pascuorum*. In *B. terrestris*, there appears to be little population substructuring within mainland Europe, suggesting that dispersal is frequent and that there are no substantial isolating barriers between populations (Estoup *et al.* 1996). However, populations on various Mediterranean islands and Tenerife (Canary Islands) were distinct, suggesting that substantial bodies of water do provide a more or less complete barrier to movement (Estoup *et al.* 1996; Widmer *et al.* 1998). Similarly, whilst mainland populations of *B. ignitus* in Asia were found to be genetically similar, distant offshore populations were significantly differentiated (Shao *et al.* 2004). In *B. pascuorum*, populations throughout most of mainland Europe are similar, but differ markedly from those found south of the Alps in Italy (Pirounakis *et al.* 1998; Widmer and Schmid-Hempel 1999). There were also small differences between populations in Scandinavia and those in the body of Europe. Widmer and Schmid-Hempel (1999) conclude that *B. pascuorum* probably invaded Europe from two refugia following the last ice-age, with one population coming to occupy most of Europe from Spain to Sweden, and the other remaining trapped in Italy. It seems therefore that genetic structuring is observed when populations are separated by appreciable barriers, like mountain ranges or large stretches of water.

Until recently, studying the population genetics of rare bee species was extremely difficult, as lethal sampling was necessary. Work in this area was greatly aided by the development of a non-lethal DNA sampling technique (Holehouse *et al.* 2003), and this has recently been applied to studies of fragmented populations of rare species: *B. muscorum* (Darvill *et al.* 2006), *B. sylvarum* (Ellis *et al.* 2006) and *B. distinguendus* (Bourke and Hammond 2002). All three studies found significant population structuring. For example in *B. muscorum*, all populations >10 km apart were significantly differentiated, as were some populations just 3 km apart. Ellis *et al.* (2006) used microsatellite markers to group workers into sisterhoods and so estimated the number of colonies (and hence  $N_e$ ) in populations of *B. sylvarum*. Estimates of  $N_e$  were very low (range 21–72) suggesting that, if isolated, these populations are very vulnerable to loss of genetic diversity through drift. Indeed, significant differentiation was found between all populations suggesting that they are genetically isolated. In all three rare species, genetic diversity (allelic richness and heterozygosity) was reduced compared to common species, and island populations showed further reductions (Table 13.1).

Comparing genetic diversity across species is of debatable validity, since different microsatellite markers vary enormously in their variability, and thus the variation observed in any particular study depends on which microsatellites were chosen. The bumblebee microsatellites in common use were developed for *B. terrestris*, which means



**Table 13.1** Genetic diversity (allelic richness and heterozygosity,  $H_E$ ) estimates for populations of a number of *Bombus* species (mean  $\pm$  SE).

Species	Population	Sample Size	Allelic Richness	$H_E$	Source
<i>B. ignitus</i>	Beijing, China	33	12.2 $\pm$ 1.53*	0.85 $\pm$ 0.02	Shao <i>et al.</i> (2004)
<i>B. ignitus</i>	Zhejiang, China	21	9.44 $\pm$ 1.34*	0.84 $\pm$ 0.03	Shao <i>et al.</i> (2004)
<i>B. ignitus</i>	Niigata, Japan	19	8.33 $\pm$ 0.97	0.82 $\pm$ 0.03	Shao <i>et al.</i> (2004)
<i>B. ignitus</i>	Nagano, Japan	26	8.22 $\pm$ 0.72*	0.83 $\pm$ 0.03	Shao <i>et al.</i> (2004)
<i>B. pascuorum</i>	Landford, UK	183	6.22 $\pm$ 1.19*	0.52 $\pm$ 0.15	Darvill <i>et al.</i> (2004)
<i>B. pascuorum</i>	Rothamsted, UK	125	5.71 $\pm$ 1.01	0.52 $\pm$ 0.11	Knight <i>et al.</i> (2005)
<i>B. pascuorum</i>	Continental Europe	22.7 average	5.49 $\pm$ 0.16*	0.56 $\pm$ 0.01	Widmer and Schmid-Hempel (1999)
<i>B. pascuorum</i>	Foix, France	29	6.57 $\pm$ 1.14	0.54 $\pm$ 0.12	Ellis <i>et al.</i> (2006)
<i>B. sylvarum</i>	Epenede, France	10	4.00 $\pm$ 0.85*	0.53 $\pm$ 0.09	Ellis <i>et al.</i> (2006)
<i>B. terrestris</i>	Continental Europe	37.5 average	5.96 $\pm$ 0.12*	0.61 $\pm$ 0.01	Estoup <i>et al.</i> (1996)
<i>B. terrestris</i>	Landford, UK	79	8.39 $\pm$ 1.15	0.74 $\pm$ 0.06	Darvill <i>et al.</i> (2004)
<i>B. terrestris</i>	Rothamsted, UK	158	7.57 $\pm$ 1.32	0.72 $\pm$ 0.06	Knight <i>et al.</i> (2005)
<i>B. lucorum</i>	Bern, Switzerland	40	7.00 $\pm$ 2.00*	0.60 $\pm$ 0.12	Estoup <i>et al.</i> (1996)
<i>B. lucorum</i>	Landford, UK	52	10.16 $\pm$ 1.58	0.80 $\pm$ 0.04	Darvill (2007)
<i>B. lapidarius</i>	Rothamsted, UK	269	6.40 $\pm$ 0.61	0.72 $\pm$ 0.03	Knight <i>et al.</i> (2005)
<i>B. pratorum</i>	Rothamsted, UK	125	5.84 $\pm$ 0.99	0.69 $\pm$ 0.05	Knight <i>et al.</i> (2005)
<i>B. hypnorum</i>	Various, Sweden	10	6.75 $\pm$ 1.03*	0.72 $\pm$ 0.14 <sup>†</sup>	Paxton <i>et al.</i> (2001)
<i>B. jonellus</i>	Outer Hebrides, UK	53.4 average	8.20 $\pm$ 0.36	0.74 $\pm$ 0.01	Darvill (2007)
<i>B. jonellus</i>	Inner Hebrides, UK	40.8 average	9.26 $\pm$ 0.24	0.74 $\pm$ 0.01	Darvill (2007)
<i>B. jonellus</i>	Mainland Scotland	42	9.76 $\pm$ 1.89	0.76 $\pm$ 0.07	Darvill (2007)
<i>B. sylvarum</i>	Southern UK	25.6 average	3.12 $\pm$ 0.10	0.39 $\pm$ 0.02	Ellis <i>et al.</i> (2006)
<i>B. muscorum</i>	Outer Hebrides, UK	43.8 average	3.22 $\pm$ 0.12	0.39 $\pm$ 0.01	Darvill <i>et al.</i> (2006)
<i>B. muscorum</i>	Inner Hebrides, UK	62.7 average	3.21 $\pm$ 0.07	0.47 $\pm$ 0.01	Darvill <i>et al.</i> (2006)
<i>B. muscorum</i>	Southern UK	35.5 average	4.01 $\pm$ 0.06	0.51 $\pm$ 0.01	Darvill <i>et al.</i> (2006)
<i>B. distinguendus</i>	Scotland, UK	7.75 average	2.63 $\pm$ 0.23*	0.42 $\pm$ 0.01 <sup>†</sup>	Bourke and Hammond (2002)
<i>B. florilegus</i>	Hokkaido, Japan	90	2.31 $\pm$ 0.33*	0.35 $\pm$ 0.08 <sup>†</sup>	Takahashi <i>et al.</i> (2008a)

Species above the gap are widespread in the study region, those below are rare, declining and exist in fragmented populations. Where possible, allelic richness is a normalized measure which takes account of differing sample sizes by using rarefaction based on a population size of 23, giving a comparable figure across populations.

\*Allelic richness was not available, and the average number of alleles per locus is presented.

<sup>†</sup>Expected heterozygosity was not available, and observed heterozygosity is given. These measures are expected to be very similar for populations that are in Hardy-Weinberg equilibrium.

that they are likely to have been selected on the basis that they are highly variable in this species. However, as data amass from a large number of bumblebee species and geographic regions, a clear pattern emerges which is hard to explain other than by inferring a causal relationship: common species consistently have more genetic diversity than rare species (Table 13.1). It would be interesting to evaluate genetic diversity in museum specimens to quantify how much genetic diversity has changed during the decline of such rare species.

Until very recently, we had no indication as to whether bumblebee species differ in their dispersal abilities. Rare species with fragmented populations exhibit more population structuring and less genetic variation than do ubiquitous species (Table 13.1), but this is as we would expect even if dispersal abilities were similar. Two complementary lines of evidence have emerged which suggest that there is considerable variation in the propensity and/or ability of different bumblebee species to disperse. Darvill (2007) compared the genetic structure of populations of *B. muscorum* (a rare species that has declined considerably in much of Europe) with that of *B. jonellus* (a species which is widespread and has probably declined little, although it is generally uncommon). The two species co-occur on most Hebridean Islands, allowing for a direct comparison between the two species in a situation where their geographic distribution is near identical. The results are very revealing; they suggest that *B. muscorum* rarely if ever crosses sea barriers of >10 km, while *B. jonellus* appears to readily cross sea barriers of >30 km (counterintuitively, *B. muscorum* is the larger of these two species). This may explain why *B. muscorum* is far more prone to population collapse; limited dispersal makes it prone to inbreeding and renders recolonization events unlikely. The second line of evidence relates to natural colonization events that have been recorded in bumblebees. *B. pratorum* and *B. monticola* both appear to have colonized Ireland from the United Kingdom during the twentieth century, while *B. hypnorum* colonized the United Kingdom from the continent in 2001 (Goulson and Williams 2001). These three species all belong to the subgenus *Pyrobombus*, which also includes *B. jonellus*, and suggests that this subgenus may be atypically dispersive. None of the UK *Pyrobombus* are included on the UK BAP list. In contrast, *B. muscorum* belongs to *Thoracobombus*, and four of the five *Thoracobombus* are on the BAP list. If dispersal abilities tend to be similar between closely related species, as we might expect, then Darvill's (2007) comparison of *B. jonellus* and *B. muscorum* may provide a more general explanation as to why *Thoracobombus* species are particularly prone to metapopulation collapse.

To summarize, it is clear that rare bumblebees surviving in habitat fragments have very low effective population sizes, and that many populations are isolated from one another. These are exactly the circumstances in which we would expect to see gradual metapopulation collapse, with chance extinction events occurring more rapidly than recolonization events, so that the metapopulation heads inexorably towards extinction. This process may be exacerbated in some species which appear to have poor powers of dispersal. It would appear that *B. subterraneus* suffered from metapopulation collapse,

and this is likely to be happening in *B. sylvarum* and *B. distinguendus*, species that may already be doomed to extinction in the United Kingdom unless suitable habitat availability increases.

### 13.1.5 Do bumblebees suffer from inbreeding depression?

Small population size and limited dispersal can in themselves lead directly to extinction, but they have a secondary effect that may reduce population fitness and accelerate extinction. In a functioning metapopulation, dispersal maintains genetic cohesion and diversity. Conversely, if dispersal is limited or absent and populations are small, they will lose genetic diversity through drift. This both reduces evolutionary potential and can lead to expression of deleterious recessive alleles which reduce individual fitness (Frankham *et al.* 2002). The data described earlier strongly suggest that loss of genetic diversity is occurring in rare bumblebees, but the evidence for a direct fitness costs to inbreeding is more ambiguous.

To date, relatively few studies have attempted to determine the consequences of inbreeding in bumblebees. There is some evidence for reduced colony foundation and hibernation success in response to brother–sister mating but no effect on reproductive output or cumulative fitness (Gerloff and Schmid-Hempel 2005; Duchateau *et al.* 1994). Beekman *et al.* (1999) however found that inbred queens laid fewer eggs. Gerloff *et al.* (2003) found no evidence for a reduced encapsulation (immune) response. These studies must all be treated with some caution as they were all performed in a laboratory situation with unlimited food and few of the stresses that bees are likely to encounter in natural situations. Nonetheless, a recent meta-analysis concluded that haplo-diploid insects suffer less from inbreeding than diploid insects, perhaps due to purging of non-sex limited recessive alleles in haploid males (Packer and Owen 2001), but that substantial inbreeding depression does occur (Henter 2003).

An additional cost may be imposed on inbred populations of many hymenopteran species as a result of their haplo-diploid sex determination mechanism. The mechanism centres on a polyallelic sex determining locus, and has important consequences for small populations (Cook and Crozier 1995). Individuals heterozygous at this locus develop into females, and homozygous (or hemizygous) individuals develop into males. In a large population, diversity at this locus is maintained by negative frequency dependent selection. As populations diminish in size, genetic drift accelerates and can lead to a reduction in the number of sex alleles in the population, increasing the probability of a ‘matched mating’. A queen that mates with a male who shares one of her sex determining alleles will produce a colony in which 50% of her workforce are diploid males. In honeybees and ants, diploid male larvae are consumed by the workers, which minimizes their cost, but in bumblebees they are reared to adulthood (Duchateau *et al.* 1994). Bumblebee diploid males are viable although presumed to have low fertility (but see Ayabe *et al.* 2004) and reduced immune response (Gerloff *et al.* 2003), and therefore represent a considerable cost to the colony best viewed as 50% worker mortality (Packer

and Owen 2001). Diploid male producing colonies generated by lab crosses die swiftly when placed out in field conditions, and fare much more poorly than outbred colonies (P. Whitehorn, unpublished data).

Diploid males represent a clear example of inbreeding depression, and have been detected in numerous wild populations of hymenopterans (e.g. Zayed and Packer 2001; Stahlhut and Cowan 2004). Their frequency has been proposed as an indicator of population fitness (Zayed *et al.* 2004) and recent modelling work has shown that diploid male production, where present, may initiate a rapid extinction vortex (Zayed and Packer 2005). Until recently, diploid male production had not been detected in naturally occurring populations of bumblebees. However, in the past few years they have been discovered in two UK bumblebee species, *B. muscorum* (Darvill *et al.* 2006) and *B. sylvarum* (Ellis *et al.* 2006), and the rare Japanese species *Bombus florilegus* (Takahashi *et al.* 2008a).

The survival of introduced populations of bumblebees provides evidence that some bumblebee species can cope with high levels of inbreeding. Genetic evidence suggests that the populations of *B. subterraneus* and *B. hortorum* introduced to New Zealand over 100 years ago went through a severe initial bottleneck (G. Lye, unpublished data). Similarly, the *B. terrestris* population in Tasmania (which came from New Zealand) appears to be thriving, but genetic studies suggest it may have originated from just one or two individuals (Schmid-Hempel *et al.* 2007). However, in both Tasmania and New Zealand there is little or no competition from other bumblebee species, a plethora of introduced weeds suitable for bumblebees to forage on, and a lack of many of the parasites that affect bumblebees in their native range (Allen *et al.* 2007). Hence it may be that these populations persist despite inbreeding depression, rather than because there is none.

We do not as yet have unequivocal evidence that inbreeding plays a major role in driving small, isolated populations of bumblebees to extinction. If reductions in the genetic diversity of neutral markers found in rare species are indicative of reductions in the diversity of functional genes, then there will be concomitant consequences for evolutionary potential and perhaps also reductions in fitness through inbreeding depression. If fragmented populations of rare bumblebee species are suffering from reduced fitness through inbreeding then we must take steps to conserve what genetic diversity remains. Management strategies in vertebrates routinely consider genetic factors, and we may need to adopt similar measures in the management of rare bumblebee populations.

## 13.2 Why are some bumblebee species still abundant?

Some bumblebee species appear to have been largely unaffected by habitat loss, fragmentation and degradation. In much of Europe, six species are widespread and common (*B. terrestris*, *B. lucorum*, *B. lapidarius*, *B. pratorum*, *B. hortorum* and *B. pascuorum*). Some species have actually expanded their range in recent years. Both *B. lapidarius*

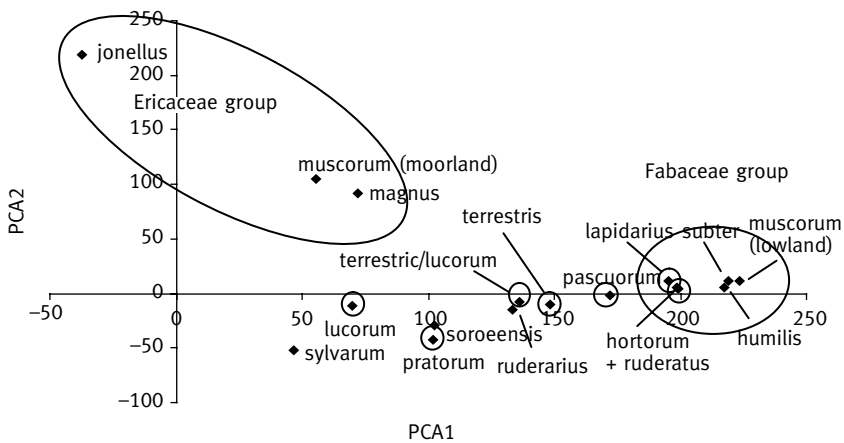
and *B. terrestris* have expanded their range northwards in Scotland in the past 10 years (MacDonald 2001), while *B. hypnorum* has recently colonized the United Kingdom from mainland Europe (Goulson and Williams 2001). We have no historical data on abundance for comparison, but it seems probable that abundance of these common species may be lower than it used to be in heavily farmed areas. Nonetheless, these species are still found in a broad range of habitats, and remain familiar sights throughout Britain and most of Europe.

How do the common species differ from those that have suffered major range contractions? Williams (1986, 1988) proposes an explanation, the 'marginal mosaic model', based on some earlier general models of species distribution and abundance (Andrewartha and Birch 1954; Brown 1984). He points out that each bumblebee species occupies a particular climatic range. Within the centre of this range the species should be able to forage most profitably, and persist in a range of habitats including those that are not ideal. However, towards the edge of their range, each species will only be able to survive in the very best habitats, and even here it would be expected to be less abundant than those species near the centre of the range. If the quality of a habitat declines, it would thus be species near the edge of their climatic range that become extinct first (and the extinction process may be hastened by competition with species that are near the centre of their range that are better adapted to local conditions). This argument does appear to explain the pattern of species loss in the United Kingdom, at least in part. Species at the northern edge of their range (e.g. *B. subterraneus*) or the southern edge (e.g. *B. distinguendus*) have been affected most by declining habitat quality. In contrast, species such as *B. terrestris*, which is near the centre of its range, remains abundant even in poor quality habitats. Williams (2005) recently showed that rare and declining species in Britain tend to occupy small climatic and geographic ranges within Europe. He suggests that these species may have more specific habitat associations or climatic requirements, which render them more susceptible to environmental change. Williams *et al.* (2007) calculate that the range contractions of *B. distinguendus* and *B. sylvarum*, probably the UK's two most endangered species, have been towards the centre of the climatic niche space occupied by each species, that is, populations further from the centre of the species' range have been more likely to go extinct. However, climatic factors cannot explain all aspects of bumblebee declines. Some species have declined much more than others even within the heart of their range. For example, *B. subterraneus* is now thought to be very rare throughout western Europe, but apparently increased near the northern edge of its range in Finland in the 1970s (Pekkarinen *et al.* 1981).

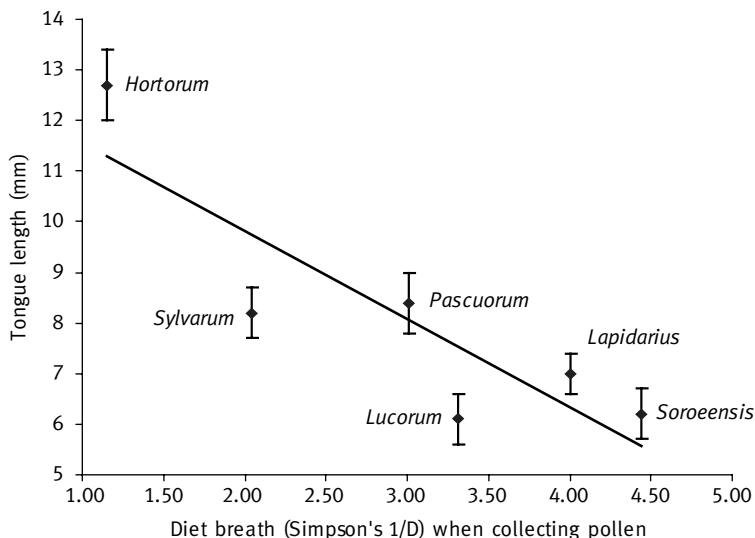
An alternative but not mutually exclusive explanation for bumblebee declines relates to forage use. It seems intuitively likely that more specialized species are more likely to be susceptible to habitat degradation or loss. A small number of bumblebee species are known to be tightly associated with just one plant species, at least within particular parts of their range; for example, *B. consobrinus* with *Aconitum septentrionale* (Løken 1973; Rasmont 1988), and inevitably such species are rare and localized. Based on studies of forage use, I have argued that the rare and declining species tend to be long tongued

and have narrower diets, with a very large proportion of the pollen they collect being from Fabaceae (many of which have deep flowers) (Goulson and Darvill 2004; Goulson *et al.* 2005, 2006, 2008b). This is supported by a substantial data set of bumblebee foraging records gathered from throughout the United Kingdom, and separated according to whether they were collecting pollen, nectar, or both. Principal Components Analysis of visitation rates of pollen-collecting bees suggested that the best separator of bee species is the proportion of their pollen-collecting visits that are to Fabaceae (Fig. 13.6). Some species tend to get 90–100% of their pollen from Fabaceae (e.g. *B. hortorum*, *B. ruderatus*, *B. subterraneus* and *B. humilis*), and these tend to be long tongued and, with the exception of *B. hortorum*, they are all declining species. Parallel studies of more diverse bumblebee communities in Poland confirm similar patterns (although it must be noted that many of the bee species overlap with those in the UK studies) (Goulson *et al.* 2008b).

Overall, there appears to be a negative relationship between diet breadth when collecting pollen, and tongue length (Fig. 13.7) (Goulson *et al.* 2005, 2008b). This is odd, because bees do not use their tongue to collect pollen. However, many of the Fabaceae from which these bees collect pollen do have deep flowers (e.g. *T. pratense*, *Anthyllis vulneraria*, *Vicia cracca*). These long-tongued Fabaceae-specialist bumblebee species tend to be associated with unimproved grasslands (calcareous grasslands, haymeadows, machair, etc.), which are rich in Fabaceae. The reason that unimproved grasslands are



**Figure 13.6** Foraging preferences of pollen-collecting bumblebees, based on >3,000 bee observations from sites across the United Kingdom. The proportion of visits to different plant families by workers of each bumblebee species was subjected to principal components analysis, and the first two components are plotted here. Combined data for *B. terrestris/lucorum* from southern UK is plotted separately to *B. terrestris* alone (New Zealand data) and *B. lucorum* alone (Hebridean data). The six common bumblebee species are circled. The first and second component account for 71.1% and 15.7% of variation in forage use, respectively. Component 1 is strongly correlated with visits to Fabaceae, while component two is correlated with visits to Ericaceae, and so separates out moorland species. From Goulson *et al.* (2005).



**Figure 13.7** Relationship between worker tongue length and diet breadth when collecting pollen as calculated using Simpson's index. This relationship remains when rarefaction is used to calculate diet breadth. Based on studies of bumblebee communities in Southern Poland (Goulson *et al.* 2008b).

rich in Fabaceae is because they occur on soils with low soil fertility; the Fabaceae have mutualistic root bacteria to obtain nitrates from the air, and this gives them a competitive advantage over other plants when soil fertility is low. Unfortunately, the addition of artificial fertilizers promotes rapid growth of grasses (boosting fodder production) at the expense of Fabaceae, and this process led to the near-eradication of unimproved grasslands in the second half of the twentieth century; more than 90% has been lost in the United Kingdom (Fuller 1987; Howard *et al.*, 2003). Hence it is easy to see why bumblebee species that formerly flourished in Fabaceae-rich haymeadows across the United Kingdom are now rare or extinct.

In contrast, the common bumblebee species tend to have broad foraging preferences and readily encompass non-native garden plants and mass-flowering crops in their diets (Goulson *et al.* 2002, 2005). *B. terrestris* in particular is the most polylectic bumblebee known, and is also the most abundant bumblebee throughout much of Europe. It is short tongued, but by nectar robbing it is also able to access some flowers with deep corollas. It has been recorded feeding on many hundreds of flower species both within and outside of its natural range (Free and Butler 1959; Proctor *et al.* 1996; Semmens 1996a,b; Ne'eman *et al.* 2000). However, it is unclear whether the large number of plant species that it has been recorded visiting are the cause of its ecological success, or simply an artefact of its abundance. There have been far more studies of *B. terrestris* than of other bumblebee species, so that it is inevitable that it has been recorded feeding on a lot of plants.

A fascinating insight into the foraging behaviour of bumblebees in the past is provided by the recent work of Kleijn and Raemakers (2008), who identified pollen on the bodies of museum specimens of bumblebees collected in Belgium, England and Holland before 1950. They obtained specimens of both common and declining species, and compared pollen preserved on their bodies with that on field-caught specimens from the same localities in 2004–2005. They concluded that, even in the past when they were relatively abundant, species that were subsequently to decline had a narrower diet breadth than the species which have remained common. The species that were about to decline also tended to visit plant species which were themselves to decline, whereas the bee species that have remained common benefited from increases in some of their preferred foodplants (such as *Trifolium repens* which is much favoured by *B. terrestris* and *B. lapidarius*). Overall, it seems clear that there is a link between the pollen collected by bees and their susceptibility to decline.

In the United Kingdom and Ireland, there seems to be a broad correlation between rarity and emergence time, with rare species tending to emerge later (Goulson *et al.* 2005; Fitzpatrick *et al.* 2007). Bumblebee species differ greatly in the time of year at which queens emerge from hibernation; the earliest species emerge in February, while other species do not appear until late May or June. It is perhaps worth noting that there are very few flowers in unimproved grasslands before May. Thus it makes sense for species such as *B. distinguendus* and *B. subterraneus* that seem to be associated with such grasslands, and the deep-flowered Fabaceae that they contain, to emerge late from hibernation. Species with a late emergence time tend to have small colonies and hence a lower intrinsic rate of increase, presumably because there is simply not time to rear lots of offspring. This may make these species less able to cope with environmental perturbations (Williams and Osborne 2009). The species that emerge late are largely the same as those that are long tongued and dependent on Fabaceae for pollen, and this may be because Fabaceae pollen is exceptionally high in protein (Hanley *et al.* 2008) and a high-quality pollen source is needed for rapid colony growth when the season available is short.

There may be other disadvantages to emerging late, aside from the short season that this strategy necessitates. It may be difficult for naïve queens emerging from hibernation to compete effectively with experienced workers when foraging (see Chapter 7). Where nesting habitat is scarce, those species in which queens emerge early in the season may be able to monopolize available nest sites, reducing the chances of colony founding for later emerging queens. In urban parks in San Francisco, *B. vosnesenskii* is the most abundant species, and is also the earliest emerging of the community of bumblebees found there (McFrederick and LeBuhn 2006). Rodent holes were found to limit bumblebee abundance and it is suggested that the earliest emerging species monopolizes nest sites.

An intriguing theory related to me by Mike Edwards is that the bee species that remain common are those that evolved in woodland and woodland edge habitats, and hence emerge early to exploit spring flowers such as bluebells which appear in March and April before bud-burst in the tree canopy above excludes the light. Gardens arguably provide a surrogate 'woodland edge' habitat, again with abundant spring forage, and



hence these species remain common in suburban areas. In contrast, the declining species are often associated with unimproved grassland habitats in which flowers appear later (and which have been largely eradicated to make way for arable crops).

One final factor merits discussion with regard to differences in bumblebee ecology that may influence their ability to thrive in modern landscapes. In recent years, it has become apparent that there are major differences between bumblebee species in their foraging range (Walther-Hellwig and Frankl 2000; Darvill *et al.* 2004; Knight *et al.* 2005). Species such as *B. terrestris* and *B. lapidarius* have been found to forage further afield than so-called 'doorstep foragers' such as *B. pascuorum*, *B. sylvarum*, *B. ruderarius* and *B. muscorum*. It is perhaps significant that the former two species remain ubiquitous in much of Europe, while three of the four doorstep foragers have declined (although as noted earlier this may also be because the males and/or queens of these *Thoracobombus* species have poor dispersal abilities; we do not as yet know whether worker foraging range and dispersal range of reproductives are correlated, but it seems probable). A larger foraging range would give a greater chance of colony survival in areas where the average density of floral resources is low or where resources are highly patchy (Fig. 6.7). Intensively farmed arable landscapes with occasional fields of mass-flowering crops provide just such a landscape, and it is probably no coincidence that *B. terrestris* and *B. lapidarius* are among the species most commonly recruited in large numbers to such crops (Goulson *et al.* 2006; Osborne *et al.* 2008a).

Overall, it is hard to disentangle the various factors that influence which species of bumblebees have declined most, and it is perhaps foolish to search for a general explanation, since differences in diet breadth, climatic niche, forage range, emergence time and nest site requirements render each species unique. Many of these factors are strongly correlated with one another (e.g. emergence time, tongue length and dietary specialization) so that separating out the relative importance of each in determining sensitivity to environmental change may not be possible.

### 13.3 Consequences of declining bumblebee numbers

The plight of our bumblebee fauna deserves particular attention because loss of bee species will have knock-on effects for other wildlife. As already mentioned, a large number of wild plants are pollinated predominantly or exclusively by bumblebees, sometimes by particular species of bumblebee (Corbet *et al.* 1991; Kwak *et al.* 1991a,b; Osborne *et al.* 1991; Rathke and Jules 1993). Reduced bumblebee numbers will result in reductions in seed set, which has obvious implications, and can also lead to reduced outcrossing and thus to inbreeding. Most bumblebees are generalist pollinators and most insect-pollinated plants use multiple pollinators (Waser *et al.* 1996), so it could be argued that pollination networks are buffered against the loss of a few pollinator species. However, a recent study simulating the effects of removal of individual pollinators from pollination networks demonstrated that removal of highly linked pollinators such as bumblebees produced the greatest rate of decline in plant species diversity, compared to

removing less polylectic pollinators (Memmott *et al.* 2004). Declining pollination services can be very detrimental when plants are already scarce and threatened directly by the same changes in land use that threaten the bees (Senft 1990; Jennersten *et al.* 1992; Lavery 1992; Oostermeijer *et al.* 1992; Kwak *et al.* 1996; Young *et al.* 1996; Fischer and Matthies 1997; Steffan-Dewenter and Tschardtke 1997). It seems probable that reductions in the abundance and species richness of bumblebees may lead to widespread changes in plant communities (Corbet *et al.* 1991). And of course these changes will have further knock-on effects for associated herbivores and other animals dependent on plant resources.

Bumblebees also directly support a diverse array of parasites, commensals and parasitoids, organisms that feed on bumblebee adults, immature stages, or on detritus in the nest. Over 100 species of insects and mites have been discovered living in bumblebee nests, and many are found nowhere else (Alford 1975). Because of their vital role in supporting a diverse range of other organisms, bumblebees can be regarded as keystone species (Kevan 1991; Corbet 1995). If our bumblebees disappear then much else will go with them.

Aside from the implications for conservation, there are good financial reasons for conserving bumblebees. The yields of many field, fruit and seed crops are greatly enhanced by bumblebee visitation (Corbet *et al.* 1991; Free 1993; Osborne and Williams 1996; Carreck and Williams 1998). For example, field beans are largely dependent on pollination by longer-tongued species such as *B. pascuorum* and *B. hortorum*, and without them, yields are reduced (Free and Williams 1976). Bumblebees are acknowledged to be more reliable pollinators than honeybees, particularly because they will continue foraging even when it is cold and wet. In a poor spring, bumblebee queens (and perhaps also solitary bees such as *Osmia rufa*) may be the only insects that remain active enough to pollinate early flowering crops such as hard fruits. Reliance on honeybee pollination is also risky since if a disease or parasite epidemic removes this one species, and no alternatives are available, then crops will fail. In the United States, there is an ongoing decline in managed honeybee populations due to disease, misuse of pesticides, loss of subsidies, dangers associated with invading Africanized honeybees (Kremen *et al.* 2002), and most recently by Colony Collapse Disorder. The value of crop pollination by honeybees in the United States has been estimated at between 5 and 14 billion US dollars per year, but beekeeping has diminished by around 50% over the past 50 years (Kremen *et al.* 2002). This has given rise to concerns over the future of insect-pollinated crops such as cucumber, pumpkin, watermelon, blueberry and cranberry (Delaplane and Mayer 2000; Richards 2001; Kremen *et al.* 2002). At sufficient densities, bumblebees pollinate many of these crops efficiently (e.g. Stubbs and Drummond 2001). However, the impoverished bumblebee communities often associated with agricultural landscapes may be insufficient to replace the services currently provided by honeybees. Thus even those with no interest in conserving biodiversity for its own sake should be concerned, for there are direct economic costs to the decline in wild bee abundance.

## 13.4 Conservation strategies

### 13.4.1 Enhancing bumblebee diversity in farmland

A major cause of bumblebee declines is undoubtedly loss of habitat to intensive farming, and the concomitant reduction in habitat heterogeneity at the landscape scale. However, there are moves to reverse this trend in Europe and North America where there is a growing emphasis on combining the goals of agriculture and conservation (Ovenden *et al.* 1998; Kleijn and Sutherland 2003). Subsidies are currently available in many countries for agri-environment schemes that promote biodiversity, including replanting of hedgerows, repair of existing hedgerows, conservation headlands, beetlebanks (strips of tussock-forming grasses planted across fields), uncropped field margins (either allowed to regenerate naturally or sown with wildflower seed mixtures) and restoring flower-rich grassland (Kaule and Krebs, 1989; Firbank *et al.* 1993; Marshall *et al.* 1994; Sotherton 1995; Kleijn *et al.* 1998).

As yet little is known as to the relative value of these various forms of management for many wildlife taxa, and they are likely to differ between faunal or floral groups. Indeed the objectives of the schemes are often rather vague, and the prescriptions developed without reference to any evidence base (Webster and Felton 1993). However, there is no doubt that broadly the schemes do benefit wildlife. For example, hedgerows and beetlebanks provide overwintering sites for beetles, and so boost the overall populations on farmland (Dennis and Fry 1992). They also provide a home for small mammals and nesting sites for birds (Boatman 1992; Aebischer *et al.* 1994; Boatman and Wilson 1988). Conservation headlands have been shown to increase abundance of farmland butterflies (Dover *et al.* 1990; Dover 1992; Feber *et al.* 1996), and to provide nectar for hoverflies (Syrphidae) (Cowgill *et al.* 1993).

Most of the management options promote floral abundance and diversity, and any form of management that increases floral resources and reduces the area of crop is likely to benefit bumblebees (Dramstad and Fry 1995), particularly since the reproductive output of bumblebee colonies is directly linked to food availability (Sutcliffe and Plowright 1988).

#### 13.4.1.1 *Field margin management and wildflower strips*

Most studies of habitat creation and management for bumblebees in the United Kingdom have focussed on field margin management options, largely because the field margin tends to have lowest agricultural productivity. Field margin management can take a number of forms:

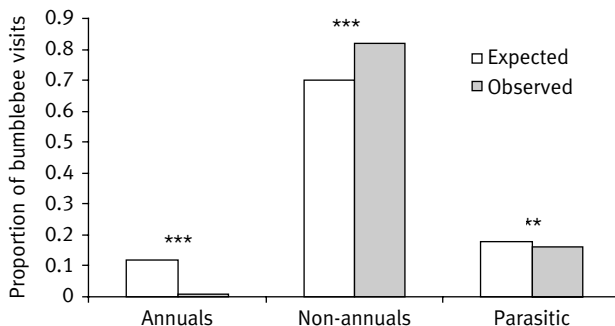
1. Conservation headlands are planted with crop, but no pesticides are applied, allowing annual arable weeds to flower.
2. Uncropped margins are not planted with crop, and are left to regenerate naturally.
3. Uncropped margins are not planted with crop but are instead sown with wildflower seed mixes.

Usually the margin consists of a 6m wide strip adjacent to the field boundary. Conservation headlands, which are necessarily cultivated every year, will clearly favour annuals (Vieting 1988). They can produce high numbers of annual arable weeds such as poppies (*Papaver rhoeas*) which are exploited by generalist bumblebees. However, it seems that perennial and biennial plants are more favoured by bumblebees than annuals, probably because, as a very broad generalization, they tend to produce more nectar (Fussell and Corbet 1992a; Dramstad and Fry 1995) (Fig. 13.8). Longer-tongued bumblebees in particular strongly favour perennials, in part probably because Fabaceae tend to be perennials and this plant family is particularly favoured by long tongued and rare bumblebees (Parrish and Bazzaz 1979; Williams 1985b; Fussell and Corbet 1991; Saville 1993; Carvell *et al.* 2006b). Thus while conservation headlands may be valuable for some groups of organisms, especially for conserving arable weeds (Firbank *et al.* 1993), they are of limited value to bumblebees, particularly the long-tongued species.

Uncropped margins are far more effective for the absence of a crop allows more space for flowers and negates the need for annual cultivation so that perennial plant communities can develop. There are four options available for these margins:

- (a) Leave them to regenerate naturally, relying on the seedbank.
- (b) Sow a 'quick-fix' nectar source such as *Phacelia tanacetifolia* or Borage (*Borago officinalis*).
- (c) Sow a perennial, clover-based pollen and nectar mix.
- (d) Sow a wildflower mix to try to recreate a natural species-rich grassland community.

There are pros and cons to these options. Natural regeneration is the cheapest, and can be effective. For example, Kells *et al.* (2001) found that naturally regenerated uncropped margins contained 6 times as many flowering plants and 10 times as many flowers as the equivalent cropped area (although it should be noted that cropped areas contained almost no flowers; six times ~zero is still not very much). The perennial plants preferred



**Figure 13.8** Foraging preferences of foraging bumblebees (data pooled for seven Norwegian species) with respect to life-history strategies of plants. Bumblebees exhibit a preference for non-annuals (biennials and perennials), and also for parasitic plant species. After Dramstad and Fry (1995), reproduced with permission of Elsevier Science.

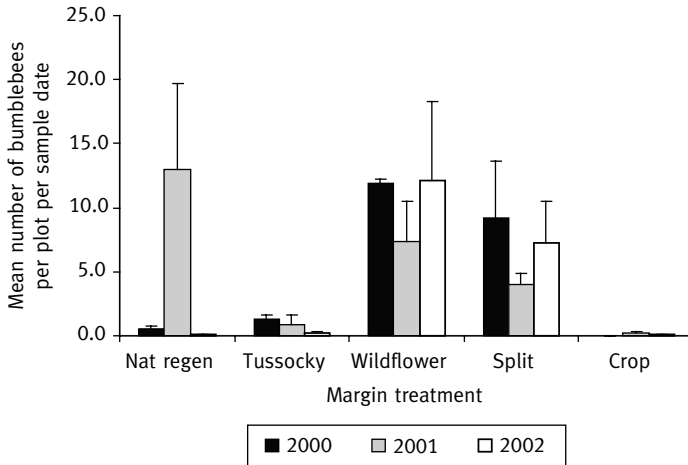
by bumblebees are often poorly represented in the seed banks in agricultural land, thus establishment of such species may be slow. Carvell *et al.* (2004) compared natural regeneration to a range of sown seed mixes in arable field margins and found that natural regeneration was patchy and often encouraged pernicious weeds. Problems with weeds such as thistles (*Cirsium* spp.), nettles (*Urtica dioica*), docks (*Rumex* spp.) and rank grasses are exacerbated by high fertility, which is likely in land that has recently been cultivated, or when allowing regeneration of arable field margins that are adjacent to crops to which fertilizers are regularly applied. Frequent mowing and removal of cuttings may help suppress growth of weeds and reduce soil fertility (Smith and MacDonald 1992). However, narrow field margin strips adjacent to arable fields and thus subject to fertilizer runoff are unlikely to ever form stable, diverse flower communities and are hence likely to need ploughing and reseeded every few years.

Quick-fix nectar sources such as *Phacelia* and borage are easy to grow, flower within a couple of months of sowing, provide a visually attractive display and are enormously attractive to short-tongued bees such as *B. terrestris* and to honeybees (Carvell *et al.* 2006b; Pontin *et al.* 2006). The drawbacks are that they need re-sowing every year and are of little interest to the longer-tongued species that are in most pressing need of conserving. On the other hand, if the farmer is interested primarily in boosting populations of common, short-tongued species to improve crop pollination, this approach is worth considering.

The most valuable form of field margin management for bumblebees has been found to be the sowing of either wildflowers or a pollen and nectar mix consisting of agricultural cultivars of legume species (Carreck and Williams 2002; Carvell *et al.* 2004, 2007; Pywell *et al.* 2005, 2006) (Fig. 13.9). Carvell *et al.* (2007) found that the pollen and nectar mixture produced the highest flower abundance with a succession of forage plants flowering over the 3-year trial period. The wildflower mixture produced few flowers in the first year but flower abundance increased over the 3 years as the mixture became established. Both treatments led to an increase in bumblebee species richness and abundance, and in the third year the wildflower mix was as valuable as the pollen and nectar mixture. Once established, the wildflower mix may persist for up to 10 years, while the agricultural cultivars in the pollen and nectar mix are likely to need re-sowing within 5 years (Pywell *et al.* 2002).

Unfortunately flower seed mixes can be expensive, which may act as a major barrier to uptake (Smith and Macdonald 1989; Smith *et al.* 1993, 1994; Corbet 1995). For example, in 2007, the Bumblebee Conservation Trust sowed an 8 Ha meadow in Scotland with a wildflower mix tailored to favour bumblebees; the cost of the seed alone was £12,000 (~US\$20,000). Few farmers can afford, or have the motivation, to use this approach on a large scale.

Studies of forage use by bumblebees suggest that it is not necessarily important to provide a great diversity of flowers on farmland to support substantial bee populations through the season (Goulson and Darvill 2004; Goulson *et al.* 2005). In coastal scrubland in California, five plant species were found to account for between 80% and 93%



**Figure 13.9** Changes in total bumblebee abundance in 6 m wide field margins subject to a range of different field margin treatments: unsown (relying on natural regeneration); sown with a ‘tussocky grass’ mix; sown with a ‘grass and wildflower’ mix; sown with 3 m each of ‘tussocky grass’ and ‘grass and wildflower’ mix; cropped. The high bee abundance in year two for the natural regeneration treatment is due to thistles, which are undesirable in an agricultural context. From Carvell *et al.* (2004).

of bumblebee visits over a 3-year study period (Thomson 2006). Similarly, in studies of 15 bumblebee species across a broad range of habitats in the United Kingdom, 80% of all pollen-collecting visits were to just 11 plant species (Goulson *et al.* 2005). Carvell *et al.* (2007) found that 92% of visits were to six flowering plants in managed field margins and that a diverse sown wildflower field margin option consisting of 18 herb species was no more beneficial than a simple sown wildflower option consisting of only three herbaceous species. Few, well chosen forage species provide suitable resources for a diverse bumblebee community.

At present, only one long-tongued and one medium-tongued species remain common in the United Kingdom and much of Europe (*B. hortorum* and *B. pascuorum*, respectively). There are probably a number of wild flowers with deep corollas that are more or less dependent on these species for pollination. Corbet (2000) makes a strong argument for giving conservation of the longer-tongued bee/deep-corolla pollinator ‘compartment’ a high priority in Europe, since the knock-on effects of losing our last longer-tongued species would probably be severe. Inclusion of deep-flowered plants such as *T. pratense*, *V. cracca* and *Lamium album* in field margin seed mixes is an obvious route by which this may be achieved.

It has often been suggested that the most critical time of the year for bumblebee colonies is the spring, when the queen has to single-handedly gather pollen and nectar to rear her offspring (Alford 1975). Provision of forage specifically for queens may thus provide great benefits. Suitable plant species for early emerging bumblebee species

in Europe include *L. album* and *Salix* spp. The latter is not infrequent in hedgerows, and it would be a simple matter for farmers to plant more (plants generate readily from cuttings pushed in to the ground). Suitable foodplants for queens of the later emerging long-tongued species include *Rhinanthus minor*, *A. vulneraria*, *Lamium* spp. and *T. pratense*.

#### 13.4.1.2 Restoring and maintaining species-rich grasslands

When large areas (e.g. whole fields) are being taken out of agricultural production for the long term, the aim is often the restoration of species-rich grasslands (haymeadows etc.) that were once common in Europe and North America. Such management is clearly beneficial to bumblebees since this habitat is favoured by numerous species, particularly those rare and declining species that are dependent on deep-flowered perennials and on Fabaceae for pollen (Goulson *et al.* 2005). Restoration of species-rich grasslands is a complex topic on which much research has been carried out, and it is beyond the scope of this book to review it in detail. The general principles are similar to those used for field margin management; restoration can rely on natural regeneration, which is often slow and is more likely to suffer from weed problems, or use a sown wildflower mix which is generally much more expensive. In either case, reducing soil fertility is key to controlling pernicious weeds and allowing development of a diverse flora, particularly if the site is a former arable field or improved pasture and has hence been subject to regular additions of fertilizer. The most extreme solution to this problem is to strip off the topsoil, but this is rarely practicable. A cheaper alternative is to deep-plough, burying the most fertile topsoil. In either of these cases, use of a sown wildflower mix is then essential as no natural seedbank will then be available. Subsequent annual cutting and removal of hay should then gradually reduce soil fertility still further over time.

Numerous seed mixes are now available from specialist wildflower seed companies, and can be tailor-made to suit particular regions and site conditions. However, as we have discussed earlier, wildflower seed mixes are expensive (at the time of writing up to £1,500 Ha<sup>-1</sup>). This can be substantially reduced by using primarily agricultural varieties of legumes which are much cheaper and more readily available than wild strains, but they tend to be shorter-lived and may flower at different times (e.g. agricultural *T. pratense* flowers a month or more later than the wild variety in the United Kingdom; Carvell *et al.* 2007). A compromise is to use both; potentially extending the flowering season and ensuring that when the agricultural varieties die off there is something to take their place; this approach has been used with success by the Bumblebee Conservation Trust in the first flower-rich grassland restoration project ever targeted specifically at bumblebees, near Kinross in Scotland (Plate 3). Inclusion of some annual arable weeds such as poppy (*P. rhoeas*) and cornflower (*Centaurea cyanus*) provides flowers suitable for bumblebees in the first year of sowing.

There have been few studies of large-scale grassland restoration and management with respect to bumblebees, but a general principle is that to maintain mid-successional

grassland communities, intermediate levels of disturbance such as mowing, cutting or seasonal grazing are required. Carvell (2002) assessed the benefits of different grassland management regimes for bumblebee populations in the United Kingdom. Grazing during the autumn and winter months was found to provide excellent bumblebee habitat, and without it coarse grasses became dominant. In some parts of Europe it is traditional for livestock to be moved to upland pastures in summer, leaving lowland meadows ungrazed for hay production, and this system works well at least for the lowland bumblebees. In contrast, if stock remain in meadows during the spring and summer this can be very detrimental since most flowers are eaten (Hatfield and LeBuhn 2007). For example in Sichuan, recent increases in yak density near towns have led to overgrazing in the summer, declines in abundance of the flowers of important forage plants, and consequent declines in bumblebee diversity (Xie *et al.* 2008). If grazing is unavoidable in summer (i.e. no upland or alternative grazing areas are available), then rotational grazing through the spring and summer is advisable so that there are always some areas that have not recently been grazed and which can therefore provide forage for bees. In general, grazing by cattle seems to be more favourable to bumblebees than grazing by sheep, and low summer grazing densities are preferable (Carvell 2002). The growth of grasses can also be suppressed by encouraging hemi-parasitic plant species such as *Rhinanthus*, with the added benefit that this is an important nectar source for some long-tongued bumblebees (Pywell *et al.* 2007).

Until recently it was possible for farmers in many parts of the EU to obtain payments for 'set-aside', and long-term set-aside (lasting 5 years or more) can eventually produce the mid-successional grassland communities preferred by bumblebees (Osborne and Corbet 1994). This scheme had the potential to go a long way towards creation of substantial areas of species-rich grasslands, a habitat that had been largely lost in most EU countries. However, in 2007 all payments for set-aside were discontinued.

#### 13.4.1.3 *Providing nest sites*

Bumblebees not only require a suitable source of forage, but also nest and hibernation sites. As long ago as 1943, Skovgaard argued for the protection of uncultivated refuges in agricultural land to provide for bumblebee nest sites. A popular agri-environment scheme in the United Kingdom is the sowing of field margins with tussocky grasses (Pywell *et al.* 2006). These habitats attract the small mammals whose abandoned holes are used by bumblebees for nest sites (Svensson *et al.* 2000), so it is likely that this form of management is of value to bumblebees. Carvell *et al.* (2004) found that field margins sown with a 'split' treatment consisting of a mixture of tussocky grasses and wildflower mix attracted almost as many bumblebees as margins sown solely with the wildflower seed suggesting that it is possible to provide both forage and nesting habitat in small areas. Replanting of hedgerows and repair of damaged hedgerows provides more sites for species that nest underground in holes, and financial support for this is available in some EU countries including the United Kingdom. In contrast, agri-environment schemes that operate on an annual rotation such as



conservation headlands will not provide suitable nest sites since the vegetation is not sufficiently dense for above-ground nesting species, and subterranean nesting species rarely use newly tilled soil.

Provision of artificial nest boxes is discussed in more detail in Chapter 12, but has only been found to be successful in New Zealand; elsewhere, take-up is invariably too low to provide a viable conservation strategy.

#### 13.4.1.4 *Organic farming*

There is a long way to go before farmland in the intensive agricultural regions of Europe such as central and southern United Kingdom will support anything like the diversity of wildlife that it did 60 years ago, and this may be an unrealistic target. But at least it is beginning to move in the right direction. Further hope is provided by the moves towards organic farming. Demand for organic produce has rocketed in the United Kingdom in recent years, and far outstrips the supply so that at present much has to be imported. Farmers are understandably reluctant to switch to organic production because they face a 4-year transition period during which they cannot market their produce as organic. Despite this, the area of land under organic regimes is steadily climbing and it seems certain that this too will aid wildlife. Rundlöf *et al.* (2008) found that organic farms in Sweden had more flowers and more bumblebees than equivalent paired conventional farms, although the effect was only significant in areas where the farming was intensive and the landscape homogenous. Rich bumblebee communities including rare species such as *B. sylvarum* have been identified on organic farms in Pembrokeshire in south-west Wales (Edwards 1999). Apart from the obvious avoidance of use of pesticides, organic farms are favourable for bees because they often depend heavily on rotations involving legumes such as clover to maintain soil fertility. Indeed, some conventional farms are reinstating leguminous ley crops to raise soil fertility as an alternative to using chemical fertilizers which have become very expensive as oil prices have risen. As we have seen, Fabaceae in general are the major source of pollen for most bumblebee species (Goulson *et al.* 2005), probably because their pollen is richer in protein than that of most other plant families (Hanley *et al.* 2008). Red clover (*T. pratense*) in particular is thought to be an important food source for longer-tongued species, and is easily the most visited pollen source for bumblebees in the United Kingdom, averaged across bumblebee species (Goulson *et al.* 2005, 2008a; Table 13.2). Similarly, in Poland, visits to *T. pratense* comprised 51% of all pollen-collecting visits averaged across bumblebee species. Bumblebee species richness in Finnish farmland was recently found to be strongly correlated with abundance of zigzag clover, *Trifolium medium* (Bäckman and Tiainen 2002). Rasmont (1988) argues that the decline of several long-tongued bumblebees in France and Belgium is largely attributable to a decline in the area of leguminous fodder crops once grown to feed horses. A shift back towards use of legumes could greatly benefit bumblebees; indeed the organic farms studied by Rundlöf *et al.* (2008) had significantly more *T. pratense* than their conventional equivalents.

**Table 13.2** Forage use by bumblebees collecting pollen (all bee species combined).

Species	% of visits	Cumulative %	Family
<i>Trifolium pratense</i>	28.8	28.8	Fabaceae
<i>Trifolium repens</i>	10.1	38.9	Fabaceae
<i>Calluna vulgaris</i>	9.0	46.7	Ericaceae
<i>Lotus corniculatus</i>	8.5	56.4	Fabaceae
<i>Erica cinerea</i>	4.4	60.8	Ericaceae
<i>Onobrychis viciifolia</i>	4.2	65.0	Fabaceae
<i>Melilotus altissima</i>	4.1	69.1	Fabaceae
<i>Echium vulgare</i>	3.6	73.5	Boraginaceae
<i>Odontites verna</i>	3.0	75.7	Scrophulariaceae
<i>Rubus fruticosus</i>	2.8	78.4	Rosaceae
<i>Hypericum perforatum</i>	1.9	80.4	Guttiferae
<i>Potentilla erecta</i>	1.5	81.8	Rosaceae
<i>Erica tetralix</i>	1.4	83.3	Ericaceae
<i>Papaver rhoeas</i>	1.2	84.5	Papaveraceae
<i>Rhinanthus minor</i>	1.1	85.6	Scrophulariaceae
<i>Taraxacum officinale</i>	1.1	86.7	Lamiaceae
<i>Prunella vulgaris</i>	0.9	26.8	Lamiaceae
<i>Vicia sepium</i>	0.9	27.7	Fabaceae
<i>Vicia cracca</i>	0.7	89.2	Fabaceae
<i>Lupinus arboreus</i>	0.7	89.8	Fabaceae

Only the 20 most visited plants are included, ranked according to the number of visits (for all bee species, castes and sites combined). Data based on 3,029 visits to flowers across 172 sites in United Kingdom and New Zealand. From Goulson *et al.* (2005).

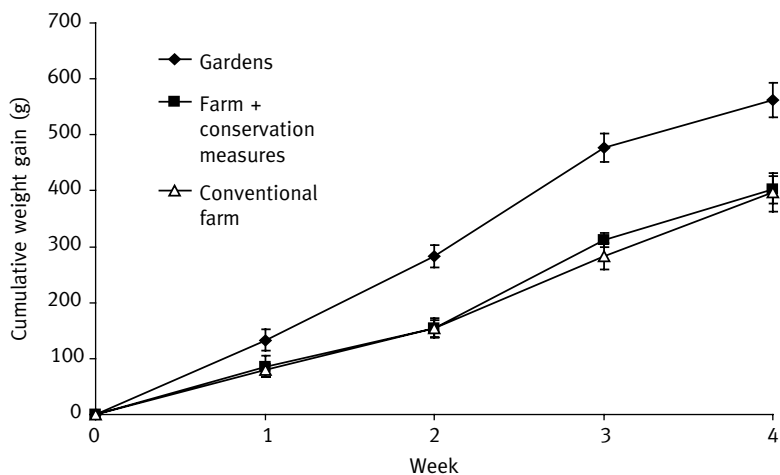
Organic livestock farms may in the long term provide excellent habitat for bumblebees. Some of the best remaining habitats in the United Kingdom are unimproved grasslands maintained by cattle or by grazing of sheep in the winter only (with the sheep moved to higher ground in the summer). Essentially all that seems to be required is a consistent regime of moderate or rotational grazing without use of artificial fertilizers, which is exactly how many organic farms are managed (and how most livestock farms were managed pre 1940). Of course, it may be many decades before land that has previously been improved will once again develop high levels of floristic diversity, but this does provide some hope for the future.

#### 13.4.2 The importance of urban areas

In the United States, 2.2 million acres of farmland and open space are converted into urban areas every year (McFrederick and LeBuhn 2006). Although conservationists would generally view this negatively, there is evidence that gardens and urban parks are particular strongholds for some species of bumblebee. Urban parks in San Francisco were found to have higher mean abundance and equal diversity of bumblebees,

compared to nearby 'wilder' areas. Abundance of bumblebees was partly explained by the openness of the matrix surrounding the park, suggesting that suburban gardens were also playing a role (McFrederick and LeBuhn 2006). In the United Kingdom, young nests of *B. terrestris* placed in suburban gardens grew more quickly and attained a larger size than nests placed in arable farmland, even when compared to farmland with agri-environment schemes in place (Goulson *et al.* 2002a) (Fig. 13.10). The foragers returning to nests in gardens were also carrying pollen from a greater variety of plants. Interestingly, the artificial nests used in this study were far more frequently attacked by the wax moth, *Aphomia sociella*, when placed in gardens than when in farmland. Since this moth only occurs in bumblebee nests, then if it is more common in gardens it is reasonable to presume that bumblebee nests occur at a higher density in gardens than in farmland. Recent support for this comes from the UK National Bumblebee Nest Survey which enlisted the help of 719 volunteers to survey small fixed areas for bumblebee nests (Osborne *et al.* 2008b). Gardens were found to have a higher nest density (36 nests Ha<sup>-1</sup>) than any of a range of rural habitats.

It is likely that gardens provide favourable habitat for several bumblebee species as a result of the density, variety and continuity of flowers that they provide; bumblebees are not constrained by garden boundaries, and with a foraging range of perhaps 500–1500 m a nest in suburbia is very likely to have numerous patches of flowers available to it at any time in the spring or summer (Goulson *et al.* 2002a). However, many commonly used garden plants are unsuitable for bumblebees. Artificial selection has often resulted



**Figure 13.10** Growth rates of nests of *B. terrestris* placed in one of three different habitats: suburban gardens; conventional farmland, or farmland with substantial areas of set-aside. The experiment was conducted in southern UK in 2000. After Goulson *et al.* (2002a).

in modern flower varieties which provide little or no reward, or which are inaccessible to insects (Corbet *et al.* 2001). For example, double flowered varieties of *Lotus corniculatus*, normally a plant favoured by bumblebees, provide no nectar (Comba *et al.* 1999; Corbet *et al.* 2001). Similarly, some exotic plants provide rewards that are inaccessible to native species. For example, *Salvia splendens*, a native of the Neotropics where it probably pollinated by hummingbirds, provides high levels of nectar but when grown in the United Kingdom is not visited by bumblebees or other day-flying insects because the corolla is too deep (Corbet *et al.* 2001). Many of the annual bedding plants sold in garden centres are sterile F<sub>1</sub> hybrids (producing no pollen), or have been the subject of such prolonged selection that the blooms do not produce nectar, or what nectar they produce is inaccessible to insects. More often than not gardeners are entirely unaware of this. It is clear that urban areas can provide a refuge for bumblebees, but they could be much better. Numerous garden plants are available that are enormously attractive to bumblebees; for example, lavender, aquilegia, sage, thyme, lupins etc. Some wildflowers are eminently suitable for growing in suburban gardens. Encouraging and educating gardeners so that they choose their plants appropriately could be particularly beneficial to wildlife in heavily populated countries where urban areas cover substantial portions of the country. In the United Kingdom, the Bumblebee Conservation Trust is championing gardening for bumblebees and other wildlife through its ~3,200 members (at the time of writing).

### 13.4.3 Translocations and reintroductions

As we have seen, habitat loss has led to fragmentation of bumblebee populations and, in some species, to metapopulation collapse. In the United Kingdom, *B. subterraneus* provides an example of a species in which this progressed to extinction (in 1988), while *B. distinguendus* and *B. sylvarum* are examples of species which appear to be advancing along the same trajectory. Provision of more habitats to enlarge and link surviving populations is the obvious solution, but it requires large-scale changes to the management of the countryside. Whether these can be achieved remains to be seen. In the meantime, a possible stopgap strategy would be to translocate breeding individuals between populations. For example, the surviving approximate seven populations of *B. sylvarum* are almost certainly entirely isolated from one another, but historically they were linked by populations that have since been lost. Artificial translocation could maintain genetic cohesion and reduce or prevent inbreeding in these populations. To our knowledge, this has never been done with bumblebees, but it is a strategy that clearly merits consideration.

Although *B. subterraneus* is extinct in the United Kingdom, a population of UK origin survives in New Zealand, to which they were introduced in ~1885. This provides the intriguing possibility that it could be reintroduced, and plans are currently underway to attempt such an introduction in 2010. It remains to be seen whether the New Zealand

population can survive in the United Kingdom; our as yet unpublished studies suggest that the New Zealand population has little genetic variation, and it has not been exposed to most of the natural enemies that occur in the United Kingdom for over 100 generations. Nonetheless, this provides an interesting flagship project for the promotion of bumblebee conservation issues.

### 13.5 Summary

Widespread declines of bumblebee species threaten pollination services to both wildflowers and crops. It is clear from studies of population structure that most bumblebee species cannot be conserved by managing small protected 'islands' of habitat within a 'sea' of unsuitable, intensively farmed land. Large areas of suitable habitat are needed to support viable populations in the long term; however, suitable habitat need not be contiguous and provision of numerous small patches (e.g. field margin strips) within a matrix of unsuitable habitat may suffice. Studies of foraging range indicate that bumblebees exploit forage patches at a landscape scale, so that the scale of management must be appropriate. An integrated approach across large areas or several farms is more likely to succeed than localized efforts. Where small, isolated populations of rare species remain in habitat fragments, targeting the adjacent farms for uptake of suitable agri-environment schemes could increase the population size and so reduce the likelihood of stochastic extinction events and inbreeding. Similarly, such schemes could be used to provide linkage between habitat islands.

Unimproved flower-rich grassland is one of the most important habitats for bumblebees, but has been largely lost to agriculture in Western Europe and North America. Restoration of areas of this habitat will boost bumblebee populations and has been shown to provide improved pollination services on nearby farmed land. Substantial benefits could also be obtained by reintroducing clover (e.g. *Trifolium pratense*) ley crops into rotations, since this is a key forage source for many declining bumblebee species. This would also reduce dependency on artificial fertilizers.

Pesticide poisoning is likely to have contributed to bumblebee declines, and the current risk assessments of the dangers of pesticides to honeybees are inadequate for bumblebees. In addition, there is a clear need to assess sub-lethal effects of pesticides on bumblebees.

In the United States, recent declines in several bumblebee species have been linked to increases in the commercialization of bumblebees for greenhouse pollination and associated introductions of parasites. There are already restrictions in place on the importation and movement of bumblebees in Canada, Mexico and the United States but there are calls for increased restrictions on transportation of bees and for stricter quarantine and monitoring systems (Winter *et al.* 2006).

Finally, increased recording of bumblebee distributions, and long-term monitoring of bumblebee populations is required in order to build up a picture of the current status of bumblebee species and to establish baselines to which future studies can refer. This is particularly important in areas such as North America where declines of some species have been documented but the extent is poorly quantified.

*This page intentionally left blank*

## Bumblebees Abroad: Effects of Introduced Bees

The devastating impacts which some exotic organisms have wreaked on native ecosystems are all too familiar, and surely ought to have taught us a lesson as to the perils of allowing release of alien species. The introduction of Nile perch to Lake Victoria, of cane toads, prickly pear, rabbits, foxes and cats amongst numerous others to Australia, and of water hyacinth, *Eichhornia crassipes*, to waterways throughout the old world tropics, are perhaps some of the best known examples, but they represent only the tip of the iceberg. Australia alone had 24 introduced mammal species, 26 birds, 6 reptiles, 1 amphibian, 31 fish, more than 200 known invertebrates and no less than 2,700 non-native plants at the last count (Alexander 1996; reviewed in Low 1999). These problems are certainly not confined to the Antipodes, although many of the most dramatic examples are to be found there. A strong case can be made that exotic species represents one of the biggest threats to global biodiversity (perhaps exceeded only by habitat loss and climate change) (Pimm *et al.* 1995; Low 1999).

The threat posed by exotic species is now widely appreciated, and many countries have rigorous measures in place to prevent further introductions. Yet we seem to have a blind spot with regard to bees. Bumblebees and a range of other bee species continue to be deliberately released in parts of the world to which they are not native. Of course bees are widely perceived to be beneficial for their role in the pollination of crops and wildflowers. Because of the economic benefits they can provide there appears to be reluctance to regard bees as potentially damaging in environments to which they are not native.

The natural range of bumblebees is largely confined to the temperate northern hemisphere and the mountains of Central and South America (Williams 1994). Various *Bombus* species have been deliberately introduced to new countries to enhance crop pollination. The earliest deliberate and successful introduction specifically for pollination was of bumblebees to New Zealand. In 1885 and again in 1906, 93 and 143 queens, respectively, were caught in the United Kingdom and released in New Zealand with the intention of improving seed set of red clover, *Trifolium pratense* (Hopkins 1914; MacFarlane and Griffin 1990). Four species became established, *B. hortorum*, *B. terrestris*, *B. subterraneus* and *B. ruderatus*. That these introductions were not well



thought through is clear from the introduction of *B. terrestris*, which is not effective as a pollinator of red clover but acts as a nectar robber (Gurr 1957). All four species have survived to this day; *B. hortorum* and *B. subterraneus* have restricted distributions within New Zealand, while *B. terrestris* and *B. ruderatus* have become ubiquitous (MacFarlane and Gurr 1995). It is interesting that of these species, *B. subterraneus* is now probably extinct in the United Kingdom while *B. ruderatus* is generally scarce.

*B. terrestris* spread into Israel in the 1960s (Dafni and Shmida 1996), perhaps as a result of the presence of introduced weeds. During the 1990s, *B. terrestris* also became established in the wild in Japan following escapes from commercial colonies used for pollination in glasshouses (Dafni 1998; Goka 1998). In 1992 *B. terrestris* arrived in Hobart, Tasmania, perhaps accidentally transported in cargo, and has since spread out to occupy about one quarter of the island (Semmens 1996a; Buttermore 1997; Stout and Goulson 2000). Recently, *B. terrestris* was introduced to Chile. This is the second UK species to arrive in Chile, for *B. ruderatus* was previously introduced in 1982 and 1983 for pollination of red clover (Arretz and MacFarlane 1986). *B. ruderatus* had spread to Argentina by 1993 (Abrahamovich *et al.* 2001), and *B. terrestris* arrived there in 2006 (Torretta *et al.* 2006). Because of its efficacy as a pollinator of glasshouse tomatoes, applications have been lodged for deliberate release in South Africa and mainland Australia, with the latter application being rejected in 2008. At present more than 1 million *B. terrestris* nests are reared each year in factories in Europe and distributed for use in more than 60 countries around the world.

Interestingly, the most recently recorded range expansion in bumblebees is in *B. hypnorum*, a species not used commercially. This native of mainland Europe was recorded for the first time in the United Kingdom in 2001 (Goulson and Williams 2001), and by 2002 appeared to be established on the south coast in the Southampton area (D.G., pers. obs.). Recent records collated by the Bees, Wasps and Ants Recording Society suggest that by 2008 this species had spread through much of England. It is not known whether this was a natural invasion or whether a queen or nest was accidentally transported to the United Kingdom from continental Europe.

Bumblebees are not the only bees to have been redistributed around the globe by man. The honeybee is thought to be native to Africa, western Asia and southeast Europe (Michener 1974), although its association with man is so ancient that it is hard to be certain of its origins. It has certainly been domesticated for at least 4,000 years (Crane 1990a). Because of its economic value, the honeybee has been introduced to more or less every country in the world, and has achieved a global distribution (being absent only from the Antarctic). It is now amongst the most widespread and abundant insects on earth. The alfalfa leafcutter bee *Megachile rotundata* (Fabr.) (Megachilidae), a native of Eurasia, has been introduced to North America, Australia and New Zealand for alfalfa pollination (Bohart 1972; Donovan 1975; Woodward 1996). At least six other Megachilidae have been introduced to the United States for pollination of various crops (Batra 1979; Parker 1981; Cooper 1984; Torchio 1987; Stubbs *et al.* 1994; Mangum and Brooks 1997; Frankie *et al.* 1998). The alkali bee, *Nomia melanderi* (Cockerell) (Halictidae), a native of

North America, was introduced to New Zealand in 1971 for pollination of alfalfa and has become established at restricted sites (Donovan 1975, 1979).

So why should these introductions be a cause for concern? There are a number of possible undesirable effects of exotic bumblebees, including

1. Competition with native flower visitors for floral resources
2. Competition with native organisms for nest sites
3. Introgression with native species
4. Transmission of parasites or pathogens to native organisms
5. Changes in seed set of native plants (either increases or decreases)
6. Pollination of exotic weeds.

I will discuss each of these in turn. Far more studies have been carried out on impacts of honeybees than on introduced bumblebees, but many of the effects are likely to be similar so I have also included a summary of this work.

### 14.1 Competition with native organisms for floral resources

For there to be the potential for competition to occur between organisms, the niches that they occupy must overlap. The diet of all bee species consists more or less exclusively of pollen and nectar collected from flowers (occasionally supplemented by honeydew, plant sap and waxes, and water) (Michener 1974). The two bee species that have proved to be most adaptable in colonizing new habitats, *A. mellifera* and *B. terrestris*, have done so largely because they are generalists. *A. mellifera* usually visits a hundred or more different species of plant within any one geographic region (Pellet 1976; O'Neal and Waller 1984; Wills *et al.* 1990; Roubik 1991; Butz Huryn 1997; Coffey and Breen 1997), and in total has been recorded visiting nearly 40,000 different species (Crane 1990b). *B. terrestris* is similarly polylectic. It has been recorded visiting 66 native plants of 21 families in Tasmania (Hingston and McQuillan 1998) and 419 introduced and native plants in New Zealand (MacFarlane 1976).

A diverse range of different organisms collect pollen and/or nectar from flowers, including birds, bats, mammals and insects. Of the insects, the main groups are the bees and wasps (Hymenoptera), butterflies and moths (Lepidoptera), beetles (Coleoptera) and flies (Diptera). Only the bees feed more or less exclusively on floral resources during all stages of their life cycle, but many of the other groups are floral specialists as adults. The wide distribution and polylectic diet of *B. terrestris* and honeybees means that potentially they might compete with many thousands of different native species. It seems reasonable to predict that introduced bees are most likely to compete with native bee species (rather than other native organisms), since these are likely to be most similar in terms of their ecological niche. Studies of niche overlap in terms of flowers visited have all concluded that both honeybees and bumblebees overlap substantially with native bees and with other flower visitors such as nectivorous birds (Donovan 1980; Roubik 1982a; Roubik *et al.* 1986; Menezes Pedro and Camargo 1991; Thorp *et al.* 1994; Wilms

*et al.* 1996; Wilms and Wiechers 1997; Hingston and McQuillan 1998; Goulson *et al.* 2008b). Thus there is the potential for competition.

Some potential competitors manage to coexist by exploiting shared resources at different times of the year or day. Honeybees and bumblebees differ from many other flower visitors in having a prolonged flight season; honeybees remain active for all of the year in warmer climates, while bumblebees commonly forage throughout the spring and summer in the temperate climates where they naturally occur. Thus, in terms of the time of year at which they are active, they overlap with almost all other flower visitors with which they co-occur. They also tend to feed throughout the day, beginning before and ending after most native organisms, so that both are feeding together through the middle of the day. Thus they share resources with native organisms, and are exploiting them at the same time.

The highest niche overlap is likely to occur when introduced and native species are closely related. In the United Kingdom, where ~60,000 nests of *B. terrestris dalmatinus* from south eastern Europe are imported every year, there is a distinct possibility of competition between the imported bees and the indigenous subspecies *B. terrestris audax*. Ings *et al.* (2006) compared the performance of nests of each subspecies when placed in the field in the United Kingdom, and found that the non-native subspecies had larger workers, brought back more nectar to the nest, and ultimately produced more new queens when compared to the native bees. This would suggest that *B. t. audax* could readily be displaced by *B. t. dalmatinus*. However, Peat *et al.* (2005a) show that *B. t. dalmatinus* has shorter hair than *B. t. audax*, so may be less able to cope with inclement weather. Only time will reveal whether *B. t. dalmatinus* establish in the wild in the United Kingdom, and if so whether they have detrimental effects on native bees.

Of course demonstration of niche overlap is not proof of competition. In fact it is notoriously difficult to provide unambiguous evidence of competition, particularly in mobile organisms. Because of this there is no clear agreement as to whether non-native bees have had a significant negative impact upon native pollinator populations (for reviews of the impacts of honeybees which draw different conclusions compare Robertson *et al.* 1989; Buchmann and Nabhan 1996; Sugden *et al.* 1996 with Butz Huryn 1997). The majority of studies to date have been carried out in the neotropics, stimulated by the recent arrival and spread of Africanized honeybees, and in Australia, where awareness of the possible impacts of introduced species is unusually high. Australia also has a large native bee fauna of over 1,500 species (Cardale 1993) that is arguably the most distinctive in the world (Michener 1965). Considerable circumstantial evidence has accumulated suggesting that introduced bees do impact upon native pollinator through effects on their foraging, but no unequivocal evidence has been found for competitive exclusion at the population level.

#### 14.1.1 Effects on foraging of native organisms

Hingston and McQuillan (1999) examined interactions between bumblebees and native bees in Tasmania and concluded that native bees were deterred from foraging by the

presence of bumblebees, perhaps because bumblebees depressed availability of floral resources (rather than because of direct interference competition). Honeybees, or the joint action of honeybees and bumblebees, have been shown to depress the availability of nectar and pollen (Paton 1990, 1996; Wills *et al.* 1990; Horskins and Turner 1999), which may explain why other flower visitors then choose to forage elsewhere. Honeybees commonly deter other bee species from foraging on the richest sources of forage, displacing them to less profitable flowers (Holmes 1964; Wratt 1968; Roubik 1978, 1980, 1996a; Schaffer *et al.* 1979, 1983; Eickwort and Ginsberg 1980; Ginsberg 1983; Wilms and Wiechers 1997) (although in at least one instance the converse had been reported; Menke 1954). For example in Panama, the presence of Africanized honeybees effectively eliminated peaks of foraging activity of Meliponine bees because these native species were prevented from visiting their preferred sources of forage; as a result the rate at which pollen was accrued in the nest was lower (Roubik *et al.* 1986).

Displacement of native organisms has been attributed to the larger size of honeybee when compared to the majority of bee species (Roubik 1980), but is not necessarily size related. For example, the presence of honeybees has been found to deter foraging by hummingbirds (Schaffer *et al.* 1983). Similarly, in a year when honeybees were naturally scarce, native bumblebees in Colorado were found to expand their diet breadth to include flowers usually visited mainly by honeybees (Pleasants 1981).

Both bumblebees and honeybees begin foraging earlier in the morning than many native bee species (Corbet *et al.* 1993; Dafni and Shmida 1996; Horskins and Turner 1999). Both bumblebees and honeybees are able to achieve this due to their large size (compared to most bees) and also due to heat retention within their large nests (Roubik 1989). It has been argued that depletion of nectar before native bees begin to forage may result in a significant asymmetry in competition in favour of these introduced species (Matthews 1984; Hopper 1987; Anderson 1989; Dafni and Shmida 1996; Schwarz and Hurst 1997). In a site in Tasmania, much of the available nectar was found to be removed by the combined action of honeybees and bumblebees before 10 am, by which time native bees had not begun to forage (D.G., pers. obs.).

Asymmetries in competition may also occur because of the ability of honeybees and bumblebees to communicate the availability and/or location of valuable food sources with nest mates, so improving foraging efficiency (von Frisch 1967; Dornhaus and Chittka 1999) (the majority of bee species are solitary, and each individual must discover the best places to forage by trial and error). Thus social species are collectively able to locate new resources more quickly, which again may enable them to gather the bulk of the resources before solitary species arrive (Roubik 1980, 1981; Schwarz and Hurst 1997). Honeybees and bumblebees also appear to be unusual in the distances over which they are capable of foraging. Honeybees are known to forage over 10 km from their nest, on occasion up to 20 km (Seeley 1985a; Schwarz and Hurst 1997), and *B. terrestris* up to at least 4 km (Goulson and Stout 2001). Little is known of the foraging range of most other bee species, but those estimates that are available suggest that they are generally lower. For example, *Melipona fasciata* travels up to 2.4 km and Trigonini over 1 km (Roubik *et al.* 1986). Solitary bee species are generally thought to travel only a few hundred metres at

most (Schwarz and Hurst 1997). A long foraging range is likely to be particularly advantageous in patchy, fragmented landscapes where resources are widely scattered, such as in intensively farmed areas.

Asymmetries in competition may not be stable, since the relative competitive abilities of bee species are likely to vary during the day according to temperature and resource availability, and are likely to vary spatially according to the types of flowers available (Corbet *et al.* 1995). Bumblebees and honeybees are large compared to most of the native species with which they might compete; *B. terrestris* weighs 109–315 mg (Prys-Jones 1982), and *A. mellifera* workers weigh  $98 \pm 2.8$  mg (Corbet *et al.* 1995). They also have longer tongues than many native species, particularly in Australia where most native species are short tongued, so they can extract nectar from deeper flowers (Armstrong 1979; Goulson *et al.* 2002c). Large bees are at a competitive advantage in cool conditions because of their ability to maintain a body temperature considerably higher than the ambient air temperature (Newsholme *et al.* 1972). They can thus forage earlier and later in the day than most smaller bees, and during cooler weather. Bees with longer tongues can also extract nectar from deeper flowers. However, large bees are not always at an advantage. The energetic cost of foraging is approximately proportional to weight, so large bees burn energy faster (Heinrich 1979b). As nectar resources decline, the marginal rate of return will be reached more quickly by large bees. Also long tongues are inefficient at handling shallow flowers (Plowright and Plowright 1997). Thus large bees are likely to be at a competitive advantage early in the day and during cool weather, and they will be favoured by the presence of deep flowers that provide them with a resource that other bees cannot access. However, small bees with short tongues can forage profitably on shallow flowers even when rewards per flower are below the minimum threshold for large bees; at these times honeybees and bumblebees may survive by using honey stores. Small bees are also able to maintain activity at high ambient temperatures when bumblebees would swiftly overheat. Thus the relative competitive abilities of different bee species are not consistent, and the strength of competition is likely to vary with time of day, season, and according to what types of flower are available.

Although, in general, honeybees and bumblebees are able to forage at cooler temperatures than native bees, there may be occasional exceptions. For example, the Australian native *Exoneura xanthoclypeata* is adapted for foraging in cool conditions (Tierney 1994). It has been argued that this species is specialized for foraging on (naturally) uncontested resources early in the day, and may be particularly susceptible to competition with exotic bees which forage at the same time (Schwarz and Hurst 1997).

The outcome of interactions between exotic and native flower visitors depends on whether floral resources are limiting. Because floral resources are usually produced continuously during the life of a flower (although often at a variable rate), they are rarely completely used up, but as they become more scarce, foraging efficiency will decline. Resource availability is likely to vary greatly during the year as different plant species come in to flower (Carpenter 1978). When an abundant or large plant flowers, it may

provide a nectar flush. Competition is unlikely to occur during such periods (Tepedino and Stanton 1981).

Overall, it seems probable that depression of resources by introduced bees is likely to have negative effects on native bee species. To determine whether these effects are largely trivial (such as forcing native bees to modify their foraging preferences) or profound (resulting in competitive exclusion), population-level studies are necessary.

#### 14.1.2 Evidence for population-level changes in native organisms

The only way to test unequivocally whether floral resources are limiting and competition is in operation is to conduct experiments in which the abundance of the introduced bee species is artificially manipulated, and the population size of native species is then monitored. If populations are substantially higher in the absence of the introduced bee, then competition is occurring. Although in principle a simple procedure, such experiments have proved to be remarkably hard to accomplish. Honeybees and bumblebees are highly mobile, foraging many kilometres from their nests (Seeley 1985a; Goulson and Stout 2001). Thus excluding them from an area is difficult. Within and between season variation is likely to be large, so such experiments need to be well replicated, with replicates situated many kilometres apart, and conducted over several years. No such study has ever been carried out.

An alternative approach, which is far easier but provides more equivocal data, is to correlate patterns of diversity or abundance of native bees with abundance of exotic bees, without manipulating their distribution. A comparison of native flower visitors in Tasmania in areas colonized by *B. terrestris* with areas outside of the current range of the exotic bee found no evidence for competition, but concluded that this may be due to an overriding abundance of honeybees at all sites (Goulson *et al.* 2002c). Aizen and Feinsinger (1994) found that fragmentation of forests in Argentina resulted in a decline in native flower visitors and an increase in honeybee populations. Similarly, Kato *et al.* (1999) studied oceanic islands in the northwest Pacific, and found that indigenous bees were rare or absent on islands where honeybees were numerous, which they concluded was evidence for competitive exclusion. On Mt Carmel in Israel, Dafni and Shmida (1996) reported declines in abundance of medium- and large-sized native bees (and also of honeybees) following the arrival of *B. terrestris* in 1978. However, such studies can be criticized on the grounds that the relationship between exotic bee abundance and declining native bee populations (if found) need not be causative (Butz Huryn 1997). Increasing honeybee populations are often associated with increased environmental disturbance by man, which may explain declines in native bees.

Some researchers have attempted to manipulate numbers of honeybees, either enhancing populations in experimental plots by placing hives within them, or conversely by removing hives from experimental plots in areas where hives have traditionally been placed. Areas without hives usually still have some honeybees, since there

are likely to be some feral nests, and also because honeybees can forage over great distances. Replicates of the treatment without hives need to be sited many kilometres from replicates with hives to ensure that bees do not travel between the two, so many studies have been carried out without adequate replication (e.g. Sugden and Pyke 1991). Despite these limitations, some interesting results have been obtained. Wenner and Thorp (1994) found that removal of feral nests and hives from part of Santa Cruz Island in California resulted in marked increases in numbers of native bees and other flower-visiting insects. Addition of honeybee hives caused the Australian nectivorous bird *Phylidonyris novaehollandiae* to expand its home foraging range and to avoid parts of inflorescences favoured by honeybees (Paton 1993), but a comparison of areas with and without hives found no difference in the density of this bird species (Paton 1995). Roubik (1978) found a decrease in abundance of native insects when he placed hives of the Africanized honeybee in forests in French Guiana. This approach has never been attempted with bumblebees.

Finding that increasing the abundance of alien bees decreases abundance of native organisms is in itself not good evidence for competition. Measures of the abundance of native organisms are generally made by recording them on flowers. In the presence of alien bees, they may simply be foraging elsewhere. Few studies have attempted to directly measure reproductive success of native flower visitors while manipulating abundance of introduced bees. This is unfortunate, since effects of competition on reproduction are likely to result in reduced population sizes. The few studies that have been carried out have found variable effects. Roubik (1982a, 1983) found no consistent detrimental effects on brood size, honey stores or pollen stores in nests of two Meliponine bee species in Panama when Africanized honeybee hives were placed nearby for 30 days. Monitoring of numbers of native bee species using light traps over many years since the arrival of Africanized bee has not revealed any clear declines in abundance (Wolda and Roubik 1986; Roubik 1991). Roubik (1996a) describes the introduction of Africanized honeybees to the neotropics as a vast experiment, but it is an experiment without replicates or controls, so interpreting the results is difficult. Sugden and Pyke (1991) and Schwarz *et al.* (1991, 1992a,b) failed to find clear evidence for a link between abundance of honeybees and reproductive success of anthophorid bees belonging to the genus *Exoneura* in Australia in experiments in which they greatly enhanced honeybee numbers at experimental sites. In contrast, Thomson (2004) experimentally manipulated the locations of honeybees and native bumblebee (*B. occidentalis*) nests in California and found that close proximity to honeybee hives significantly reduced the foraging rates and reproductive success of the bumblebee colonies. In most of the studies to date, the native bees under consideration are themselves abundant generalists, visiting a broad range of flowers (Schwarz and Hurst 1997; Goulson *et al.* 2002c). As such they are the species least likely to be affected by competition.

The majority of bee species are specialized; in a review of data for 960 solitary bee species, Schemske (1983) found that 64% gathered pollen from only one plant family, often only one genus. For example, some Australian halictine bees have only been

recorded on flowers of *Wahlenbergia* sp. (Michener 1965). Very little is known about such species, and no studies have been carried out to determine whether they are adversely affected by exotic bees (Schwarz and Hurst 1997). Also, the Australian studies of Sugden and Pyke (1991) and Schwarz *et al.* (1991, 1992a,b) were carried out in flower-rich heathlands; floral resources are more likely to be limiting in arid regions of Australia (Schwarz and Hurst 1997), and these areas often contain the highest native bee diversity (Michener 1979; O'Toole and Raw 1991). The *Exoneura* species studied in Australia had coexisted with honeybees for 180 years, so it is not surprising that they are not greatly affected by competition with this species. If there are species that are excluded by competition with exotic bees, there is no point looking for them in places where these bees are abundant.

Overall, there is no indisputable evidence that introduced bees have had a substantial impact via competition with native species. Given the difficulties involved in carrying out rigorous manipulative experiments (and the rather small number of attempts to do so) this should certainly not be interpreted as the absence of competition. The abundance of exotic bees, the high levels of niche overlap and evidence of resource depression and displacement of native pollinators, all point to the likelihood that competition is occurring. But we do not know whether such competition results (or resulted) in competitive exclusion. The best way to test for such competition is to carry out replicated experiments in which exotic bee numbers are manipulated and native pollinator numbers and reproductive success monitored over long periods. Ideally, such studies should target native species that are not generalists, and areas where floral resources are not abundant.

## 14.2 Competition for nest sites

Of the bumblebees that have been introduced outside their native range, *B. terrestris* and *B. subterraneus* generally nest in existing cavities below ground. *B. terrestris* often uses abandoned rodent holes, and spaces beneath man-made structures such as garden sheds (Alford 1975; Donovan and Weir 1978), while rather less is known of the nesting preferences of *B. subterraneus*. *B. hortorum* and *B. ruderatus* are more variable in their nesting preferences, often nesting just above the ground surface under dense vegetation, but also sometimes using holes.

To my knowledge there have been no studies to determine which native organisms are likely to use nest sites similar to bumblebees in New Zealand, Tasmania or South America. Numerous organisms including diverse arthropods and small mammals might be expected to come in to contact with subterranean bee nests, but little is known of the outcome of such interactions. Overall, Donovan (1980) considered it unlikely that bumblebees compete with native bee species for nest sites in New Zealand. In contrast, there is strong circumstantial evidence for competition between *B. terrestris* and the native *B. hypocrita* in Japan (Inoue *et al.* 2008); the two species occupy the same habitats, choose very similar nest sites, usurpation is common among *B. terrestris* queens



(suggesting a shortage of nest sites) and the invasion by *B. terrestris* has coincided with a decline in *B. hypocrita*.

### 14.3 Introgression with native bees

The global trade in *B. terrestris* poses a threat to the genetic diversity of the species which has received very little attention. The trade is largely in *B. t. dalmatinus* from South East Europe, which are shipped throughout the range of *B. terrestris*. *B. terrestris* consists of a number of distinct subspecies: *B. terrestris terrestris* in much of western Europe, *B. t. audax* in Great Britain and Ireland, *B. t. lusitanicus* in Iberia and various named subspecies on different islands in the Mediterranean and Canary Islands (Rasmont *et al.* 2008b). The subspecies differ morphologically and behaviourally, and are considered distinct species by some authors. In a laboratory setting, the subspecies readily interbreed (e.g. Ings *et al.* 2005; Rasmont *et al.* 2008b), but this does not necessarily mean that they will interbreed in a natural setting where pheromonal cues are likely to be important (in a cage male bumblebees will readily try to mate with gynes of distantly related species). The transport of *B. t. dalmatinus* throughout Europe poses the threat that the distinct local races will be lost through introgression, resulting in an overall loss of genetic diversity within the species. However, to my knowledge there has been no attempt to ascertain whether introgression is occurring in any European region to which non-native races of *B. terrestris* are being imported.

Non-native bees also pose a different threat through interspecific matings. In Japan, nearly 30% of native *B. hypocrita* queens mate with feral *B. terrestris* males, matings that result in no viable offspring and so effectively sterilize the queens (Kanbe *et al.* 2008). Such interspecific mating is to be expected among closely related species (both belong to the subgenus *Bombus*) that do not naturally encounter one another. Closely related species that are sympatric have generally evolved mate-location behaviours or differences in sex pheromones that prevent hybridization (see Chapter 4).

### 14.4 Transmission of parasites or pathogens to native organisms

Bees and their nests support a diverse microflora, including pathogenic, commensal and mutualistic organisms (Gilliam and Taber 1991; Goerzen 1991; Gilliam 1997). Although there is a rich literature on bee parasites, it is fair to say that we still have a pretty feeble grasp of the effects they have on their hosts, as demonstrated by the recent outbreaks of colony collapse disorder (CCD) in honeybees. This is characterized by the sudden disappearance of the majority of workers within a hive followed swiftly by death of the colony, and has affected significant numbers of colonies in North America in 2007 and 2008. Similar colony losses have been reported elsewhere, and also at intervals in the historical past, but in no case is the cause clear. At the time of writing, most experts

suggest that it is the result of an interaction between one or more viruses and their mite vectors, but various different viruses have been implicated and the overall situation remains confused.

There is no doubt that many bee parasites are likely to have been transported to new regions with their hosts, particularly where introductions were made many years ago when awareness of bee natural enemies was low. Thus, for example, the honey-bee disease chalkbrood, caused by the fungus *Ascosphaera apis*; foulbrood, caused by the bacteria *Paenibacillus larvae*; the microsporidian *Nosema apis*; and the mite *Varroa destructor* now occur throughout much of the world. Similarly, bumblebees in New Zealand are host to a parasitic nematode and three mite species, all of which are thought to have come from the United Kingdom with the original introduction of bees (Donovan 1980).

During some more recent deliberate introductions of exotic bees, such as that of *N. melanderi* to New Zealand, care has been taken to eliminate pathogens or parasites before bees were released (Donovan 1979). However, this is not always the case, and some parasites and pathogens can be hard to detect. Recent studies in Japan have demonstrated that *B. terrestris* imported from the Netherlands are frequently infested with the tracheal mite *Locustacarus buchneri* (Goka *et al.* 2001). Although this mite also occurs in Japan, the European race is genetically distinct. In addition to importing *B. terrestris*, queens of a Japanese bumblebee, *B. ignitus*, have been sent to the Netherlands and the established nests re-imported back to Japan. The re-imported nests have been found to be infected with the European race of the mite. In laboratory studies, these mites are able to infest various Japanese bumblebee species, and by 2001 mites of the European haplotype were identified in native Japanese bees (Goka *et al.* 2006). It seems likely that the worldwide trade in bumblebees has led to a global redistribution of various strains of the mite (Goka *et al.* 2006). Exposure of hosts to novel strains of mite can have dramatic consequences, as demonstrated by the recent spread of *V. destructor*.

There is strong circumstantial evidence that the most dramatic declines that have been observed in any bumblebee species are the result of exposure to a non-native pathogen. In the 1990s, queens of various North American species were taken from North America to Europe and rearing in factories alongside the European *B. terrestris*. The established nests were then returned to North America. Shortly afterwards, *B. occidentalis*, *B. terricola* and *B. affinis*, all widespread and abundant species, disappeared from much of their range (Thorp 2005; Thorp and Shepherd 2005; Winter *et al.* 2006; Rao and Stephen 2007). It is perhaps relevant that these species are all closely related, belong to the subgenus *Bombus*. The only other nearctic member of this subgenus, *B. franklini*, was always very rare but has recently disappeared from former localities and is possibly now globally extinct (last recorded in 2006). Thus an entire subgenus has been devastated across a continent in the space of a few short years. To put this in context for European readers, this would be the equivalent of ubiquitous species such as *B. terrestris* or *B. pascuorum* disappearing from most of Europe in a couple of years. It is hard to conceive of an explanation for this decline that does not invoke a disease

epizootic. Anecdotal evidence suggests that a non-native strain of *Nosema bombi* was transported to North America with the commercial colonies, but in truth we shall probably never know. Almost nothing is known about the bumblebee diseases that were present in North America *before* the 1990s. Studying the few survivors is unlikely to be revealing as they are presumably those that were resistant to the disease.

It is hard to exaggerate our ignorance of the natural enemies of most bee species, particularly their pathogens. We do not know what species infect them, or what the host ranges of these pathogens are. Thus very little is known of the susceptibility of native organisms to the parasites and pathogens that have been introduced with exotic bees. In a survey of natural enemies of native and introduced bees in New Zealand, Donovan (1980) concluded that no enemies of introduced bees were attacking native bees, but that the converse was true. A chalcidoid parasite was found to attack the introduced species *M. rotundata* and *B. terrestris* (but the latter only rarely). One fungus, *Beetsia alvei*, which is a pathogen of honeybee hives elsewhere in the world, was recorded infecting a native bee in New Zealand, but it is not known whether the fungus is also native to New Zealand. Indeed the natural geographic range of bee pathogens is almost wholly unknown. Some bee pathogens have a broad host range; for example chalkbrood (*A. apis*), is also known to infect *A. cerana* (Gilliam *et al.* 1993) and the distantly related *Xylocopa californica* (Gilliam *et al.* 1994). The related chalkbrood fungus *Ascosphaera aggregata* is commonly found infecting *M. rotundata*; in Canada, where *M. rotundata* is an exotic species, this fungus also infects the native bees *Megachile pugnata* (Goerzen *et al.* 1992) and *Megachile relativa* (Goerzen *et al.* 1990).

If we are ignorant of the parasitoid, fungal and protozoan parasites of wild bee species, then the same is doubly true of our knowledge of bee viruses. Until quite recently only apparent viral infections could be easily detected, but new and cheap molecular detection methods have revealed a diversity of viruses in honeybees. Some honeybee viruses also occur in bumblebees: for example, Bailey and Gibbs (1964) detected acute bee paralysis virus (ABPV) in various bumblebee species. Recently, Genersch *et al.* (2006) found deformed wing virus (DWV) in about 10% of commercial *B. terrestris* colonies, and also found the virus in a wild nest of *B. pascuorum* located near honeybee hives (infected bees are unable to fly so that a heavily infected nest is doomed). To my knowledge most commercial bumblebee rearing facilities do little or no testing for viruses, so it seems certain that the global trade in bumblebees is leading to the redistribution of viral diseases of bees, with unknown consequences. Given the current collapse of honeybee populations in North America and perhaps also in Europe, thought to be driven by one or more viral diseases perhaps interacting with parasitic mites, there is an urgent need to improve our understanding of the cross-infectivity of bee diseases.

It seems likely that these few recorded instances of exotic bee pathogens infecting native species are just the tip of the iceberg, since so few studies have been carried out. As to whether these pathogens have had, or are having, a significant impact on native species, we do not know; if the introduction of a new pathogen were to lead to an

epizootic in native insects, it would generally go unnoticed unless it were a comparatively well-studied insect such as *B. terricola*. More studies of the incidence and identity of pathogen and parasite infestations of wild populations of native bees are urgently needed. In the meantime, legislation to enforce strict quarantine of bees before transportation would seem to be necessary.

## 14.5 Effects on pollination of native flora

Concerns have been expressed that exotic bees may reduce pollination of native plants, or alter the population structure of these plants by mediating different patterns of pollen transfer to those brought about by native pollinators (Butz Huryn 1997; Gross and Mackay 1998). Efficient pollination requires a match between the morphology of the flower and that of the pollinator (reviews in Ramsey 1988; Burd 1994). If there is a mismatch, then floral rewards may be gathered without efficient transfer of pollen, a process known as floral parasitism (McDade and Kinsman 1980). Specialized obligate relationships between plants and pollinators do exist (reviewed in Goulson 1999) but are the exception (Waser *et al.* 1996). Most flowers are visited by a range of pollinator species, each of which will provide a different quality of pollinator service.

The efficiency of honeybees as pollinators of native plants in Australia and North America was reviewed by Butz Huryn (1997). She concluded that honeybees provide an effective pollination service to the majority of the flower species that they visit, although they do act as floral parasites when visiting a small number of plant species such as *Grevillea X gaudichaudii* in Australia (Taylor and Whelan 1988) and *Impatiens capensis* and *Vaccinium ashei* in North America (Cane and Payne 1988, 1990; Wilson and Thomson 1991). Similar results have been found for honeybees visiting Jamaican flora (Percival 1974). That honeybees are effective pollinators of many plants, even ones with which they did not co-evolve is not surprising. After all, they have been used for centuries to pollinate a broad range of crops. Thus pollination of the native Australian *Banksia ornata* was increased by the presence of honeybee hives (Paton 1995), and honeybees have proved to be as effective as native bees in pollinating wild cashews, *Anacardium occidentale* in South America (Freitas and Paxton 1998). However, their presence may result in reduced seed set of some native plants. Roubik (1996b) reported lower seed set in the neotropical plant *Mimosa pudica* when honeybees were the dominant visitors, compared to sites where native bees were the more abundant, while Aizen and Feinsinger (1994) found reduced pollination of a range of Argentinian plant species in areas where forests were fragmented and honeybees more abundant. Gross and Mackay (1998) demonstrated that honeybees were poor pollinators of the Australian native *Melastoma affine*, so that when honeybees were the last visitors to a flower, seed set was reduced. As Roubik (1996b) points out, if native pollinators are lost (be it through competition with exotic bees, habitat loss or use of pesticides) then we cannot expect honeybees to provide an adequate replacement pollination service for all wild plants and crops.

Few studies have yet examined the effects of exotic bumblebees on the seed set of native plants. Madjidian *et al.* (2008) found that the invading *B. ruderatus* appears to be providing an *improved* pollination service to the native herb *Alstroemeria aurea* in South America, while seemingly displacing the native pollinator *B. dahlbomii*. The far more widespread invasive bumblebee *B. terrestris* has the potential to disrupt pollinator services through nectar robbing. When the structure of the flower renders the nectaries inaccessible, *B. terrestris* (and some other bee species) may use their powerful mandibles to bite through the base of the corolla (Inouye 1980b, 1983). In this way they act as floral parasites, removing nectar without effecting pollination. In Tasmania, they rob some bird-pollinated plants in this way (Goulson *et al.* 2002c). The effects of this behaviour are hard to predict. Clearly, it could result in reduced seed set if the lowered floral resources render the flowers less attractive to pollinators (Darwin 1876). In some instances, robbers have been found to reduce the amount of reward available and hence decrease visitation rates by pollinators (McDade and Kinsman 1980) and reduce seed set (Roubik 1982b; Roubik *et al.* 1985; Irwin and Brody 1999). However, robbing does not always result in adverse effects on seed set (see Chapter 12). Kenta *et al.* (2007) examined the possible effects of *B. terrestris* invasion in Japan on pollination of seven native plant species in greenhouse experiments in which plants were exposed to either *B. terrestris*, native bumblebees or a mixture of the two. Five of the seven plant species had lower fruit set or fruit quality when exposed exclusively to *B. terrestris*, but this was largely because these plants had deep corollas which only the long-tongued native bees could legitimately visit; they were either robbed or ignored by *B. terrestris*. Such effects would only be manifest in natural situations if *B. terrestris* excluded long-tongued native bumblebees, which seems unlikely.

A second possible detrimental effect of exotic bees is that rather than reducing seed set of native flowers, they may alter the population structure by effecting a different pattern of pollen transport to native pollinators. There is some evidence to support this. In South Australia, Paton (1990, 1993) found that honeybees extracted more nectar and pollen from a range of flower species than did birds, the primary native pollinators. However, honeybees moved between plants far less than did birds, and so were less effective in cross-pollinating. This seems to be a general pattern, for several other studies have reported that inter-plant movement by both bumblebees and honeybees is lower than that of other visitors (McGregor *et al.* 1959; Heinrich and Raven 1972; Silander and Primack 1978). Of course other pollinators often also move small distances; in terms of maximizing foraging efficiency it makes obvious sense to do so (Waddington 1983b), and it has been argued that honeybees are not unusual in this respect (Butz Huryn 1997). However, this is not true. Workers of all social bees are unusual in that they are not constrained in their foraging behaviour by the need to find mates, locate oviposition sites or guard a territory; they are single-minded in their task. In contrast, for example, butterflies intersperse visits to flowers with long patrolling flights in which they search for mates (males) or oviposition sites (females) (Goulson *et al.* 1997a,b). Thus, honeybees, bumblebees and other social bees do tend to engage in fewer long

flights than other species (Schmitt 1980, Waser 1982a). The most obvious possible effect of exotic social bees in this respect is increased self-pollination, which could also result in reduced seed set if the plant is self-infertile. Reduced inter-patch pollen movement could result in reproductive fragmentation of plant populations. However, rare long-distance pollen flow is exceedingly hard to quantify, and currently there are no data available with which to assess whether exotic bees have had a significant impact on the genetic structure of native plant populations.

Clearly it is not possible to generalize as to the effects that exotic bees will have on seed set of native flowers. For some species they will provide effective pollination, for others they will not. Where native pollinators have declined for other reasons, for example as a result of habitat loss and fragmentation, exotic bees may provide a valuable replacement pollinator service of native flowers. Where exotic bees are floral parasites, the effect will depend on whether rates of parasitism are sufficient to deter native pollinators. Any change in seed set (including increases) of plant species within a community could lead to long-term ecological change, but such effects would be difficult to detect amongst the much larger environmental changes that are currently taking place.

## 14.6 Pollination of exotic weeds

As we have seen, both honeybees and bumblebees visit a broad range of flowers. They also appear to prefer to visit exotic flowers (Telleria 1993; Thorp *et al.* 1994). For example, in Ontario, 75% of pollen collected by honeybees was from introduced plants (Stimec *et al.* 1997). Across a range of sites in Tasmania, overall 72.6% of flower visits by honeybees and 83.5% of visits by *B. terrestris* were to introduced weeds (Goulson *et al.* 2002c). Indeed it has been argued that the distribution of *B. terrestris* in Tasmania is largely limited to areas where European weeds are abundant, since some of these plants provide a protected resource in the form of nectar presented in deep corollas, which the shorter-tongued native bees cannot access (Goulson *et al.* 2002c). In New Zealand, *B. terrestris* has been recorded visiting 400 exotic plants but only 19 native species (MacFarlane 1976; Goulson and Hanley 2004). The three other introduced *Bombus* species also visit mainly introduced plants (Donovan 1980; Goulson and Hanley 2004). In the highlands of New Zealand, honeybees rely almost exclusively on introduced plants for pollen during most of the season (Pearson and Braiden 1990). These preferences presumably occur because the bees tend to gain more rewards by visiting flowers with which they are coadapted; most of the insect-pollinated native flowers in New Zealand and Tasmania are small, shallow, and provide small quantities of nectar.

So do visits by exotic bees improve seed set of weeds? By virtue of their abundance and foraging preferences, they often make up a very large proportion of insect visits to weeds. For example in a site dominated by European weeds in Tasmania, honeybees and bumblebees were the major flower visitors and comprised 98% of all insect visits to the problematic weed creeping thistle, *Cirsium arvense* (D.G., unpublished data). In North America, honeybees increase seed set of the yellow star thistle, *Centaurea*

*solstitialis* (Barthell *et al.* 1994) and are the main pollinators of the major weed purple loosestrife, *Lythrum salicaria* (Mal *et al.* 1992). Donovan (1980) reports that bumblebees are major pollinators of introduced weeds in New Zealand. It thus seems obvious and inevitable that exotic bees will prove to be important pollinators of various weeds (Sugden *et al.* 1996).

Remarkably, this view has been challenged. It is hard to agree with the conclusions of Butz Huryn and Moller (1995) that 'Although honey bees may be important pollinators of some weeds, they probably do not contribute substantially to weed problems'. Butz Huryn (1997) argues that most weeds do not rely on insect pollination, either because they are anemophilous, self-pollinating, apomictic or primarily reproduce vegetatively. This is undoubtedly true of some weed species. For example, of the 33 worst environmental weeds in New Zealand (Williams and Timmins 1990), nine fall into one of these categories (Butz Huryn and Moller 1995). However, 16 require pollination and are visited by honeybees, and one is pollinated more or less exclusively by them (the barberry shrub, *Berberis darwinii*). Eight more are listed as having 'unknown' pollination mechanisms (Butz Huryn and Moller 1995). This group includes the tree lupin, *Lupinus*



**Figure 14.1** A non-native *B. terrestris* worker pollinating non-native lupins in New Zealand.

*arboreus*, and broom, *Cytisus scoparius*, which are self-incompatible and rely on pollination by bumblebees (Stout 2000; Stout *et al.* 2002) (Fig. 14.1). It also includes gorse, *Ulex europeaus*, which is thought to depend on honeybee pollination, and in which seed set is greatly reduced by a lack of pollinators in the Chatham Islands where honeybees and bumblebees are absent (MacFarlane *et al.* 1992). Thus, at least four major weeds in New Zealand are pollinated primarily by exotic bees.

*L. arboreus* is currently a minor weed in Tasmania. However, seed set in areas recently colonized by *B. terrestris* has increased, and it is likely that *L. arboreus* may become as problematic in Tasmania as it is in New Zealand now that it has an effective pollinator (Stout *et al.* 2002). Its zygomorphic flowers have to be forced apart to expose the stamens and stigma; only a large, powerful bee is able to do this, and no such bees are native to Tasmania. *L. arboreus* is only one of many weeds in Tasmania, New Zealand and southern Australia that originated in the temperate northern hemisphere and are coadapted for pollination by bumblebees.

Demonstrating that exotic bees increase seed set of weeds is not sufficient in itself to conclusively show that the action of the bees will increase the weed population (Butz Huryn 1997). No long-term studies of weed population dynamics in relation to the presence or absence of exotic bees have been carried out. Since most weed species are short-lived and dependent on high reproductive rates, it seems probable that seed production is a crucial factor in determining their abundance. Key factor analysis of the life history could reveal whether seed set is directly related to population size.

At present, Australia alone has 2,700 exotic weed species, and the costs of control and loss of yields due to these weeds costs an estimated AU\$3 billion per year (Commonwealth of Australia 1997). The environmental costs are less easy to quantify but are certainly large. The majority of these 2,700 exotic weeds are at present scarce and of trivial ecological and economic importance. The recent arrival of bumblebees in Tasmania may awake some of these 'sleeper' weeds, particularly if they are adapted for bumblebee pollination. Positive feedback between abundance of weeds and abundance of bumblebees is probable, since an increase in weed populations will encourage more bumblebees, and vice versa. If even one new major weed occurs in Australia due to the presence of bumblebees, the economic and environmental costs could be substantial. The recent (2008) decision by the Australian government to refuse permission for the use of bumblebees for crop pollination on mainland Australia was a wise one.

## 14.7 Summary and conclusions

Both *A. mellifera* and *B. terrestris* are now abundant over large areas where they naturally did not occur. They are both polylectic, and thus use resources utilized by a broad range of native species. It seems almost certain that abundant and widespread exotic organisms which single-handedly utilize a large proportion of the available floral resources do impact on local flower-visiting fauna. Consider, for example, the Tasmania native bee community. One hundred and eighty years ago this presumably consisted of a



large number of small, solitary and sub-social species. Over 100 species have recently been recorded, and many more probably exist. Nowadays, by far the most abundant flower-visiting insects at almost every site is the honeybee, often outnumbering all other flower-visiting insects by a factor of 10 or more (D.G., pers. obs.). In the southeast, the second most abundant flower visitor is usually the bumblebee *B. terrestris*. The majority of floral resources are gathered by these bees, often during the morning before native bees have become active. It is hard to conceive how the introduction of these exotic species and their associated pathogens could not have substantially altered the diversity and abundance of native bees. Unfortunately, we will never know what the abundance and diversity of the Tasmanian bee fauna was like before the introduction of the honeybee.

Of course the same applies to most other regions such as North America where the honeybee has now been established for nearly 400 years. It is quite possible that some, perhaps many, native bee species were driven to extinction by the introduction of this numerically dominant species or by exotic pathogens that arrived with it. Even were it practical or considered desirable to eradicate honeybees from certain areas, it would be too late for such species.

The introduction of exotic bees must increase seed set and hence weediness of some exotic plants, particularly when, as in the case of the bumblebee in Australia, many of the weeds were introduced from the same geographic region and are coadapted with the introduced bee.

It must be remembered that introduced bees provide substantial benefits to man in terms of pollination of crops, and in the case of the honeybee in providing honey. Ideally these quantifiable benefits should be weighed against the likely costs. In areas where weeds pollinated by exotic bees are a serious threat, and/or where native communities of flora and fauna are particularly valued, it may be that the benefits provided by these species are outweighed by the costs. Clearly further research, particularly rigorous manipulative experiments, are needed to determine how much introduced bees contribute to weed problems and whether they do substantially impact upon native pollinator communities. Also, further investigation of the potential of native bees to provide adequate crop pollination is needed. A ban on the import of *B. terrestris* to North America led to the swift development of *B. impatiens* as an alternative pollinator for tomatoes. In most parts of the world there are probably native bee species that could be exploited, although there are disease risks associated with use of any bee species at high density. There are native Australian bee species such as carpenter bees (*Xylocopa* sp.) and the blue-banded bee *Amegilla* that are able to pollinate tomatoes, but adequate means of rearing these bees for glasshouse use have not yet been developed (Hogendoorn *et al.* 2000, 2007).

The precautionary principle argues that in the meantime we should prevent further deliberate release of exotic bee species (such as of bumblebees in mainland Australia and South Africa). If bees are to be moved between countries (regardless of whether they are native to the country of importation), rigorous screening should be used to

ensure that they are not carrying parasites or pathogens. Remarkably, at present most of the bumblebee trade appears to be unregulated in this respect. Most of the commercial bumblebee rearers now take steps to ensure that their product is free of the better known bumblebee diseases, but it is not clear exactly which diseases and parasites they test for and there is little or nothing in the way of independent checks in most countries. As recently as 2004, Niwa *et al.* detected the pathogen *N. bombi* in commercial bumblebee nests originating in Europe.

It is sometimes argued that the use of bumblebees in glasshouses in areas where they are non-native should be acceptable as they are contained, and hence competitive interactions with wild bees and possible establishment in the wild are unlikely. However, glasshouses require ventilation, and there is clear evidence that bumblebee colonies placed in glasshouses use vents to forage outside: for example, Whittington *et al.* (2004) found that up to 73% of pollen collected by bumblebee colonies in tomato glasshouses came from *outside*.

Escape of bumblebees can be reduced by use of netting on vents and doors. This is now routine practice in Japan, where it is legally enforced (although rather too late since *B. terrestris* is well established in the wild; a classic example of shutting the stable door after the horse has bolted). This is probably sensible as a means of reducing the threat of pathogen spillover when native bees are being kept at artificially high densities (and also forces the bees to forage on the commercial crop in the glasshouse). However, it is absurdly optimistic to expect this to provide a barrier to invasion of a non-native species. Some bees will always escape from commercial glasshouses (windows get broken, netting torn, doors left open, etc.). The horticulture industry in Australia has lobbied (so far without success) to be allowed to use *B. terrestris* in netted glasshouses, but if this occurs the constant trickle of inevitable escapees would almost certainly eventually establish in the wild. Unlike many of the other impacts that man has on the environment, introduction of exotic species is usually irreversible. Once feral bee populations are established, removal is probably impossible (Oldroyd 1998). Similarly, if an exotic pathogen escapes into wild bee populations there is no way it can be eradicated. Since genetic studies of the Tasmanian *B. terrestris* population suggest that it was founded by perhaps one or two queens (Schmid-Hempel *et al.* 2007), even a single mated queen escaping from a glasshouse might be enough. Just because it is hard to measure potential competitive effects, and to quantify long-term impacts on plant communities, does not mean that these processes are not occurring. Given the numerous potential interactions between alien bees and their pathogens, on the one hand, and native flower visitors, native plants and non-native weeds, on the other, it seems almost certain that introducing new bee species has serious impacts on natural ecosystems that we have not yet begun to appreciate.

*This page intentionally left blank*

# References

- Able, K.P. 1994. Magnetic orientation and magnetoreception in birds. *Progress in Neurobiology* 42: 449–473.
- Abrahamovich, A.H., Telleria, M.C. and Díaz, N.B. 2001. Bombus species and their associated flora in Argentina. *Bee World* 82: 76–87.
- Ackerman, D.J., Mesler, M.R., Lu, K.L. and Montalvo, A.M. 1982. Food-foraging behavior of male euglossinin (Hymenoptera: Apidae): vagabonds or trapliners? *Biotropica* 14: 241–248.
- Aebischer, N.J., Blake, K.A. and Boatman, N.D. 1994. Field margins as habitats for game. In: *Field Margins: Integrating Agriculture and Conservation. Brighton Crop Protection Conference Monograph No. 58* (ed. by N.D. Boatman), pp. 95–104. British Crop Protection Council, Farnham.
- Aizen, M.A. and Feinsinger, P. 1994. Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology* 75: 330–351.
- Alaux, C., Boutot, M., Jaisson, P. and Hefetz, A. 2007. Reproductive plasticity in bumblebee workers (*Bombus terrestris*)—reversion from fertility to sterility under queen influence. *Behavioral Ecology and Sociobiology* 62: 213–222.
- Alaux, C., Jaisson, P. and Hefetz, A. 2006. Regulation of worker reproduction in bumblebees (*Bombus terrestris*): workers eavesdrop on a queen signal. *Behavioral Ecology and Sociobiology* 60: 439–446.
- Alaux, C., Savarit, F., Jaisson, P. and Hefetz, A. 2004. Does the queen win it all? Queen-worker conflict over male production in the bumblebee, *Bombus terrestris*. *Naturwissenschaften* 91: 400–403.
- Alcock, J. and Alcock, J.P. 1983. Male behaviour in two bumblebees, *Bombus nevadensis auricomus* and *B. griseicollis* (Hymenoptera: Apidae). *Journal of Zoology* 200: 561–570.
- Alcock, J. and Smith, A.P. 1987. Hilltopping, leks and female choice in the carpenter bee *Xylocopa (neoxylocopa) varipuncta*. *Journal of Zoology* 211: 1–10.
- Alexander, H.M. 1990. Dynamics of plant-pathogen interactions in natural plant communities. In: *Pests, Pathogens and Plant Communities* (eds J.J. Burdon and S.R. Leather), pp. 31–45. Blackwell Scientific publications, Oxford.
- Alexander, N. (ed.) 1996. *Australia: State of the Environment 1996*. CSIRO publishing, Melbourne.
- Alfken, J.D. 1913. Die Bienenfauna von Bremen. *Abhandlungen Naturwissenschaftlicher Verein, Bremen* 22: 1–220.
- Alford, D.V. 1968. The biology and immature stages of *Syntretus splendidus* (Marshall) (Hymenoptera: Braconidae, Euphorinae), a parasite of adult bumblebees. *Transactions of the Royal Entomological Society of London* 120: 375–393.
- Alford, D.V. 1969. *Sphaerularia bombi* as a parasite of bumble bees in England. *Journal of Apicultural Research* 8: 49–54.

## 240 References

- Alford, D.V. 1973. *Syntretus splendidus* attacking *Bombus pascuorum* in Hampshire. *Bee World* 54: 176.
- Alford, D.V. 1975. *Bumblebees*. Davis-Poynter, London.
- Alford, D.V. (ed.) 1980. Atlas of the Bumblebees of the British Isles. Institute of Terrestrial Ecology Publications, No. 30.
- Alghamdi, A., Dalton, L., Phillis, A., Rosato, E. and Mallon, E.B. 2008. Immune response impairs learning in free-flying bumble-bees. *Biology Letters* 4: 479–481.
- Allander, K. and Schmid-Hempel, P. 2000. Immune defence reaction in bumble-bee workers after a previous challenge and parasitic coinfection. *Functional Ecology* 14: 711–717.
- Allen, G.R., Seeman, O.D., Schmid-Hempel, P. and Buttermore, R.E. 2007. Low parasite loads accompany the invading population of the bumblebee, *Bombus terrestris* in Tasmania. *Insectes Sociaux* 54: 56–63.
- Allen, J.A. 1989. Searching for search image. *Trends in Ecology and Evolution* 4: 361.
- Allen, T., Cameron, S., McGinley, R. and Heinrich, B. 1978. The role of workers and new queens in the ergonomics of a bumblebee colony (Hymenoptera: Apoidea). *Journal of the Kansas Entomological Society* 51: 329–342.
- Anasiewicz, A. 1971. Observations on the bumble-bees in Lublin. *Polish Journal of Ecology* 19: 401–417.
- Anasiewicz, A. and Warakomska, Z. 1977. Pollen food of the bumblebees (*Bombus* Latr., Hymenoptera) and their associations with the plant species in the Lublin region. *Polish Journal of Ecology* 25: 309–322.
- Anderson, J.M.E. (1989) Honeybees in natural ecosystems. In: *Mediterranean Landscapes in Australia: Mallee Ecosystems and their Management* (eds J.C. Noble and R.A. Bradstock), pp. 300–304. CSIRO, East Melbourne.
- Andersson, S. 1988. Size-dependent pollination efficiency in *Anchusa officinalis* (Boraginaceae): causes and consequences. *Oecologia* 76: 125–130.
- Andrewartha, H.G. and Birch, L.C. 1954. *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago.
- Appelgren, M., Bergström, G., Svensson, B.G. and Cederberg, B. 1991. Marking pheromones of *Megabombus* bumble bee males. *Acta Chemica Scandinavica* 45: 972–974.
- Arizmendi, M.C., Dominguez, C.A. and Dirzo, R. 1995. The role of an avian nectar robber and of hummingbird pollinators in the reproduction of two plant species. *Functional Ecology* 10: 119–127.
- Armstrong, J.A. 1979. Biotic pollination mechanisms in the Australian flora—a review. *New Zealand Journal of Botany* 17: 467–508.
- Arretz, P.V. and Macfarlane, R.P. 1986. The introduction of *Bombus ruderatus* to Chile for red clover pollination. *Bee World* 67: 15–22.
- Asada, S. and Ono, M. 2000. Difference in colony development of two Japanese bumblebees, *Bombus hypocrita* and *B. ignitus* (Hymenoptera: Apidae). *Applied Entomology and Zoology* 35: 597–603.
- Awram, W.J. 1970. Flight Route Behaviour of Bumblebees. Ph.D. thesis, University of London, London.
- Ayabe, T., Hoshihara, H. and Ono, M. 2004. Cytological evidence for triploid males and females in the bumblebee, *Bombus terrestris*. *Chromosome Research* 12: 215–223.
- Bäckman, J.C. and Tiainen, J. 2002. Habitat quality of field margins in a Finnish farmland area for bumblebees (Hymenoptera: *Bombus* and *Psithyrus*). *Agriculture, Ecosystems and Environment* 89: 53–68.

- Baer, B. 2003. Bumblebees as model organisms to study male sexual selection in social insects. *Behavioral Ecology and Sociobiology* 54: 521–533.
- Baer, B., Maile, R., Schmid-Hempel, P., Margan, E.D. and Jones, G.R. 2000. Chemistry of a mating plug in bumblebees. *Journal of Chemical Ecology* 26: 1869–1875.
- Baer, B., Morgan, E.D. and Schmid-Hempel, P. 2001. A nonspecific fatty acid within the bumblebee mating plug prevents females from remating. *Proceedings of the National Academy of Sciences USA* 98: 3926–3928.
- Baer, B. and Schmid-Hempel, P. 1999. Experimental variation in polyandry affects parasite load and fitness in a bumble-bee. *Nature* 397: 151–154.
- Baer, B. and Schmid-Hempel, P. 2000. The artificial insemination of bumblebee queens. *Insectes Sociaux* 47: 183–187.
- Baer, B. and Schmid-Hempel, P. 2001. Unexpected consequences of polyandry for parasitism and fitness in the bumblebee, *Bombus terrestris*. *Evolution* 55: 1639–1643.
- Baer, B. and Schmid-Hempel, P. 2003. Bumblebee workers from different sire groups vary in susceptibility to parasite infection. *Ecology Letters* 6: 106–110.
- Baer, B. and Schmid-Hempel, P. 2005. Sperm influences female hibernation success, survival and fitness in the bumble-bee *Bombus terrestris*. *Proceedings of the Royal Society B-Biological Sciences* 272: 319–323.
- Baer, B. and Schmid-Hempel, P. 2006. Phenotypic variation in male and worker encapsulation response in the bumblebee *Bombus terrestris*. *Ecological Entomology* 31: 591–596.
- Bailey, L. and Gibbs, A.J. 1964. Acute infection of bees with paralysis virus. *Journal of Insect Pathology* 6: 395–407.
- Banaszak, J. 1983. Ecology of bees (Apoidea) of agricultural landscapes. *Polish Ecological Studies* 9: 421–505.
- Banaszak, J. 1992. Strategy for conservation of wild bees in an agricultural landscape. *Agriculture, Ecosystems and Environment* 40: 179–192.
- Banaszak, J. 1996. Ecological bases of conservation of wild bees. In: *The Conservation of Bees* (eds A. Matheson, S.L. Buchmann, C. O'Toole, P. Westrich and I.H. Williams), pp. 55–62. Academic Press, London.
- Banda, H.J. and Paxton, R.J. 1991. Pollination of greenhouse tomatoes by bees. *Acta Horticulturae* 288: 194–198.
- Barnett, E.A., Charlton, A.J. and Fletcher, M.R. 2007. Incidents of bee poisoning with pesticides in the United Kingdom, 1994–2003. *Pest Management Science* 63: 1051–1057.
- Barron, M.C., Wratten, S.D. and Donovan, B.J. 2000. A four-year investigation into the efficiency of domiciles for enhancement of bumble bee populations. *Agricultural and Forest Entomology* 2: 141–146.
- Barrow, D.A. 1983. Ecological Studies on Bumblebees in South Wales with Special Reference to Resource Partitioning and Bee Size Variation. PhD thesis, University of Wales, UK, 161 pp.
- Barrow, D.A. and Pickard, R.S. 1984. Size-related selection of food plants by bumblebees. *Ecological Entomology* 9: 369–373.
- Barth, F.G. 1985. *Insects and Flowers, the Biology of a Partnership*. George Allen and Unwin, London.
- Barthell, J.F., Randall, J.M., Thorp, R.W. and Wenner, A.M. 1994. Invader assisted invasion: pollination of yellow star-thistle by feral honey bees in island and mainland ecosystems [abstract]. *Supplement to the Bulletin of the Ecological Society of America* 75: 10.

## 242 References

- Batra, S.W.T. 1979. *Osmia cornifrons* and *Pithitis smaragdula*, two asian bees introduced into the United States for crop pollination. In: Proc. IV Internat. Symposium of Pollination. MD Agric. Exp. Stn. Sp. Misc. Pub. I. (ed. M.C. Dewey), University of Maryland, College Park.
- Batra, S.W.T. 1995. Bees and pollination in our changing environment. *Apidologie* 26: 361–370.
- Beattie, A.J. 1976. Plant dispersion, pollination and gene flow in *Viola*. *Oecologia* 25: 291–300.
- Beekman, M. and Bin Lew, J. 2008 Foraging in honeybees—when does it pay to dance? *Behavioral Ecology* 19: 255–262.
- Beekman, M. and Van Stratum, P. 1998. Bumblebee sex ratios: why do bumblebees produce so many males? *Proceedings of the Royal Society of London B* 265: 1535–1543.
- Beekman, M., Van Stratum, P. and Lingeman, R. 1998. Diapause survival and post-diapause performance in bumblebee queens (*Bombus terrestris*). *Entomologia Experimentalis et Applicata* 89: 207–214.
- Beekman, M., Van Stratum, P. and Veerman, A. 1999. Selection for non-diapause in the bumblebee *Bombus terrestris*, with notes on the effect of inbreeding. *Entomologia Experimentalis et Applicata* 93: 69–75.
- Bell, G. 1985. On the function of flowers. *Proceedings of the Royal Society of London B-Biological Sciences* 224: 223–265.
- Bell, G., Lefebvre, L., Geraldeae, L.-A. and Weary, D. 1984. Partial preference of insects for the male flowers of an annual herb. *Oecologia* 64: 287–294.
- Bell, W.G. 1991. *Searching Behaviour: The Behavioral Ecology of Finding Resources*. Chapman and Hall, London.
- Bennett, A.W. 1884. On the constancy of insects in their visits to flowers. *The Journal of the Linnean Society* 17: 175–185.
- Benton, T. 2006. *Bumblebees*. Collins New Naturalist Series, London.
- Bergman, P. and Bergström, G. 1997. Scent marking, scent origin, and species specificity in male premating behaviour of two Scandinavian bumblebees. *Journal of Chemical Ecology* 23: 1235–1251.
- Bergman, P., Bergström, G. and Appelgren, M. 1996. Labial gland marking secretion in males of two Scandinavian cuckoo bumblebee species. *Chemoecology* 7: 140–145.
- Bergström, G., Bergman, P., Appelgren, M. and Smith, J.O. 1996. Labial gland chemistry of three species of bumblebees (Hymenoptera, Apidae) from North America. *Bioorganic and Medicinal Chemistry* 4: 515–519.
- Bergström, G., Kullenberg, B., Stållberg-Stenhagen, S. and Stenhagen, E. 1968. Studies on natural odiferous compounds. II. Identification of a 2,3-dihydro-farnesol as the main component of the marking perfume of male bumblebees of the species *Bombus terrestris*. *Arkiv För Kemi* 28: 453–469.
- Bergström, G., Svensson, B.G., Appelgren, M. and Groth, I. 1981. Complexity of bumblebee marking pheromones: biochemical, ecological and systematical interpretations. In: *Biosystematics of Social Insects* (eds P.E. Howse and J.L. Clement), pp. 175–183. Academic Press, London.
- Bertin, R.I. 1982. Floral biology, hummingbird pollination and fruit production of Trumpet Creeper (*Campsis radicans*, Bignoniaceae). *American Journal of Botany* 69: 122–134.
- Bertsch, A., Schweer, H., Titze, A. and Tanaka, H. 2005. Male labial gland secretions and mitochondrial DNA markers support, species status of *Bombus cryptarum* and *B. magnus* (Hymenoptera, Apidae). *Insectes Sociaux* 52: 45–54.
- Bertsch, A.H. 1983. Nectar production of *Epilobium augustifolium* L. at different air humidities; nectar sugar in individual flowers and the optimal foraging theory. *Oecologia* 59: 40–48.

- Bertsch, A.H. 1987. Flowers as food sources and the cost of outcrossing. *Ecological Studies* 61: 277–293.
- Best, L.S. and Bierzychudek, P. 1982. Pollinator foraging on foxglove (*Digitalis purpurea*): a test of a new model. *Evolution* 36: 70–79.
- Betts, A.D. 1920. Nosema in humble bees. *Bee World* 1: 171.
- Biernaskie, J.M., Cartar, R.V. and Hurly, T.A. 2002. Risk-averse inflorescence departure in hummingbirds and bumble bees: could plants benefit from variable nectar rewards. *Oikos* 98: 98–104.
- Bierzychudek, P. 1981. Pollinator limitation of plant reproductive effort. *American Naturalist* 117: 838–840.
- Birmingham, A.L., Hoover, S.E., Winston, M.L. and Ydenberg, R.C. 2004. Drifting bumble bee (Hymenoptera: Apidae) workers in commercial greenhouses may be social parasites. *Canadian Journal of Zoology* 82: 1843–1853.
- Bloch, G. 1999. Regulation of queen-worker conflict in bumble-bee (*Bombus terrestris*) colonies. *Proceedings of the Royal Society of London B* 266: 2465–2469.
- Bloch, G., Borst, D.W., Huang, Z.-Y., Robinson, G.E. and Hefetz, A. 1996. Effects of social conditions on juvenile hormone mediated reproductive development in *Bombus terrestris* workers. *Physiological Entomology* 21: 257–267.
- Bloch, G. and Hefetz, A. 1999. Regulation of reproduction by dominant workers in bumblebee (*Bombus terrestris*) queenright colonies. *Behavioral Ecology and Sociobiology* 45: 125–135.
- Blough, D.S. 1979. Effects of the number and form of stimuli on visual search in the pigeon. *Journal of Experimental Psychology* 5: 211–223.
- Blum, M.S. 1981. *Chemical Defenses of Arthropods*. Academic Press, New York.
- Blum, M.S. 1987. Specificity of pheromonal signals: a search for its recognitive bases in terms of a unified chemisociality. In: *Chemistry and Biology of Social Insects* (eds J. Eder and H. Rembold), pp. 401–405. J. Peperny, München.
- Boatman, N.D. 1992. Herbicides and the management of field boundary vegetation. *Pesticide Outlook* 3: 30–34.
- Boatman, N.D. and Wilson, P.J. 1988. Field edge management for game and wildlife conservation. *Aspects of Applied Biology* 16: 53–61.
- Boetius, J. 1948. Über den Verlauf der Nektarabsonderung einiger Blütenpflanzen. *Beihefte Schweizerische Bienenzeitung* 2: 257–317.
- Bogler, D.J., Neff, J.L. and Simpson, B.B. 1995. Multiple origins of the yucca-yucca moth association. *Proceedings of the National Academy of Sciences of the USA*, 92: 6864–6867.
- Bohart, G.E. 1970. The Evolution of Parasitism among Bees. Utah State University, pp. 30. Logan, Utah.
- Bohart, G.E. 1972. Management of wild bees for the pollination of crops. *Annual Review of Entomology* 17: 287–312.
- Bohart, G.E. and Knowlton, G.F. 1953. Yearly population fluctuations of *Bombus morrisoni* at Fredonia, Arizona. *Journal of Economic Entomology* 45: 890.
- Bond, A.B. 1983. Visual-search and selection of natural stimuli in the pigeon—the attention threshold hypothesis. *Journal of Experimental Psychology* 9: 292–306.
- Bond, A.B. and Riley, D.A. 1991. Searching image in the pigeon: a test of three hypothetical mechanisms. *Ethology* 87: 203–224.
- Bond, H.W. and Brown, W.L. 1979. The exploitation of floral nectar in *Eucalyptus incrassata* by honeyeaters and honeybees. *Oecologia* 44: 105–111.
- Boomsma, J.J. and Grafen, A. 1991. Colony-level sex ratio selection in the eusocial Hymenoptera. *Journal of Evolutionary Biology* 3: 383–407.



- Boomsma, J.J. and Ratnieks, F.L.W. 1996. Paternity in eusocial Hymenoptera. *Philosophical Transactions of the Royal Society of London B* 351: 947–975.
- Borneck, R. and Merle, B. 1989. Essai d'une évaluation de l'incidence économique de l'abeille pollinisatrice dans l'agriculture européenne. *Apiacta* 24: 33–38.
- Bortolotti, L., Duchateau, M.J. and Sbrenna, G. 2001. Effect of juvenile hormone on caste determination and colony processes in the bumblebee *Bombus terrestris*. *Entomologia Experimentalis et Applicata* 101: 143–158.
- Boucher, D.H., James, S. and Keeler, K. 1982. The ecology of mutualism. *Annual Review of Ecology and Systematics* 13: 315–347.
- Bourke, A.F.G. 1994. Worker matricide in social bees and wasps. *Journal of Theoretical Biology* 167: 283–292.
- Bourke, A.F.G. 1997. Sex ratios in bumble bees. *Philosophical Transactions of the Royal Society of London B* 352: 1921–1933.
- Bourke, A.F.G. and Hammond, R.L. 2002. Genetics of the scarce bumble bee, *Bombus distinguendus*, and nonlethal sampling of DNA from bumble bees. A Report for the RSPB, January 2002.
- Bourke, A.F.G. and Ratnieks, F.L.W. 1999. Kin conflict over caste determination in social Hymenoptera. *Behavioral Ecology and Sociobiology* 46: 287–297.
- Bourke, A.F.G. and Ratnieks, F.L.W. 2001. Kin-selected conflict in the bumble-bee *Bombus terrestris* (Hymenoptera: Apidae). *Proceedings of the Royal Society of London B* 268: 347–355.
- Bowers, M.A. 1985a. Bumblebee colonization, extinction, and reproduction in subalpine meadows in Northeastern Utah. *Ecology* 66: 914–927.
- Bowers, M.A. 1985b. Experimental analyses of competition between two species of bumble bees (Hymenoptera: apidae). *Oecologia* 67: 224–230.
- Boyle, R.M.D. and Philogène, B.J.R. 1983. The native pollinators of an apple orchard: variations and significance. *Journal of Horticultural Science* 58: 355–363.
- Brand, C.J. and Westgate, J.M. 1909. Alfalfa in cultivated rows for seed production in semiarid regions. United States Department of Agriculture, Bureau of Plant Industry, Circular No. 24: 1–23.
- Brasse, D. 2003. Poisoning incidents involving honeybees in Germany (1999–2002) and new problems for beekeeping. *Bulletin of Insectology* 56: 199.
- Brian, A.D. 1952. Division of labour and foraging in *Bombus agrorum* Fabricius. *Journal of Animal Ecology* 21: 223–240.
- Brian, A.D. 1954. The foraging of bumble bees Part 1. Foraging behaviour. *Bee World* 35: 61–67.
- Brian, A.D. 1957. Differences in the flowers visited by four species of bumble-bees and their causes. *Journal of Animal Ecology* 21: 223–240.
- Brian, M.V. 1965a. *Social Insect Populations*. Academic Press, London.
- Brian, M.V. 1965b. Caste differentiation in social insects. *Symposia of the Zoological Society of London* 14: 13–38.
- Brian, M.V. 1983. *Social Insects*. Chapman and Hall, London.
- Bringer, B. 1973. Territorial flight of bumble-bee males in the coniferous forests on the northernmost part of the island of Öland. *Zoon, Supplement* 1: 15–22.
- Brink, D. 1982. Abonanza-blank pollinatorrewardschedule in *Delphinium nelsonii* (Ranunculaceae). *Oecologia* 52: 292–294.

- Brink, D. and Wet, J.M.J. De 1980. Interpopulation variation in nectar production in *Aconitum columbianum* (Ranunculaceae). *Oecologia* 47: 160–163.
- Brittain, W.H. and Newton, D.E. 1933. A study in the relative constancy of hive bees and wild bees in pollen gathering. *Canadian Journal of Research* 9: 334–349.
- Brody, A.K. and Mitchell, R.J. 1997. Effects of experimental manipulation of inflorescence size on pollination and pre-dispersal seed predation in the hummingbird-pollinated plant *Ipomopsis aggregata*. *Oecologia* 110: 86–93.
- Bromley, S.W. 1934. The robber flies of Texas (Diptera, Asilidae). *Annals of the Entomological Society of America* 27: 74–113.
- Bromley, S.W. 1936. Asilids feeding on bumblebees in New England. *Psyche* 43: 14.
- Bromley, S.W. 1949. The Missouri bee-killer, *Proctacanthus milbertii* Macq. (Asilidae: Diptera). *Bulletin of the Brooklyn Entomological Society* 44: 21–28.
- Bronstein, J.L. 1995. The plant-pollinator landscape. In: *Mosaic Landscapes and Ecological Processes* (eds L. Hansson, L. Fahrig and G. Merriam), pp. 256–288. Chapman and Hall, London, UK.
- Brower, J.P., Brower, J.V.Z. and Westcott, P.W. 1960. Experimental studies of mimicry. 5. The reactions of toads (*Bufo terrestris*) to bumblebees (*Bombus americanorum*) and their robberfly mimics (*Mallophora bomboides*), with a discussion of aggressive mimicry. *American Naturalist* 94: 343–355.
- Brown, C.J.D. 1929. A morphological and systematical study of Utah Asilidae (Diptera). *Transactions of the American Entomological Society* 54: 295–320.
- Brown, J.H. 1984. On the relationship between abundance and distribution of species. *American Naturalist* 124: 644–645.
- Brown, M.J.F. and Baer, B. 2005. The evolutionary significance of long copulation duration in bumble bees. *Apidologie* 36: 157–167.
- Brown, M.J.F., Baer, B., Schmid-Hempel, R. and Schmid-Hempel, P. 2002. Dynamics of multiple-mating in the bumblebee *Bombus hypnorum*. *Insectes Sociaux* 49: 315–319.
- Brown, M.J.F., Loosli, R. and Schmid-Hempel, P. 2000. Condition-dependent expression of virulence in a trypanosome infecting bumblebees. *Oikos* 91: 421–427.
- Brown, M.J.F., Moret, Y. and Schmid-Hempel, P. 2003. Activation of host constitutive immune defence by an intestinal trypanosome parasite of bumble bees. *Parasitology* 126: 253–260.
- Brown, M.J.F., Schmid-Hempel, R. and Schmid-Hempel, P. 2003a. Strong context-dependent virulence in a host-parasite system: reconciling genetic evidence with theory. *Journal of Animal Ecology* 72: 994–1002.
- Brown, M.J.F., Schmid-Hempel, R. and Schmid-Hempel, P. 2003b. Queen-controlled sex ratios and worker reproduction in the bumble bee *Bombus hypnorum*, as revealed by microsatellites. *Molecular Ecology* 12: 599–1605.
- Buchmann, S.L. 1985. Bees use vibration to aid pollen collection from non-poricidal flowers. *Journal of the Kansas Entomological Society* 58: 517–525.
- Buchmann, S.L. and Nabhan, G.P. 1996. *The Forgotten Pollinators*. Island Press, Washington, DC.
- Bulmer, M.G. 1981. Worker-queen conflict in annual social Hymenoptera. *Journal of Theoretical Biology* 93: 239–251.
- Bulmer, M.G. 1983. The significance of protandry in the social Hymenoptera. *Journal of Theoretical Biology* 93: 239–251.
- Burd, M. 1994. Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. *Botanical Review* 60: 83–139.

## 246 References

- Burkle, L.A., Irwin, R.E. and Newman, D.A. 2007. Predicting the effects of nectar robbing on plant reproduction: implications of pollen limitation and plant mating system. *American Journal of Botany* 94: 1935–1943.
- Burns, J.G. and Thomson, J.D. 2006. A test of spatial memory and movement patterns of bumblebees at multiple spatial and temporal scales. *Behavioral Ecology* 17: 48–55.
- Buttermore, R.E. 1997. Observations of successful *Bombus terrestris* (L.) (Hymenoptera: Apidae) colonies in southern Tasmania. *Australian Journal of Entomology* 36: 251–254.
- Butz Huryn, V.M. 1997. Ecological impacts of introduced honey bees. *The Quarterly Review of Biology* 72: 275–297.
- Butz Huryn, V.M. and Moller, H. 1995. An assessment of the contribution of honeybees (*Apis mellifera*) to weed reproduction in New Zealand protected natural areas. *New Zealand Journal of Ecology* 19: 111–122.
- Bulmer, M.G. 1983. The significance of protandry in social Hymenoptera. *American Naturalist* 121: 540–551.
- Calam, D.H. 1969. Species and sex-specific compounds from the heads of male bumblebees (*Bombus* spp.). *Nature* 221: 856–857.
- Camargo, C.A. de 1979. Sex determination in bees. XI Production of diploid males and sex determination in *Melipona quadrifasciata*. *Journal of Apicultural Research* 18: 77–84.
- Cameron, S.A. 1981. Chemical signals in bumble bee foraging. *Behavioral Ecology and Sociobiology* 9: 257–260.
- Cameron, S.A., Hines, H.M. and Williams, P.H. 2007. A comprehensive phylogeny of the bumble bees (*Bombus*). *Biological Journal of the Linnean Society* 91: 161–188.
- Cameron, S.A. and Robinson, G.E. 1993. Juvenile hormone does not affect division of labour in bumble bee colonies (Hymenoptera: Apidae). *Annals of the Entomological Society of America* 83: 626–631.
- Cane, J.H. and Payne, J.A. 1988. Foraging ecology of the bee *Habropoda laboriosa* (Hymenoptera: Anthophoridae), an oligolege of blueberries (Ericaceae: Vaccinium) in the southeastern United States. *Annals of the Entomological Society of America* 81: 419–427.
- Cane, J.H. and Payne, J.A. 1990. Native bee pollinates rabbiteye blueberry. *Alabama Agricultural Experiment Station, Highlights of Agricultural Research* 37: 4.
- Capaldi, E.A. and Dyer, F.C. 1999. The role of orientation flights on homing performance in honeybees. *Journal of Experimental Biology* 202: 1655–1666.
- Cardale, J.C. 1993. Hymenoptera: Apoidea. In: *Zoological catalogue of Australia*, Vol. 10 (eds W.W.K. Houston and G.V. Maynard). Australian Government Printing Service, Canberra, 1–406.
- Carpenter, F.L. 1976. Plant-pollinator interactions in Hawaii: pollination energetics of *Metrosideros collina* (Myrtaceae). *Ecology* 57: 1125–1144.
- Carpenter, F.L. 1978. A spectrum of nectar-eater communities. *American Zoologist* 18: 809–819.
- Carreck, N.L. and Williams, I.H. 2002. Food for insect pollinators on farmland: insect visits to flowers of annual seed mixtures. *Journal of Insect Conservation* 6: 13–23.
- Cartar, R.V. 1989. Condition-dependent foraging behavior of bumble bees. PhD thesis, Simon Fraser University, Burnaby, B.C., Canada.
- Cartar, R.V. 1992a. Adjustment of foraging effort and task-switching in energy-manipulated wild bumble bee colonies. *Animal Behaviour* 44: 75–87.
- Cartar, R.V. 1992b. Morphological senescence and longevity: an experiment relating wing wear and life span in foraging wild bumble bees. *Journal of Animal Ecology* 61: 225–231.

- Cartar, R.V. 2004. Resource tracking by bumble bees: Responses to plant-level differences in quality. *Ecology* 85: 2764–2771.
- Cartar, R.V. and Dill, L.M. 1990. Colony energy requirements affect the foraging currency of bumble bees. *Behavioral Ecology and Sociobiology* 27: 377–383.
- Carreck, N.L. and Williams, I.H. 1998. The economic value of bees in the UK. *Bee World*.79: 115–123.
- Carvell, C. 2000. Studies of the distribution and habitat requirements of *Bombus sylvarum* (the shrill carder bee) and other bumblebees at Castlemartin range, Pembrokeshire and Kenfig National Nature Reserve, Glamorgan and surrounding areas. Unpublished report for Countryside Council for Wales/UK Biodiversity Action Plan Bumblebee Working Group.
- Carvell, C. 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. *Biological Conservation* 103: 33–49.
- Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D. and Nowakowski, M. 2007. Comparing the efficiency of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology* 44: 29–40.
- Carvell, C., Meek, W.R., Pywell, R.F. and Nowakowski, M. 2004. The response of bumblebees to successional change in newly created arable field margins. *Biological Conservation* 118: 327–339.
- Carvell, C., Rothery, P., Pywell, R.F. and Heard, M.S. 2008. Effects of resource availability and social parasite invasion on field colonies of *Bombus terrestris*. *Ecological Entomology* 33: 321–327.
- Carvell, C., Roy, D.B., Smart, S.M., Pywell, R.F., Preston, C.D. and Goulson, D. 2006a. Declines in forage availability for bumblebees at a national scale. *Biological Conservation* 132: 481–489.
- Carvell, C., Westrich, P., Meek, W.R., Pywell, R.F. and Nowakowski, M. 2006b. Assessing the value of annual and perennial forage mixtures for bumblebees by direct observation and pollen analysis. *Apidologie* 37: 326–340.
- Cederberg, B., Svensson, B.G., Bergström, G., Appelgren, M. and Groth, I. 1984. Male marking pheromones in North European cuckoo bumble bees, *Psithyrus* (Hymenoptera, Apidae). *Nova Acta Regiae Societatis Scientiarum Upsaliensis, Series V:C*, 3: 161–166.
- Charnov, E.L. 1976. Optimal foraging: the marginal value theorem. *Theoretical Population Biology* 9: 129–136.
- Cheverton, J., Kacelnik, A. and Krebs, J.R. 1985. Optimal foraging: constraints and currencies. In: *Experimental Behavioural Ecology and Sociobiology* (eds B. Holldobler and M. Lindauer), pp. 109–126. Sinauer, Sunderland, MA.
- Chen, P.S., Stumm Zollinger, E., Aigaki, T., Balmer, J., Beinz, M. and Bohlen, P. 1988. A male accessory gland peptide that regulates reproductive behaviour of female *Drosophila melanogaster*. *Cell* 54: 291–298.
- Chittka, L. 1998. Sensorimotor learning in bumblebees: long-term retention and reversal training. *Journal of Experimental Biology* 201: 515–524.
- Chittka, L., Gumbert, A. and Kunze, J. 1997. Foraging dynamics of bumblebees: correlates of movements within and between plant species. *Behavioural Ecology and Sociobiology* 8: 239–249.
- Chittka, L., Kunze, J. and Geiger, K. 1995. The influence of landmarks on distance estimation of honeybees. *Animal Behaviour* 50: 23–31.
- Chittka, L., Shmida, A., Troje, N. and Menzel, R. 1994. Ultraviolet as a component of flower reflections, and the colour perception of Hymenoptera. *Vision Research* 34: 1489–1508.
- Chittka, L. and Thomson, J.D. 1997. Sensori-motor learning and its relevance for task specialization in bumble bees. *Behavioural Ecology and Sociobiology* 41: 385–398.
- Chittka, L., Thomson, J.D. and Waser, N.M. 1999a. Flower constancy, insect psychology, and plant evolution. *Naturwissenschaften* 86: 361–377.

- Chittka, L., Williams, N.M., Rasmussen, H. and Thomson, J.D. 1999b. Navigation without vision: bumblebee orientation in complete darkness. *Proceedings of the Royal Society of London Series B-Biological Sciences* 266: 45–50.
- Chmielewski, W. 1969. Obserwacje nad biologią nowego dla akarofauny polskiej gatunku *Kunizia laevis* (Dujardin 1849) (Acarina, Acaridae). *Polskie Pismo Entomologiczne* 39: 603–617.
- Chmurzynski, J.A., Kieruzel, M., Krzysztofiak, A. and Krzysztofiak, L. 1998. Long-distance homing ability in *Dasypoda altercator* (Hymenoptera, Melittidae). *Ethology* 104: 421–429.
- Cibula, D.A. and Zimmerman, M. 1987. Bumblebee foraging behaviour: changes in departure decisions as a function of experimental manipulations. *American Midlands Naturalist* 117: 386–394.
- Clark, M.G. 1976. Effect of 2-deoxy-D-glucose on flight and flight muscle substrate cycling by the bumble-bee. *Comparative Biochemistry and Physiology* 55B: 409–415.
- Clark, M.G., Bloxham, D.P., Holland, P.C. and Lardy, H.A. 1973. Estimation of the fructose diphosphatase-phosphofructokinase substrate cycle in the flight muscle of *Bombus affinis*. *Biochemistry Journal* 134: 589–597.
- Clark, T.B. 1977. Spiroplasma as a new pathogen in the honeybees. *Journal of Invertebrate Pathology* 29: 112–113.
- Clark, T.B. 1982. Entomopoxvirus-like particles in three species of bumble-bees. *Journal of Invertebrate Pathology* 39: 119–122.
- Clark, T.B., Whitcomb, R.F., Tully, J.G., Mouches, G., Saillard, C., Bové, J.M., Wroblewski, H., Carle, P., Rose, D.L., Henegar, R.B. and Williamson, D.L. 1985. *Spiroplasma melliferum*, a new species from the honeybee (*Apis mellifera*). *International Journal of Systematic Bacteriology* 35: 296–308.
- Clausen, C.P. 1940. *Entomophagous Insects*. McGraw-Hill, New York.
- Clifford, P.T.P. and Anderson, A.C. 1980. Herbage seed production. In: *Proceedings of the New Zealand Grassland Association* (ed. J.A. Lancashire), pp. 76–79. New Zealand Grassland Association, New Zealand.
- Cnaani, J., Borst, D.W., Huang, Z.-Y., Robinson, G.E. and Hefetz, A. 1997. Caste determination in *Bombus terrestris*: differences in development and rates of JH biosynthesis between queen and worker larvae. *Journal of Insect Physiology* 43: 373–381.
- Cnaani, J. and Hefetz, A. 1994. The effect of workers size frequency-distribution on colony development in *Bombus terrestris*. *Insectes Sociaux* 41: 301–307.
- Cnaani, J. and Hefetz, A. 1996. The effect of social environment in the colony on caste determination and JH synthesis in *Bombus terrestris* larvae. In: *Proceedings of the XXth International Congress of Entomology*, p. 390. Florence, Italy.
- Cnaani, J., Robinson, G.E., Bloch, G., Borst, D.W. and Hefetz, A. 2000. The effect of queen-worker conflict on caste determination in the bumblebee *Bombus terrestris*. *Behavioral Ecology and Sociobiology* 47: 346–352.
- Coffey, M.F. and Breen, J. 1997. Seasonal variation in pollen and nectar sources of honey bees in Ireland. *Journal of Apicultural Research* 36: 63–76.
- Cole, B.J. 1983. Multiple mating and the evolution of social behaviour in the Hymenoptera. *Behavioral Ecology and Sociobiology* 12: 191–291.
- Colla, S.R., Otterstatter, M.C., Gegeer, R.J. and Thomson, J.D. 2006. Plight of the bumble bee: pathogen spillover from commercial to wild populations. *Biological Conservation* 129: 461–467.
- Colla, S.R. and Packer, L. 2008. Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidae), with special focus on *Bombus affinis* Cresson. *Biodiversity and Conservation* 17: 1379–1391.

- Colville, F.V. 1890. Notes on bumble-bees. *Proceedings of the Entomological Society of Washington* 1: 197–202.
- Colwell, R.K. 1973. Competition and coexistence in a simple tropical community. *American Naturalist* 107: 737–760.
- Comba, L., Corbet, S.A., Barron, A., Bird, A., Collinge, S., Miyazaki, N. and Powell, M. 1999. Garden flowers: insect visits and the floral reward of horticulturally-modified variants. *Annals of Botany* 83: 73–86.
- Commonwealth of Australia 1997. *The National Weeds Strategy*. Commonwealth of Australia, Canberra.
- Cook, J.M. and Crozier, R.H. 1995. Sex determination and population biology in the Hymenoptera. *Trends in Ecology And Evolution* 10: 281–286.
- Cook, S.M., Awmack, C.S., Murray, D.A. and Williams, I.H. 2003. Are honey bees' foraging preferences affected by pollen amino acid composition? *Ecological Entomology* 28: 622–627.
- Cooper, K.W. 1984. Discovery of the first resident population of the European bee, *Megachile apicalis*, in the United States (Hymenoptera: Megachilidae). *Entomological News* 95: 225–226.
- Corbet, S.A. 1987. More bees make better crops. *New Scientist* 115: 40–43.
- Corbet, S.A. 1995. Insects, plants and succession—advantages of long-term set-aside. *Agriculture Ecosystems and Environment* 53: 201–217.
- Corbet, S.A. 2000. Conserving compartments in pollination webs. *Conservation Biology* 14: 1229–1231.
- Corbet, S.A., Bee, J., Dasmahapatra, K., Gale, S., Gorringer, E., La Ferla, B., Moorhouse, T., Trevail, A., Van Bergen, Y. and Vorontsova, M. 2001. Native or exotic? Double or single? Evaluating plants for pollinator-friendly gardens. *Annals of Botany* 87: 219–232.
- Corbet, S.A., Cuthill, I., Fallows, M., Harrison, T. and Hartley, G. 1981. Why do nectar-foraging bees and wasps work upwards on inflorescences? *Oecologia* 51: 79–83.
- Corbet, S.A., Fussell, M., Ake, R., Fraser, A., Gunson, C., Savage, A. and Smith, K. 1993. Temperature and the pollinating activity of social bees. *Ecological Entomology* 18: 17–30.
- Corbet, S.A., Kerslake, C.J.C., Brown, D. and Morland, N.E. 1984. Can bees select nectar-rich flowers in a patch? *Journal of Apicultural Research* 23: 234–242.
- Corbet, S.A. and Morris, R.J. 1999. Mites on bumble bees and bluebells. *Entomologist's Monthly Magazine* 135: 77–83.
- Corbet, S.A., Saville, N.M., Fussell, M., Prys-Jones, O.E. and Unwin, D.M. 1995. The competition box: a graphical aid to forecasting pollinator performance. *Journal of Applied Ecology* 32: 707–719.
- Corbet, S.A., Williams, I.H. and Osborne, J.L. 1991. Bees and the pollination of crops and wild flowers in the European Community. *Bee World* 72: 47–59.
- Corbet, S.A. and Willmer, P.G. 1980. Pollination of the yellow passionfruit: nectar, pollen and carpenter bees. *Journal of Agricultural Science* 95: 655–666.
- Corbet, S.A., Willmer, P.G., Beament, J.W.L., Unwin, D.M. and Prys-Jones, O.E. 1979. Post-secretory determinants of sugar concentration in nectar. *Plant Cell and Environment* 2: 293–308.
- Corbetta, M., Miezin, F.M., Dobmeyer, S., Shulman, G.L. and Peterson, G.L. 1990. Attentional modulation of neural processing of shape, colour, and velocity in humans. *Science* 248: 1556–1559.
- Cowgill, S.E., Wratten, S.D. and Sotherton, N.W. 1993. The selective use of floral resources by the hoverfly *Episyrphus balteatus* (Diptera: Syrphidae) on farmland. *Annals of Applied Biology* 122: 223–231.
- Crane, E. 1975. *Honey: A Comprehensive Survey*. Heinemann in co-operation with International Bee Research Association, London.

## 250 References

- Crane, E. 1990a. *Bees and Beekeeping: Science, Practice, and World Resources*. Cornstock Publishing Associates, Cornell University Press, Ithaca, NY.
- Crane, E. 1990b. *Bees and Beekeeping*. Heinemann Newnes, Oxford.
- Cresswell, J.E. 1990. How and why do nectar-foraging bumblebees initiate movements between inflorescences of wild bergamot *Monarda fistulosa* (Lamiaceae). *Oecologia* 82: 450–460.
- Cresswell, J.E. 1997. Spatial heterogeneity, pollinator behaviour and pollinator-mediated gene-flow: bumblebee movements in variously aggregated rows of oil-seed rape. *Oikos* 78: 546–556.
- Cresswell, J.E. 1999. The influence of nectar and pollen availability on pollen transfer by individual flowers of oilseed rape (*Brassica napus*) when pollinated by bumblebees (*Bombus lapidarius*). *Journal of Ecology* 87: 670–677.
- Cresswell, J.E. and Galen, C. 1991. Frequency-dependent selection and adaptive surfaces for floral character combinations—the pollination of *Polemonium viscosum*. *American Naturalist* 138: 1342–1353.
- Cresswell, J.E. and Osborne, J.L. 2004. The effect of patch size and separation on bumblebee foraging in oilseed rape: implications for gene flow. *Journal of Applied Ecology* 41: 539–546.
- Cresswell, J.E., Osborne, J.L. and Bell, S. 2002. A model of pollinator-mediated gene flow between plant populations, with numerical solutions for bumble bees pollinating oilseed rape. *Oikos* 98: 375–384.
- Cresswell, J.E., Osborne, J.L. and Goulson, D. 2000. An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees. *Ecological Entomology* 25: 249–255.
- Cresswell, J.E. and Robertson, A.W. 1994. Discrimination by pollen-collecting bumblebees among differentially rewarding flowers of an alpine wildflower, *Campanula rotundifolia* (Campanulaceae). *Oikos* 69: 304–308.
- Cribb, D. 1990. Pollination of tomato crops by honeybees. *Bee Craft* 72: 228–231.
- Crosswhite, F.S. and Crosswhite, C.D. 1970. Pollination of *Castilleja sessiflora* in southern Wisconsin. *Bulletin of the Torrey Botanical Club* 97: 100–105.
- Croxton, P.J., Carvell, C., Mountford, J.O. and Sparks, T.H. 2002. A comparison of green lanes and field margins as bumblebee habitat in an arable landscape. *Biological Conservation* 107: 365–374.
- Crozier, R.H. 1979. Genetics of sociality. In: *Social Insects* (ed. H.R. Hermann), vol. I, pp. 223–286. Academic Press, New York.
- Crozier, R.H. and Page, R.E. 1985. On being the right size: male contributions and multiple mating in social hymenoptera. *Behavioral Ecology and Sociobiology* 18: 105–116.
- Crozier, R.H. and Pamilo, P. 1996. *Evolution of Social Insect Colonies*. Oxford University Press, Oxford.
- Cruden, R.W., Hermanutz, L. and Shuttleworth, J. 1984. The pollination biology and breeding system of *Monarda fistulosa* (Labiatae). *Oecologia* 64: 104–110.
- Cruzan, M.B., Neal, P.R. and Willson, M.F. (1988) Floral display in *Phyla incisa*: consequences for male and female reproductive success. *Evolution* 42: 505–515.
- Cumber, R.A. 1949a. The biology of humblebees, with special reference to the production of the worker caste. *Transactions of the Royal Entomological Society of London* 100: 1–45.
- Cumber, R.A. 1949b. An overwintering nest of the bumble-bee *Bombus terrestris*. *New Zealand Science Review* 7: 76–77.
- Cumber, R.A. 1949c. Humble-bee parasites and commensals found within a thirty mile radius of London. *Proceedings of the Royal Entomological Society of London (A)* 24: 119–127.

- Cumber, R.A. 1953. Some aspects of the biology and ecology of bumble-bees bearing upon the yields of red-clover seed in New Zealand. *New Zealand Journal of Science and Technology* 11: 227–240.
- Cushman, J.H. and Beattie, A.J. 1991. Mutualisms: assessing the benefits to hosts and visitors, *Trends in Ecology and Evolution* 6: 191–195.
- Dafni, A. 1998. The threat of *Bombus terrestris* spread. *Bee World* 79: 113–114.
- Dafni, A. and Shmida, A. 1996. The possible ecological implications of the invasion of *Bombus terrestris* (L.) (Apidae) at Mt Carmel, Israel. In: *The Conservation of Bees* (eds A. Matheson, S.L. Buchmann, C. O’Toole, P. Westrich and I.H. Williams), pp. 183–200. Academic Press, London.
- Dalla Torre, K.W. v1880. Unsere hummel-(Bombus) Arten. *Naturhistoriker* 2: 40–41.
- Dalla Torre, K.W. v1882. Bemerkungen zur Gattung Bombus Latr., II. 3. Zur Synonymie und geographischen Verbreitung der Gattung Bombus Latr. *Bericht Naturwissenschaftlichmedizinischen Vereins in Innsbruck* 12: 14–31.
- Damgaard, C. and Kjellsson, G. 2005. Gene flow of oilseed rape (*Brassica napus*) according to isolation distance and buffer zone. *Agriculture, Ecosystems and Environment* 108: 291–301.
- Damgaard, C., Simonsen, V. and Osborne, J.L. 2008. Prediction of pollen-mediated gene flow between fields of red clover (*Trifolium pratense*). *Environmental Modelling and Assessment* 13: 483–490.
- Darvill, B. 2007. The conservation genetics of the bumblebees *Bombus muscorum* and *Bombus jonellus* in a model island system. PhD thesis, University of Southampton.
- Darvill, B., Ellis, J.S., Lye, G.C. and Goulson, D. 2006. Population structure and inbreeding in a rare and declining bumblebee, *Bombus muscorum* (Hymenoptera: Apidae). *Molecular Ecology* 15: 601–611.
- Darvill, B., Knight, M.E. and Goulson, D. 2004. Use of genetic markers to quantify bumblebee foraging range and nest density. *Oikos* 107: 471–478.
- Darvill, B., Lye, G.C. and Goulson, D. 2007. Aggregations of male *Bombus muscorum* (Hymenoptera: Apidae) at mature nests. Incestuous brothers or amorous suitors? *Apidologie* 38: 518–524.
- Darwin, C. 1865. On the flight paths of male humble bees (translated from German by R.B. Freeman). *The Works of Charles Darwin: An Annotated Bibliographical Handlist. Appendix*. Dawson’s of Pall Mall, London.
- Darwin, C. 1876. *On the Effects of Cross and Self Fertilization in the Vegetable Kingdom*. John Murray, London.
- Darwin, C. 1886. Über die Wege der Hummelmännchen. In: Krause, E. Gesammelte kleinere Schriften von Charles Darwin. Ein Supplement zu seinen grösseren Werken. Vol. 2. Leipzig.
- Davidson, A. 1894. On the parasites of wild bees in California. *Entomological News* 5: 170–172.
- Davies, N.B. 1977. Prey selection and the search strategy of the spotted flycatcher (*Muscicapa striata*): a field study on optimal foraging. *Animal Behaviour* 25: 1016–1033.
- Davis, A.R. and Shuel, R.W. 1988. Distribution of carbofuran and dimethoate in flowers and their secretion in nectar as related to nectary vascular supply. *Canadian Journal of Botany* 66: 1248–1255.
- Day, H.D. and Day, K.C. 1997. Directional preferences in the rotational play behaviors of young children. *Developmental Psychobiology* 30: 213–223.
- De Jonghe, R. 1986. Crossing experiments with *Bombus terrestris terrestris* (Linnaeus, 1758) and *Bombus terrestris xanthopus* (Kriechbaumer, 1870) and some notes on diapause and nose-ose (Hymenoptera: Apoidea). *Phegea* 14: 19–23.
- Delaplane, K.S. and Mayer, D.F. 2000. *Crop Pollination by Bees*. CABI publishing, Wallingford, UK.



- Delbrassinne, S. and Rasmont, P. 1988. Contribution à l'étude de la pollinisation du colza, *Brassica napus* L. var. *oleifera* (Moench) Delile, en Belgique. *Bulletin des Recherches Agronomique de Gembloux* 23: 123–152.
- Delph, L.F. and Lively, C.M. 1989. The evolution of floral colour change: pollinator attraction versus physiological constraints in *Fuchsia excorticata*. *Evolution* 43: 1252–1262.
- Delph, L.F. and Lively, C.M. 1992. Pollinator visitation, floral display, and nectar production of the sexual morphs of a gynodioecious shrub. *Oikos* 63: 161–170.
- Dennis, P.D. and Fry, G.L.A. 1992. Field-margins: can they enhance natural enemy populations and general arthropod diversity on farmland. *Agriculture, Ecosystems and Environment* 40: 95–116.
- Descoins, C., Frerot, B., Gallois, M., Lettere, M., Bergström, G., Appelgren, M., Svensson, B.G. and Ågren, L. 1984. Identification des composé de la phéromone de marquage produite par les glandes labiales des mâles de *Megabombus pascuorum* (Scopoli) (Hymenoptera, Apidae). *Nova Acta Regiae Societatis Scientiarum Upsaliensis, Series V:C* 3: 149–152.
- Desjardins, E.C. and De Oliveira, D. 2006. Commercial bumble bee *Bombus impatiens* (Hymenoptera: Apidae) as a pollinator in lowbush blueberry (Ericale: Ericaceae) fields. *Journal of Economic Entomology* 99: 443–449.
- Devlin, B. and Stephenson, A.G. 1985. Sex differential floral longevity, nectar secretion, and pollinator foraging in a protandrous species. *American Journal of Botany* 72: 303–310.
- Dias, D. 1958. Contribuição para o conhecimento da bionomia de *Bombus incarum* Franklin da Amazônia (Hymenoptera: Bombidae). *Revista Brasileira Entomologia* 8: 1–20.
- Dimou, M., Taraza, S., Thrasyvoulou, A. and Vasilakakis, M. 2008. Effect of bumble bee pollination on greenhouse strawberry production. *Journal of Apicultural Research* 47: 99–101.
- Donovan, B.J. 1975. Introduction of new bee species for pollinating lucerne. *Proceedings of the New Zealand Grasslands Association* 36: 123–128.
- Donovan, B.J. 1979. Importation, establishment and propagation of the alkali bee *Nomia melanderi* Cockerell (Hymenoptera: Halictidae) in New Zealand. Proceedings of the IVth International Symposium on Pollination. *Maryland Agricultural Experimental Station Special Miscellaneous Publication* 1: 257–268.
- Donovan, B.J. 1980. Interactions between native and introduced bees in New Zealand. *New Zealand Journal of Ecology* 3: 104–116.
- Donovan, B.J. and Wier, S.S. 1978. Development of hives for field population increase, and studies on the life cycle of the four species of introduced bumble bees in New Zealand. *New Zealand Journal of Agricultural Research* 21: 733–756.
- Dornhaus, A., Brockman, A. and Chittka, L. 2003. Bumble bees alert to food with pheromone from tergal gland. *Journal of Comparative Physiology A* 189: 47–51.
- Dornhaus, A. and Chittka, L. 1999. Insect behaviour—evolutionary origins of bee dances. *Nature* 401: 38.
- Dornhaus, A. and Chittka, L. 2001. Food alert in bumblebees (*Bombus terrestris*): possible mechanisms and evolutionary implications. *Behavioral Ecology and Sociobiology* 50: 570–576.
- Dornhaus, A. and Chittka, L. 2005. Bumble bees (*Bombus terrestris*) store both food and information in honeypots. *Behavioral Ecology* 16: 661–666.
- Douglas, J.M. 1973. Double generations of *Bombus jonellus subborealis* Rich. (Hym. Apidae) in an Arctic summer. *Entomologica Scandinavica* 4: 283–284.
- Doums, C., Moret, Y., Benelli, E., Schmid-Hempel, P. 2002. Senescence of immune defence in *Bombus* workers. *Ecological Entomology* 27: 138–144.

- Doums, C. and Schmid-Hempel, P. 2000. Immunocompetence in workers of a social insect, *Bombus terrestris* L., in relation to foraging activity and parasitic infection. *Canadian Journal of Zoology* 78: 1060–1066.
- Dover, J. 1992. The conservation of insects on arable farmland. In: *The Conservation of Insects and their Habitats* (eds N.W. Collins and J. Thomas), pp. 294–318. Academic Press, London.
- Dover, J., Sotherton, N. and Gobbet, K. 1990. Reduced pesticide inputs in cereal field margins: effects on butterfly abundance. *Ecological Entomology* 15: 17–24.
- Dramstad, W.E. 1996. Do bumblebees (Hymenoptera: Apidae) really forage close to their nests? *Journal of Insect Behaviour* 2: 163–182.
- Dramstad, W. and Fry, G. 1995. Foraging activity of bumblebees (*Bombus*) in relation to flower resources in arable land. *Agriculture, Ecosystems and Environment* 53: 123–135.
- Dramstad, W.E., Fry, G.L.A. and Schaffer, M.J. 2003. Bumblebee foraging—is closer really better? *Agriculture Ecosystems and Environment* 95: 349–357.
- Dreisig, H. 1985. Movement patterns of a clear-wing hawkmoth, *Hemaris fuciformis*, foraging at red catchfly, *Viscaria vulgaris*. *Oecologia* 67: 360–366.
- Dreisig, H. 1995. Ideal free distributions of nectar foraging bumblebees. *Oikos* 72: 161–172.
- Duchateau, M.J. 1989. Agonistic behaviours in colonies of the bumblebee *Bombus terrestris*. *Journal of Ethology* 7: 141–151.
- Duchateau, M.J., Hishiba, H. and Velthuis, H.H.W. 1994. Diploid males in the bumble bee *Bombus terrestris*. *Entomologia Experimentalis et Applicata* 71: 263–269.
- Duchateau, M.J. and Mariën, J. 1995. Sexual biology of haploid and diploid males in the bumble bee *Bombus terrestris*. *Insectes Sociaux* 42: 255–266.
- Duchateau, M.J. and Velthuis, H.H.W. 1988. Development and reproductive strategies in *Bombus terrestris* colonies. *Behaviour* 107: 186–217.
- Duchateau, M.J. and Velthuis, H.H.W. 1989. Ovarian development and egg laying in workers of *Bombus terrestris*. *Entomologia Experimentalis et Applicata* 51: 199–213.
- Duchateau, M.J., Velthuis, H.H.W. and Boomsma, J.J. 2004. Sex ratio variation in the bumblebee *Bombus terrestris*. *Behavioral Ecology* 15: 71–82.
- Dudley, R. and Ellington, C.P. 1990. Mechanics of forward flight in bumblebees I. Kinematics and morphology. *Journal of Experimental Biology* 148: 19–52.
- Duffield, G.E., Gibson, R.C., Gilhooly, P.M., Hesse, A.J., Inkley, C.R., Gilbert, F.S. and Barnard, C.J. 1993. Choice of flowers by foraging honey-bees (*Apis mellifera*)—possible morphological cues. *Ecological Entomology* 18: 191–197.
- Dukas, R. 1995. Transfer and interference in bumblebee learning. *Animal Behaviour* 49: 1481–1490.
- Dukas, R. 2005. Bumble bee predators reduce pollinator density and plant fitness. *Ecology* 86: 1401–1406.
- Dukas, R. and Edelman-Keshet, L. 1998. The spatial distribution of colonial food provisioners. *Journal of Theoretical Biology* 190: 121–134.
- Dukas, R. and Ellner, S. 1993. Information processing and prey detection. *Ecology* 74: 1337–1346.
- Dukas, R. and Real, L.A. 1991. Learning foraging tasks by bees: a comparison between social and solitary species. *Animal Behaviour* 42: 269–276.
- Dukas, R. and Real, L.A. 1993a. Learning constraints and floral choice behaviour in bumblebees. *Animal Behaviour* 46: 637–644.
- Dukas, R. and Real, L.A. 1993b. Effects of recent experience on foraging decisions by bumblebees. *Oecologia* 94: 244–246.

- Dukas, R. and Real, L.A. 1993c. Effects of nectar variance on learning by bumblebees. *Animal Behaviour* 45: 37–41.
- Dukas, R. and Waser, N.M. 1994. Categorization of food types enhances foraging performance of bumblebees. *Animal Behaviour* 48: 1001–1006.
- Durrer, S. and Schmid-Hempel, P. 1994. Shared use of flowers leads to horizontal pathogen transmission. *Proceedings of the Royal Society London B* 258: 299–302.
- Duvoisin, N., Baer, B. and Schmid-Hempel, P. 1999. Sperm transfer and male competition in a bumblebee. *Animal Behaviour* 58: 743–749.
- Dyer, A.G. and Chittka, L. 2004. Bumblebees (*Bombus terrestris*) sacrifice foraging speed to solve difficult colour discrimination tasks. *Journal of Comparative Physiology A-Neuroethology Sensory Neural and Behavioral Physiology* 190: 759–763.
- Dyer, A.G., Whitney, H.M., Arnold, S.E.J., Glover, B.J. and Chittka, L. 2006. Bees associate warmth with floral colour. *Nature* 442: 7102.
- Dyer, F.C. 1996. Spatial memory and navigation by honeybees on the scale of the foraging range. *Journal of Experimental Biology* 199: 147–154.
- Eaton, G.W. and Stewart, M.G. 1969. Blueberry blossom damage caused by bumblebees. *The Canadian Entomologist* 101: 149–150.
- Eckhart, V.M. 1991. The effects of floral display on pollinator visitation vary among populations of *Phacelia linearis* (Hydrophyllaceae). *Evolutionary Ecology* 5: 370–384.
- Edwards, M. 1998. U.K. Biodiversity Action Plan Bumblebee Working Group Report 1998. Unpublished report for the UK BAP bumblebee working group, Midhurst, UK.
- Edwards, M. 1999. U.K. Biodiversity Action Plan Bumblebee Working Group Report 1999. Unpublished report for the UK BAP bumblebee working group, Midhurst, UK.
- Edwards, M. 2000. U.K. Biodiversity Action Plan Bumblebee Working Group Report 2000. Unpublished report for the UK BAP bumblebee working group, Midhurst, UK.
- Edwards, M. 2001. U.K. Biodiversity Action Plan Bumblebee Working Group Report 2001. Unpublished report for the UK BAP bumblebee working group, Midhurst, UK.
- Ehrlén, J. 1992. Proximate limits to seed production in a herbaceous perennial legume, *Lathyrus vernus*. *Ecology* 73: 1820–1831.
- Ehrlén, J. and Eriksson, O. 1995. Pollen limitation and population growth in a herbaceous perennial legume. *Ecology* 76: 652–656.
- Eickwort, G.C. 1994. Evolution and life-history patterns of mites associated with bees. In: *Mites* (ed. M.A. Houck), pp. 218–251. Chapman and Hall, New York.
- Eickwort, G.C. and Ginsberg, H.S. 1980. Foraging and mating behaviour in Apoidea. *Annual Review of Entomology* 25: 421–426.
- Eijnde, J.V.D. and Vette, N. 1993. Nosema infection in honeybees (*Apis mellifera* L.) and bumble bees (*Bombus terrestris* L.). *Proceedings of the Section Experimental and Applied Entomology of the Netherlands Entomological Society* 4: 205–208.
- Ellington, C.P., Machin, K.E. and Casey, T.M. 1990. Oxygen consumption of bumblebees in forward flight. *Nature* 347: 472–473.
- Ellis, J.S., Knight, M.E., Darvill, B. and Goulson, D. 2006. Extremely low effective population sizes, genetic structuring and reduced genetic diversity in a threatened bumblebee species, *Bombus sylvarum* (Hymenoptera: Apidae). *Molecular Ecology* 15: 4375–4386.
- Eltz, T. 2006. Tracing pollinator footprints on natural flowers. *Journal of Chemical Ecology* 32: 907–915.

- Endler, J.A. 1981. An overview of the relationships between mimicry and crypsis. *Biological Journal of the Linnean Society* 16: 25–31.
- Ernst, W.R., Pearce, P.A. and Pollock, T.L. 1989. *Environmental Effects of Fenitrothion Use in Forestry*. Conservation and Protection, Environment Canada, Atlantic Region, Canada.
- Esch, H. 1967. Die Bedeutung der Lauterzeugung für die Verständigung der stachellosen Bienen. *Zeitschrift fuer Vergleichende Physiologie* 56: 199–220.
- Esch, H., Goller, F. and Heinrich, B. 1991. How do bees shiver? *Naturwissenschaften* 78: 325–328.
- Estoup, A., Scholl, A., Pouvreau, A. and Solignac, M. 1995. Monandry and polyandry in bumble bees (Hymenoptera, Bombinae) as evidenced by highly variable microsatellites. *Molecular Ecology* 4: 89–93.
- Estoup, A., Slignac, M., Cornuet, J.-M., Goudet, J. and Scholl, A. 1996. Genetic differentiation of continental and island populations of *Bombus terrestris* (Hymenoptera: Apidae) in Europe. *Molecular Ecology* 5: 19–31.
- Evans, D.L. and Waldbauer, G.P. 1982. Behaviour of adult and naïve birds when presented with a bumblebee and its mimic. *Zeitschrift für Tierpsychologie* 59: 247–259.
- Evans, G.O. 1992. *Principles of Acarology*. Cambridge University Press, Cambridge.
- Eysenck, M.W. and Keane, M.T. 1990. *Cognitive Psychology*. Lawrence Erlbaum, London.
- Fabre J.-H., 1882. *Souvenirs Entomologiques Études sur l'Instinct et les Moeurs des Insectes* (2me Sér.). Delagrave, Paris 1882.
- Fantham, H.B. and Porter, A. 1914. The morphology, biology and economic importance of *Nosema bombi* n. sp. parasitic in various humble bees (*Bombus* sp.). *Annals of Tropical Medicine and Parasitology* 8: 636–638.
- Farrar, C.L. and Bain, H.F. 1946. Honey bees as pollinators of cranberry. 86: 503–504.
- Fattig, P.W. 1933. Food of the robber fly, *Mallophora orcina* (Wied.) (Diptera). *The Canadian Entomologist* 65: 119–120.
- Feber, R.E., Smith, H. and Macdonald, D.W. 1996. The effects on butterfly abundance of the management of uncropped edges of arable fields. *Journal of Applied Ecology* 33: 1191–1205.
- Ferguson, A.W. and Free, J.B. 1979. Production of forage-marking pheromone by the honeybee. *Journal of Apicultural Research* 18: 128–135.
- Ferton, C. 1901. Sur l'époque du reveil des bourdons et des Psithyres à Bonifacio. *Annales de la Société Entomologique de France* 70: 84–85.
- Firbank, L.G., Arnold, H.R., Eversham, B.C., Mountford, J.O., Radford, G.L., Telfer, M.G., Treweek, J.R., Webb, N.R.C. and Wells, T.C.E. 1993. *Managing Set-aside for Wildlife*. HMSO, London.
- Fischer, M. and Matthies, D. 1997. Mating structure and inbreeding and outbreeding depression in the rare plant *Gentianella germanica* (Genitanaceae). *American Journal of Botany* 84: 1685–1692.
- Fisher, R.A. 1930. *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.
- Fisher, R.M. 1984. Evolution and host specificity: a study of the invasion success of a specialized bumblebee social parasite. *Canadian Journal of Zoology* 62: 1641–1644.
- Fisher, R.M. 1987. Queen-worker conflict and social parasitism in bumble bees (Hymenoptera: Apidae). *Animal Behaviour* 35: 1026–1036.
- Fisher, R.M. 1988. Observations on the behaviours of three European bumblebee species (*Psithyrus*). *Insectes Sociaux* 35: 341–354.

## 256 References

- Fisher, R.M. 1989. Incipient colony manipulation, Nosema incidence and colony productivity of the bumble bee *Bombus terrestris* (Hymenoptera, Apidae). *Journal of the Kansas Entomological Society* 62: 581–589.
- Fisher, R.M. 1992. Sex ratios in bumble bee social parasites: support for queen-worker conflict theory? (Hymenoptera: Apidae). *Sociobiology* 20: 205–217.
- Fisher, R.M. and Pomeroy, N. 1989a. Pollination of greenhouse muskmelons by bumble bees (Hymenoptera: Apidae). *Entomological Society of America* 82: 1061–1066.
- Fisher, R.M. and Pomeroy, N. 1989b. Incipient colony manipulation, Nosema incidence and colony productivity of the bumble bee *Bombus terrestris* (Hymenoptera, Apidae). *Journal of the Kansas Entomological Society* 62: 581–589.
- Fitzpatrick, U., Murray, T.E., Paxton, R.J., Breen, J., Cotton, D., Santorum, V. and Brown, M.J.F. 2007. Rarity and decline in bumblebees—a test of causes and correlates in the Irish fauna. *Biological Conservation* 136: 185–194.
- Fontaine, C., Collin, C.L. and Dajoz, I. 2008. Generalist foraging of pollinators: diet expansion at high density. *Journal of Ecology* 96: 1002–1010.
- Forbes, W.T.M. 1923. *The Lepidoptera of New York and Neighboring States*. New York State College of Agriculture, New York.
- Forster Johnson, A.P. 2002. Bumblebee queens form part of the spring diet of the great tit (*Parus major* L.) in southern Finland. *Entomologist's Monthly Magazine* 138: 138.
- Forup, M.L. and Memmott, J. 2005. The relationship between the abundances of bumblebees and honeybees in a native habitat. *Ecological Entomology* 30: 47–57.
- Foster, R.L. 1992. Nestmate recognition as an inbreeding avoidance mechanism in bumble bees (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society* 65: 238–243.
- Foster, R.L., Brunskill, A., Verdirame, D. and O'Donnell, S. 2004. Reproductive physiology, dominance interactions, and division of labour among bumble bee workers. *Physiological Entomology* 29: 327–334.
- Frank, A. 1941. Eigenartige Flugbahnen bei Hummel Männchen. *Zeitschrift fuer Vergleichende Physiologie* 28: 467–484.
- Frankham, R., Ballou, J.D. and Briscoe, D.A. 2002. *Introduction to Conservation Genetics*. Cambridge University Press, Cambridge, UK, 617 pp.
- Frankie, G. and Vinson, S.B. 1977. Scent-marking of passion flowers in Texas by females of *Xylocopa virginica texana* (Hym. Anthophoridae). *Journal of the Kansas Entomological Society* 50: 613–625.
- Frankie, G.W., Thorp, R.W., Newstrom-Lloyd, L.E., Rizzardi, M.A., Barthell, J.F., Griswold, T.L., Kim, J.Y. and Kappagoda, S. 1998. Monitoring solitary bees in modified wildland habitats: implications for bee ecology and conservation. *Environmental Entomology* 27: 1137–1148.
- Franklin, M.T., Winston, M.L. and Morandin, L.A. 2004. Effects of clothianidin on *Bombus impatiens* (Hymenoptera: Apidae) colony health and foraging ability. *Ecotoxicology* 97: 369–373.
- Free, J.B. 1955a. The division of labour within bumblebee colonies. *Insectes Sociaux* 2: 195–212.
- Free, J.B. 1955b. The collection of food by bumblebees. *Insectes Sociaux* 2: 303–311.
- Free, J.B. 1955c. Queen production in colonies of bumblebees. *Proceedings of the Royal Entomological Society of London A* 30: 19–25.
- Free, J.B. 1958. The defence of bumblebee colonies. *Behaviour* 12: 233–242.
- Free J.B. 1962. The behaviour of honeybees visiting field beans (*Vicia faba*). *Journal of Animal Ecology* 31: 497–502.

- Free, J.B. 1963. The flower constancy of honeybees. *Journal of Animal Ecology* 32: 119–131.
- Free, J.B. 1970. The flower constancy of bumblebees. *Journal of Animal Ecology* 39: 395–402.
- Free, J.B. 1971. Stimuli eliciting mating behaviour of bumblebee (*Bombus pratorum* L.) males. *Behaviour* 40: 55–61.
- Free, J.B. 1987. *Pheromones of Social Bees*. Chapman and Hall, London.
- Free, J.B. 1993. *Insect Pollination of Crops*, 2nd edn. Academic Press, London.
- Free, J.B. and Butler, C.G. 1959. *Bumblebees*. Collins, London.
- Free, J.B. and Ferguson, A.W. 1986. Foraging of bees on oil-seed rape (*Brassica napus* L.) in relation to the flowering of the crop and pest control. *Journal of Agricultural Science, Cambridge* 94: 151–154.
- Free, J.B., Ferguson, A.W., Pickett, J.A. and Williams, I.H. 1982b. Use of unpurified Nasonov pheromone components to attract clustering honeybees. *Journal of Apicultural Research* 21: 26–29.
- Free, J.B., Weinberg, I. and Whiten, A. 1969. The egg-eating behaviour of *Bombus lapidarius* L. *Behaviour* 35: 313–317.
- Free, J.B. and Williams, I.H. 1972. The role of the Nasonov gland pheromone in crop communication by honeybees (*Apis mellifera* L.). *Behaviour* 41: 314–318.
- Free, J.B. and Williams, I.H. 1973. The foraging behaviour of honeybees (*Apis mellifera*) on Brussels sprouts (*Brassica oleracea* L.). *Journal of Applied Ecology* 10: 489–499.
- Free, J.B. and Williams, I.H. 1976. Pollination as a factor limiting the yield of field beans (*Vicia faba* L.). *Journal of Agricultural Science, UK* 87: 395–399.
- Free, J.B., Williams, I.H., Pickett, J.A., Ferguson, A.W. and Martin, A.P. 1982a. Attractiveness of (Z)-11-eicosen-1-ol to foraging honeybees. *Journal of Apicultural Research* 21: 151–156.
- Freeman, B.A. 1966. Notes on the conopid flies including insect hostplant and phoretic relationships (Diptera: Conopidae). *Journal of the Kansas Entomological Society* 39: 123–131.
- Frehn, E. and Schwammberger, K. 2001. Social parasitism of *Psithyrus vestalis* in free-foraging colonies of *Bombus terrestris* (Hymenoptera: Apidae). *Entomologia Generalis* 25: 103–105.
- Freitas, B.M. and Paxton, R.J. 1998. A comparison of two pollinators: the introduced honey bee *Apis mellifera* and an indigenous bee *Centris tarsata* on cashew *Anacardium occidentale* in its native range of NE Brazil. *Journal of Applied Ecology* 35: 109–121.
- Fretwell, S.D. and Lucas, H.L. 1970. Territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19: 16–36.
- Fries, I., de Ruijter, A., Paxton, R.J., da Silva, A.J., Slemenda, S.B. and Pieniasek, N.J. 2001. Molecular characterization of *Nosema bombi* (Microsporidia) and a note on its sites of infection in *Bombus terrestris* (Hymenoptera: Apoidea). *Journal of Apicultural Research* 40: 91–96.
- Frison, T.H. 1917. Notes on Bombidae, and on the life history of *Bombus auricomis* Robt. *Annals of the Entomological Society of America* 10: 277–286.
- Frison, T.H. 1926. Contribution to the knowledge of the inter-relations of the bumblebees of Illinois with their animate environment. *Annals of the Entomological Society of America* 19: 203–235.
- Frison, T.H. 1928. A contribution to the knowledge of the life history of *Bremus bimaculatus* (Cresson) (Hym.). *Entomologica Americana* 8: 159–223.
- Frison, T.H. 1929. A contribution to the knowledge of the bionomics of *Bremus impatiens* (Cresson) (Hym.). *Bulletin of the Brooklyn Entomological Society* 24: 261–285.

- Frison, T.H. 1930. Observations of the behavior of bumblebees (*Bremus*). The orientation flight. *The Canadian Entomologist* 62: 49–54.
- von Frisch, K. 1923. Über die 'Sprache' der Beinen, eine tierpsychologische Untersuchung. *Zoologische Jahrbucher: Abteilung für Allgemeine Zoologie und Physiologie* 40: 1–186.
- von Frisch, K. 1952. Hummeln als unfreiwillige Transportflieger. *Natur u. Volk* 82: 171–174.
- von Frisch, K. 1967. *The Dance Language and Orientation of Bees*. Harvard University Press, Cambridge, MA.
- Frost, S.K. and Frost, P.G.H. 1981. Sunbird pollination of *Strelitzia nicolai*. *Oecologia*, 49: 379–384.
- Fuchs, R. and Muller, M. 2004. Pollination problems in Styrian oil pumpkin plants: can bumblebees be an alternative to honeybees? *Phyton-Annales Rei Botanicae* 44: 155–165.
- Fuller, R.M. 1987. The changing extent and conservation interest of lowland grasslands in England and Wales: a review of grassland surveys 1930–84. *Biological Conservation* 40: 281–300.
- Fussell, M. and Corbet, S.A. 1991. Forage for bumble bees and honey bees in farmland: a case study. *Journal of Apicultural Research* 30: 87–97.
- Fussell, M. and Corbet, S.A. 1992a. Flower usage by bumblebees—a basis for forage plant management. *Journal of Applied Ecology* 29: 451–465.
- Fussell, M. and Corbet, S.A. 1992b. Observations on the patrolling behaviour of male bumblebees (Hym.). *Entomologist's Monthly Magazine* 128: 229–235.
- Fussell, M. and Corbet, S.A. 1992c. The nesting places of some British bumblebees. *Journal of Apicultural Research* 31: 32–41.
- Fussell, M., Osborne, J.L. and Corbet, S.A. 1991. Seasonal and diurnal patterns of insect visitors to winter sown field bean flowers in Cambridge. *Aspects of Applied Biology* 27: 95–99.
- Fye, R.E. and Medler, J.T. 1954. Field domiciles for bumblebees. *Journal of Economic Entomology* 47: 672–676.
- Galen, C. 1983. The effects of nectar thieving ants on seedset in floral scent morphs of *Polemonium viscosum*. *Oikos* 41: 245–249.
- Galen, C. 1985. Regulation of seed-set in *Polemonium viscosum*: floral scents, pollination, and resources. *Ecology* 66: 792–797.
- Galen, C. 1989. Measuring pollinator-mediated selection on morphometric traits: bumblebees and the alpine sky pilot, *Polemonium viscosum*. *Evolution* 43: 882–890.
- Galen, C. and Newport, M.E.A. 1987. Bumble bee behaviour and selection on flower size in the sky pilot, *Polemonium viscosum*. *Oecologia* 74: 20–23.
- Galen, C. and Newport, M.E.A. 1988. Pollination quality, seed set, and flower traits in *Polemonium viscosum*: complementary effects of variation in flower scent and size. *American Journal of Botany* 75: 900–905.
- Ganskopp, D. 1995. Free-ranging Angora-goats—left-handed or right-handed tendencies while grazing. *Applied Animal Behaviour Science* 43: 141–146.
- Gardner, K.E., Foster, R.L. and O'Donnell, S. 2007. Experimental analysis of worker division of labor in bumblebee nest thermoregulation (*Bombus huntii*, Hymenoptera: Apidae). *Behavioral Ecology and Sociobiology* 61: 783–792.
- Garófalo, C.A. 1974. Aspectos evolutivos da biologia da reprodução em abelhas (Hymenoptera, Apoidea). Dissertation thesis, Universidade de São Paulo, Ribeirão Preto, Brazil.
- Garófalo, C.A. 1976. Evolução do comportamento social visualizada através da ecologia de *Bombus morio* (Hymenoptera: Bombinae). PhD thesis, Universidade de São Paulo, Ribeirão Preto, Brazil.

- Gathmann, A., Greiler, J.H. and Tscharrntke, T. 1994. Trap-nesting bees and wasps colonizing set-aside fields: succession and body size, management by cutting and sowing. *Oecologia* 98: 8–14.
- Gathmann, A. and Tscharrntke, T. 2002. Foraging ranges of solitary bees. *Journal of Animal Ecology* 71: 757–764.
- Gawleta, N., Zimmermann, Y. and Eltz, T. 2005. Repellent foraging scent recognition across bee families. *Apidologie* 36: 325–330.
- Geber, M.A. 1985. The relationship of plant size to self-pollination in *Mertensia ciliata*. *Ecology* 66: 762–772.
- Gegeer, R.J. and Lavery, T.M. 1995. Effect of flower complexity on relearning flower-handling skills in bumble bees. *Canadian Journal of Zoology* 73: 2052–2058.
- Gegeer, R.J. and Lavery, T.M. 1998. How many flower types can bumble bees work at the same time? *Canadian Journal of Zoology* 76: 1358–1365.
- Gegeer, R.J. and Lavery, T.M. 2004. Effect of a colour dimorphism on the flower constancy of honey bees and bumble bees. *Canadian Journal of Zoology* 82: 587–593.
- Gegeer, R.J. and Lavery, T.M. 2005. Flower constancy in bumblebees: a test of the trait variability hypothesis. *Animal Behaviour* 69: 939–949.
- Gegeer, R.J., Otterstatter, M.C. and Thomas, J.D. 2005. Does parasitic infection impair the ability of bumblebees to learn flower-handling techniques? *Animal Behaviour* 70: 209–215.
- Gegeer, R.J., Otterstatter, M.C. and Thomas, J.D. 2006. Bumble-bee foragers infected by a gut parasite have an impaired ability to utilize floral information. *Proceedings of the Royal Society of London B* 273: 1073–1078.
- Genersch, E., Yue, C., Fries, I. and de Miranda, J.R. 2006. Detection of Deformed Wing Virus, a honey bee viral pathogen, in bumble bees (*Bombus terrestris* and *Bombus pascuorum*) with wing deformities. *Journal of Invertebrate Pathology* 91: 61–63.
- Génissel, A., Aupinel, P., Bressac, C., Tasei, J.N. and Chevrier, C. 2002. Influence of pollen origin on performance of *Bombus terrestris* micro-colonies. *Entomologia Experimentalis et Applicata* 104: 329–336.
- Gentry, A.H. 1978. Anti-pollinators for mass-flowering plants? *Biotropica* 10: 68–69.
- Gerloff, C.U., Ottmer, B.K. and Schmid-Hempel, P. 2003. Effects of inbreeding on immune response and body size in a social insect, *Bombus terrestris*. *Functional Ecology* 17: 582–589.
- Gerloff, C.U. and Schmid-Hempel, P. 2005. Inbreeding depression and family variation in a social insect, *Bombus terrestris* (Hymenoptera: Apidae). *Oikos* 111: 67–80.
- Ghazoul, J. 2005. Buzziness as usual? Questioning the global pollination crisis. *Trends in Ecology and Evolution* 20: 367–373.
- Gilbert, F.S. 1981. Foraging ecology of hoverflies: morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species. *Ecological Entomology* 6: 245–262.
- Gilbert, F.S., Azmeh, S., Barnard, C., Behnke, J., Collins, S.A., Hurst, J., Shuker, D., and the behavioural ecology field course. 2001. Individually recognizable scent marks on flowers made by a solitary bee. *Animal Behaviour* 61: 217–229.
- Gilbert, F.S., Haines, N. and Dickson, K. 1991. Empty flowers. *Functional Ecology* 5: 29–39.
- Gilbert, L.E. 1975. Ecological consequences of a coevolved mutualism between butterflies and plants. In: *Coevolution of Animals and Plants* (eds L.E. Gilbert and P.H. Raven), pp. 210–240. University of Texas Press, Austin, Texas.
- Gill, R.A. 1991. The value of honeybee pollination to society. *Acta Horticulturae* 288: 62–68.



## 260 References

- Gilliam, M. 1997. Identification and roles of non-pathogenic microflora associated with honey bees. *Fems Microbiology Letters* 155: 1–10.
- Gilliam, M., Lorenz, B.J., Prest, D.B. and Camazine, S. 1993. *Ascosphaera apis* from *Apis cerana* from South Korea. *Journal of Invertebrate Pathology* 61: 111–112.
- Gilliam, M., Lorenz, B.J. and Buchmann, S.L. 1994. *Ascosphaera apis*, the chalkbrood pathogen of the honeybee, *Apis mellifera*, from larvae of a carpenter-bee, *Xylocopa californica arizonensis*. *Journal of Invertebrate Pathology* 63: 307–309.
- Gilliam, M. and Taber, S. 1991. Diseases, pests, and normal microflora of honeybees, *Apis mellifera*, from feral colonies. *Journal of Invertebrate Pathology* 58: 286–289.
- Ginsberg, H.S. 1983. Foraging ecology of bees in an old field. *Ecology* 64: 165–175.
- Ginsberg, H.S. 1985. Foraging movements of *Halictus ligatus* (Hymenoptera: Halictidae) and *Ceratina calcarata* (Hymenoptera: Anthophoridae) on *Chrysanthemum leucanthemum* and *Erigeron annuus* (Asteraceae). *Journal of the Kansas Entomological Society* 58: 19–26.
- Ginsberg, H.S. 1986. Honey bee orientation behaviour and the influence of flower distribution on foraging movements. *Ecological Entomology* 11: 173–179.
- Giurfa, M. 1993. The repellent scent-mark of the honeybee *Apis mellifera ligustica* and its role as a communication cue during foraging. *Insectes Sociaux* 40: 59–67.
- Giurfa, M., Eichmann, B. and Menzel, R. 1996. Symmetry perception in an insect. *Nature* 382: 458–461.
- Giurfa, M. and Núñez, J.A. 1992a. Foraging by honeybees on *Carduus acanthoides*—pattern and efficiency. *Ecological Entomology* 17: 326–330.
- Giurfa, M. and Núñez, J.A. 1992b. Honeybees mark with scent and reject recently visited flowers. *Oecologia* 89: 113–117.
- Giurfa, M., Núñez, J.A. and Backhaus, W. 1994. Odour and colour information in the foraging choice behavior of the honeybee. *Journal of Comparative Physiology* 175: 773–779.
- Goerzen, D.W. 1991. Microflora associated with the alfalfa leafcutting bee, *Megachile rotundata* (Fab) (Hymenoptera, Megachilidae) in Saskatchewan, Canada. *Apidologie* 22: 553–561.
- Goerzen, D.W., Dumouchel, L. and Bissett, J. 1992. Occurrence of chalkbrood caused by *Ascosphaera aggregata* Skou in a native leafcutting bee, *Megachile pugnata* Say (Hymenoptera, Megachilidae), in Saskatchewan. *The Canadian Entomologist* 124: 557–558.
- Goerzen, D.W., Erlandson, M.A. and Bissett, J. 1990. Occurrence of chalkbrood caused by *Ascosphaera aggregata* Skou in a native leafcutting bee, *Megachile relativa* Cresson (Hymenoptera, Megachilidae), in Saskatchewan. *The Canadian Entomologist* 122: 1269–1270.
- Goka, K. 1998. Influences of invasive species on native species—will the European bumblebee, *Bombus terrestris*, bring genetic pollution into Japanese native species? *Bulletin of the Biographical Society of Japan* 53: 91–101.
- Goka, K., Okabe, K. and Yoneda, M. 2006. Worldwide migration of parasitic mites as a result of bumblebee commercialization. *Population Ecology* 48: 285–291.
- Goka, K., Okabe, K., Yoneda, M. and Niwa, S. 2001. Bumblebee commercialization will cause worldwide migration of parasitic mites. *Molecular Ecology* 10: 2095–2099.
- Goldblatt, J.W. 1984. Parasites and parasitization rates in bumble bee queens *Bombus* spp. (Hymenoptera, Apidae) in Southwestern Virginia. *Environmental Entomology* 13: 1661–1665.
- Goldblatt, J.W. and Fell, R.D. 1987. Adult longevity of workers of the bumble bee *Bombus fervidus* (F.) and *Bombus pennsylvanicus* (De Geer) (Hymenoptera: Apidae). *Canadian Journal of Zoology* 65: 2349–2353.

- Golick, D.A. and Ellis, M.D. 2006. An update on the distribution and diversity of *Bombus* in Nebraska (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society* 79: 341–347.
- Gomez, J.M., Bosch, J., Perfectti, F., Fernandez, J.D., Abdelaziz, M. and Camacho, J.P.M. 2008. Spatial variation in selection on corolla shape in a generalist plant is promoted by the preference patterns of its local pollinators. *Proceedings of the Royal Society B-Biological Sciences* 275: 2241–2249.
- Gonzalez, A., Rowe C.L., Weeks, P.J., Whittle, D., Gilbert, F.S. and Barnard, C.J. 1995. Flower choice by honey-bees (*Apis mellifera* L.)—sex-phase of flowers and preferences among nectar and pollen foragers. *Oecologia* 101: 258–264.
- Goodwin, S.G. 1995. Seasonal phenology and abundance of early-, mid- and long-season bumble bees in southern England, 1985–1989. *Journal of Apicultural Research* 34: 79–87.
- Gori, D.F. 1983. Post-pollination phenomena and adaptive floral changes. In: *Handbook of Experimental Pollination Biology* (eds C.E. Jones and R.J. Little), pp. 31–49. Van Nostrand Reinhold Co. Inc., New York.
- Gori, D.F. 1989. Floral colour change in *Lupinus argenteus* (Fabaceae): why should plants advertise the location of unrewarding flowers to pollinators? *Evolution* 43: 870–881.
- Goulson, D. 1994. A model to predict the role of flower constancy in inter-specific competition between insect pollinated flowers. *Journal of Theoretical Biology* 168: 309–314.
- Goulson, D. 1999. Foraging strategies for gathering nectar and pollen in insects. *Perspectives in Plant Ecology, Evolution and Systematics* 2: 185–209.
- Goulson, D. 2000a. Are insects flower constant because they use search images to find flowers? *Oikos* 88: 547–552.
- Goulson, D. 2000b. Why do pollinators visit proportionally fewer flowers in large patches? *Oikos* 91: 485–492.
- Goulson, D. 2003. Effects of introduced bees on native ecosystems. *Annual Review of Ecology Evolution and Systematics* 34: 1–26.
- Goulson, D. 2004. Keeping bees in their place: impacts of bees outside their natural range. *Bee World* 85: 45–46.
- Goulson, D., Chapman, J.W. and Hughes, W.O.H. 2001. Discrimination of unrewarding flowers by different bee species; direct detection of rewards and use of repellent scent marks. *Journal of Insect Behavior* 14: 669–678.
- Goulson, D. and Cory, J.S. 1993. Flower constancy and learning in the foraging behaviour of the green-veined white butterfly, *Pieris napi*. *Ecological Entomology* 18: 315–320.
- Goulson, D., Cruise, J.L., Sparrow, K.R., Harris, A.J., Park, K.J., Tinsley, M.C. and Gilburn, A.S. 2007. Choosing rewarding flowers; perceptual limitations and innate preferences influence decision making in bumblebees and honeybees. *Behavioural Ecology and Sociobiology* 61: 1523–1529.
- Goulson, D. and Darvill, B. 2004. Niche overlap and diet breadth in bumblebees; are rare species more specialized in their choice of flowers? *Apidologie* 35: 55–64.
- Goulson, D., Darvill, B., Ellis, J., Knight, M.E. and Hanley, M.E. 2004. Interspecific differences in response to novel landmarks in bumblebees. *Apidologie* 35: 619–622.
- Goulson, D. and Hanley, M.E. 2004. Distribution and forage use of exotic bumblebees in South Island, New Zealand. *New Zealand Journal of Ecology* 28: 225–232.
- Goulson, D., Hanley, M.E., Darvill, B. and Ellis, J.S. 2006. Biotope associations and the decline of bumblebees (*Bombus* spp.). *Journal of Insect Conservation* 10: 95–103.
- Goulson, D., Hanley, M.E., Darvill, B., Ellis, J.S. and Knight, M.E. 2005. Causes of rarity in bumblebees. *Biological Conservation* 122: 1–8.

## 262 References

- Goulson, D., Hawson, S.A. and Stout, J.C. 1998b. Foraging bumblebees avoid flowers already visited by conspecifics or by other bumblebee species. *Animal Behaviour* 55: 199–206.
- Goulson, D., Hughes, W.O.H., Derwent, L.C. and Stout, J.C. 2002a. Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. *Oecologia* 130: 267–273.
- Goulson, D. and Jerrim, K. 1997. Maintenance of the species boundary between *Silene dioica* and *S. latifolia* (red and white campion). *Oikos* 78: 254–266.
- Goulson, D., Lye, G.C. and Darvill, B. 2008a. Decline and conservation of bumblebees. *Annual Review of Entomology* 53: 191–208.
- Goulson, D., Lye, G.C. and Darvill, B. 2008b. Diet breadth, coexistence and rarity in bumblebees. *Biodiversity and Conservation* 17: 3269–3288.
- Goulson, D., Ollerton, J. and Sluman, C. 1997a. Foraging strategies in the small skipper butterfly, *Thymelicus flavus*: when to switch? *Animal Behaviour* 53: 1009–1016.
- Goulson, D., Peat, J., Stout, J.C., Tucker, J., Darvill B., Derwent, L.C. and Hughes, W.O.H. 2002b. Can alloethism in workers of the bumblebee *Bombus terrestris* be explained in terms of foraging efficiency? *Animal Behaviour* 64: 123–130.
- Goulson, D. and Sparrow, K.R. 2009. Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. *Journal of Insect Conservation* 13: 177–181.
- Goulson, D. and Stout, J.C. 2001. Homing ability of the bumblebee *Bombus terrestris*. *Apidologie* 32: 105–112.
- Goulson, D., Stout, J.C. and Hawson, S.A. 1997b. Can flower constancy in nectaring butterflies be explained by Darwin's interference hypothesis? *Oecologia* 112: 225–231.
- Goulson, D., Stout, J.C., Hawson, S.A. and Allen, J.A. 1998a. The effects of floral display size and colour on recruitment of three bumblebee species to comfrey, *Symphytum officinale* L. (Boraginaceae), and subsequent seed set. *Oecologia* 113: 502–508.
- Goulson, D., Stout, J.C. and Kells, A.R. 2002c. Do alien bumblebees compete with native flower-visiting insects in Tasmania? *Journal of Insect Conservation* 6: 179–189.
- Goulson, D., Stout, J.C., Langley, J. and Hughes, W.O.H. 2000. The identity and function of scent marks deposited by foraging bumblebees. *Journal of Chemical Ecology* 26: 2897–2911.
- Goulson, D. and Williams, P.H. 2001. *Bombus hypnorum* (Hymenoptera: Apidae), a new British bumblebee? *British Journal of Entomology and Natural History* 14: 129–131.
- Goulson, D. and Wright, N.P. 1998. Flower constancy in the hoverflies *Episyrphus balteatus* (Degeer) and *Syrphus ribesii* (L.) (Syrphidae). *Behavioural Ecology and Sociobiology* 9: 213–219.
- Graham, L. and Jones, K.N. 1996. Resource partitioning and per-flower foraging efficiency in 2 bumble bee species. *American Midlands Naturalist* 136: 401–406.
- Granero, A.M., Sanz, J.M.G., Gonzalez, F.J.E., Vidal, J.L.M., Dornhaus, A., Ghani, J., Serrano, A.R. and Chittka, L. 2005. Chemical compounds of the foraging recruitment pheromone in bumblebees. *Naturwissenschaften* 92: 371–374.
- Grant, V. 1949. Pollination systems as isolating mechanisms in angiosperms. *Evolution* 3: 82–97.
- Grant, V. 1950. The flower constancy of bees. *Botanical Review* 3: 82–97.
- Grant, V. 1952. Isolation and hybridization between *Aquilegia formosa* and *A. pubescens*. *Aliso* 2: 341–360.
- Grant, V. 1992. Floral isolation between ornithophilous and sphingophilous species of *Ipomopsis* and *Aquilegia*. *Proceedings of the National Academy of Sciences USA* 89: 11828–11831.

- Grant, V. 1993. Origins of floral isolation between ornithophilous and sphingophilous plant species. *Proceedings of the National Academy of Sciences USA* 90: 7729–7733.
- Grant, V. 1994. Modes and origins of mechanical and ethological isolation in angiosperms. *Proceedings of the National Academy of Sciences USA* 91: 3–10.
- Gray, H.E. 1925. Observations of tripping of alfalfa blossoms. *The Canadian Entomologist* 57: 235–237.
- Greco, C.F., Holland, D. and Kevan, P.G. 1996. Foraging behavior of honey-bees (*Apis mellifera* L.) on staghorn sumac [*Rhus hirta* Sudworth (ex-typhina L)]—differences and dioecy. *The Canadian Entomologist* 128: 355–366.
- Greenleaf, S.S. and Kremen, C. 2006. Wild bee species increase tomato production and respond differently to surrounding land use in Northern California. *Biological Conservation* 133: 81–87.
- Greenleaf, S.S., Williams, N.M., Winfree, R. and Kremen, C. 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153: 589–596.
- Greggers, U. and Menzel, R. 1993. Memory dynamics and foraging strategies of honeybees. *Behavioural Ecology and Sociobiology* 32: 17–29.
- Grindeland, J.M., Sletvold, N. and Ims, R.A. 2005. Effects of floral display size and plant density on pollinator visitation rate in a natural population of *Digitalis purpurea*. *Functional Ecology* 19: 383–390.
- Grixti, J.C. and Packer, L. 2006. Changes in the bee fauna (Hymenoptera: Apoidea) of an old field site in southern Ontario, revisited after 34 years. *The Canadian Entomologist* 138: 147–164.
- Grixti, J.C., Wong, L.T., Cameron, S.A. and Favret, C. 2009. Decline of bumble bees (*Bombus*) in the North American Midwest. *Biological Conservation* 142: 75–84.
- Grönlund, S., Itämies, J. and Mikkola, H. 1970. On the food and feeding habits of the great grey shrike *Lanius excubitor* in Finland. *Ornis Fennica* 47: 167–171.
- Gross, C.L. and Mackay, D. 1998. Honeybees reduce fitness in the pioneer shrub *Melastoma affine* (Melastomataceae). *Biological Conservation* 86: 169–178.
- Guilford, T. and Dawkins, M.S. 1987. Search images not proven: a reappraisal of recent evidence. *Animal Behaviour* 35: 1838–1845.
- Gumbert, A. 2000. Color choices by bumble bees (*Bombus terrestris*): innate preferences and generalization after learning. *Behavioral Ecology and Sociobiology* 48: 36–43.
- Gumbert, A. and Kunze, J. 2001. Colour similarity to rewarding model plants affects pollination in a food deceptive orchid, *Orchis boryi*. *Biological Journal of the Linnean Society* 72: 419–433.
- Gupta, A.P. (ed.) 1986. *Hemocytic and Humoral Immunity in Arthropods*. John Wiley and Sons, New York.
- Gurr, L. 1955. A note on the efficiency of *Bombus terrestris* (L.) as a pollinator of lucerne (*Medicago sativa* L.). *New Zealand Journal of Science and Technology* A37: 300.
- Gurr, L. 1957. Bumble bee species present in the South Island of New Zealand. *New Zealand Journal of Science and Technology* A38: 997–1001.
- Haas, A. 1949. Arttpische Flugbahnen von Hummelmännchen. *Zeitschrift Fuer Vergleichende Physiologie* 31: 281–307.
- Haas, A. 1960. Vergleichende Verhaltensstudien zum Paarungsschwarm solitärer Apiden. *Zeitschrift fur Tierpsychologie* 17: 402–416.
- Haas, C.A. and Cartar, R.V. 2008. Robust flight performance of bumble bees with artificially induced wing wear. *Canadian Journal of Zoology* 86: 668–675.

## 264 References

- von Hagen, E., 1994. *Hummeln bestimmen. Ansiedeln, Vermehren, Schützen*. Naturbuch-Verlag, Augsburg.
- Haldane, J.B.S. 1949. Disease and evolution. *La Ricerca Scientifica* 19(Suppl.): 68–76.
- Hamilton, W.D. 1964. The genetical evolution of social behavior. *Journal of Theoretical Biology* 7, I: 1–16; II: 17–32.
- Hamilton, W.D. 1967. Extraordinary sex ratios. *Science* 156: 477–488.
- Hamilton, W.D. 1980. Sex vs. non-sex vs. parasite. *Oikos* 35: 282–290.
- Hamilton, W.D. 1987. Kinship, recognition, disease, and intelligence: constraints of social evolution. In: *Animal Societies: Theory and Facts* (eds Y. Itô, J.L. Brown and J. Kikkawa), pp. 81–102. Japanese Scientific Society Press, Tokyo.
- Hanley, M.E., Franco, M., Pichon, S., Darvill, B. and Goulson, D. 2008. Breeding system, pollinator choice and variation in pollen quality in British herbaceous plants. *Functional Ecology* 22: 592–598.
- Harder, L.D. 1985. Morphology as a predictor of flower choice by bumblebees. *Ecology* 66: 198–210.
- Harder, L.D. 1986. Effects of nectar concentration and flower depth on handling efficiency of bumblebees. *Oecologia* 69: 309–315.
- Harder, L.D. and Barrett, S.C.H. 1995. Mating cost of large floral displays in hermaphrodite plants. *Nature* 373: 512–515.
- Harder, L.D. and Real, L.A. 1987. Why are bumblebees risk averse? *Ecology* 68: 1104–1108.
- Hartfelder, K., Cnaani, J. and Hefetz, A. 2000. Caste-specific differences in ecdysteroid titers in early larval stages of the bumblebee *Bombus terrestris*. *Journal of Insect Physiology* 46: 1433–1439.
- Hartling, L.K. and Plowright, R.C. 1978. Foraging by bumblebees on artificial flowers: a laboratory study. *Canadian Journal of Botany* 63: 488–491.
- Hatfield, R.G. and LeBuhn, G. 2007. Patch and landscape factors shape community assemblage of bumble bees, *Bombus* spp. (Hymenoptera: Apidae), in montane meadows. *Biological Conservation* 139: 1–2.
- Haughton, A.J., Champion, G., Hawes, C., Heard, M., Brooks, D.R., Bohan, D.A., Clark, S.A., Dewar, A., Firbank, L.G., Osborne, J.L., Perry, J.N., Rothery, P., Roy, D.B., Scott, R., Woiwod, I.P., Birchall, C., Skellern, M.P., Walker, J., Baker, P., Browne, E., Dewar, A.J.G., Garner, B., Haylock, L., Horne, S., Mason, N., Sands, R. and Walker, M.J. 2003. Invertebrate responses to the management of genetically modified herbicide-tolerant and conventional spring crops. II. Within-field epigeal and aerial arthropods. *Philosophical Transactions of the Royal Society B, Biology* 358: 1863–1877.
- Hawes, C., Haughton, A., Osborne, J.L., Roy, D., Clark, S., Perry, J., Rothery, P., Bohan, D., Brooks, D., Champion, G., Dewar, A., Heard, M., Woiwod, I., Daniels, R., Young, M., Parish, A., Scott, R., Firbank, L. and Squire, G. 2003. Responses of plants and invertebrate trophic groups to contrasting herbicide regimes in the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. *Philosophical Transactions of the Royal Society B* 358: 1899–1913.
- Hasselrot, T.B. 1960. Studies on Swedish bumblebees (genus *Bombus* Latr.): their domestication and biology. *Opuscula Entomologica, Supplementum* 17: 1–192.
- Haydak, M.H. 1943. Larval food and development of castes in the honeybee. *Journal of Economic Entomology* 36: 778–792.
- Hedenström, A., Ellington, C.P. and Wolf, T.J. 2001. Wing wear, aerodynamics and flight energetics in bumblebees (*Bombus terrestris*): an experimental study. *Functional Ecology* 15: 417–422.
- Hefetz, A., Taghizadeh, T. and Francke, W. 1996. The exocrinology of the queen bumble bee *Bombus terrestris* (Hymenoptera: Apidae, Bombini). *Zeitschrift für Naturforschung* 51: 409–422.

- Heinrich, B. 1971. Temperature regulation of the sphinx moth, *Manduca sexta*. II. *Journal of Experimental Biology* 54: 141–166.
- Heinrich, B. 1972a. Patterns of endothermy in bumblebee queens, drones and workers. *Journal of Comparative Physiology* 77: 65–79.
- Heinrich, B. 1972b. Physiology of brood incubation in the bumblebee queen, *Bombus vosnesenskii*. *Nature* 239: 223–225.
- Heinrich, B. 1972c. Energetics of temperature regulation and foraging in a bumblebee, *Bombus terricola* Kirby. *Journal of Comparative Physiology* 77: 49–64.
- Heinrich, B. 1972d. Temperature regulation in the bumblebee *Bombus vagans*: a field study. *Science* 175: 185–187.
- Heinrich, B. 1974. Thermoregulation in bumblebees. I. Brood incubation by *Bombus vosnesenskii* queens. *Journal of Comparative Physiology* 88: 129–140.
- Heinrich, B. 1975a. Thermoregulation in bumblebees. II. Energetics of warmup and free flight. *Journal of Comparative Physiology* 96: 155–166.
- Heinrich, B. 1975b. Energetics of pollination. *Annual Reviews in Ecology and Systematics* 6: 139–170.
- Heinrich, B. 1976a. Resource partitioning among some eusocial insects: bumblebees. *Ecology* 57: 874–889.
- Heinrich, B. 1976b. The resource specializations of individual bumblebees. *Ecological Monographs* 46: 105–128.
- Heinrich, B. 1976c. Heat exchange in relation to blood flow between thorax and abdomen in bumblebees. *Journal of Experimental Biology* 64: 561–585.
- Heinrich, B. 1979a. Resource heterogeneity and patterns of movement in foraging bumblebees. *Oecologia* 40: 235–245.
- Heinrich, B. 1979b. *Bumblebee Economics*. Harvard University Press, Cambridge.
- Heinrich, B. 1979c. ‘Majoring’ and ‘minoring’ by foraging bumblebees, *Bombus vagans*: an experimental analysis. *Ecology* 60: 245–255.
- Heinrich, B. 1993. *The Hot-Blooded Insects*. Springer-Verlag, New York.
- Heinrich, B. 1996. *The Thermal Warriors*. Harvard University Press, Cambridge.
- Heinrich, B. and Heinrich, M.J.E. 1983a. Size and caste in temperature regulation by bumblebees. *Physiological Zoology* 56: 552–562.
- Heinrich, B. and Heinrich, M.J.E. 1983b. Heterothermia in foraging workers and drones of the bumblebee *Bombus terricola*. *Physiological Zoology* 56: 563–567.
- Heinrich, B. and Mommsen, T.P. 1985. Flight of winter moths near 0°C. *Science* 228: 177–179.
- Heinrich, B., Mudge, P.R. and Deringis, P.G. 1977. Laboratory analysis of flower constancy in foraging bumblebees: *Bombus ternarius* and *B. terricola*. *Behavioral Ecology and Sociobiology* 2: 247–265.
- Heinrich, B. and Raven, P.H. 1972. Energetics and pollination ecology. *Science* 176: 597–602.
- Helms, K.R. 1999. Colony sex ratios, conflict between queens and workers, and apparent queen control in the ant *Pheidole desertorum*. *Evolution* 53: 1470–1478.
- Henslow, G. 1867. Note on the structure of *Medicago sativa* as apparently affording facilities for the intercrossing of distinct flowers. *Journal of the Linnean Society of London (Botany)* 9: 327–329.
- Henter, H.J. 2003. Inbreeding depression and haplodiploidy: experimental measures in a parasitoid and comparisons across diploid and haplodiploid insect taxa. *Evolution* 57: 1793–1803.

- Herrmann, F., Westphal, C., Moritz, R.F.A. and Steffan-Dewenter, I. 2007. Genetic diversity and mass resources promote colony size and forager densities of a social bee (*Bombus pascuorum*) in agricultural landscapes. *Molecular Ecology* 16: 1167–1178.
- Higashi, S., Ohara, M., Arai, H. and Matsuo, K. 1988. Robber-like pollinators: overwintering queen bumblebees foraging on *Corydalis ambigua*. *Ecological Entomology* 13: 411–418.
- Hines, H.M. 2008. Historical biogeography, divergence times, and diversification patterns of bumble bees (Hymenoptera: Apidae: Bombus). *Systematic Biology* 57: 58–75.
- Hines, H.M., Cameron, S.A. and Deans, A.R. 2007. Nest architecture and foraging behavior in *Bombus pullatus* (Hymenoptera: Apidae), with comparisons to other tropical bumble bees. *Journal of the Kansas Entomological Society* 80: 1–15.
- Hines, H.M. and Hendrix, S.D. 2005. Bumble bee (Hymenoptera: Apidae) diversity and abundance in tallgrass prairie patches: effects of local and landscape floral resources. *Environmental Entomology* 34: 1477–1484.
- Hingston, A.B. 2006. Is the exotic bumblebee *Bombus terrestris* really invading Tasmanian native vegetation? *Journal of Insect Conservation* 10: 289–293.
- Hingston, A.B. and McQuillan, P.B. 1998. Does the recently introduced bumblebee *Bombus terrestris* (Apidae) threaten Australian ecosystems? *Australian Journal of Ecology* 23: 539–549.
- Hingston, A.B. and McQuillan, P.B. 1999. Displacement of Tasmanian native megachilid bees by the recently introduced bumblebee *Bombus terrestris* (Linnaeus, 1758) (Hymenoptera: Apidae). *Australian Journal of Zoology* 47: 59–65.
- Hobbs, G.A. 1962. Further studies on the food-gathering behaviour of bumble bees (Hymenoptera: Apoidea) in Alberta. *The Canadian Entomologist* 94: 538–541.
- Hobbs, G.A. 1964a. Phylogeny of bumble bees based on brood-rearing behaviour. *The Canadian Entomologist* 96: 115–116.
- Hobbs, G.A. 1964b. Ecology of species of *Bombus* Latr. (Hymenoptera: Apidae) in southern Alberta. I. Subgenus *Alpinobombus* Skor. *The Canadian Entomologist* 96: 1465–1470.
- Hobbs, G.A. 1965a. Ecology of species of *Bombus* (Hymenoptera: Apidae) in southern Alberta. II. Subgenus *Bombias* Robt. *The Canadian Entomologist* 97: 120–123.
- Hobbs, G.A. 1965b. Ecology of species of *Bombus* (Hymenoptera: Apidae) in southern Alberta. III. Subgenus *Cullumanobombus* Vogt. *The Canadian Entomologist* 97: 1293–1302.
- Hobbs, G.A. 1966a. Ecology of species of *Bombus* (Hymenoptera: Apidae) in southern Alberta. IV. Subgenus *Fervidobombus* Skorikov. *The Canadian Entomologist* 98: 33–39.
- Hobbs, G.A. 1966b. Ecology of species of *Bombus* (Hymenoptera: Apidae) in southern Alberta. V. Subgenus *Subterraneobombus* Vogt. *The Canadian Entomologist* 98: 288–294.
- Hobbs, G.A. 1967a. Ecology of species of *Bombus* (Hymenoptera: Apidae) in southern Alberta. VI. Subgenus *Pyrobombus*. *The Canadian Entomologist* 99: 1272–1292.
- Hobbs, G.A. 1967b. Obtaining and protecting red-clover pollinating species of *Bombus* (Hymenoptera: Apidae). *The Canadian Entomologist* 99: 943–951.
- Hobbs, G.A., Nummi, W.O. and Virostek, J.F. 1961. Food-gathering behaviour of honey, bumble, and leaf-cutter bees (Hymenoptera: Apoidea) in Alberta. *The Canadian Entomologist* 93: 409–419.
- Hobbs, G.A., Nummi, W.O. and Virostek, J.F. 1962. Managing colonies of bumblebees (Hymenoptera: Apidae) for pollination purposes. *The Canadian Entomologist* 94: 1121–1132.
- Hobbs, G.A., Virostek, J.F. and Nummi, W.O. 1960. Establishment of *Bombus* spp. (Hymenoptera: Apidae) in artificial domiciles in southern Alberta. *The Canadian Entomologist* 92: 868–872.

- Hodges, C.M. 1981. Optimal foraging in bumblebees: hunting by expectation. *Animal Behaviour* 29: 1166–1171.
- Hodges, C.M. 1985a. Bumble bees foraging: the threshold departure rule. *Ecology* 66: 179–187.
- Hodges, C.M. 1985b. Bumble bees foraging: energetic consequences of using a threshold departure rule. *Ecology* 66: 188–197.
- Hoffer, E. 1882–1883. *Die Hummeln Steiermarks*. Lebensgeschichte und Beschreibung derselben, Graz.
- Hoffmann, D., Pettis, J.S. and Neumann, P. 2008. Potential host shift of the small hive beetle (*Aethina tumida*) to bumblebee colonies (*Bombus impatiens*). *Insectes Sociaux* 55: 153–162.
- Hogendoorn, K., Coventry, S. and Keller, M.A. 2007. Foraging behaviour of a blue banded bee, *Amegilla chlorocyanea* in greenhouses: implications for use as tomato pollinators. *Apidologie* 38: 86–92.
- Hogendoorn, K., Steen, Z. and Schwarz, M.P. 2000. Native Australian carpenter bees as a potential alternative to introducing bumble bees for tomato pollination in greenhouses. *Journal of Apicultural Research* 39: 67–74.
- Høiland, K. 1993. *Threatened Plants in the Cultural Landscape in Norway. 1. Weeds in Arable Environments*. Norwegian Institute for Nature Research, Trondheim.
- Holehouse, K.A., Hammond, R.L. and Bourke, A.F.G. 2003. Non-lethal sampling of DNA from bumble bees for conservation genetics. *Insectes Sociaux* 50: 277–285.
- Hölldobler, B. and Wilson, E.O. 1990. *The Ants*. Springer-Verlag, Berlin.
- Holm, S.N. 1966. The utilization and management of bumblebees for red clover and alfalfa seed production. *Annual Review of Entomology* 11: 155–182.
- Holm, S.N. 1972. Weight and life length of hibernating bumble bee queens (Hymenoptera: Bombidae) under controlled conditions. *Entomologica Scandinavica* 3: 313–320.
- Holmes, F.O. 1964. The distribution of honey bees and bumblebees on nectar secreting plants. *American Bee Journal* 12–13.
- Hopkins, I. 1914. History of the bumblebee in New Zealand: its introduction and results. *New Zealand Department of Agriculture, Industry and Commerce* 46: 1–29.
- Hopper, S.D. 1987. Impact of honeybees on Western Australia's nectarivorous fauna. In: *Beekeeping and Land Management* (ed. J. Blyth), pp. 59–71. CALM, Western Australia.
- Horskins, K. and Turner, V.B. 1999. Resource use and foraging patterns of honeybees, *Apis mellifera*, and native insects on flowers of *Eucalyptus costata*. *Australian Journal of Ecology* 24: 221–227.
- Hovorka, O., Urbanová, K. and Valterová, I. 1998. Premating behavior of *Bombus confusus* males and analysis of their labial gland secretion. *Journal of Chemical Ecology* 24: 183–193.
- Howard, D.C., Watkins, J.W., Clarke, R.T., Barnett, C.L. and Stark, G.J. 2003. Estimating the extent and change in broad habitats in Great Britain. *Journal of Environmental Management* 67: 219–227.
- Huck, K., Schwarx, H.H. and Schmid-Hempel, P. 1998. Host choice in the phoretic mite *Parasitellus fucorum* (Mesostigmata: Parasitidae): which bumblebee caste is best? *Oecologia* 115: 385–390.
- Huber, P. 1802. Observations on several species of the genus *Apis*, known by the name of humblebees, and called *Bombinatrices* by Linnaeus. *Transactions of the Linnean Society of London* 6: 214–298.
- Hughes, W.O.H., Howse, P.E. and Goulson, D. 2001. Polyethism and the importance of context in the alarm reaction of *Atta capiguara*. *Behavioural Ecology and Sociobiology* 49: 503–508.
- Hunter, P.E. and Husband, R.W. 1973. *Pneumolaelaps* (Acarina: Laelapidae) mites from North America and Greenland. *Florida Entomologist* 56: 77–91.



- Husband, R.W. and Sinha, R.N. 1970. A revision of the genus *Locustacarus* with a key to genera of the family Podapolipidae (Acarina). *Annals of the Entomological Society of America* 63: 1152–1162.
- Imhoof, B. and Schmid-Hempel, P. 1998. Patterns of local adaptation of a protozoan parasite to its bumblebee host. *Oikos* 82: 59–65.
- Imhoof, B. and Schmid-Hempel, P. 1999. Colony success of the bumble bee, *Bombus terrestris*, in relation to infections by two protozoan parasites, *Crithidia bombi* and *Nosema bombi*. *Insectes Sociaux* 46: 233–238.
- Ingelög, T. 1988. Floraläget i Sverige. *Svensk Botanisk Tidskrift* 82: 376–378.
- Inglesfield, C. 1989. Pyrethroids and terrestrial non-target organisms. *Pesticide Science* 27: 387–428.
- Ings, T.C., Raine, N.E. and Chittka, L. 2005. Mating preferences of the commercially imported bumblebee species *Bombus terrestris* in Britain (Hymenoptera: Apidae). *Entomologia Generalis* 28: 233–238.
- Ings, T.C., Ward, N.L. and Chittka, L. 2006. Can commercially imported bumble bees out-compete their native conspecifics? *Journal of Applied Ecology* 43: 940–948.
- Inoue, M.N. and Yokoyama, J. 2006. Morphological variation in relation to flower use in bumblebees. *Entomological Science* 9: 147–159.
- Inoue, M.N., Yokoyama, J. and Washitani, I. 2008. Displacement of Japanese native bumblebees by the recently introduced *Bombus terrestris* (L.) (Hymenoptera: Apidae). *Journal of Insect Conservation* 12: 135–146.
- Inouye, D.W. 1976. Resource partitioning and community structure: a study of bumblebees in the Colorado Rocky Mountains. Doctoral dissertation. University of North Carolina, Chapel Hill, North Carolina, USA.
- Inouye, D.W. 1978. Resource partitioning in bumblebees: experimental studies of foraging behavior. *Ecology* 59: 672–678.
- Inouye, D.W. 1980a. The effects of proboscis and corolla tube lengths on patterns and rates of flower visitation by bumblebees. *Oecologia* 45: 197–201.
- Inouye, D.W. 1980b. The terminology of floral larceny. *Ecology* 61: 1251–1253.
- Inouye, D.W. 1983. The ecology of nectar robbing. In: *The Biology of Nectaries* (eds T.S. Elias and B. Bentley), pp. 152–173. Columbia University Press, New York.
- Internicola, A.I., Bernasconi, G. and Gigord, L.D.B. 2008. Should food-deceptive species flower before or after rewarding species? An experimental test of pollinator visitation behaviour under contrasting phenologies. *Journal of Evolutionary Biology* 21: 1358–1365.
- Irwin, R.E. 2003. Impact of nectar robbing on estimates of pollen flow: conceptual predictions and empirical outcomes. *Ecology* 84: 485–495.
- Irwin, R.E. and Brody, A.K. 1999. Nectar-robbing bumble bees reduce the fitness of *Ipomopsis aggregata* (Polemoniaceae). *Ecology* 80: 1703–1712.
- Ito, M. 1985. Supraspecific classification of bumblebees based on the characters of male genitalia. *Contributions from the Institute of Low Temperature Science, Hokkaido University (B)* 20: 143.
- Ito, M. 1987. Geographic variation of an eastern Asian bumble bee *Bombus diversus* in some morphometric characters (Hymenoptera, Apidae). *Kontyu* 55: 188–201.
- Jacobs-Jessen, U.F. 1959. Zur Orientierung der Hummeln und einiger anderer Hymenopteren. *Zeitschrift fuer Vergleichende Physiologie* 41: 597–641.

- Janzen D.H. 1971. Euglossine bees as long-distance pollinators of tropical plants. *Science* 171: 203–205.
- Jennersten, O., Loman, J., Møller, A.P., Robertson, J. and Widén, B. 1992. Conservation biology in agricultural habitat islands. In: *Ecological Principles of Nature Conservation* (ed. L. Hansson), 99. 394–424. Elsevier Applied Science, London.
- Johnson, R.A. 1986. Intraspecific resource partitioning in the bumble bees *Bombus ternarius* and *B. pensylvanicus*. *Ecology* 67: 133–138.
- Johnson, S.D. and Bond, W.J. 1992. Habitat dependent pollination success in a cape orchid. *Oecologia* 91: 455–456.
- Johnson, S.D., Peter, C.I., Nilsson, L.A. and Agren, J. 2003. Pollination success in a deceptive orchid is enhanced by co-occurring rewarding magnet plants. *Ecology* 84: 2919–2927.
- Johnston, M.O. 1991. Pollen limitation of female reproduction in *Lobelia cardinalis* and *L. siphilitica*. *Ecology* 72: 1500–1503.
- Jones, C.E. 1978 Pollinator constancy as a pre-pollination isolating mechanism between sympatric species of *Cercidium*. *Evolution* 32: 189–198.
- Jones, C.E. and Buchmann, S.L. 1974. Ultraviolet floral patterns as functional orientation cues in hymenopterous pollination systems. *Animal Behaviour* 22: 481–485.
- Kadmon, R. 1992. Dynamics of forager arrivals and nectar renewal in flowers of *Anchusa strigosa*. *Oecologia* 92: 552–555.
- Kadmon, R. and Shmida, A. 1992. Departure rules used by bees foraging for nectar: a field test. *Evolutionary Ecology* 6: 142–151.
- Kanbe, Y., Okada, I., Yoneda, M., Goka, K. and Tsuchida, K. 2008. Interspecific mating of the introduced bumblebee *Bombus terrestris* and the native Japanese bumblebee *Bombus hypocrita sapporoensis* results in inviable hybrids. *Naturwissenschaften* 95: 1003–1008.
- Kapustjanskij, A., Streinzer, M., Paulus, H.F. and Spaethe, J. 2007. Bigger is better: implications of body size for flight ability under different light conditions and the evolution of alloethism in bumblebees. *Functional Ecology* 21: 1130–1136.
- Katayama, E. 1973. Observations on the brood development in *Bombus ignitus* (Hymenoptera: Apidae): II. Brood development and feeding habits. *Kontyû* 41: 203–216.
- Katayama, E. 1975. Egg laying habits and brood development in *Bombus hypocrita* (Hymenoptera: Apidae): II. Brood development and feeding habits. *Kontyû* 43: 478–496.
- Katayama, E. 1996. Survivorship curves and longevity for workers of *Bombus ardens* Smith and *Bombus diversus* Smith (Hymenoptera, Apidae). *Japanese Journal of Entomology* 64: 111–121.
- Kato, M. 1988. Bumble bee visits to *Impatiens* spp.: pattern and efficiency. *Oecologia* 76: 364–370.
- Kato, M., Shibata, A., Yasui, T. and Nagamasu, H. 1999. Impact of introduced honeybees, *Apis mellifera*, upon native bee communities in the Bonin (Ogasawara) Islands. *Researches on Population Ecology* 2: 217–228.
- Kaule, G. and Krebs, S. 1989. Creating new habitats in intensively used farmland. In: *Biological Habitat Reconstruction* (ed. G.P. Buckley), pp. 161–170. Belhaven Press, London.
- Kawaguchi, L.G., Ohashi, K. and Toquenaga, Y. 2006. Do bumble bees save time when choosing novel flowers by following conspecifics? *Functional Ecology* 20: 239–244.
- Kawaguchi, L.G., Ohashi, K. and Toquenaga, Y. 2007. Contrasting responses of bumble bees to feeding conspecifics on their familiar and unfamiliar flowers. *Proceedings of the Royal Society B - Biological Sciences* 274: 2661–2667.

- Kawakita, A., Sota, T., Ito, M., Ascher, J.S., Tanaka, H., Kato, M. and Roubik, D.W. 2004. Phylogeny, historical biogeography, and character evolution in bumble bees (*Bombus*: Apidae) based on simultaneous analysis of three nuclear gene sequences. *Molecular Phylogenetics and Evolution* 32: 422–423.
- Kay, Q.O.N. 1982. Intraspecific discrimination by pollinators and its role in evolution. In: *Pollination and Evolution* (eds J.A. Armstrong, J.M. Powell and A.J. Richards), pp. 9–28. Royal Botanical Gardens, Sydney.
- Keasar, T., Motro, U., Shur, Y. and Shmida, A. 1996. Overnight memory retention of foraging skills by bumblebees is imperfect. *Animal Behaviour* 52: 95–104.
- Keller, L. and Nonacs, P. 1993. The role of queen pheromones in social insects: queen control or queen signal? *Animal Behaviour* 45: 787–794.
- Kells, A.R. and Goulson, D. 2001. Evidence for handedness in bumblebees. *Journal of Insect Behaviour* 14: 47–55.
- Kells, A.R. and Goulson, D. 2003. Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems. *Biological Conservation* 109: 164–174.
- Kells, A.R., Holland, J. and Goulson, D. 2001. The value of uncropped field margins for foraging bumblebees. *Journal of Insect Conservation* 5: 283–291.
- Kendall, D.A. and Smith, B.D. 1976. The pollinating efficiency of honeybee and bumblebee visits to flowers of the runner bean *Phaseolus coccineus* L. *Journal of Applied Ecology* 13: 749–752.
- Kenta, T., Inari, N., Nagamitsu, T., Goka, K. and Hiura, T. 2007. Commercialized European bumblebee can cause pollination disturbance: an experiment on seven native plant species in Japan. *Biological Conservation* 134: 298–309.
- Kerr, W.E. 1969. Some aspects of the evolution of social bees (Apidae). *Evolutionary Biology* 3: 119–175.
- Kevan, P.G. 1976. Fluorescent nectar (technical comment). *Science* 194: 341–342.
- Kevan, P.G. 1978. Floral coloration, its colormetric analysis and significance in anthecology. In: *The Pollination of Flowers by Insects* (ed. A.J. Richards), pp. 51–78. Academic Press, London.
- Kevan, P.G. 1983. Floral colours through the insect eye: what they are and what they mean. In: *Handbook of Experimental Pollination Ecology* (eds C.E. Jones and R.J. Little). Van Nostrand Reinhold, New York.
- Kevan, P.G. 1991. Pollination: keystone process in sustainable global productivity. *Acta Horticulturae* 288: 103–110.
- Kevan, P.G., Clark, E.A. and Thomas, V.G. 1990. Insect pollinators and sustainable agriculture. *American Journal of Alternative Agriculture* 5: 13–22.
- Kevan, P.G. and Gadawski, S.D. 1984. Pollination of cranberries, *Vaccinium macrocarpon*, on cultivated marshes in Ontario. *Proceedings of the Entomological Society of Ontario* 114: 45–53.
- Kindl, J., Oldrich, H., Urbanová, K. and Valterová, I. 1999. Scent marking in male pre-mating behaviour of *Bombus confusus*. *Journal of Chemical Ecology* 25: 1489–1500.
- King, M.J. 1993. Buzz foraging mechanism of bumble bees. *Journal of Apicultural Research* 32: 41–49.
- Kipp, L.R. 1987. The flight directionality of honeybees foraging on real and artificial inflorescences. *Canadian Journal of Zoology* 65: 587–593.
- Kipp, L.R., Knight, W. and Kipp, E.R. 1989. Influence of resource topography on pollinator flight directionality of two species of bees. *Journal of Insect Behavior* 2: 453–472.
- Kleijn, D., Joenje, W., Lecoecur, D. and Marshall, E.J.P. 1998. Similarities in vegetation development of newly established herbaceous strips along contrasting European field boundaries. *Agriculture, Ecosystems and Environment* 68: 13–26.

- Kleijn, D. and Raemakers, I. 2008. A retrospective analysis of pollen host plant use by stable and declining bumble bee species. *Ecology* 89: 1811–1823.
- Kleijn, D. and Sutherland, W.J. 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology* 40: 947–969.
- Klinkhamer, P.G.L. and de Jong, T.L. 1990. Effects of plant density and sex differential reward visitation in the protandrous *Echium vulgare* (Boraginaceae). *Oikos* 57: 399–405.
- Klinkhamer, P.G.L., de Jong, T.L. and de Bruyn, G.J. 1989. Plant size and pollinator visitation in *Cynoglossum officinale*. *Oikos* 54: 201–204.
- Knee, W.J. and Medler, J.T. 1965. The seasonal size increase of bumblebee workers (Hymenoptera: Bombus). *The Canadian Entomologist* 97: 1149–1155.
- Knight, M.E., Bishop, S., Martin, A.P., Osborne, J.L., Hale, R.J., Sanderson, R.A. and Goulson, D. 2005. An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular Ecology* 14: 1811–1820.
- Knudsen, J.T. 1994. Floral scent variation in the *Pyrola rotundifolia* complex in Scandinavia and western Greenland. *Nordic Journal of Botany* 14: 277–282.
- Koeman-Kwak, M. 1973. The pollination of *Pedicularis palustris* by nectar thieves (short-tongued bumblebees). *Acta Botanica Neerlandica* 22: 608–615.
- Koltermann, R. 1969. Lern- und Vergessensprozesse bei der Honigbiene aufgezeigt anhand von Duftdressuren. *Zeitschrift fuer Vergleichende Physiologie* 63: 310–334.
- Komai, Y. 2001. Direct measurement of oxygen partial pressure in a flying bumblebee. *Journal of Experimental Biology* 204: 2999–3007.
- König, C. and Schmid-Hempel, P. 1995. Foraging activity and immunocompetence in workers of the bumble bee, *Bombus terrestris* L. *Proceedings of the Royal Society London B* 260: 225–227.
- Konovalova, I. 2007. The first record of the rare oligolectic bumblebee *Bombus gerstaeckeri* Morawitz (Hymenoptera: Apidae: Bombini) from Ukraine. *Annales de la Societe Entomologique de France* 43: 441–443.
- Kosior, A. 1995. Changes in the fauna of bumble-bees (*Bombus* Latr.) and cuckoo-bees (*Psithyrus* Lep.) of selected regions in southern Poland. In: *Changes in Fauna of Wild Bees in Europe* (ed. J. Banaszak), pp. 103–111. Pedagogical University, Bydgoszcz.
- Kosior, A., Celary, W., Olejniczak, P., Fijal, J., Krol, W., Solarz, W. and Plonka, P. 2007. The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of Western and Central Europe. *Oryx* 41: 79–88.
- Kremen, C., Williams, N.M. and Thorp, R.W. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences USA* 99: 16812–16816.
- Kreyer, D., Oed, A., Walther-Hellwig, K. and Frankl, R. 2004. Are forests potential landscape barriers for foraging bumblebees? Landscape scale experiments with *Bombus terrestris* agg. and *Bombus pascuorum* (Hymenoptera, Apidae). *Biological Conservation* 116: 111–118.
- Krieger, G.M., Duchateau, M.J., van Doorn, A., Ibarra, F., Francke, W. and Ayasse, M. 2006. Identification of queen sex pheromone components of the bumblebee *Bombus terrestris*. *Journal of Chemical Ecology* 32: 453–471.
- Krüger, E. 1917. Zur Systematik der mitteleuropäischen Hummeln (Hym.). *Entomologische Mitteilungen* 6: 55–66.
- Krüger, E. 1920. Beiträge zur Systematik und Morphologie der mitteleuropäischen Hummeln. *Zoologische Jahrbücher (Systematik, Ökologie und Geographie der Tiere)* 42: 289–464.
- Krüger, E. 1951. Über die Bahnflüge der Männchen der Gattungen *Bombus* und *Psithyrus*. *Zeitschrift für Tierpsychologie* 8: 61–75.

## 272 References

- Kugler, H. 1936. Die Ausnutzung der Saftmalsumfärbung bei den Roszkastanienblüten durch Bienen und Hummeln. *Berichte. Deutsche Botanische Gesellschaft* 60: 128–134.
- Kugler, H. 1940. Die Bestäubung von Blumen durch Furchenbienen (*Halictus* Latr.). *Planta* 30: 780–799.
- Kugler, H. 1943. Hummeln als Blütenbesucher. *Ergebnisse der Biologie* 19: 143–323.
- Kugler, H. 1950. Der Blütenbesuch der Schammfliege (*Eristalomyia tenax*). *Zeitschrift für Vergleichende Physiologie* 32: 328–347.
- Kukuk, P.F. and May, B. 1990. Diploid males in a primitely eusocial bee, *Lasioglossum (Dialictus) zephyrum* (Hymenoptera: Halictidae). *Evolution* 44: 1522–1528.
- Kulahci, I.G., Dornhaus, A. and Papaj, D.R. 2008. Multimodal signals enhance decision making in foraging bumble-bees. *Proceedings of the Royal Society B-Biological Sciences* 275: 797–802.
- Kullenberg, B. 1956. Field experiments with chemical sexual attractants in Aculeate Hymenoptera males I. *Zoologiska Bidrag Uppsala* 31: 253–354.
- Kullenberg, B. 1973. Field experiments with chemical sexual attractants in Aculeate Hymenoptera males II. *Zoon Supplement* 1: 31–42.
- Kullenberg, B., Bergström, G., Bringer, B., Carlberg, B. and Cederberg, B. 1973. Observations on the scent marking by *Bombus* Latr. and *Psithyrus* Lep. males (Hym., Apidae) and localization of site of production of the secretion. *Zoon, Supplement* 1: 23–30.
- Kullenberg, B., Bergström, G. and Ställberg-Stenhagen, S. 1970. Volatile components of the cephalic marking secretion of male bumblebees. *Acta Chemica Scandinavica* 24: 1481–1483.
- Kunin, W.E. 1993. Sex and the single mustard: population density and pollinator behaviour effects on seed set. *Ecology* 74: 2145–2160.
- Kunin, W.E. 1997. Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. *Journal of Ecology* 85: 225–234.
- Kunin, W.E. and Iwasa, Y. 1996. Pollinator foraging strategies in mixed floral arrays—density effects and floral constancy. *Theoretical Population Biology* 49: 232–263.
- Kwak, M.M. 1988. Pollination ecology and seed-set in the rare annual species *Melampyrum arvense* L. (Scrophulariaceae). *Acta Botanica Neerlandica* 37: 153–163.
- Kwak, M.M., Kremer, P., Boerrichter, E. and van den Brand, C. 1991a. Pollination of the rare species *Phyteuma nigrum* (Campanulaceae): flight distances of bumblebees. *Proceedings of Experimental and Applied Entomology, N.E.V. Amsterdam* 2: 131–136.
- Kwak, M.M., van den Brand, C., Kremer, P. and Boerrichter, E. 1991b. Visitation, flight distances and seed set in the rare species, *Phyteuma nigrum* (Campanulaceae). *Acta Horticulturae* 288: 303–307.
- Kwak, M.M., Velterop, O. and Boerrichter, E. 1996. Insect diversity and the pollination of rare plant species. In: *The Conservation of Bees* (ed. A. Matheson, S.L. Buchmann, C. O'Toole, P. Westrich, I.H. Williams), pp. 115–124. Academic Press, London.
- Langley, C.M. 1996. Search images: selective attention to specific visual features of prey. *Journal of Experimental Psychology* 22: 152–163.
- Lanne, B.S., Bergström, G., Wassgren, A.-B. and Törnback, B. 1987. Biogenetic pattern of straight chain marking compounds in male bumble bees. *Comparative Biochemistry and Physiology B. Biochem* 88: 631–636.
- Laverty, T.M. 1980. Bumble bee foraging: floral complexity and learning. *Canadian Journal of Zoology* 58: 1324–1335.

- Laverty, T.M. 1992. Plant interactions for pollinator visits: a test of the magnet species effect. *Oecologia* 89: 502–508.
- Laverty, T.M. 1994a. Costs to foraging bumblebees of switching plant species. *Canadian Journal of Zoology* 72: 43–47.
- Laverty, T.M. 1994b. Bumblebee learning and flower morphology. *Animal Behaviour* 47: 531–545.
- Laverty, T.M. and Plowright, R.C. 1988. Flower handling by bumblebees—a comparison of specialists and generalists. *Animal Behaviour* 36: 733–740.
- Lawrence, E.S. and Allen, J.A. 1983. On the term ‘search image’. *Oikos* 40: 313–314.
- Leadbeater, E. and Chittka, L. 2008. Social transmission of nectar-robbing behaviour in bumblebees. *Proceedings of the Royal Society B-Biological Sciences* 275: 1669–1674.
- Leatherdale, D. 1970. The arthropod hosts of entomogenous fungi in Britain. *Entomophaga* 15: 419–435.
- Levin, D.A. 1978. Pollinator behaviour and the breeding structure of plant populations. In: *The Pollination of Flowers by Insects* (ed. A.J. Richards), pp. 133–150. Academic Press, London.
- Levin, M.D. 1983. Value of bee pollination to US agriculture. *Bulletin of the Entomological Society of America* 29: 50–51.
- Levins, R. and MacArthur, R. 1969. An hypothesis to explain the incidence of monophagy. *Ecology* 50: 910–911.
- Lewis, A.C. 1986. Memory constraints and flower choice in *Pieris rapae*. *Science* 232: 863–865.
- Lewis, A.C. 1989. Flower visit consistency in *Pieris rapae*, the cabbage butterfly. *Journal of Animal Ecology* 58: 1–13.
- Lewis, A.C. 1993. Learning and the evolution of resources: pollinators and flower morphology. In: *Insect Learning: Ecology and Evolutionary Perspectives* (eds D.R. Papaj and A.C. Lewis), pp. 219–242. Chapman and Hall, New York.
- Lex, T. 1954. Duftmale an Blüten. *Zeitschrift für Vergleichende Physiologie* 36: 212–234.
- Lie-Pettersen, O.J. 1901. Biologiske Beobachtungen an norwegischen Hummeln. *Bergens Museum Årbok* 6: 3–10.
- Liersch, S. and Schmid-Hempel, P. 1998. Genetic variation within social insect colonies reduces parasite load. *Proceedings of the Royal Society of London B* 265: 221–225.
- Linhard, E. 1912. Humlebiens som Husdyr. Spredte Traek af nogle danske Humlebiarters Biologi. *Tidsskrift PlAvtl.* 19: 335–352.
- Lloyd, J.E. 1981. Sexual selection: individuality, identification, and recognition in a bumblebee and other insects. *Florida Entomologist* 64: 89–111.
- Lockey, K.H. 1980. Insect cuticular hydrocarbons. *Comparative Biochemistry and Physiology* 65B: 457–462.
- Løken, A. 1949. Bumble bees in relation to *Aconitum septentrionale* in central Norway. *Nytt Magasin for Naturvidenskapene* 87: 1–60.
- Løken, S. 1973. Studies on Scandinavian bumble bees (Hymenoptera, Apidae). *Norsk Entomologisk Tidsskrift* 20: 1–218.
- Lopez-Vaamonde, C., Brown, R.M., Lucas, E.R., Pereboom, J.J.M., Jordan, W.C. and Bourke, A.F.G. 2007. Effect of the queen on worker reproduction and new queen production in the bumble bee *Bombus terrestris*. *Apidologie* 38: 171–180.
- Lopez-Vaamonde, C., Koning, J.W., Brown, R.M., Jordan, W.C. and Bourke, A.F.G. 2004. Social parasitism by male-producing reproductive workers in a eusocial insect. *Nature* 430: 557–560.

- Lopez-Vaamonde, C., Koning, J.W., Jordan, W.C. and Bourke, A.F.G. 2003. No evidence that reproductive bumblebee workers reduce the production of new queens. *Animal Behaviour* 66: 577–584.
- Lopez-Vaamonde, C., Koning, J.W., Jordan, W.C. and Bourke, A.F.G. 2004. A test of information use by reproductive bumblebee workers. *Animal Behaviour* 68: 811–818.
- Lovell, J.H. 1918. *The Flower and the Bee*. Scribner's, New York.
- Low, T. 1999. *Feral Future*. Penguin Books Australia Ltd, Ringwood, Australia.
- Ludwig, F. 1885. Die biologische Bedeutung des Farbenwechsels mancher Blumen. *Biologische Centralblatt* 4: 196.
- Ludwig, F. 1887. Einige neue Falle von Farbenwechsel in verblühenden Blütenständen. *Biologische Centralblatt* 6: 1–3.
- Lunau, K. 1990. Colour saturation triggers innate reactions to flower signals: flower dummy experiments with bumblebees. *Journal of Comparative Physiology A* 166: 827–834.
- Lunau, K., Wacht, S. and Chittka, L. 1996. Colour choice of naïve bumble bees and their implications for colour perception. *Journal of Comparative Physiology* 178: 477–489.
- Lundberg, H. and Svensson, B.G. 1975. Studies on the behaviour of *Bombus* Latr. species (Hymenoptera: Apidae) parasitized by *Sphaerularia bombi* Dufour (Nematoda) in an alpine area. *Norwegian Journal of Entomology* 22: 129–134.
- MacDonald, M.A. 2001. The colonisation of Northern Scotland by *Bombus terrestris* (L.) and *B. lapidarius* (L.) (Hym., Apidae), and the possible role of climate change. *The Entomologist's Monthly Magazine* 137: 1–13.
- MacFarlane, R.P. 1976. Bees and Pollination. In: *New Zealand Insect Pests* (ed. D.N. Ferro), pp. 221–229. Lincoln University College of Agriculture, New Zealand.
- MacFarlane, R.P. and Griffin, R.P. 1990. New Zealand distribution and seasonal incidence of the nematode *Sphaerularia bombi* Dufour, a parasite of bumblebees. *New Zealand Journal of Zoology* 17: 191–199.
- MacFarlane, R.P., Griffin, R.P. and Read, P.E.C. 1983. Bumble bee management options to improve 'grasslands pawera' red clover seed yields. *Proceedings of the New Zealand Grasslands Association* 44: 47–53.
- MacFarlane, R.P., Grundell, J.M. and Dugdale, J.S. 1992. Gorse on the Chatham Islands: seed formation, arthropod associates and control. *Proceedings of the 45th New Zealand Plant Protection Conference* 251–255.
- MacFarlane, R.P. and Gurr, L. 1995. Distribution of bumble bees in New Zealand. *New Zealand Entomologist* 18: 29–36.
- MacFarlane, R.P., Lipa, J.J. and Liu, H. 1995. Bumble bee pathogens and internal enemies. *Bee World* 76: 130–148.
- MacFarlane, R.P. and Pengelly, D.H. 1974. Conopidae and Sarcophidae (Diptera) as parasites of adult Bombinae (Hymenoptera) in Ontario. *Proceedings of the Entomological Society of Ontario* 105: 55–59.
- Macior, L.W. 1966. Foraging behavior of *Bombus* (Hymenoptera: Apidae) in relation to *Aquilegia* pollination. *American Journal of Botany* 53: 302–309.
- Macior, L.W. 1968. *Bombus* (Hym. Apid.) queen foraging in relation to vernal pollination in Wisconsin. *Ecology* 49: 20–25.
- Mackensen, O. 1951. Viability and sex determination in the honey bee (*Apis mellifera* L.). *Genetics* 36: 500–509.

- MacKenzie, K.E. 1994. The foraging behaviour of oney bees (*Apis mellifera* L) and bumble bees (*Bombus* spp) on cranberry (*Vaccinium macrocarpon* Ait). *Apidologie* 25: 375–383.
- Macuda, T., Gegeer, R.J., Laverty, T.M. and Timney, B. 2001. Behavioural assessment of visual acuity in bumblebees (*Bombus impatiens*). *The Journal of Experimental Biology* 204: 559–564.
- Madjidian, J.A., Morales, C.L. and Smith, H.G. 2008. Displacement of a native by an alien bumblebee: lower pollinator efficiency overcome by overwhelmingly higher visitation frequency. *Oecologia* 156: 835–845.
- Makino, T.T., Ohashi, K. and Sakai, S. 2007. How do floral display size and the density of surrounding flowers influence the likelihood of bumble bee revisitation to a plant? *Functional Ecology* 21: 87–95.
- Makino, T.T. and Sakai, S. 2004. Findings on spatial foraging patterns of bumblebees (*Bombus ignitus*) from a bee-tracking experiment in a net cage. *Behavioral Ecology and Sociobiology* 56: 155–163.
- Makino, T.T. and Sakai, S. 2007. Experience changes pollinator responses to floral display size: from size-based to reward-based foraging. *Functional Ecology* 21: 854–863.
- Mal, T.K., Lovett-Doust, J., Lovett-Doust, L. and Mulligan, G.A. 1992. The biology of Canadian weeds. 100. *Lythrum salicaria*. *Canadian Journal of Plant Science* 72: 1305–1330.
- Mallet, J. 1999. Causes and consequences of a lack of coevolution in Müllerian mimicry. *Evolutionary Ecology* 13: 777–806.
- Mallon E.B., Brockman, A. and Schmid-Hempel, P. 2003a. Immune function inhibits memory formation in the honeybee *Apis mellifera*. *Proceedings of the Royal Society of London B* 270: 1843–1847.
- Mallon, E.B., Loosli, R. and Schmid-Hempel, P. 2003b. Specific versus nonspecific immune defense in the bumblebee, *Bombus terrestris* L. *Evolution* 57: 1444–1447.
- Malooof, J.E. 2000. The ecological effect of nectar robbers, with an emphasis on the reproductive biology of *Corydalis caseana*. Dissertation, University of Maryland, College Park, Maryland, USA.
- Malooof, J.E. 2001. The effects of a bumble bee nectar robber on plant reproductive success and pollinator behavior. *American Journal of Botany* 88: 1960–1965.
- Malooof, J.E. and Inouye, D.W. 2000. Are nectar robbers cheaters or mutualists? *Ecology* 81: 2651–2661.
- Mänd, M., Mänd, R. and Williams, I.H. 2002. Bumblebees in the agricultural landscape of Estonia. *Agriculture, Ecosystems and Environment* 89: 69–76.
- Mangel, M. 1990. Dynamic information in uncertain and changing worlds. *Journal of Theoretical Biology* 146: 317–332.
- Mangum, W.A. and Brooks, R.W. 1997. First records of *Megachile* (*Callomegachile*) *sculpturalis* Smith (Hymenoptera: Megachilidae) in the continental United States. *Journal of the Kansas Entomological Society* 70: 140–142.
- Manning, A. 1956. Some aspects of the foraging behaviour of bumblebees. *Behaviour* 9: 164–201.
- Mapalad, K.S., Leu, D. and Nieh, J.C. 2008. Bumble bees heat up for high quality pollen. *Journal of Experimental Biology* 211: 2239–2242.
- Marden, J.H. 1984. Intrapopulation variation in nectar secretion in *Impatiens capensis*. *Oecologia* 63: 418–422.
- Markow, T.A. 1995. Evolutionary ecology and developmental instability. *Annual Review of Entomology* 40: 105–120.



- Marloth, R. 1895. The fertilisation of '*Disa uniflora*' Berg, by insects. *Transactions of the South African Philosophical Society* 8: 93–95.
- Marshall, E.J.P. and Smith, B.D. 1987. Field margin flora and fauna; interactions with agriculture. In: *Field Margins* (eds. J.M. Way and P.W. Greig-Smith), pp. 22–33. British Crop Protection Council, Thornton Heath, UK; Monograph no. 35.
- Marshall, E.J.P., Thomas, C.F.G., Joenje, W., Kleijn, D., Burel, F. and Lecoeur, D. 1994. Establishing vegetation strips in contrasted European Farm situations. In: *British Crop Protection Monograph No. 58. Field margins: integrating agriculture and conservation* (Ed. N.D. Boatman), pp. 335–340. Farnham, British Crop Protection Council.
- Martin, A.P., Carreck, N.L., Swain, J.L., Goulson, D., Knight, M.E., Hale, R.J., Sanderson, R.A. and Osborne, J.L. 2006. A modular system for trapping and mass-marking bumblebees: applications for studying food choice and foraging range. *Apidologie* 37: 341–350.
- Marucci, P.E. and Moulter, H.J. 1977. Cranberry pollination in New Jersey. *Acta Horticulturae* 61: 217–222.
- Matsumura, C., Yokoyama, J. and Washitani, I. 2004. Invasion status and potential impacts of an invasive alien bumblebee, *Bombus terrestris* L. (Hymenoptera: Apidae) naturalized in southern Hokkaido, Japan. *Global Environmental Research* 8: 51–66.
- Matthews, E. 1984. To Bee or Not? Bees in National Parks—The Introduced Honeybee in Conservation Parks in South Australia, pp. 9–14. Magazine of the South Australia National Parks Association, Adelaide.
- McDade, L.A. and Kinsman, S. 1980. The impact of floral parasitism in two neotropical hummingbird-pollinated plant species. *Evolution* 34: 944–958.
- McFrederick, Q.S. and LeBuhn, G. 2006. Are urban parks refuges for bumble bees? *Biological Conservation* 129: 372–382.
- McGregor, S.E. 1976. *Insect Pollination of Cultivated Crops*. USDA Agriculture Handbook No. 496, US Government Printing Office, Washington, DC.
- McGregor, S.E., Alcorn, E.B., Kuitz, E.B., Jr. and Butler, G.D., Jr. 1959. Bee visitors to Saguaro flowers. *Journal of Economic Entomology* 52: 1002–1004.
- McIvor, C.A. and Malone, L.A. 1995. *Nosema bombi*, a microsporidian pathogen of the bumble bee *Bombus terrestris* (L.). *New Zealand Journal of Zoology* 22: 25–31.
- Medler, J.T. 1962a. Morphometric studies on bumblebees. *Annals of the Entomological Society of America* 55: 212–218.
- Medler, J.T. 1962b. Morphometric analyses of bumblebee mouthparts. *Transactions of the XI International Congress of Entomology* 2: 517–521.
- Meidell, O. 1934. Fra dagliglivet I et homlebol. *Naturen* 58: 85–95, 108–116.
- Meidell, O. 1944. Notes of the pollination of *Malampyrum pratense* and the 'honey stealing' of bumblebees. *Bergens Museum Årbok* 11: 5–11.
- Meijere, J.C.H. de 1904. Beiträge zur Kenntnis der Biologie und der systematischen Verwandtschaft der Conopiden. *Tijdschrift voor Entomologie* 46: 144–224.
- Meijere, J.C.H. de 1912. Neue Beiträge zur Kenntnis der Conopiden. *Tijdschrift voor Entomologie* 55: 184–207.
- Meineke, H. 1978. Umlernen einer Honigbiene zwischen gelb und blau-Belohnung im Dauerversuch. *Journal of Insect Physiology* 24: 155–163.
- Meisels, S. and Chiasson, H. 1997. Effectiveness of *Bombus impatiens* Cr. as pollinators of greenhouse sweet peppers (*Capsicum annuum* L.). *Acta Horticulturae* 437: 425–429.

- Memmott, J., Waser, N.M. and Price, M.V. 2004. Tolerance of pollination networks to species extinctions. *Proceedings of the Royal Society of London B* 271: 2605–2611.
- Menezes Pedro, S.R. and Camargo, J.M.F. 1991. Interactions on floral resources between the Africanized honey bee *Apis mellifera* L and the native bee community (Hymenoptera: Apoidea) in a natural 'cerrado' ecosystem in southeast Brazil. *Apidologie* 22: 397–415.
- Menke, H.F. 1954. Insect pollination in relation to alfalfa seed production in Washington. *Washington Agricultural Experiment Station Bulletin* 555: 24.
- Menzel, R. 1967. Untersuchungen zum Erlernen von Spektralfarben durch die Honigbiene (*Apis mellifica*). *Zeitschrift fuer Vergleichende Physiologie* 56: 22–62.
- Menzel, R. 1969. Das Gedächtnis der Honigbiene für Spaktralfarben. II. Umlernen und Mehrfachlernen. *Zeitschrift für Vergleichende Physiologie* 63: 290–309.
- Menzel, R. 1979. Behavioral access to short-term memory in bees. *Nature* 281: 368–369.
- Menzel, R. 1990. Learning, memory and 'cognition' in honey bees. In: *Neurobiology of Comparative Cognition* (eds R.P. Kesner and D.S. Olten), pp. 237–292. Erlbaum Inc., Hillsdale, NJ.
- Menzel, R. 1999. Memory dynamics in the honeybee. *Journal of Comparative Physiology A* 185: 323–340.
- Menzel, R. and Erber, I. 1978. Learning and memory in bees. *Scientific American* 239: 102–110.
- Menzel, R., Geiger, K., Chittka, L., Joerges, J., Kunze, J. and Muller, U. 1996. The knowledge base of bee navigation. *Journal of Experimental Biology* 199: 141–146.
- Menzel, R., Geiger, K., Joerges, J., Muller, U. and Chittka, L. 1998. Bees travel novel homeward routes by integrating separately acquired vector memories. *Animal Behaviour* 55: 139–152.
- Menzel, R., Greggers, U. and Hammer, M. 1993. Functional organization of appetitive learning and memory in a generalist pollinator, the honey bee. In: *Insect Learning: Ecological and Evolutionary Perspectives* (eds D. Papaj and A.C. Lewis, A.C.), pp.79–125. Chapman and Hall, New York.
- Menzel, R., Gumbert, A., Kunze, J., Shmida, A. and Vorobyev, M. 1997. Pollinators' strategies in finding flowers. *Israel Journal of Plant Sciences* 45: 141–156.
- Menzel, R. and Müller, U. 1996. Learning and memory in honeybees: from behaviour to neural substrates. *Annual Review of Neuroscience* 19: 379–404.
- Michener, C.D. 1965. A classification of the bees of the Australian and South Pacific regions. *Bulletin of the American Museum of Natural History* 130: 1–324.
- Michener, C.D. 1974. *The Social Behavior of the Bees: A Comparative Study*. Second Edition. Harvard University Press (Belknap Press), Cambridge, 404 pp.
- Michener, C.D. 1979. Biogeography of bees. *Annals of the Missouri Botanical Garden* 66: 277–347.
- Michener, C.D. 1990. Classification of the Apidae (Hymenoptera). *University of Kansas Science Bulletin* 54: 75–164.
- Michener, C.D. and Amir, M. 1977. The seasonal cycle and habitat of a tropical bumble bee. *Pacific Insects* 17: 75–164.
- Michener, C.D. and Grimaldi, D.A. 1988. The oldest fossil bee: apoid history, evolutionary stasis, and antiquity of social behavior. *Proceedings of the National Academy of Sciences USA* 85: 6424–6426.
- Michener, C.D. and Laberge, W.E. 1954. A large *Bombus* nest from Mexico. *Psyche* 61: 63–67.
- Mikkola, K. 1978. Spring migrations of wasps and bumblebees on the southern coast of Finland (Hymenoptera, Vespidae and Apidae). *Annual Entomology Fennici* 44: 10–26.

## 278 References

- Mikkola, K. 1984. Migration of wasp and bumblebee queens across the Gulf of Finland (Hymenoptera: Vespidae and Apidae). *Notulae Entomologicae* 64: 125–128.
- Milliron, H.E. 1971. A monograph of the western hemisphere bumblebees (Hymenoptera: Apidae; Bombinae). I. The genera *Bombus* and *Megabombus* subgenus *Bombias*. Memoirs of the Entomological Society of Canada, No. 82.
- Milliron, H.E. and Oliver, D.R. 1966. Bumblebees from northern Ellesmere Island, with observations on usurpation by *Megabombus hyperboreus* (Schöhn). *The Canadian Entomologist* 98: 207–213.
- Minckley, R.L., Buchmann, S.L. and Wcislo, W.T. 1991. Bioassay evidence for a sex attractant pheromone in the large carpenter bee, *Xylocopa varipuncta* (Anthophoridae, Hymenoptera). *Journal of Zoology* 224: 285–291.
- Minckley, R.L. and Roulston, T.H. 2006. Incidental mutualisms and pollen specialisation among bees. In: *Plant-Pollinator Interactions: From Specialisation to Generalisation* (eds N.M. Wasser and J. Ollerton), pp. 69–98. University of Chicago Press, London.
- Mitchell, R.J., Karron, J.D., Holmquist, K.G. and Bell, J.M. 2004. The influence of *Mimulus ringens* floral display size on pollinator visitation patterns. *Functional Ecology* 18: 116–124.
- Miyake, Y.C. and Sakai, S. 2005. Effects of number of flowers per raceme and number of racemes per plant on bumblebee visits and female reproductive success in *Salvia nipponica* (Labiatae). *Ecological Research* 20: 395–403.
- Miyamoto, S. 1957. Behavior study on *Bombus ardens* Smith in early stage of nesting. *Science Reports of the Hyogo University of Agriculture* 3: 1–5.
- Mohr, N.A. and Kevan, P.G. 1987. Pollinators and pollination requirements of lowbush blueberry (*Vaccinium angustifolium* Ait. and *V. myrtilloides* Michx.) and cranberry (*V. macrocarpon* Ait.) in Ontario with notes on highbush blueberry (*V. corymbosum* L.) and lignonberry (*V. vitis-idaea* L.). *Proceedings of the Entomological Society of Ontario* 118: 149–154.
- Molet, M., Chittka, L., Stelzer, R.J., Streit, S. and Raine, N.E. 2008. Colony nutritional status modulates worker responses to foraging recruitment pheromone in the bumblebee *Bombus terrestris*. *Behavioral Ecology and Sociobiology* 62: 1919–1926.
- Møller, A.P. 1993. Developmental stability, sexual selection, and the evolution of secondary sexual characters. *Etologia* 3: 199–208.
- Møller, A.P. 1995. Bumblebee preference for symmetrical flowers. *Proceedings of the National Academy of Science* 92: 2288–2292.
- Møller, A.P. and Eriksson, M. 1995. Pollinator preference for symmetrical flowers and sexual selection in plants. *Oikos* 73: 15–22.
- Møller, A.P. and Pomiankowski, A. 1993. Fluctuating asymmetry and sexual selection. *Genetica* 89: 267–279.
- Møller, A.P. and Sorci, G. 1998. Insect preference for symmetrical artificial flowers. *Oecologia* 114: 37–42.
- Møller, A.P. and Thornhill, R. 1998. Bilateral symmetry and sexual selection: a meta-analysis. *American Naturalist* 151: 174–192.
- Mommaerts, V., Sterk, G. and Smaghe, G. 2006. Hazards and uptake of chitin synthesis inhibitors in bumblebees *Bombus terrestris*. *Pest Management Science* 62: 752–758.
- Morandin, L.A., Lavery, T.M. and Kevan, P.G. 2001. Bumble bee (Hymenoptera: Apidae) activity and pollination levels in commercial tomato greenhouses. *Journal of Economic Entomology* 94: 462–467.
- Morandin, L.A. and Winston, M.L. 2003. Effects of novel pesticides on bumble bee (Hymenoptera: Apidae) colony health and foraging ability. *Environmental Entomology* 32: 555–563.

- Morandin, L.A., Winston, M.L., Abbott, V.A. and Franklin, M.T. 2007. Can pastureland increase wild bee abundance in agriculturally intense areas? *Basic and Applied Ecology* 8: 117–124.
- Morandin, L.A., Winston, M.L., Franklin, M.T. and Abbott, V.A. 2005. Lethal and sub-lethal effects of spinosad on bumble bees (*Bombus impatiens* Cresson). *Pest Management Science* 61: 619–626.
- Moret, Y. and Schmid-Hempel, P. 2000. Survival for immunity: the price of immune system activation for bumblebee workers. *Science* 290: 1166–1168.
- Moret, Y. and Schmid-Hempel, P. 2001. Immune defence in bumble-bee offspring. *Nature* 414: 506.
- Moret, Y. and Schmid-Hempel, P. 2004. Social life-history response to individual immune challenge of workers of *Bombus terrestris* L.: a possible new cooperative phenomenon. *Ecology Letters* 7: 146–152.
- Moritz, R.F.A. 1985. The effects of multiple mating on the worker-queen conflict in *Apis mellifera* L. *Behavioral Ecology and Sociobiology* 16: 375–377.
- Moritz, R.F.A., Kryger, P., Koeniger, G., Koeniger, N., Estoup, A. and Tingek, S. 1995. High degree of polyandry in *Apis dorsata* queens detected by DNA microsatellite variability. *Behavioral Ecology and Sociobiology* 37: 357–363.
- Morris, W.F. 1996. Mutualism denied—nectar-robbing bumble bees do not reduce female or male success of bluebells. *Ecology* 77: 1451–1462.
- Morse, D.H. 1977. Resource partitioning in bumble bees: the role of behavioral factors. *Science* 197: 678–680.
- Morse, D.H. 1978a. Foraging rate, foraging position and worker size in Bumble-Bee workers. Proceedings of the IVth International Symposium on Pollination. *Maryland Agricultural Experimental Station Special Miscellaneous Publications* 1: 447–452.
- Morse, D.H. 1978b. Size-related foraging differences of bumble bee workers. *Ecological Entomology* 3: 189–192.
- Morse, D.H. 1986a. Inflorescence choice and time allocation by insects foraging on milkweed. *Oikos* 46: 229–236.
- Morse, D.H. 1986b. Predatory risk to insects foraging at flowers. *Oikos* 46: 223–228.
- Morse, D.H. 1981. Interactions among syrphid flies and bumblebees on flowers. *Ecology* 62: 81–88.
- Morse, R.A. and Calderone, N.W. 2000. The value of honey bees as pollinators of U.S. crops in 2000. *Bee Culture* 128(Special Suppl): 1–15.
- De Los Mozos Pascual, M. and Domingo, L.M. 1991. Flower constancy in *Heliotaurus ruficollis* (Fabricius 1781, Coleoptera: Alleculidae). *Elytron (Barc)* 5: 9–12.
- Müller, C.B. 1994. Parasite-induced digging behaviour in bumble bee workers. *Animal Behaviour* 48: 961–966.
- Müller, C.B. and Schmid-Hempel, P. 1992a. Variation in life history pattern in relation to worker mortality in the bumblebee *Bombus lucorum*. *Functional Ecology* 6: 48–56.
- Müller, C.B. and Schmid-Hempel, P. 1992b. Correlates of reproductive success among field colonies of *Bombus lucorum*: the importance of growth and parasites. *Ecological Entomology* 17: 343–353.
- Müller, C.B. and Schmid-Hempel, P. 1993a. Exploitation of cold temperature as defense against parasitoids in bumblebees. *Nature* 363: 65–67.
- Müller, C.B. and Schmid-Hempel, P. 1993b. Correlates of reproductive success among field colonies of *Bombus lucorum* L.: the importance of growth and parasites. *Ecological Entomology* 17: 343–353.

- Müller, C.B., Shykoff, J.A. and Sutcliffe, G.H. 1992. Life history patterns and opportunities for queen-worker conflict in bumblebees (Hymenoptera: Apidae). *Oikos* 65: 242–248.
- Müller, H. 1883. The effect of the change of colour in the flowers of *Pulmonaria officinalis* upon its fertilizers. *Nature* 28: 81.
- Murray, T.E., Fitzpatrick, U., Brown, M.J.F. and Paxton, R.J. 2008. Cryptic species diversity in a widespread bumble bee complex revealed using mitochondrial DNA RFLPs. *Conservation Genetics* 9: 653–666.
- Nakamura, H. and Toquenaga, Y. 2002. Estimating colony locations of bumble bees with moving average model. *Ecological Research* 17: 39–48.
- Neal, P.R., Dafni, A. and Giurfa, M. 1998. Floral symmetry and its role in plant-pollinator systems: terminology, distribution, and hypotheses. *Annual Review of Ecology and Systematics* 29: 345–373.
- Ne'eman, G., Dafni, A. and Potts, S.G. 2000. The effect of fire on flower visitation and fruit set in four core-species in east Mediterranean scrubland. *Plant Ecology* 146: 157–164.
- Newman, D.A. and Thomson, J.D. 2005 Interactions among nectar robbing, floral herbivory, and ant protection in *Linaria vulgaris*. *Oikos* 110: 497–506.
- Newman, H.W. 1851. Habits of the Bombinatrices. *Proceedings of the Entomological Society of London* 1851: 86–92.
- Newsholme, E.A., Crabtree, B., Higgins, S.J., Thornton, S.D. and Start, C. 1972. The activities of fructose diphosphatase in flight muscles from the bumble-bee and the role of this enzyme in heat generation. *Biochemical Journal* 128: 89–97.
- Newton, S.D. and Hill, G.D. 1983. Robbing of field bean flowers by the short-tongued bumble bee *Bombus terrestris* L. *Journal of Apicultural Research* 22: 124–129.
- Nilsson, L.A. 1992. Orchid pollination biology. *Trends in Ecology and Evolution* 7: 255–259.
- Nieh, J.C., Leon, A., Cameron, S. and Vandame, R. 2006. Hot bumble bees at good food: thoracic temperature of feeding *Bombus wilmattae* foragers is tuned to sugar concentration. *Journal of Experimental Biology* 209: 4185.
- Nielsen, D.M., Visker, K.E., Cunningham, M.J., Keller, R.W., Glick, S.D. and Carlson, J.N. 1997. Paw preference, rotation, and dopamine function in collins HI and LO mouse strains. *Physiology and Behavior* 61: 525–535.
- Niwa, S., Iwano, H., Asada, S., Matsuura, M. and Goka, K. 2004. A microsporidian pathogen isolated from a colony of the European bumblebee, *Bombus terrestris*, and infectivity on Japanese bumblebee. *Japanese Journal of Applied Entomology and Zoology* 48: 60–64.
- Núñez, J.A. 1967. Sammelbienen markieren versiegte Futterquellen durch Duft. *Naturwissenschaften* 54: 322–323.
- Nuttman, C. and Willmera, P. 2003. How does insect visitation trigger floral colour change? *Ecological Entomology* 28: 467–474.
- Oberrath, R., Zanke, C. and Bohninggaese, K. 1995. Triggering and ecological significance of floral color-change in lungwort (*Pulmonaria spec.*). *Flora* 190: 155–159.
- Ockinger, E. and Smith, H.G. 2007. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology* 44: 50–59.
- O'Donnell, S. and Foster, R.L. 2001. Thresholds of response in nest thermoregulation by worker bumble bees, *Bombus bifarius nearcticus* (Hymenoptera: Apidae). *Ethology* 107: 387–399.
- O'Donnell, S. and Jeanne, R.L. 1992. Forager success increases with experience in *Polybia occidentalis* Olivier (Hymenoptera: Vespidae). *Insectes Sociaux* 39: 451–454.

- O'Donnell, S. and Jeanne, R.L. 1995. Implications of senescence patterns for the evolution of age polyethism in eusocial insects. *Behavioural Ecology and Sociobiology* 6: 269–273.
- O'Donnell, S., Reichardt, M. and Foster, R. 2000. Individual and colony factors in bumble bee division of labor (*Bombus bifarius nearcticus* Handl; Hymenoptera, Apidae). *Insectes Sociaux* 47: 164–170.
- Ohara, M. and Higashi, S. 1994. Effects of inflorescence size on visits from pollinators and seed set of *Corydalis ambigua* (Papaveraceae). *Oecologia* 98: 25–30.
- Ohashi, K., Leslie, A. and Thomson, J.D. 2008. Trapline foraging by bumble bees: V. Effects of experience and priority on competitive performance. *Behavioral Ecology* 19: 936–948.
- Ohashi, K. and Yahara, T. 1998. Effects of variation in flower number on pollinator visits in *Cirsium purpuratum* (Asteraceae). *American Journal of Botany* 85: 219–224.
- Ohashi, K. and Yahara, T. 1999. How long to stay on, and how often to visit a flowering plant?—a model for foraging strategy when floral displays vary in size. *Oikos* 86: 386–392.
- Ohashi, K. and Yahara, T. 2002. Visit larger displays but probe proportionally fewer flowers: counterintuitive behaviour of nectar-collecting bumble bees achieves an ideal free distribution. *Functional Ecology* 16: 492–503.
- Oldham, N.J., Billen, J. and Morgan, E.D. 1994. On the similarity of Dufour gland secretion and their cuticular hydrocarbons of some bumblebees. *Physiological Entomology* 19: 115–123.
- Oldroyd, B.P. 1998. Controlling feral honey bee, *Apis mellifera* L. (Hymenoptera: Apidae), populations in Australia: methodologies and costs. *Australian Journal of Entomology* 37: 97–100.
- Oldroyd, B.P., Smolenski, A.J., Cornuet, J.M., Wongsiri, S., Estoup, A., Rinderer, T.E. and Crozier, R.H. 1995. Levels of polyandry and intracolony genetic relationships in *Apis florea*. *Behavioral Ecology and Sociobiology* 37: 329–335.
- Olesen, J.M. and Knudsen, J.T. 1994. Scent profiles of flower color morphs of *Corydalis cava* (Fumariaceae) in relation to foraging behavior of bumblebee queens (*Bombus terrestris*). *Biochemical Systematics and Ecology* 22: 231–237.
- Olmstead, A.L. and Wooten, D.B. 1987. Bee pollination and productivity growth: the case of alfalfa. *American Journal of Agricultural Economics* 69: 56–63.
- O'Neill, K.M., Evans, H.E. and Bjostad, L.B. 1991. Territorial behaviour in males of three North American species of bumblebees (Hymenoptera: Apidae, *Bombus*). *Canadian Journal of Zoology* 69: 604–613.
- O'Neal, R.J. and Waller, G.D. 1984. On the pollen harvest by the honey bee (*Apis mellifera* L.) near Tucson, Arizona (1976–1981). *Desert Plants* 6: 81–94.
- Oostermeijer, J.G.B., den Nijs, J.C.M., Raijmann, L.E.L. and Menken, S.B.J. 1992. Population biology and management of the marsh gentian (*Gentiana pneumoanthe* L.), a rare species in The Netherlands. *Botanical Journal of the Linnean Society* 108: 117–130.
- Osborne, J.L. 1994. Evaluating a pollination system: *Borago officinalis* and bees. Ph.D. thesis, Cambridge University, UK
- Osborne J.L., Clark S.J., Morris R.J., Williams I.H., Riley J.R., Smith A.D., Reynolds D.R. and Edwards A.S. 1999. A landscape study of bumble bee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology* 36: 519–533.
- Osborne, J.L. and Corbet, S.A. 1994. Managing habitats for pollinators in farmland. *Aspects of Applied Biology* 40: 207–215.
- Osborne, J.L., Martin, A.P., Carreck, N.L., Swain, J.L., Knight, M.E.; Goulson, D., Hale, R.J. and Sanderson, R.A. 2008a. Bumblebee flight distances in relation to the forage landscape. *Journal of Animal Ecology* 77: 401–415.

- Osborne, J.L., Martin, A.P., Shortall, C.R., Todd, A.D., Goulson, D., Knight, M.E., Hale, R.J. and Sanderson, R.A. 2008b. Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *Journal of Applied Ecology* 45: 784–792.
- Osborne, J.L. and Williams, I.H. 1996. Bumble bees as pollinators of crops and wild flowers. In: *Bumble Bees for Pleasure and Profit* (ed. A. Matheson), pp. 24–32. IBRA, Cardiff.
- Osborne, J.L. and Williams, I.H. 2001. Site constancy of bumble bees in an experimentally patchy habitat. *Agriculture, Ecosystems and Environment* 83: 129–141.
- Osborne, J.L., Williams, I.H., Carreck, N.L., Poppy, G.M., Riley J.R., Smith A.D., Reynolds D.R. and Edwards A.S. 1997. Harmonic radar: a new technique for investigating bumble bee and honey bee foraging flight. *Acta Horticulturae* 437: 159–163.
- Osborne, J.L., Williams, I.H. and Corbet, S.A. 1991. Bees, pollination and habitat change in the European community. *Bee World* 72: 99–116.
- Oster, G. and Heinrich, B. 1976. Why do bumblebees major? A mathematical model. *Ecological Monographs* 46: 129–133.
- Oster, G.F. and Wilson, E.O. 1978. *Caste and Ecology in the Social Insects*. Princeton University Press, Princeton, NJ.
- O'Toole, C. 1994. Who cares for solitary bees? In: *Forage for Bees in an Agricultural Landscape* (ed. A. Matheson), pp. 47–56. IBRA, Cardiff.
- O'Toole, C. and Raw, A. 1991. *Bees of the World*. Blandford, London.
- Ott, J.R., Real, L.A. and Silverfine, E.M. 1985. The effect of nectar variance on bumblebee patterns of movement and potential gene dispersal. *Oikos* 45: 333–340.
- Otterstatter, M.C. 2004. Patterns of parasitism among conopid flies parasitizing bumblebees. *Entomologia Experimentalis et Applicata* 111: 133–139.
- Otterstatter, M.C., Gegeer, R.J., Colla, S.R. and Thompson, J.D. 2005. Effects of parasitic mites and protozoa on the flower constancy and foraging rate of bumble bees. *Behavioral Ecology and Sociobiology* 58: 383–389.
- Otterstatter, M.C. and Thompson, J.D. 2006. Within-host dynamics of an intestinal pathogen of bumble bees. *Parasitology* 133: 749–761.
- Otterstatter, M.C. and Thompson, J.D. 2007. Contact networks and transmission of an intestinal pathogen in bumble bee (*Bombus impatiens*) colonies. *Oecologia* 154: 411–421.
- Otterstatter, M.C. and Thomson, J.D. 2008. Does pathogen spillover from commercially reared bumble bees threaten wild pollinators? *PloS ONE* 3: e2771.
- Otterstatter, M.C. and Whidden, T.L. 2004. Patterns of parasitism by tracheal mites (*Locustacarus buchneri*) in natural bumble bee populations. *Apidologie* 35: 351–357.
- Otti, O. and Schmid-Hempel, P. 2007. *Nosema bombi*: a pollinator parasite with detrimental fitness effects. *Journal of Invertebrate Pathology* 96: 118–124.
- Otti, O. and Schmid-Hempel, P. 2008. A field experiment on the effects of *Nosema bombi* in colonies of the bumblebee *Bombus terrestris*. *Ecological Entomology* 33: 577–582.
- Ovenden, G.N., Swash, A.R.H. and Smallshire, D. 1998. Agri-environment schemes and their contribution to the conservation of biodiversity in England. *Journal of Applied Ecology* 35: 955–960.
- Owen, J.H. 1948. The larder of the red-backed shrike. *British Birds* 41: 200–203.
- Owen, R.E. 1988. Body size variation and optimal body size of bumble bee queens (Hymenoptera: Apidae). *The Canadian Entomologist* 120: 19–27.
- Owen, R.E., Mydnyski, L.J., Packer, L. and McCorquodale, D.B. 1992. Allozyme variation in bumble bees (Hymenoptera: Apidae). *Biochemical Genetics* 30: 443–453.

- Owen, R.E. and Plowright, R.C. 1982. Worker-queen conflict and male parentage in bumble bees. *Behavioural Ecology and Sociobiology* 11: 91–99.
- Owen, R.E., Rodd, F.H. and Plowright, R.C. 1980. Sex ratio in bumble bee colonies: complications due to orphaning? *Behavioral Ecology and Sociobiology* 7: 287–291.
- Packer, L. and Owen, R. 2001. Population genetic aspects of pollinator decline. *Conservation Ecology* 5: 4.
- Palm, N.B. 1949. The pharyngeal gland in *Bombus* Latr. And *Psithyrus* Lep. *Opuscula Entomologica* 14: 27–47.
- Palmer, A.R. 1994. Fluctuating asymmetry analyses: a primer. In: *Developmental Instability: Its Origins and Evolutionary Implications* (ed. T.A. Markow), pp. 335–364. Kluwer, Dordrecht, The Netherlands.
- Palmer, A.R. 1996. Waltzing with asymmetry. *Bioscience* 46: 518–532.
- Palmer, T.P. 1968. Establishment of bumble bees in nest boxes at Christchurch. *New Zealand Journal of Agricultural Research* 11: 737–739.
- Palmer-Jones, T., Forster, I.W. and Clinch, P.G. 1966. Observations of the pollination of Montgomery red clover (*Trifolium pratense* L.). *New Zealand Journal of Agricultural Research* 9: 738–747.
- Pamilo, P. 1991. Evolution of colony characteristics in social insects. 2. Number of reproductive individuals. *American Naturalist* 137: 83–107.
- Pamilo, P., Pekkarinen, A. and Varvio, S.-L. 1987. Clustering of bumblebee subgenera based on interspecific genetic relationships (Hymenoptera: Apidae: *Bombus* and *Psithyrus*). *Annales Zoologici Fennici* 24: 19–27.
- Pamilo, P., Varvio, S.-L. and Pekkarinen, A. 1984. Genetic variation in bumblebees (*Bombus*, *Psithyrus*) and putative sibling species of *Bombus lucorum*. *Hereditas* 101: 245–251.
- Parker, F.D. 1981. A candidate for red clover, *Osmia coerulescens* L. *Journal of Apicultural Research* 20: 62–65.
- Parker, F.D., Batra, S.W.T. and Tepedino, V.J. 1987. New pollinators for our crops. *Agricultural Zoology Reviews* 2: 279–304.
- Parrish, J.A.D. and Bazzaz, F.A. 1979. Difference in pollination niche relationships in early and late successional plant communities. *Ecology* 60: 597–610.
- Paton, D.C. 1990. Budgets for the use of floral resources in mallee heath. In: *The Mallee Lands: A Conservation Perspective* (eds J.C. Noble, P.J. Joss and G.K. Jones), pp. 189–193. CSIRO, Melbourne.
- Paton, D.C. 1993. Honeybees in the Australian Environment—does *Apis mellifera* disrupt or benefit the native biota? *Bioscience* 43: 95–103.
- Paton, D.C. 1995. Impact of honeybees on the flora and fauna of Banksia heathlands in Ngarkat Conservation Park. *SASTA Journal* 95: 3–11.
- Paton, D.C. 1996. *Overview of Feral and Managed Honeybees in Australia: Distribution, Abundance, Extent of Interactions with Native Biota, Evidence of Impacts and Future Research*. Australian Nature Conservation Agency, Canberra.
- Paxton, R.J., Thorén, P.A., Estoup, A. and Tengö, J. 2001. Queen-worker conflict over male production and the sex ratio in a facultatively polyandrous bumblebee, *Bombus hypnorum*: the consequences of nest usurpation. *Molecular Ecology* 10: 2489–2498.
- Paxton, R.J., Thorén, P.A., Gyllenstrand, N. and Tengö, J. 2000. Microsatellite DNA analysis reveals low diploid male production in a communal bee with inbreeding. *Biological Journal of the Linnean Society* 69: 483–502.



- Payne, C.M., Lavery, T.M. and Lachance, M.A. 2003. The frequency of multiple paternity in bumble bee (*Bombus*) colonies based on microsatellite DNA at the B10 locus. *Insectes Sociaux* 50: 375–378.
- Pearson, W.D. and Braiden, V. 1990. Seasonal pollen collection by honeybees from grass shrub highlands in Canterbury, New Zealand. *Journal of Apicultural Research* 29: 206–213.
- Peat, J., Darvill, B., Ellis, J. and Goulson, D. 2005a. Effects of climate on intra- and inter-specific size variation in bumblebees. *Functional Ecology* 19: 145–151.
- Peat, J. and Goulson, D. 2005. Effects of experience and weather on foraging efficiency and pollen versus nectar collection in the bumblebee, *Bombus terrestris*. *Behavioural Ecology and Sociobiology* 58: 152–156.
- Peat J., Tucker, J. and Goulson, D. 2005b. Does intraspecific size variation in bumblebees allow colonies to efficiently exploit different flowers? *Ecological Entomology* 30: 176–181.
- Pedersen, B.V. 1996. A phylogenetic analysis of cuckoo bumblebees (*Psithyrus*, Lepeletier) and bumblebees (*Bombus*, Latreille) inferred from sequences of the mitochondrial gene cytochrome oxidase I. *Molecular Phylogenetics and Evolution* 5: 289–297.
- Pekkarinen, A. 1979. Morphometric, colour and enzyme variation in bumblebees (Hymenoptera, Apidae, *Bombus*) in Fennoscandia and Denmark. *Acta Zoologica Fennica* 158: 1–60.
- Pekkarinen, A., Teräs, I., Viramo, J. and Paatela, J. 1981. Distribution of bumblebees (Hymenoptera, Apidae: *Bombus* and *Psithyrus*) in eastern Fennoscandia. *Notulae Entomologicae* 61: 71–89.
- Pekkarinen, A., Varvio-Aho, S.-L. and Pamilo, P. 1979. Evolutionary relationships in northern European *Bombus* and *Psithyrus* species (Hymenoptera, Apidae) studied on the basis of allozymes. *Annales Entomologici Fennici* 45: 77–80.
- Pellet, F.C. 1976. *American Honey Plants*. Fifth Edition. Hamilton (IL), Dadant and Sons.
- Pelletier, L. and McNeil, J.N. 2003. The effects of food supplementation on reproductive success in bumblebee field colonies. *Oikos* 103: 688–694.
- Pelletier, L. and McNeil, J.N. 2004. Do bumblebees always forage as much as they could? *Insectes Sociaux* 51: 271–274.
- Pellmyr, O. 1986. Three pollination morphs in *Cimicifuga simplex*; incipient speciation due to inferiority in competition. *Oecologia* 68: 304–307.
- Pendrel, B.A. and Plowright, R.C. 1981. Larval feeding by adult Bumble-bee workers (Hymenoptera: Apidae). *Behavioral Ecology and Sociobiology* 8: 71–76.
- Peters, G. 1972. Ursachen für den Rückgang der seltenen heimischen Hummelarten (Hym., *Bombus* et *Psithyrus*). *Entomologische Berichten* 1972: 85–90.
- Percival, M. 1974. Floral ecology of coastal scrub in Southeast Jamaica. *Biotropica* 6: 104–129.
- Pereboom, J.J.M. 1997. 'While they banquet splendidly the future mother': the significance of trophogenic and social factors on caste determination and differentiation in the bumblebee *Bombus terrestris*. PhD thesis, University of Utrecht, The Netherlands.
- Pereboom, J.J.M. 2000. The composition of larval food and the significance of exocrine secretions in the bumblebee *Bombus terrestris*. *Insectes Sociaux* 47: 11–20.
- Pereboom, J.J.M., Velthuis, H.H.W. and Duchateau, M.J. 2003. The organisation of larval feeding in bumblebees (Hymenoptera, Apidae) and its significance to caste differentiation. *Insectes Sociaux* 50: 127–133.
- Pierce, G.J. and Ollason, J.G. 1987. 8 reasons why optimal foraging theory is a complete waste of time. *Oikos* 49: 111–118.
- Pirounakis, K., Koulianos, S. and Schmid-Hempel, P. 1998. Genetic variation among European populations of *Bombus pascuorum* (Hymenoptera, Apidae) using mitochondrial DNA sequence data. *European Journal of Entomology* 95: 27–33.

- Pimm, S.L., Russell, G.J., Gittleman, J.L. and Brookes, T.M. 1995. The future of biodiversity. *Science* 269: 347–350.
- Plateau, F. 1901. Observations sur le phénomène de la constance chez quelques hyménoptères. *Annales de la Société Entomologique de Belgique* 45: 56–83.
- Plath, O.E. 1923a. Notes on the egg-eating habits of bumblebees. *Psyche* 30: 193–202.
- Plath, O.E. 1923b. The bee-eating proclivity of the skunk. *American Naturalist* 57: 571–574.
- Plath, O.E. 1934. *Bumblebees and their Ways*. The Macmillan Company, New York.
- Pleasant, J.M. 1981. Bumblebee response to variation in nectar availability. *Ecology* 62: 1648–1661.
- Pleasant, J.M. 1983. Nectar production patterns in *Ipomopsis aggregata* (Polemoniaceae). *American Journal of Botany* 70: 1468–1475.
- Pleasant, J.M. 1989. Optimal foraging by nectarivores: a test of the marginal-value theorem. *American Naturalist* 134: 51–71.
- Pleasant, J.M. and Chaplin, S.J. 1983. Nectar production rates of *Asclepias quadrifolia*: causes and consequences of individual variation. *Oecologia* 59: 232–238.
- Pleasant, J.M. and Zimmerman, M. 1979. Patchiness in the dispersion of nectar resources: evidence for hot and cold spots. *Oecologia* 41: 283–288.
- Pleasant, J.M. and Zimmerman, M. 1983. The distribution of standing crop of nectar: what does it really tell us? *Oecologia* 57: 412–414.
- Pleasant, J.M. and Zimmerman, M. 1990. The effect of inflorescence size on pollinator visitation of *Delphinium nelsonii* and *Aconitum columbianum*. *Collectanea Botanica* 19: 21–39.
- Plowright, C.M.S. and Plowright, R.C. 1997. The advantage of short tongues in bumble bees (*Bombus*)—Analyses of species distributions according to flower corolla depth, and of working speeds on white clover. *The Canadian Entomologist* 129: 51–59.
- Plowright, R.C. and Galen, C. 1985. Landmarks or obstacles: the effects of spatial heterogeneity on bumble bee foraging behaviour. *Oikos* 44: 459–464.
- Plowright, R.C. and Jay, S.C. 1968. Caste differentiation in bumblebees (*Bombus* Latr.: Hym.) 1. The determination of female size. *Insectes Sociaux* 15: 171–192.
- Plowright, R.C. and Lavery, T.M. 1987. Bumble bees and crop pollination in Ontario. *Proceedings of the Entomological Society of Ontario* 118: 155–160.
- Plowright, R.C. and Owen, R.E. 1980. The evolutionary significance of bumble bee colour patterns: a mimetic interpretation. *Evolution* 34: 622–637.
- Plowright, R.C. and Pallet, J.M. 1979. Worker-male conflict and inbreeding in bumble bees (Hymenoptera: Apidae). *The Canadian Entomologist* 111: 289–294.
- Plowright, R.C. and Pendrel, B.A. 1977. Larval growth in bumble bees (Hymenoptera, Apidae). *The Canadian Entomologist* 109: 967–973.
- Plowright, R.C. and Silverman, A. 2000. Nectar and pollen foraging by bumble bees (Hymenoptera: Apidae): choice and tradeoffs. *The Canadian Entomologist* 132: 677–679.
- Plowright, R.C. and Stephen, W.P. 1973. A numerical taxonomic analysis of the evolutionary relationships of *Bombus* and *Psithyrus* (Apidae: Hymenoptera). *The Canadian Entomologist* 105: 733–743.
- Posner, M.I. and Peterson, S.E. 1990. The attention system of the human brain. *Annual Review of Neuroscience* 13: 25–42.
- Poinar, G.O. and van del Laan, P.A. 1972. Morphology and life history of *Sphaerularia bombi*. *Nematologica* 18: 239–252.
- Pomeroy, N. 1979. Brood bionomics of *Bombus ruderatus* in New Zealand (Hymenoptera: Apidae). *The Canadian Entomologist* 111: 865–874.

- Pomeroy, N. 1981. Use of natural field sites and field hives by a long-tongued bumble bee *Bombus ruderatus*. *New Zealand Journal of Agricultural Research* 24: 409–414.
- Pomeroy, N. and Plowright, R.C. 1982. The relation between worker numbers and the production of males and queens in the bumble bee *Bombus perplexus*. *Canadian Journal of Zoology* 60: 954–957.
- Pontin, D.R., Wade, M.R., Kehrl, P. and Wratten, S.D. 2006. Attractiveness of single and multiple species flower patches to beneficial insects in agroecosystems. *Annals of Applied Biology* 148: 39–47.
- Possingham, H.P. 1989. The distribution and abundance of resources encountered by a forager. *American Naturalist* 133: 42–60.
- Postner, M. 1952. Biologische-ökologische Untersuchungen an Hummeln und ihren Nestern. *Veröf. Übersee-Museum Bremen (A)*. 2: 45–86.
- Poulsen, M.H. 1973. The frequency and foraging behaviour of honeybees and bumble bees on field beans in Denmark. *Journal of Apicultural Research* 12: 75–80.
- Pouvreau, A. 1967. Contribution à l'étude morphologique et biologique d'*Aphomia sociella* L. (Lepidoptera, Heteroneura, Pyraloidea, Pyralididae), parasite des nids de bourdons (Hymenoptera, Apoidea, *Bombus* Latr.). *Insectes Sociaux* 14: 57–72.
- Pouvreau, A. 1974. Les ennemis des bourdons. II. Organismes affectant les adultes. *Apidologie* 5: 39–62.
- Pouvreau, A. 1989. Contribution à l'étude du polyéthisme chez les bourdons, *Bombus* Latr. (Hymenoptera, Apidae). *Apidologie* 20: 229–244.
- Pouvreau, A. 1991. Morphology and histology of tarsal glands in bumble bees of the genera *Bombus*, *Pyrobombus* and *Megabombus*. *Canadian Journal of Zoology* 69: 866–872.
- Prescott, C. and Allen, R. 1986. *The First Resource; Wild Species in the North American Economy*. Yale University Press, New Haven, Connecticut, USA.
- Primack, R.B. and Hall, P. 1990. Cost of reproduction in the pink lady's slipper orchid: a four year experimental study. *American Naturalist* 136: 638–656.
- Proctor, M. and Yeo, P. 1973. *The Pollination of Flowers*. William Collins Sons, Glasgow.
- Proctor, M., Yeo, P. and Lack, A. 1996. *The Natural History of Pollination*. Harper Collins, London.
- Prys-Jones, O.E. 1982. Ecological studies of foraging and life history in bumblebees. Ph.D. thesis, University of Cambridge.
- Prys-Jones, O.E. 1986. Foraging behaviour and the activity of substrate cycle enzymes in bumblebees. *Animal Behaviour* 34: 609–611.
- Prys-Jones, O.E. and Corbet, S.A. 1991. *Bumblebees*. Richmond Publishing Co. Ltd. Slough, England.
- Prys-Jones, O.E., Ólafsson, E. and Kristjánsson, K. 1981. The Icelandic bumblebee fauna and its distributional ecology. *Journal of Apicultural Research* 20: 189–197.
- Ptáček, V. 1991. Trials to rear bumblebees. *Acta Horticulturae* 288: 144–148.
- Pyke, G.H. 1978a. Optimal foraging: movement patterns of bumblebees between inflorescences. *Theoretical Population Biology* 13: 72–98.
- Pyke, G.H. 1978b. Optimal foraging in bumblebees and coevolution with their plants. *Oecologia* 36: 281–293.
- Pyke, G.H. 1978c. Optimal foraging in hummingbirds: testing the marginal value theorem. *American Zoologist* 18: 739–752.
- Pyke, G.H. 1978d. Optimal body size in bumblebees. *Oecologia* 34: 255–266.

- Pyke, G.H. 1979. Optimal foraging in bumblebees: rules of movement between flowers within inflorescences. *Animal Behaviour* 27: 1167–1181.
- Pyke, G.H. 1981. Honeyeater foraging: a test of optimal foraging theory. *Animal Behaviour* 29: 878–888.
- Pyke, G.H. 1982. Local geographic distributions of bumblebees near Crested Butte, Colorado: competition and community structure. *Ecology* 63: 555–573.
- Pyke, G.H. 1983. Animal movements: an optimal foraging approach. In: *The Ecology of Animal Movement* (eds I.R. Swingland and P.J. Greenwood ), pp. 7–31. Clarendon, Oxford.
- Pyke, G.H. 1984. Optimal foraging: a critical review. *Annual Reviews in Ecology and Systematics* 15: 523–575.
- Pyke, G.H. and Cartar, R.V. 1992. The flight directionality of bumblebees—do they remember where they came from. *Oikos* 65: 321–327.
- Pywell, R.F., Bullock, J.M., Tallowin, J.B., Walker, K.J., Warman, E.A. and Masters, G. 2007. Enhancing diversity of species-poor grasslands: an experimental assessment of multiple constraints. *Journal of Applied Ecology* 44: 81–94.
- Pywell, R.F., Bullock, J.M., Hopkins, A., Walker, K.J., Sparks, T.H., Burke, M.J.W. and Peel, S. 2002. Restoration of a species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. *Journal of Applied Ecology* 39: 294–309.
- Pywell, R.F., Warman, E.A., Carvell, C., Sparks, T.H., Dicks, L.V., Bennett, D., Wright, A., Critchley, C.N.R. and Sherwood, A. 2005. Providing forage resources for bumblebees in intensively farmed landscapes. *Biological Conservation* 121: 479–494.
- Pywell, R.F., Warman, E.A., Hulmes, L., Hulmes, S., Nuttall, P., Sparks, T.H., Critchley, C.N.R. and Sherwood, A. 2006. Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation* 129: 192–206.
- Rackham, O. 1976. *Trees and Woodland in the British Landscape*. Dent, London.
- Raine, N.E. and Chittka, L. 2007a. Pollen foraging: learning a complex motor skill by bumblebees (*Bombus terrestris*). *Naturwissenschaften* 94: 459–464.
- Raine, N.E. and Chittka, L. 2007b. Flower constancy and memory dynamics in bumblebees (Hymenoptera: Apidae: *Bombus*). *Entomologia Generalis* 29: 179–199.
- Raine, N.E., Ings, T.C., Dornhaus, A., Saleh, N. and Chittka, L. 2006a. Adaptation, genetic drift, pleiotropy, and history in the evolution of bee foraging behaviour. *Advances in the Study of Behavior* 36: 305–354.
- Raine, N.E., Ings, T.C., Ramos-Rodriguez, O. and Chittka, L. 2006b. Intercolony variation in learning performance of a wild British bumblebee population (Hymenoptera: Apidae: *Bombus terrestris audax*). *Entomologia Generalis* 28: 241–256.
- Raju, B.C., Nyland, G., Meikle, T. and Purcell, A.H. 1981. Helical, motile mycoplasmas associated with flowers and honeybees in California. *Canadian Journal of Microbiology* 27: 249–253.
- Ramsey, M.W. 1988. Differences in pollinator effectiveness of birds and insects visiting *Banksia menziesii* (Protaceae). *Oecologia* 76: 119–124.
- Ramirez, S. and Cameron, S.A. 2003. Army ant attacks by *Eciton hamatum* and *E. rapax* (Hymenoptera: Formicidae) on nests of the Amazonian bumble bee, *Bombus transversalis* (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society* 76: 533–535.
- Ranta, E. 1982. Species structure of North European bumblebee communities. *Oikos* 38: 202–209.
- Ranta, E. 1983. Proboscis length and the coexistence of bumblebee species. *Oikos* 43: 189–196.

- Ranta, E. and Lundberg, H. 1980. Resource partitioning in bumblebees: the significance of differences in proboscis length. *Oikos* 35: 298–302.
- Ranta E., Lundberg, H. and Teräs, I. 1980. Patterns of resource utilization in two Fennoscandian bumblebee communities. *Oikos* 36: 1–11.
- Ranta, E. and Tiainen, M. 1982. Structure in seven bumblebee communities in eastern Finland in relation to resource availability. *Holarctic Ecology* 5: 48–54.
- Ranta, E. and Vepsäläinen K. 1981. Why are there so many species? Spatio-temporal heterogeneity and northern bumblebee communities. *Oikos* 36: 28–34.
- Rao, S. and Stephen, W.P. 2007. *Bombus (Bombus) occidentalis* (Hymenoptera: Apiformes): In decline or recovery? *Pan-Pacific Entomologist* 83: 360–362.
- Rasheed, S.A. and Harder, L.D. 1997. Economic motivation for plant species preferences of pollen-collecting bumble bees. *Economic Entomology* 22: 209–219.
- Rasmont, P. 1983. Catalogue of the bumble bees of the west Palearctic region. *Notes faunique de Gembloux* 7: 71 pp.
- Rasmont, P. 1988. Monographie écologique et zoogéographique des bourdons de France et de Belgique (Hymenoptera, Apidae, Bombinae). Ph.D. thesis, Faculté des Sciences Agronomique de l'Etat, Gembloux, Belgium.
- Rasmont, P. 1995. How to restore the apoid diversity in Belgium and France? Wrong and right ways, or the end of protection paradigm! In: *Changes in Fauna of Wild Bees in Europe* (ed. J. Banaszak), pp. 53–64. Pedagogical University, Bydgoszcz.
- Rasmont, P., Aytekin, A.M and Kaçar, M.S. 2008a. Ousting of the common redstart (Aves: Turdidae: *Phoenicurus phoenicurus*) from its nests by the bumblebee *Bombus niveatus vorticoides* (Hymenoptera: Apidae). *Annales de la Societe Entomologique de France* 44: 251–255.
- Rasmont, P., Coppée, A., Michez, D. and De Meulemeester, T. 2008b. An overview of the *Bombus terrestris* (L. 1758) subspecies (Hymenoptera: Apidae). *Annales de la Societe Entomologique de France* 44: 243–250.
- Rasmont, P. and Mersch, P. 1988. Première estimation de la dérive faunique chez les bourdons de la Belgique (Hymenoptera, Apidae). *Annales de la Société Royale Zoologique de Belgique* 118: 141–147.
- Rathcke, B. 1983. Competition and facilitation among plants for pollination. In: *Pollination Ecology* (ed. L. Real), pp. 305–325. Academic Press, New York.
- Rathcke, B.J. and Jules, E.S. 1993. Habitat fragmentation and plant-pollinator interactions. *Current Science* 65: 273–277.
- Ratnieks, F. and Boomsma, J.J. 1995. Facultative sex allocation by workers and the evolution of polyandry by queens in social Hymenoptera. *American Naturalist* 145: 969–993.
- Rau, P. 1929. Experimental studies in the homing of carpenter and mining bees. *Journal of Comparative Physiology* 9: 35–70.
- Reader, T., MacLeod, I., Elliott, P.T., Robinson, O.J. and Manica, A. 2005. Inter-order interactions between flower-visiting insects: foraging bees avoid flowers previously visited by hoverflies. *Journal of Insect Behavior* 18: 51–57.
- Real, L. 1981. Uncertainty and pollinator-plant interactions: the foraging behaviour of bees and wasps on artificial flowers. *Ecology* 62: 20–26.
- Real, L. 1983. Microbehavior and macrostructure in pollinator plant interactions. In: *Pollination Ecology*. (ed. L. Real), pp. 287–302. Academic Press, New York.
- Real, L., Ott, J.R. and Silverfine, E. 1982. On the tradeoff between the mean and the variance in foraging: effect of spatial distribution and colour preference. *Ecology* 63: 1617–1623.

- Real, L. and Rathcke, B.J. 1988. Patterns of individual variability of floral resources. *Ecology* 69: 728–735.
- Reid, P.J. and Shettleworth, S.J. 1992. Detection of cryptic prey: search image or search rate? *Journal of Experimental Psychology* 18: 273–286.
- Reinig, W.F. 1972. Ökologische Studien an mittel- und südosteuropäischen Hummeln (Bombus Latr., 1802; Hym. Apidae). *Mitteilungen der Muncher Entomologischen Gesellschaft* 60: 1–56.
- Reuter, K. 1998. Anzucht und experimentelle Untersuchungen zur fütterungsabhängigen Kastendetermination von *Bombus pascuorum* (Scopoli), (Hymenoptera: Apidae). PhD Thesis, Ruhr-Universität Bochum.
- Reynolds, A.M., Smith, A.D., Menzel, R., Greggers, U., Reynolds, D.R. and Riley, J.R. 2007a. Displaced honey bees perform optimal scale-free search flights. *Ecology* 88: 1955–1961.
- Reynolds, A.M., Smith, A.D., Reynolds, D.R., Carreck, N.L. and Osborne, J.L. 2007b. Honeybees perform optimal scale-free searching flights when attempting to locate a food source. *Journal of Experimental Biology* 210: 3763–3770.
- Ribbands, C.R. 1949. The foraging method of individual honeybees. *Journal of Animal Ecology* 18: 47–66.
- Ribeiro M.F. 1994. Growth in bumble bee larvae—relation between development time, mass, and amount of pollen ingested. *Canadian Journal of Zoology* 72: 1978–1985.
- Ribeiro, M.F., Velthuis, H.H.W., Duchateau, M.J. and van der Tweel, I. 1999. Feeding frequency and caste differentiation in *Bombus terrestris* larvae. *Insectes Sociaux* 46: 306–314.
- Rich, T.C.G. and Woodruff, E.R. 1996. Changes in the vascular plant floras of England and Scotland between 1930–1960 and 1987–1988: The BSBI monitoring scheme. *Biological Conservation* 75: 217–229.
- Richards, A.J. 2001. Does low biodiversity resulting from modern agricultural practice affect crop pollination and yield? *Annals of Botany* 88: 165–172.
- Richards, K.W. 1973. Biology of *Bombus polaris* Curtis and *B. hyperboreus* Schönherr at Lake Hazen, Northwest Territories (Hymenoptera: Bombini). *Quaestiones Entomologicae* 9: 115–157.
- Richards, K.W. 1978. Nest site selection by bumble bees (Hymenoptera: Apidae) in southern Alberta. *The Canadian Entomologist* 110: 301–318.
- Richards, K.W. 1993. Non-Apis bees as crop pollinators. *Revue Suisse de Zoologie* 100: 807–822.
- Richards, L.A. and Richards, K.W. 1976. Parasitid mites associated with bumblebees in Alberta, Canada (Acarina, Parasitidae; Hymenoptera: Apidae). II. Biology. *University of Kansas Science Bulletin* 51: 1–18.
- Richards, O.W. 1931. Some notes on the humblebees allied to *Bombus alpinus* L. *Tromsø Museum Årshefter* 50: 1–32.
- Richards, O.W. 1946. Observations on *Bombus agrorum* Fabricius. (Hymen. Bombidae) *Proceedings of the Royal Entomological Society of London A* 21: 66–71.
- Richardson, S.C. 2004. Are nectar-robbers mutualists or antagonists? *Oecologia* 139: 246–254.
- Rick, C.M. 1950. Pollination relations of *Lycopersicon esculentum* in native and foreign regions. *Evolution* 4: 110–122.
- Riddell C.E. and Mallon E.B. 2006. Insect psychoneuroimmunology: immune response reduces learning in protein starved bumblebees (*Bombus terrestris*). *Brain Behaviour and Immunity* 20: 135–138.
- Rieger, M.A., Lamond, M., Preston, C., Powles, S.B. and Roush, R.T. 2002. Pollen-mediated movement of herbicide resistance between commercial canola fields. *Science* 296: 2386–2388.

- Riley, J.R., Reynolds, D.R., Smith, A.D., Edwards, A.S., Osborne, J.L. and Williams, I.H. 1999. Compensation for wind drift by bumblebees. *Nature* 400: 126.
- Riley, J.R. and Smith, A.D. 2002. Design considerations for an harmonic radar to investigate the flight of insects at low altitude. *Computers and Electronics in Agriculture* 35: 151–169.
- Riley, J.R., Smith, A.D., Reynolds, D.R., Edwards, A.S., Osborne, J.L. and Williams, I.H., Carreck, N.L. and Poppy, G.M. 1996. Tracking bees with harmonic radar. *Nature* 379: 29–30.
- Riley, J.R., Valeur, P., Smith, A.D., Reynolds, D.R., Poppy, G.M. and Löfstedt, C. 1998. Harmonic radar as a means of tracking the pheromone-finding and pheromone-following flight in male moths. *Journal of Insect Behavior* 11: 287–296.
- Roberts, R.H. and Struckmeyer, B.E. 1942. Growth and fruiting of the cranberry. *Proceedings of the American Society for Horticultural Science* 40: 373–379.
- Robertson, A.W. 1991. A mid-winter colony of *Bombus terrestris* L. (Hym., Apidae) in Devon. *Entomologists's Monthly Magazine* 127: 165–166.
- Robertson, A.W. and Macnair, M.R. 1995. The effects of floral display size on pollinator service to individual flowers of *Myosotis* and *Mimulus*. *Oikos* 72: 106–114.
- Robertson, A.W., Mountjoy, C., Faulkner, B.E., Roberts, M.V. and Macnair, M.R. 1999. Bumblebee selection of *Mimulus guttatus* flowers: the effects of pollen quality and reward depletion. *Ecology* 80: 2594–2606.
- Robertson, J.L. and Wyatt, R. 1990. Reproductive biology of the Yellow-Fringed Orchid, *Platanthera ciliaris*. *American Journal of Botany* 77: 388–398.
- Robertson, P., Bennett, A.F., Lumsden, L.F., Silveira, C.E., Johnson, P.G., Yen, A.L., Milledge, G.A., Lillywhite, P.K. and Pribble, H.J. 1989. Fauna of the Mallee study area north-western Victoria. National Parks and Wildlife Division Technical Report Series, Number 87. Victoria (Australia): Department of Conservation, Forests and Lands. pp 41–42.
- Robinson, W.S. 1979. Influence of 'Delicious' apple blossom morphology on the behavior of nectar-gathering honey bees. Proceedings of the IVth International Symposium on Pollination, Maryland Agricultural Experimental Station Special Miscellaneous Publications 1. pp. 393–399.
- Robinson, W.S., Nowodgrodzki, R. and Morse, R.A. 1989. The value of bees as pollinators of U.S. crops. *American Bee Journal* 129: 411–423 and 477–487.
- Rodd, F.H., Plowright, R.C. and Owen, R.E. 1980. Mortality rates of adult bumble bee workers (Hymenoptera: Apidae). *Canadian Journal of Zoology* 58: 1718–1721.
- Rodríguez, I., Gumbert, A., de Ibarra, N.H., Kunze, J. and Giurfa, M. 2004. Symmetry is in the eye of the 'beeholder': innate preference for bilateral symmetry in flower-naive bumblebees. *Naturwissenschaften* 91: 374–377.
- Röseler, P.-F. 1967. Arbeitsteilung und Drüsenzustände in Hummelvölkern. *Naturwissenschaften* 54: 146–147.
- Röseler, P.-F. 1970. Unterschiede in der Kastendetermination zwischen den Hummelarten *Bombus hypnorum* und *Bombus terrestris*. *Zeitschrift für Naturforschung* 25: 543–548.
- Röseler, P.-F. 1973. Die Anzahl Spermien im Receptaculum seminis von Hummelköniginnen (Hymenoptera, Apidae, Bombinae). *Apidologie* 4: 267–274.
- Röseler, P.-F. 1991. Roles of morphogenetic hormones in caste polymorphism in bumblebees. In: *Morphogenetic Hormones in Arthropods: Roles in Histogenesis, Organogenesis, and Morphogenesis* (ed. A.P. Gupta), pp. 384–399. New Brunswick, NJ, Rutgers University Press.
- Röseler, P.-F. 2002. A scientific note on the reproduction of two bumblebee queens (*Bombus hypnorum*) infected by the nematode *Sphaerularia bombi*. *Apidologie* 33: 423–424.

- Röseler, P.-F. and Van Honk, C.G.J. 1990. Castes and reproduction in bumblebees. In: *Social Insects: An Evolutionary Approach to Castes and Reproduction* (ed. W. Engels), pp. 147–166. Springer, Berlin.
- Röseler, P.-F. and Röseler, I. 1974. Morphologische und physiologische Differenzierung der Kasten bei den Hummelarten *Bombus hypnorum* (L.) und *Bombus terrestris* (L.). *Zoologische Jahrbucher Abteilung fuer Allgemeine Zoologie und Physiologie der Tiere* 78: 175–198.
- Röseler, P.-F. and Röseler, I. 1977. Dominance in bumblebees. Proceedings of the 8th International Congress of the International Union for the Study of Social Insects 232–235.
- Röseler, P.-F., Röseler, I. and Van Honk, C.G.J. 1981. Evidence for inhibition of corpora allata activity in workers of *Bombus terrestris* by a pheromone from the queen's mandibular glands. *Experientia* 37: 348–351.
- Rosenkrantz, P. and Wallner, K. 2008. The chronology of honey bee losses in the Rhine Valley during spring 2008: an example of a worst case scenario. In: *Eurbee3; 3rd European Conference of Apidology* (eds J. Teal, J.L. Osborne and R.J. Paxton), pp. 94–95. Queen's University, Belfast.
- Roubik, D.W. 1978. Competitive interactions between neotropical pollinators and Africanized honey bees. *Science* 201: 1030–1032.
- Roubik, D.W. 1980. Foraging behavior of commercial Africanized honeybees and stingless bees. *Ecology* 61: 8336–845.
- Roubik, D.W. 1981. Comparative foraging behaviour of *Apis mellifera* and *Trigona corvina* (Hymenoptera: Apidae) on *Baltimora recta* (Compositae). *Revista de Biología Tropical* 29: 177–184.
- Roubik, D.W. 1982a. Ecological impact of Africanized honeybees on native neotropical pollinators. In: *Social Insects of the Tropics* (ed. P. Jaisson), pp. 233–247. Université Paris-Nord.
- Roubik, D.W. 1982b. The ecological impact of nectar robbing bees and pollinating hummingbirds on a tropical shrub. *Ecology* 63: 354–360.
- Roubik, D.W. 1983. Experimental community studies: time series tests of competition between African and neotropical bees. *Ecology* 64: 971–978.
- Roubik, D.W. 1989. *Ecology and Natural History of Tropical Bees*. Cambridge University Press, Cambridge.
- Roubik, D.W. 1991. Aspects of Africanized honey bee ecology in tropical America. In: *The 'African' Honey Bee* (eds M. Spivak *et al.*), pp. 259–281. Westview Press, Boulder (CO).
- Roubik, D.W. 1996a. Measuring the meaning of honeybees. In: *The Conservation of Bees* (eds A. Matheson, S.L. Buchmann, C. O'Toole, P. Westrich and I.H. Williams), pp. 163–172. Academic Press, London.
- Roubik, D.W. 1996b. African honey bees as exotic pollinators in French Guiana. In: *The Conservation of Bees* (eds A. Matheson, S.L. Buchmann, C. O'Toole, P. Westrich and I.H. Williams), pp. 173–182. Academic Press, London.
- Roubik, D.W. and Aluja, M. 1983. Flight ranges of *Melipona* and *Trigona* in tropical forests. *Journal of the Kansas Entomological Society* 56: 217–222.
- Roubik, D.W. and Hanson, P.E. 2004. *Abejas de Orquídeas de la América Tropical: Biología y Guía de Campo—Orchid Bees of Tropical America: Biology and Field Guide*. Editorial INBio, Santo Domingo de Heredia, Costa Rica.
- Roubik, D.W., Holbrook, N.M. and Parrav, G. 1985. Roles of nectar robbers in reproduction of the tropical treelet *Quassia amara* (Simaroubaceae).—*Oecologia* 66: 161–167.
- Roubik, D.W., Moreno, J.E., Vergara, C. and Wittman, D. 1986. Sporadic food competition with the African honey bee: projected impact on neotropical social species. *Journal of Tropical Ecology* 2: 97–111.



- Roulston, T.H., Cane, J.H. and Buchmann, S.L. 2000. What governs protein content of pollen: pollinator preferences, pollen-pistil interactions, or phylogeny? *Ecological Monographs* 70: 617–643.
- Ruiz-González, M.X. and Brown, M.J.F. 2006a. Honey bee and bumblebee trypanosomatids: specificity and potential for transmission. *Ecological Entomology* 31: 616–622.
- Ruiz-González, M.R.X. and Brown, M.J.F. 2006b. Males vs. workers: testing the assumptions of the haploid susceptibility hypothesis in bumblebees. *Behavioral Ecology and Sociobiology* 60: 501–509.
- Rundlöf, M., Nilsson, H. and Smith, H.G. 2008. Interacting effects of farming practice and landscape context on bumblebees. *Biological Conservation* 141: 417–426.
- Rutrecht, S.T. and Brown, M.J.F. 2008a. The life history impact and implications of multiple parasites for bumble bee queens. *International Journal of Parasitology* 38: 799–808.
- Rutrecht, S.T. and Brown, M.J.F. 2008b. Within colony dynamics of *Nosema bombi* infections: disease establishment, epidemiology and potential vertical transmission. *Apidologie* 39: 504–514.
- Rutrecht, S.T., Klee, J. and Brown, M.J.F. 2007. Horizontal transmission success of *Nosema bombi* to its adult bumble bee hosts: effects of dosage, spore source and host age. *Parasitology* 134: 1719–1726.
- Sadd, B.M. and Schmid-Hempel, P. 2006. Insect immunity shows specificity in protection upon secondary pathogen exposure. *Current Biology* 16: 1206–1210.
- Sadd, B.M. and Schmid-Hempel, P. 2007. Facultative but persistent trans-generational immunity via the mother's eggs in bumblebees. *Current Biology* 17: R1046–R1047.
- Sakagami, S.F. 1976. Species differences in the bionomic characters of bumblebees. A comparative review. *Journal of the Faculty of Science, Hokkaido University, ser. 6, Zoology* 20: 390–447.
- Sakagami, S.F. and Zucchi, R. 1965. Winterverhalten einer neotropischen Hummel, *Bombus atratus*, innerhalb des Beobachtungskastens. *Ein Beitrag zur Biologie der Hummeln. Journal of the Faculty of Science, Hokkaido University, ser. 6, Zoology* 15: 712–762.
- Saleh, N. and Chittka, L. 2006. The importance of experience in the interpretation of conspecific chemical signals. *Behavioural Ecology and Sociobiology* 61: 215–220.
- Saleh, N., Ohashi, K., Thomson, J.D. and Chittka, L. 2006. Facultative use of the repellent scent mark in foraging bumblebees: complex versus simple flowers. *Animal Behaviour* 71: 847–854.
- Saleh, N., Scott, A.G., Bryning, G.P. and Chittka, L. 2007. Distinguishing signals and cues: bumblebees use general footprints to generate adaptive behaviour at flowers and nest. *Arthropod-Plant Interactions* 1: 119–127.
- Sarospataki, M., Novak, J. and Molnar, V. 2005. Assessing the threatened status of bumble bee species (Hymenoptera: Apidae) in Hungary, Central Europe. *Biodiversity and Conservation* 14: 2437–2446.
- Saunders, E. 1907. *Wild bees, Wasps and Ants*. G. Routledge & Sons Ltd. London.
- Saunders, E. 1909. Bombi and other aculeates collected in 1908 in the Berner Oberland by the Rev. A.E. Easton, M.A. *Entomologist's monthly Magazine* 45: 83–84.
- Sauter, A., Brown, M.J.F., Baer, B. and Schmid-Hempel, P. 2001. Males of social insects can prevent queens from multiple mating. *Proceedings of the Royal Society* 268: 1449–1454.
- Saville, N.M. 1993. Bumblebee ecology in woodlands and arable farmland. Ph.D. Thesis, University of Cambridge.
- Saville, N.M., Dramstad, W.E., Fry, G.L.A. and Corbet, S.A. 1997. Bumblebee movement in a fragmented agricultural landscape. *Agriculture, Ecosystems and Environment* 61: 145–154.
- Schaal, B.A. and Leverich, W.J. 1980. Pollination and banner markings in *Lupinus texensis* (Leguminosae). *Southwestern Naturalist*, 25: 280–282.

- Schaffer, M.J. 1996. Spatial aspects of bumble bee (*Bombus* spp: Apidae) foraging in farm landscapes. M. Appl. Sci. Thesis. Lincoln University, Lincoln, New Zealand.
- Schaffer, M. and Wratten, S.D. 1994. Bumblebee (*Bombus terrestris*) movement in an intensive farm landscape. In: *Proceedings of the 47th New Zealand Plant Protection Conference* (ed. A.J. Popay), pp. 253–256. New Zealand Plant Protection Society, Rotorua, New Zealand.
- Schaffer, W.M., Jensen, D.B., Hobbs, D.E., Gurevitch, J., Todd, J.R. and Valentine Schaffer M. 1979. Competition, foraging energetics, and the cost of sociality in three species of bees. *Ecology* 60: 976–987.
- Schaffer, W.M., Zeh, D.W., Buchmann, S.L., Kleinhans, S., Valentine Schaffer, M. and Antrim, J. 1983. Competition for nectar between introduced honey bees and native North American bees and ants. *Ecology* 64: 564–577.
- Shelly, T.E., Buchmann, S.L., Villalobos, E.M. and O'Rourke, M.K. 1991. Colony ergonomics for a desert-dwelling bumblebee species (Hymenoptera: Apidae). *Ecological Entomology* 16: 361–370.
- Schemske, D.W. 1983. Limits to specialization and coevolution in plant-animal mutualisms. In *Coevolution*. (ed. M.H. Nitecki), pp. 67–109. The University of Chicago Press, Chicago.
- Sherman, P.W., Seeley, T.D. and Reeve, H.K. 1988. Parasites, pathogens and polyandry in social Hymenoptera. *American Naturalist* 131: 602–610.
- Schmid-Hempel, P. 1984. The importance of handling time for the flight directionality in bees. *Behavioral Ecology and Sociobiology* 15: 303–309.
- Schmid-Hempel, P. 1985. How do bees choose flight direction while foraging? *Physiological Entomology* 10: 439–442.
- Schmid-Hempel, P. 1986. The influence of reward sequence on flight directionality in bees. *Animal Behaviour* 34: 831–837.
- Schmid-Hempel, P. 1998. *Parasites in Social Insects*. Princeton University Press, Princeton, New Jersey.
- Schmid-Hempel, P. and Loosli, R. 1998. A contribution to the knowledge of *Nosema* infections in bumble bees, *Bombus* spp. *Apidologie* 29: 525–535.
- Schmid-Hempel, P. Müller, C.B., Schmid-Hempel, R. and Shykoff, J.A. 1990. Frequency and ecological correlates of parasitism by conopid flies (Conopidae, Diptera) in populations of bumblebees. *Insectes Sociaux* 37: 14–30.
- Schmid-Hempel, P., Pühr, K., Kruger, N., Reber, C. and Schmid-Hempel, R. 1999. Dynamic and genetic consequences of variation in horizontal transmission for a microparasite infection. *Evolution* 53: 426–434.
- Schmid-Hempel, P. and Schmid-Hempel, R. 1986. Nectar-collecting bees use distance-sensitive movement rules. *Animal Behaviour* 34: 605–607.
- Schmid-Hempel, P. and Schmid-Hempel, R. 1990. Endoparasitic larvae of conopid flies alter pollination behaviour of bumblebees. *Naturwissenschaften* 77: 450–452.
- Schmid-Hempel, P. and Schmid-Hempel, R. 1993. Transmission of a pathogen in *Bombus terrestris*, with a note on division of labour in social insects. *Behavioral Ecology and Sociobiology* 33: 319–327.
- Schmid-Hempel, P., Schmid-Hempel, R., Brunner, P.C., Seeman, O.D., Allen, G.R. 2007. Invasion success of the bumblebee, *Bombus terrestris*, despite a drastic genetic bottleneck. *Heredity* 99: 414–422.
- Schmid-Hempel, P. and Speiser, B. 1988. Effects of inflorescence size on pollination in *Epilobium angustifolium*. *Oikos* 53: 98–104.

- Schmid-Hempel, R. 1994. Evolutionary ecology of a host-parasitoid interaction. PhD dissertation, Basel University.
- Schmid-Hempel, R. and Müller, C.B. 1991. Do parasitised bumblebees forage for their colony? *Animal Behaviour* 41: 910–912.
- Schmid-Hempel, R. and Schmid-Hempel, P. 1989. Superparasitism and larval competition in conopid flies (Dipt., Conopidae), parasitising bumblebees (Hym., Apidae). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 62: 279–289.
- Schmid-Hempel, R. and Schmid-Hempel, P. 1991. Endoparasitic flies, pollen-collection by bumblebees and a potential host-parasite conflict. *Oecologia* 87: 222–232.
- Schmid-Hempel, R. and Schmid-Hempel, P. 1996a. Host choice and fitness correlates for conopid flies parasitising bumblebees. *Oecologia* 107: 71–78.
- Schmid-Hempel, R. and Schmid-Hempel, P. 1996b. Larval development of two parasitic flies (Conopidae) in the common host *Bombus pascuorum*. *Ecological Entomology* 21: 63–70.
- Schmid-Hempel, R. and Schmid-Hempel, P. 1998. Colony performance and immuno-competence of a social insect, *Bombus terrestris*, in poor and variable environments. *Functional Ecology* 12: 22–30.
- Schmid-Hempel, R. and Schmid-Hempel, P. 2000. Female mating frequencies in *Bombus* spp. from Central Europe. *Insectes Sociaux* 47: 36–41.
- Schmitt, J. 1980. Pollinator foraging behaviour and gene dispersal in *Senecio* (Compositae). *Evolution* 34: 934–943.
- Schmitt, J. 1983. Flowering plant density and pollinator visitation in *Senecio*. *Oecologia* 60: 97–102.
- Schmitt, U. 1990. Hydrocarbons in tarsal glands of *Bombus terrestris*. *Experientia* 46: 1080–1082.
- Schmitt, U. and Bertsch, A. 1990. Do foraging bumblebees scent-mark food sources and does it matter? *Oecologia* 82: 137–144.
- Schmitt, U., Lübke, G. and Franke, W. 1991. Tarsal secretion marks food sources in bumblebees (Hymenoptera: Apidae). *Chemoecology* 2: 35–40.
- Schneider, S.S. and McNally, L.C. 1992. Factors influencing seasonal absconding in colonies of the African honeybee, *Apis mellifera scutellata*. *Insectes Sociaux* 39: 403–423.
- Schneider, S.S. and McNally, L.C. 1993. Spatial foraging patterns and colony energy status in the African honeybee, *Apis mellifera scutellata*. *Journal of Insect Behaviour* 6: 195–210.
- Schoener, T.W. 1969. Optimal size and specialization in constant and fluctuating environments: an energy-time approach. *Brookhaven Symposium on Biology* 22: 103–114.
- Scholl, A., Obrecht, E. and Owen, R.E. 1990. The genetic relationship between *Bombus moderatus* Cresson and the *Bombus lucorum* auct. species complex (Hymenoptera: Apidae). *Canadian Journal of Zoology* 68: 2264–2268.
- Schöne H., Harris A.C., Schöne H. and Mahalski P. 1993a. Homing after displacement in open or closed containers by the diggerwasp *Argogorytes carbonarius* (Hymenoptera: Sphecidae). *Ethology* 95: 152–156.
- Schöne H., Tengö J., Kühme D., Schöne H. and Kühme L. 1993b. Homing with or without sight of surroundings and sky during displacement in the digger wasp *Bembix rostrata* (Hymenoptera: Sphecidae). *Ethology, Ecology and Evolution* 5: 549–552.
- Schousboe, C. 1986. On the biology of *Scutacarus acarorum* Goeze (Acarina: Trombidiformes). *Acarologia* 27: 151–158.
- Schousboe, C. 1987. Deutonymphs of *Parasitellus* phoretic on Danish bumble bees (Parasitidae, Mesostigmata; Apidae, Hymenoptera). *Acarologia* 28: 37–41.

- Schremmer, F. 1972. Beobachtungen zum Paarungsverhalten der Männchen von *Bombus confusus* Schenk. *Zeitschrift für Tierpsychologie* 31: 503–512.
- Schwarz, H.H. and Huck, K. 1997. Phoretic mites use flowers to transfer between foraging bumblebees. *Insectes Sociaux* 44: 303–310.
- Schwarz, H.H., Huck, K. and Schmid-Hempel, P. 1996. Prevalence and host preferences of mesostigmatic mites (Acari: Anactinochaeta) phoretic on Swiss bumble bees (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society* 69 (suppl.): 35–42.
- Schwarz, M.P., Gross, C.L. and Kukuk, P.F. 1991. Assessment of competition between honeybees and native bees. July 1991 Progress Report to the World Wildlife Fund, Australia, Project P158.
- Schwarz, M.P., Gross, C.L. and Kukuk, P.F. 1992a. Assessment of competition between honeybees and native bees. January 1992 Progress Report to the World Wildlife Fund, Australia, Project P158.
- Schwarz, M.P., Gross, C.L. and Kukuk, P.F. 1992b. Assessment of competition between honeybees and native bees. July 1992 Progress Report to the World Wildlife Fund, Australia, Project P158.
- Schwarz, M.P. and Hurst, P.S. 1997. Effects of introduced honey bees on Australia's native bee fauna. *Victorian Naturalist* 114: 7–12.
- Scott, P.E., Buchmann, S.L. and O'Rourke, M.K. 1993. Evidence for mutualism between flower-piercing carpenter bee and ocotillo: use of pollen and nectar by nectaring bees. *Ecological Entomology* 18: 234–240.
- Sechser B. and Freuler J. 2003. The impact of thiomethoxam on bumble bee broods (*Bombus terrestris* L.) following drip application in covered tomato crops. *Journal of Pesticide Science* 76: 74–77.
- Seeley, T.D. 1985a. *Honeybee Ecology*. Princeton University Press, Princeton, NJ.
- Seeley, T.D. 1985b. The information-center strategy of honey bee foraging. In: *Experimental Behavioral Ecology and Sociobiology* (eds B. Hölldobler and M. Lindauer), pp. 75–90. Sinauer Associates, Sunderland, MA.
- Seeley, T.D. and Heinrich, B. 1981. Regulation of temperature in nests of social insects. In: *Insect Thermoregulation* (ed. B. Heinrich), pp. 159–234. J. Wiley, New York.
- Semmens, T.D. 1996a. Flower visitation by the bumble bee *Bombus terrestris* (L.) (Hymenoptera: Apidae) now established in Tasmania. *Journal of the Australian Entomological Society* 32: 346.
- Semmens, T.D. 1996b. Flower visitation by the bumble bee *Bombus terrestris* (L.) (Hymenoptera: Apidae) in Tasmania. *Australian Entomologist* 23: 33–35.
- Senft, D. 1990. Protecting endangered plants. *Agricultural Research* May 1990: 16–18.
- Shao, Z.Y., Mao, H.X. and Fu, W.J. 2004. Genetic structure of Asian populations of *Bombus ignitus* (Hymenoptera: Apidae). *Journal of Heredity* 95: 46–52.
- Shelly, T.E., Buchmann, S.L., Villalobos, E.M. and O'Rourke, M.K. 1991. Colony ergonomics for a desert-dwelling bumblebee species (Hymenoptera: Apidae). *Ecological Entomology* 16: 361–370.
- Shykoff, J.A. and Bucheli, E. 1995. Pollinator visitation patterns, floral rewards and the probability of transmission of *Microbotryum violaceum*, a venereal disease of plants. *Journal of Ecology* 83: 189–198.
- Shykoff, J.A., Bucheli, E. and Kaltz, O. 1997. Anther smut disease in *Dianthus silvester* (Caryophyllaceae): natural selection on floral traits. *Evolution* 51: 383–392.
- Shykoff, J.A. and Muller, C.B. 1995. Reproductive decisions in bumble-bee colonies: the influence of worker mortality in *Bombus terrestris* (Hymenoptera, Apidae). *Functional Ecology* 9: 106–112.
- Shykoff, J.A. and Schmid-Hempel, P. 1991a. Genetic relatedness and eusociality: parasite-mediated selection on the genetic composition of groups. *Behavioural Ecology and Sociobiology* 28: 371–376.

- Shykoff, J.A. and Schmid-Hempel, P. 1991b. Parasites and the advantage of genetic variability within social insect colonies. *Proceedings of the Royal Society of London B* 243: 55–58.
- Shykoff, J.A. and Schmid-Hempel, P. 1991c. Parasites delay worker reproduction in bumblebees: consequences for eusociality. *Behavioral Ecology* 2: 242–248.
- Shykoff, J.A. and Schmid-Hempel, P. 1991d. Incidence and effects of four parasites in natural populations of bumble bees in Switzerland. *Apidologie* 22: 117–125.
- Sih, A. and Baltus, M.S. 1987. Patch size, pollinator behaviour and pollinator limitation in catnip. *Ecology* 68: 1679–1690.
- Silander, J.A. and Primack, R.B. 1978. Pollination intensity and seed set in the Evening Primrose (*Oenothera fruticosa*). *American Midland Naturalist* 100: 213–216.
- Silva-Matos, E.V. and Garófalo, C.A. 2000. Worker life tables, survivorship, and longevity in colonies of *Bombus (Fervidobombus) atratus* (Hymenoptera: Apidae). *Revista de Biología Tropical* 48: 657–664.
- Silvola, J. 1984. Respiration and energetics of the bumblebee *Bombus terrestris* queen. *Holarctic Ecology* 7: 177–181.
- Skorikov, A.S. 1922. Palearctic bumble bees. Part I. General biology (including zoogeography). *Izvestiya Severnoi Oblastnoi Stantsii Zashchity Rastenii ot Vreditelei* 4: 1–160.
- Skou, J.P., Holm, S.N. and Haas, H. 1963. Preliminary investigations on diseases in bumble bees (*Bombus* Latr.). *Kongelige Veterinaerskole og Landbohøjskole Danmark* (1963): 27–41.
- Skovgaard, O.S. 1943. Humlebiernes bopladser og overvintringssteder. *Tidsskrift Planteavlfsforsk.* 47: 285–305.
- Sladen, F.W.L. 1912. *The Humble-bee, its Life History and how to Domesticate it. Including The Humble Bee (1892)*. Logaston Press, London.
- Smith, F. 1851. Notes on the nest of *Bombus derhamellus*. *Transactions of the Entomological Society of London* 1: 111–112.
- Smith, F. 1858. Notes on Aculeate Hymenoptera, with some observations on their economy. *Entomology Annual* (1858): 34–46.
- Smith, F. 1865. Notes on Hymenoptera. *Entomology Annual* (1865): 81–96.
- Smith, F. 1876. *Catalogue of the British bees in the Collection of the British Museum*. British Museum, London.
- Smith, H., Feber, R.E., Johnson, P.J, McCallum, K., Plesner Jensen, S., Younes, M. and Macdonald, D.W. 1993. *The Conservation Management of Arable Field Margins*. English Nature, Peterborough, UK.
- Smith, H., Feber, R.E. and Macdonald, D.W. 1994. The role of wild flower seed mixtures in field margin restoration. In: *Field Margins: Integrating Agriculture and Conservation* (ed. N. Boatman), pp. 289–294. Monograph No. 58, British Crop Protection Council, Farnham, UK.
- Smith, H. and Macdonald, D.W. 1989. Secondary succession on extended arable field margins: its manipulation for wildlife benefit and weed control. Proc. of 1989 British Crop Protection Conference—Weeds. British Crop Protection Council, Farnham, UK, pp. 1063–1068.
- Smith, H. and Macdonald, D.W. 1992. The impacts of mowing and sowing on weed populations and species richness of field margin set-aside. In: *Set-aside* (ed. J. Clarke), pp. 117–122. BCPC Monograph No. 50. BCPC publications, Bracknell.
- Smith, K.G.V. 1959. The distribution and habits of the British Conopidae (Dipt.). *Transactions of the Society for British Entomology* 13: 113–136.
- Smith, K.G.V. 1966. The larva of *Thecophora occidentis*, with comments upon the biology of Conopidae (Diptera). *Journal of Zoology, London* 149: 263–276.

- Smith, K.G.V. 1969. Diptera: Conopidae. *Handbook for the Identification of British Insects* 10: 1–18.
- Snow, A.A. and Whigham, D.F. 1989. Cost of flower and fruit production in *Tipularia discolor*. *Ecology* 70: 1286–1293.
- Soltz, R.L. 1986. Foraging path selection in bumblebees: hindsight or foresight? *Behaviour* 99: 1–21.
- Sotherton NW. 1995. Beetle Banks—helping nature to control pests. *Pesticide Outlook* 6: 13–17.
- Southern, H.N. and Watson, J.S. 1941. Summer food of the red fox in Great Britain: a preliminary report. *Journal of Animal Ecology* 10: 1–11.
- Southwick, A.K. and Southwick, E.E. 1983. Aging effects on nectar production in two clones of *Asclepias syriaca*. *Oecologia* 56: 121–125.
- Southwick, E.E. and Buchmann, S.L. 1995. Effects of horizon landmarks on homing success of honeybees. *American Naturalist* 146: 748–764.
- Southwick, E.E. and Southwick, L. 1992. Estimating the economic value of honeybees (Hymenoptera: Apidae) as agricultural pollinators in the United States. *Journal of Economic Entomology* 85: 621–633.
- Sowig, P. 1989. Effects of flowering plant's patch size on species composition of pollinator communities, foraging strategies, and resource partitioning in bumble-bees (Hymenoptera: Apidae). *Oecologia* 78: 550–558.
- Spaethe, J., Brockmann, A., Halbig, C. and Tautz, J. 2007. Size determines antennal sensitivity and behavioral threshold to odors in bumblebee workers. *Naturwissenschaften* 94: 733–739.
- Spaethe, J. and Chittka, L. 2003. Interindividual variation of eye optics and single object resolution in bumblebees. *Journal of Experimental Biology* 206: 3447–3453.
- Spaethe, J., Tautz, J. and Chittka, L. 2001. Visual constraints in foraging bumblebees: flower size and color affect search time and flight behavior. *Proceedings of the National Academy of Sciences USA*, 98: 3898–3903.
- Spaethe, J. and Weidenmuller, A. 2002. Size Variation and Foraging Rate in Bumblebees (*Bombus terrestris*). *Insectes Sociaux* 49: 142–146.
- Spangler, H.G. and Moffett, J.O. 1977. Honeybee visits to tomato flowers in polyethylene greenhouses. *American Bee Journal* 117: 580–582.
- Spiewok, S. and Neumann, P. 2006. Infestation of the commercial bumblebee (*Bombus impatiens*) field colonies by small hive beetles (*Aethina tumida*). *Ecological Entomology* 31: 623–628.
- Stahlhut, J.K. and Cowan, D.P. 2004. Inbreeding in a natural population of *Euodynerus foraminatus* (Hymenoptera: Vespidae), a solitary wasp with single-locus complementary sex determination. *Molecular Ecology* 13: 631–638.
- Stanghellini, M.S., Ambrose, J.T. and Schultheis, J.R. 1997. The effects of *A. mellifera* and *B. impatiens* pollination on fruit set and abortion of cucumber and watermelon. *American Bee Journal* 137: 386–391.
- Stanghellini, M.S., Ambrose, J.T. and Schultheis, J.R. 1998. Seed production in watermelon: a comparison between two commercially available pollinators. *HortScience* 33: 28–30.
- Stanghellini, M.S., Ambrose, J.T. and Schultheis, J.R. 2002. Diurnal activity, floral visitation and pollen deposition by honey bees and bumble bees on field-grown cucumber and watermelon. *Journal of Apicultural Research* 41: 27–34.
- Stanton, M.L. and Preston, R. 1988. A qualitative model for evaluating the effects of flower attractiveness on male and female fitness in plants. *American Journal of Botany* 75: 540–544.

- Stapel, C. 1933. Undersøgelser over Humlebier (*Bombus* Latr.), deres Udbredelse, Trækplanter og Betydning for Bestøvningen of Rødkløver (*Trifolium pratense* L.). *Tidsskrift Planteavlsforskog* 39: 193–294.
- Stapledon, R.G. 1935. *The Land, Now and Tomorrow*. Faber and Faber, London.
- Staples, J.F., Koen, E.L. and Laverty, T.M. 2004. 'Futile cycle' enzymes in the flight muscles of North American bumblebees. *Journal of Experimental Biology* 207: 749–754.
- Stebbing, P.D. 1965. A study of the mite *Parasitus bomborum*. *Essex Naturalist* 3: 284–287.
- Steffan-Dewenter, I. and Tscharnkte, T. 1997. Bee diversity and seed set in fragmented habitats. *Acta Horticulturae* 437: 231–234.
- Steffan-Dewenter, I. and Tscharnkte, T. 1999. Effects of habitat isolation on pollinator communities and seed set. *Oecologia* 121: 432–440.
- Steen, J.J.M. van der 1994. Method development for the determination of the contact LD<sub>50</sub> of pesticides for bumblebees (*Bombus terrestris* L.). *Apidologie* 25: 463–465.
- Steen, J.J.M. van der 2001. Review of the methods to determine the hazard and toxicity of pesticides to bumblebees. *Apidologie* 32: 399–406.
- Stein, G. 1963. Über den Sexuallockstoff von Hummelmännchen. *Naturwissenschaften* 50: 305.
- Stevenson, A.G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* 12: 245–279.
- Stimec, J., ScottDupree, C.D. and McAndrews, J.H. 1997. Honey Bee, *Apis mellifera*, pollen foraging in southern Ontario. *Canadian Field-Naturalist* 111: 454–456.
- Stoddard, F.L. and Bond, D.A. 1987. The pollination requirements of the faba bean. *Bee World* 68: 564–577.
- Stone, G.N. and Willmer, P.G. 1989. Warm-up rates and body temperatures in bees: the importance of body size, thermal regime and phylogeny. *Journal of Experimental Biology* 147: 303–328.
- Stout, J.C. 2000. Does size matter? Bumblebee behaviour and the pollination of *Cytisus scoparius* L. (Fabaceae). *Apidologie* 31: 129–139.
- Stout, J.C., Allen, J.A. and Goulson, D. 2000. Nectar robbing, forager efficiency and seed set: bumblebees foraging on the self incompatible plant *Linaria vulgaris* Mill. (Scrophulariaceae). *Acta Oecologia* 21: 277–283.
- Stout, J.C. and Goulson, D. 2000. Bumblebees in Tasmania: their distribution and potential impact on Australian flora and fauna. *Bee World*, 81: 80–86.
- Stout, J.C. and Goulson, D. 2001. The use of conspecific and interspecific scent marks by foraging bumblebees and honeybees. *Animal Behaviour* 62: 183–189.
- Stout, J.C. and Goulson, D. 2002. The influence of nectar secretion rates on the responses of bumblebees (*Bombus* spp.) to previously visited flowers. *Behavioral Ecology and Sociobiology* 52: 239–246.
- Stout, J.C., Goulson, D. and Allen, J.A. 1998. Repellent scent marking of flowers by a guild of foraging bumblebees (*Bombus* spp.). *Behavioral Ecology and Sociobiology* 43: 317–326.
- Stout J.C., Kells A.R. and Goulson D. 2002. Pollination of the invasive exotic shrub *Lupinus arboreus* (Fabaceae) by introduced bees in Tasmania. *Biological Conservation* 106: 425–434.
- Stubbs, C.S. and Drummond, F.A. 2001. *Bombus impatiens* (Hymenoptera: Apidae): an alternative to *Apis mellifera* (Hymenoptera: Apidae) for lowbush blueberry pollination. *Journal of Economic Entomology* 94: 609–616.
- Stubbs, C.S., Drummond, F.A. and Osgood, E.A. 1994. *Osmia ribifloris biedermannii* and *Megachile rotundata* (Hymenoptera: Megachilidae) introduced into the lowbush blueberry agroecosystem in Maine. *Journal of the Kansas Entomological Society* 67: 173–185.

- Sugden, E.A. and Pyke, G.H. 1991. Effects of honey bees on colonies of *Exoneura asimillima*, an Australian native bee. *Australian Journal of Ecology* 16: 171–181.
- Sugden, E.A., Thorp, R.W. and Buchmann, S.L. 1996. Honey bee native bee competition: focal point for environmental change and apicultural response in Australia. *Bee World* 77: 26–44.
- Sundström, L. 1994. Sex ratio bias, relatedness asymmetry and queen mating frequency in ants. *Nature* 367: 266–268.
- Surholt, B., Greive, H., Baal, T. and Bertsch, A. 1990. Non-shivering thermogenesis in asynchronous flight muscles of bumblebees? Comparative studies on males of *Bombus terrestris*, *Xylocopa sulcatipes* and *Acherontia atropos*. *Comparative Biochemistry and Physiology* 97: 493–499.
- Surholt, B., Greive, H., Baal, T. and Bertsch, A. 1991. Warm-up and substrate cycling in flight muscles of male bumblebees, *Bombus terrestris*. *Comparative Biochemistry and Physiology* 98: 299–303.
- Sutcliffe, G.H. and Plowright, R.C. 1988. The effects of food supply on adult size in the bumblebee *Bombus terricola* Kirby (Hymenoptera: Apidae). *The Canadian Entomologist* 120: 1051–1058.
- Sutcliffe, G.H. and Plowright, R.C. 1990. The effects of pollen availability on the development time in the bumble bee *Bombus terricola* K. (Hymenoptera: Apidae). *Canadian Journal of Zoology* 68: 1120–1123.
- Svensson, B., Lagerlöf, J. and Svensson, B.G. 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. *Agriculture, Ecosystems and Environment* 77: 247–255.
- Svensson, B.G. 1979. *Pyrobombus lapponicus* Auct., in Europe recognised as two species: *P. lapponicus* (Fabricius, 1793) and *P. monticola* (Smith, 1849) (Hymenoptera: Apoidea: Bombinae). *Entomologica Scandinavica* 10: 275–296.
- Svensson, B.G. 1980. Patrolling behaviour of bumble bee males (Hymenoptera, Apidae) in a sub-alpine/alpine area, Swedish Lapland. *Zoon* 7: 67–94.
- Svensson, B.G., Appelgren, M. and Bergström, G. 1984. Geranylgeranyl acetate and 2-heptadecanone as the dominant marking secretion components of the labial glands in the bumble bee *Alpigenobombus wurfleini*. *Nova Acta regiae Societatis Scientiarum Upsalla, Ser. V:C* 3: 145–147.
- Svensson, B.G. and Bergström, G. 1977. Volatile marking secretions from the labial gland of north European *Pyrobombus* D.T. males (Hymenoptera: Apidae). *Insectes Sociaux* 24: 213–214.
- Svensson, B.G. and Bergström, G. 1979. Marking pheromones of *Alpinobombus* males. *Journal of Chemical Ecology* 5: 603–615.
- Swift, J. 1733. *The Poetical Works of Jonathan Swift*, Published 1833–34, W. Pickering, London.
- Takahashi, J., Ayabe, T., Mitsuhashi, M., Shimizu, I. and Ono, M. 2008a. Diploid male production in a rare and locally distributed bumblebee, *Bombus florilegus* (Hymenoptera, Apidae). *Insectes Sociaux* 55: 43–50.
- Takahashi, J., Itoh, M., Shimizu, I. and Ono, M. 2008b. Male parentage and queen mating frequency in the bumblebee *Bombus ignitus* (Hymenoptera: bombinae). *Ecological Research* 23: 937–942.
- Taneyhill, D.E. and Thomson, J.D. 2007. Behavior of inexperienced bumble bees toward spatial clumping of nectar (Hymenoptera: Apidae). *Entomologia Generalis* 29: 149–164.
- Tasei, J.N. and Aupinel, P. 2008. Nutritive value of 15 single pollens and pollen mixes tested on larvae produced by bumblebee workers (*Bombus terrestris*, Hymenoptera: Apidae). *Apidologie* 39: 397–409.
- Tay, W.T., O'Mahony, E.M. and Paxton, R.J. 2005. Complete rRNA gene sequences reveal that the microsporidium *Nosema bombi* infects diverse bumble bee (*Bombus* spp.) hosts and contains multiple polymorphic sites. *Journal of Eukaryotic Microbiology* 52: 505–513.



## 300 References

- Taylor, G. and Whelan, R.J. 1988. Can honeybees pollinate Grevillea? *Australian Zoologist* 24: 193–196.
- Taylor, O.M. and Cameron, S.A. 2003. Nest construction and architecture of the Amazonian bumble bee (Hymenoptera: Apidae). *Apidologie* 34: 321–331.
- Telleria, M.C. 1993. Flowering and pollen collection by the honeybee (*Apis mellifera* L Var *ligustica*) in the Pampas region of Argentina. *Apidologie* 24: 109–120.
- Tepedino, V.J. and Stanton, N.L. 1981. Diversity and competition in bee-plant communities on short-grass prairie. *Oikos* 36: 35–44.
- Tengö, J., Hefetz, A., Bertsch, A., Schmitt, U., Lübke, G. and Francke, W. 1991. Species specificity and complexity of Dufour's gland secretion of bumble bees. *Comparative Biochemistry and Physiology* 99B: 641–646.
- Teräs, I. 1976. Flower visits of bumblebees, *Bombus* Latr. (Hymenoptera: Apidae) during one summer. *Annales Zoologici Fennici* 13: 200–232.
- Teräs, I. 1985. Food plants and flower visits of bumble-bees (*Bombus*: Hymenoptera, Apidae) in southern Finland. *Acta Zoologica Fennica* 179: 1–120.
- Teuber, L.R. and Barnes, D.K. 1979. Breeding alfalfa for increased nectar production. Proceedings of the IVth International Symposium on Pollination, Maryland Agricultural Experimental Station Special Miscellaneous Publications 1, pp.109–116.
- Thomas, J.A. 1983. The ecology and conservation of *Lysandra bellargus* (Lepidoptera, Lycaenidae) in Britain. *Journal of Applied Ecology* 20: 59–83.
- Thomson, D.M. 2004. Detecting the effects of introduced species: a case study of competition between *Apis* and *Bombus*. *Oikos* 114: 407–418.
- Thomson, D.M. 2006. Competitive interactions between the invasive European honey bee and native bumble bees. *Ecology* 85: 458–470.
- Thomson, J.D. 1981. Spatial and temporal components of resource assessment by flower-feeding insects. *Journal of Animal Ecology* 50: 49–60.
- Thomson, J.D. 1988. Effects of variation in inflorescence size and floral rewards on the visitation rates of trap lining pollinators of *Aralia hispida*. *Evolutionary Ecology* 2: 65–76.
- Thomson, J.D. and Goodell, K. 2001. Pollen removal and deposition by honeybee and bumblebee visitors to apple and almond flowers. *Journal of Applied Ecology* 38: 1032–1044.
- Thomson, J.D., Maddison, W.P. and Plowright, R.C. 1982. Behaviour of bumblebee pollinators on *Aralia hispida* Vent. (Araliaceae). *Oecologia* 54: 326–336.
- Thomson, J.D., Peterson, S.C. and Harder, L.D. 1987. Response of traplining bumble bees to competition experiments: shifts in feeding location and efficiency. *Oecologia* 71: 295–300.
- Thomson, J.D., Slatkin, M. and Thomson, B.A. 1997. Trapline foraging by bumble bees 2. Definition and detection from sequence data. *Behavioral Ecology* 8: 199–210.
- Thompson, H.M. 2001. Assessing the exposure and toxicity of pesticides to bumblebees (*Bombus* sp.). *Apidologie* 32: 305–321.
- Thompson, H.M. and Hunt, L.V. 1999. Extrapolating from honeybees to bumblebees in pesticide risk assessment. *Ecotoxicology* 8: 147–166.
- Thompson, J.N. 1982. *Interactions and Coevolution*. Wiley-Interscience, New York.
- Thorp, R.N., Briggs, D.L., Estes, J.R. and Erikson, E.H. 1975. Nectar fluorescence under ultraviolet irradiation. *Science* 189: 476–478.
- Thorp, R.N., Briggs, D.L., Estes, J.R. and Erikson, E.H. 1976. (Reply to Kevan). *Science* 194: 342.
- Thorp, R.W. 1979. Structural, behavioral and physiological adaptations of bees (Apoidea) for collecting pollen. *Annals of the Missouri Botanical Garden* 66: 788–812.

- Thorp, R.W. 2005. Species profile: *Bombus franklini*. In: *Red List of Pollinator Insects of North America*. (eds. M.D. Shepherd, D.M. Vaughan and S.H. Black). The Xerces Society for Invertebrate Conservation, Portland, Oregon.
- Thorp, R.W. and Shepherd, M.D. 2005. Profile: Subgenus *Bombus*. In: *Red List of Pollinator Insects of North America* (eds. M.D. Shepherd, D.M. Vaughan and S.H. Black). The Xerces Society for Invertebrate Conservation, Portland, Oregon.
- Thorp, R.W., Wenner, A.M. and Barthell, J.F. 1994. Flowers visited by honeybees and native bees on Santa Cruz Island. In: *The Fourth Californian Islands Symposium: Update on the Status of Resources* (eds W.L. Halvorson and G.J. Maender), pp. 351–365. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- Tierney, S.M. 1994. Life cycle and social organisation of two native bees in the subgenus *Brevineura*. Unpublished BSc (Hons) thesis, Flinders University of South Australia.
- Tinbergen, L. 1960. The natural control of insects in pine woods. 1. Factors influencing the intensity of predation by songbirds. *Archives Néerlandaises de Zoologie* 13: 265–343.
- Tollsten, L. and Bergstrom, L.G. 1993. Fragrance chemotypes of *Platanthera* (Orchidaceae)—the result of adaptation to pollinating moths. *Nordic Journal of Botany* 13: 607–613.
- Tollsten, L. and Ovstedal, D.O. 1994. Differentiation in floral scent chemistry among populations of *Conopodium majus* (Apiaceae). *Nordic Journal of Botany* 14: 361–367.
- Tooby, J. 1982. Pathogens, polymorphism, and the evolution of sex. *Journal of Theoretical Biology* 97: 557–576.
- Torchio, P.F. 1987. Use of non-honey bee species as pollinators of crops. *Proceedings of the Entomological Society of Ontario* 118: 111–124.
- Torchio, P.F. 1990. Diversification of pollination strategies for U.S. crops. *Environmental Entomology* 19: 1649–1656.
- Torretta, J.P., Medan, D. and Arahamovich, A.H. 2006. First record of the invasive bumblebee *Bombus terrestris* (L.) (Hymenoptera, Apidae) in Argentina. *Transactions of the American Entomological Society* 132: 285–289.
- Townsend, T.H.C. 1936. The mature larva and puparium of *Brachycoma sarcophagina* (Townsend) (Diptera: Metopiidae). *Proceedings of the Entomological Society of Washington* 38: 92–98.
- Tremblay, R.L. 2005. Variation in sexual reproduction in orchids and its evolutionary consequences: a spasmodic journey to diversification. *Biological Journal of the Linnean Society* 84: 1–54.
- Trivers, R.L. and Hare, H. 1976. Haplodiploidy and the evolution of the social insects. *Science* 191: 249–263.
- Tuck, W.H. 1897. Note on the habits of *Bombus latreillellus*. *Entomologist's monthly Magazine* 33: 234–235.
- Tyler, E.R., Adams, S. and Mallon, E.B. 2006. An immune response in the bumble bee, *Bombus terrestris*, leads to increased food consumption. *BMC Physiology* 6: 6.
- Urbanova, K., Cahlikova, L., Hovorka, O., Ptacek, V. and Valterova, I. 2008. Age-dependent changes in the chemistry of exocrine glands of *Bombus terrestris* queens. *Journal of Chemical Ecology* 34: 458–466.
- Urbanová, K., Valterová, I., Hovorka, O. and Kindl, J. 2001. Chemotaxonomical characterisation of males of *Bombus lucorum* (Hymenoptera: Apidae) collected in the Czech Republic. *European Journal of Entomology* 98: 111–115.
- Vallet, A., Cassier, P. and Lensky, Y. 1991. Ontogeny of the fine structure of the mandibular glands of the honeybee (*Apis mellifera* L.) workers and the pheromonal activity of 2-heptanone. *Journal of Insect Physiology* 37: 789–804.

- Valterová, I., Urbanová, K., Hovorka, O. and Kindl, J. 2001. Composition of the labial gland secretion of the bumblebee males *Bombus pomorum*. *Verlad der Zeitschrift für Naturforschung* 56c: 430–436.
- Van den Eijnde, J., de Ruijter, A. and Van der Steen, J. 1991. Method for rearing *Bombus terrestris* continuously and the production of bumble bee colonies for pollination purposes. *Acta Horticulturae* 288: 154–158.
- Van der Blom, J. 1986. Reproductive dominance within colonies of *Bombus terrestris* (L.). *Behaviour* 97: 37–49.
- Van Doorn, A. 1987. Investigations into the regulation of dominance behaviour and the division of labour in bumble bee colonies (*Bombus terrestris*). *Netherlands Journal of Zoology* 37: 255–276.
- Van Doorn, A. and Heringa, J. 1986. The ontogeny of a dominance hierarchy in colonies of the bumble bee *Bombus terrestris*. *Insectes Sociaux* 33: 3–25.
- Van Heemert, C., de Ruijter, A., Van den Eijnde, J. and Van der Steen, J. 1990. Bees in agriculture; Year round production of bumble bee colonies for crop production. *Bee World* 71: 54–56.
- Van Honk, C.G.J. and Hogeweg, P. 1981. The ontogeny of social structure in a captive *Bombus terrestris* colony. *Behavioural Ecology and Sociobiology* 9: 111–119.
- Van Honk, C.G.J., Röseler, P.-F. Velthuis, H.H.W. and Hoogeven, J.C. 1981. Factors influencing the egg-laying of workers in a captive *Bombus terrestris* colony. *Behavioral Ecology and Sociobiology* 9: 9–14.
- Van Honk, C.G.J., Velthuis, H.H.W. and Röseler, P.-F. 1978. A sex pheromone from the mandibular glands in bumblebee queens. *Experientia* 34: 838.
- Vergara, C.H., Schroder, S., Almanza, M.T. and Wittmann, D. 2003. Suppression of ovarian development of *B. terrestris* workers by *B. terrestris* queens, *Psithyrus vestalis* and *Psithyrus bohemicus* females. *Apidologie* 34: 563–568.
- Vieting, U.K. 1988. Untersuchungen in Hessen über Auswirkung und Bedeutung von Ackerschonstreifen. 1. Konzeption des Projektes und der Botanische Aspekt. *Mitteilungen aus der Biologischen Bundesanstalt für Land- und Forstwirtschaft Berlin-Dahlem* 247: 29–41.
- Villalobos, E.M. and Shelly, T.E. 1987. Observations on the behavior of male *Bombus sonorus* (Hymenoptera: Apidae). *Journal of the Kansas Entomological Society* 60: 541–548.
- Visscher, P.K. and Seeley, T.D. 1982. Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology* 63: 1790–1801.
- Vogt, D.F. 1986. Thermoregulation in bumblebee colonies. I. Thermoregulatory versus brood-maintenance behaviors during acute changes in ambient temperature. *Physiological Zoology* 59: 55–59.
- Vogt, D.F. and Heinrich, B. 1994. Abdominal temperature regulation by Arctic bumblebees. *Physiological Zoology* 66: 257–269.
- Vogt, D.F., Heinrich, B., Dabolt, T.O. and McBath, H.L. 1994. Ovary development and colony founding in subarctic and temperate-zone bumblebee queens. *Canadian Journal of Zoology* 72: 1551–1556.
- Volynchik, S., Plotkin, M., Ermakov, N.Y., Bergman, D.J. and Ishay, J.S. 2006. Presence of a thermoregulatory hotspot in the prothorax of the large carpenter bee and the bumble bee. *Microscopy Research and Technique* 69: 903–912.
- Voss, R., Turner, M., Inouye, R., Fisher, M. and Cort, R. 1980. Floral biology of *Markea neurantha* Hemsley (Solanaceae), a bat-pollinated epiphyte. *American Midland Naturalist* 103: 262–268.
- Vrieling, K., Saumitou-Laprade, P., Cuguen, J., van Dijk, H., de Jong, T. and Klinkhamer, P. 1999. Direct and indirect estimates of the selfing rate in small and large individuals of the bumblebee pollinated *Cynoglossum officinale* L. (Boraginaceae). *Ecology Letters* 2: 331–337.

- Waddington, K.D. 1980. Flight patterns of foraging bees relative to density of artificial flowers and distribution of nectar. *Oecologia* 44: 199–204.
- Waddington, K.D. 1983a. Floral-visitation-sequences by bees: models and experiments. In: *Handbook of Experimental Pollination Ecology* (eds. C.E. Jones and R.J. Little), pp. 461–473. Van Nostrand Reinhold, New York.
- Waddington, K.D. 1983b. Foraging Behaviour of pollinators. In: *Pollination Biology* (ed. L.A. Real), pp. 213–239. Academic Press, New York.
- Waddington, K.D., Allen, T. and Heinrich, B. 1981. Floral preferences of bumblebees (*Bombus edwardsii*) in relation to intermittent versus continuous rewards. *Animal Behaviour* 29: 779–784.
- Waddington, K.D. and Heinrich, B. 1979. The foraging movements of bumblebees on vertical 'inflorescences': an experimental analysis. *Journal of Comparative Physiology* 134: 113–117.
- Waddington, K.D. and Heinrich, B. 1981. Patterns of movement and floral choice by foraging bees. In: *Foraging Behavior: Ecological, Ethological, and Psychological Approaches* (eds. A. Kamil and T. Sargent), pp. 215–230. Garland STPM Press, New York.
- Waddington, K.D., Visscher, P.K., Herbert, T.J. and Richter, M.R. 1994. Comparisons of forager distributions from matched honey bee colonies in suburban environments. *Behavioural Ecology and Sociobiology* 35: 423–429.
- Waller, R. 1962. *Prophet of the New Age*. Faber and Faber, London.
- Wallraff, H.G. 1980. Does pigeon homing depend on stimuli perceived during displacement? I. Experiments in Germany. *Journal of Comparative Physiology* 139: 193–201.
- Wallraff, H.G. 1990. Navigation by homing pigeons. *Ethology, Ecology and Evolution* 2: 81–115.
- Wallraff, H.G., Foà A. and Ioalè P. 1980. Does pigeon homing depend on stimuli perceived during displacement? II. Experiments in Italy. *Journal of Comparative Physiology* 139: 203–208.
- Walther-Hellwig, K., Fokul, G., Frankl, R., Buechler, R., Ekschmitt, K. and Wolters, V. 2006. Increased density of honeybee colonies affects foraging bumblebees. *Apidologie* 37: 517–532.
- Walther-Hellwig K. and Frankl, R. 2000. Foraging distances of *Bombus muscorum*, *Bombus lapidarius* and *Bombus terrestris* (Hymenoptera, Apidae). *Journal of Insect Behavior* 13: 239–246.
- Waser, N.M. 1982a. A comparison of distances flown by different visitors to flowers of the same species. *Oecologia* 55: 251–257.
- Waser, N.M. 1982b. Competition for pollination and floral character differences among sympatric plant species: a review of evidence. In: *Handbook of Experimental Pollination Ecology* (eds. C.E. Jones and R.J. Little), pp. 277–293. Van Nostrand Reinhold, New York.
- Waser, N.M. 1983. The adaptive significance of floral traits: ideas and evidence. In: *Pollination biology* (ed. L.A. Real), pp. 241–285. Academic Press, New York.
- Waser, N.M. 1986. Flower constancy: definition, cause and measurement. *American Naturalist* 127: 593–603.
- Waser, N.M. 1998. Pollination, angiosperm speciation, and the nature of species boundaries. *Oikos* 81: 198–201.
- Waser, N.M., Chittka, L., Price, M.V., Williams, N.M. and Ollerton, J. 1996. Generalization in pollination systems, and why it matters. *Ecology* 77: 1043–1060.
- Waser, N.M. and Mitchell, R.J. 1990. Nectar standing crops in *Delphinium nelsonii* flowers: spatial autocorrelation among plants? *Ecology* 71: 116–123.
- Watson, P.J. and Thornhill, R. 1994. Fluctuating asymmetry and sexual selection. *Trends in Ecology and Evolution* 9: 21–25.

- Webster, S. and Felton, M. 1993. Targeting for nature conservation in agricultural policy. *Land Use Policy*, January: 67–82.
- Weekes, R., Deppe, C., Allnutt, T., Boffey, C., Morgan, D., Morgan, S., Bilton, M., Daniels, R. and Henry, C. 2005. Crop-to-crop gene flow using farm scale sites of oilseed rape (*Brassica napus*) in the UK. *Transgenic Research* 14: 749–759.
- Wehner, R. 1981. Spatial vision in arthropods. In: *Handbook of Sensory Physiology* (eds H. Autrum, R. Jury, W.R. Loewenstein, D.M. Mackay, H-L. Teuber.), Vol VII/6C, pp. 98–201. Springer Verlag, Berlin.
- Wehner, R. 1994. The polarization-vision project: championing organismic biology. In: *Neural Basis of Behavioural Adaptation* (eds K. Schildberger, N. Elsner and G. Fischer), pp. 102–207. Stuttgart, New York.
- Wehner, R. 1996. Middle scale navigation: the insect case. *Journal of Experimental Biology* 199: 125–127.
- Weidenmuller, A. 2004. The control of nest climate in bumblebee (*Bombus terrestris*) colonies: interindividual variability and self reinforcement in fanning response. *Behavioral Ecology* 15: 120–128.
- Weidenmüller, A., Kleineidam, C. and Tautz, J. 2002. Collective control of nest climate parameters in bumblebee colonies. *Animal Behaviour* 63: 1065–1071.
- Weislo, W.T. 1981. The roles of seasonality, host synchrony, and behaviour in the evolutions and distributions of nest parasites in Hymenoptera (Insecta), with special reference to bees (Apoidea). *Biological Reviews* 62: 515–543.
- Weiss, M.R. 1995a. Associative color learning in a nymphalid butterfly. *Ecological Entomology* 20: 298–301.
- Weiss, M.R. 1995b. Floral color-change—a widespread functional convergence. *American Journal of Botany* 82: 167–185.
- Weiss, M.R. and Lamont, B.B. 1997. Floral color change and insect pollination: a dynamic relationship. *Israel Journal of Plant Sciences* 45: 185–199.
- Wells, H. and Wells, P.H. 1983. Honeybee foraging ecology: optimal diet, minimal uncertainty or individual constancy? *Journal of Animal Ecology* 52: 829–836.
- Wells, H. and Wells, P.H. 1986. Optimal diet, minimal uncertainty and individual constancy in the foraging of honeybees, *Apis mellifera*. *Journal of Animal Ecology* 55: 881–891.
- Wells, H., Hill, P.S. and Wells, P.H. 1992. Nectarivore foraging ecology—rewards differing in sugar types. *Ecological Entomology* 17: 280–288.
- Wenner, A.M. and Thorp, R.W. 1994. Removal of feral honey bee (*Apis mellifera*) colonies from Santa Cruz Island. In: *The Fourth Californian Islands Symposium: Update on the Status of Resources* (eds W.L. Halvorson and G.J. Maender), pp. 513–522. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- Wenner, A.M. and Wells, P.H. 1990. *Anatomy of a Controversy*. Columbia University Press, New York.
- West, E.L. and Laverty, T.M. 1998. Effect of floral symmetry on flower choice and foraging behaviour of bumble bees. *Canadian Journal of Zoology* 76: 730–739.
- Westergaard, G.C. and Suomi, S.J. 1996. Lateral bias for rotational behavior in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology* 110: 199–202.
- Westerkamp, C. 1991. Honeybees are poor pollinators—why? *Plant Systematics and Evolution* 177: 71–75.
- Westphal, C., Steffen-Dewenter, I. and Tsharntke, T. 2003. Mass-flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters* 6: 961–965.

- Westphal, C., Steffan-Dewenter, I. and Tschardt, T. 2006. Bumblebees experience landscapes at different spatial scales: possible implications for coexistence. *Oecologia* 149: 289–300.
- Westrich, P. 1989. *Die Bienen Baden-Württembergs*. Vol. 1., Ulmer Verlag, Stuttgart, 431pp.
- Westrich, P. 1996. Habitat requirements of central European bees and the problems of partial habitats. In: *The Conservation of Bees* (eds. A. Matheson, S.L. Buchmann, C. O'Toole and P. Westrich), pp. 2–16. Academic Press, Williams, I.H. London.
- Westrich, P., Schwenninger, H.-R., Dathe, H., Riemann, H., Saure, C., Voith, J. and Weber, K. 1998. Rote Liste der Bienen (Hymenoptera: Apidae). In: *Rote Liste Gefährdeter Tiere Deutschlands* (Ed. By Bundesamt für Naturschutz), pp. 119–129. Naturschutz 55, Bonn, Schriftenr, Landschaftspf.
- Wetherwax, P.B. 1986. Why do honeybees reject certain flowers? *Oecologia* 69: 567–570.
- Whidden, T.L. 1996. The fidelity of commercially reared colonies of *Bombus impatiens* Cresson (Hymenoptera: Apidae) to lowbush blueberry in southern New Brunswick. *The Canadian Entomologist* 128: 957–958.
- Whitehorn, P., Tinsley, M., Darvill, B. and Goulson, D. In prep. Impacts of inbreeding on bumblebee colony fitness under field conditions.
- Whitfield, J.B. and Cameron, S.A. 1993. Comparative notes on hymenopteran parasitoids in bumble bee and honey bee colonies (Hymenoptera: Apidae) reared adjacently. *Entomological News* 104: 240–248.
- Whitfield, J.B., Cameron, S.A., Ramírez, S.R., Roesch, K., Messinger, S., Taylor, O.M. and Cole, D. 2001. Review of the *Apanteles* species (Hymenoptera: Braconidae) attacking Lepidoptera in *Bombus (Fervidobombus)* (Hymenoptera: Apidae) colonies in the New World, with description of a new species from South America. *Annals of the Entomological Society of America* 96: 851–857.
- Whitney, H.M., Dyer, A., Chittka, L., Rands, S.A. and Glover, B.J. 2008. The interaction of temperature and sucrose concentration on foraging preferences in bumblebees. *Naturwissenschaften* 95: 845–850.
- Whittington, R. and Winston, M.L. 2003. Effects of *Nosema bombi* and its treatment fumagillin on bumble bee (*Bombus occidentalis*) colonies. *Journal of Invertebrate Pathology* 84: 54–58.
- Whittington, R., Winston, M.L., Tucker, C. and Parachnowitsch, A.L. 2004. Plant-species identity of pollen collected by bumblebees placed in greenhouses for tomato pollination. *Canadian Journal of Plant Science* 84: 599–602.
- Widmer, A. and Schmid-Hempel, P. 1999. The population genetic structure of a large temperate pollinator species, *Bombus pascuorum* (Scopoli) (Hymenoptera: Apidae). *Molecular Ecology* 8: 387–398.
- Widmer, A., Schmid-Hempel, P., Estoup, A. and Scholl, A. 1998. Population genetic structure and colonisation history of *Bombus terrestris* s.l. (Hymenoptera: apidae) from the Canary Islands and Madeira. *Heredity* 81: 563–572.
- Wiebes, J.T. 1979. Co-evolution of figs and their insect pollinators. *Annual Review of Ecology and Systematics* 10: 1–12.
- Wiegmann, D.D., Wiegmann, D.A. and Waldron, F.A. 2003. Effects of a reward downshift on the consummatory behavior and flower choices of bumblebee foragers. *Physiology and Behavior* 79: 561–566.
- Wilcove, D.S., Rothstein, D., Dubrow, J., Phillips, A. and Losos, E. 1998. Quantifying threats to imperiled species in the United States. *Bioscience* 48: 607–615.
- Wilfert, L., Gadau, J., Baer, B. and Schmid-Hempel, P. 2007. Natural variation in the genetic architecture of a host-parasite interaction in the bumblebee *Bombus terrestris*. *Molecular Ecology* 16: 1327–1339.

- Wilfert, L., Gadau, J. and Schmid-Hempel, P. 2007. The genetic architecture of immune defense and reproduction in male *Bombus terrestris* bumblebees. *Evolution* 61: 804–815.
- Williams, A.A., Hollands, T.A and Tucknott, O.G. 1981. The gas chromatographic-mass spectrometric examination of the volatiles produced by the fermentation of a sucrose solution. *Zeitschrift fuer Lebensmittel-Untersuchung und Forschung* 172: 377–381.
- Williams, C.S. 1995. Conserving Europe's bees: why all the buzz? *Trends in Ecology And Evolution* 10: 309–310.
- Williams, C.S. 1998. The identity of the previous visitor influences flower rejection by nectar-collecting bees. *Animal Behaviour* 56: 673–681.
- Williams, I.H. and Christian, D.G. 1991. Observations on *Phacelia tanacetifolia* Bentham (Hydrophyllaceae) as a food plant for honey bees and bumble bees. *Journal of Apicultural Research* 21: 236–245.
- Williams, I.H., Martin, A.P. and White, R.P. 1987. The effect of insect pollination on plant development and seed production in winter oilseed rape (*Brassica napus* L.). *Journal of Agricultural Science* 109: 135–139.
- Williams, N.H. 1982. Floral fragrances as cues in animal behavior. In: *Handbook of Experimental Pollination Ecology* (eds C.E. Jones and R.J. Little), pp. 50–72. Van Nostrand Reinhold, New York.
- Williams, N.M. and Kremen, C. 2007. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications* 17: 910–921.
- Williams, N.M. and Thomson, J.D. 1998. Trapline foraging by bumble bees: III. Temporal patterns of visitation and foraging success at single plants. *Behavioral Ecology* 9: 612–621.
- Williams, P.A. and Timmins, S.M. 1990. *Weeds in New Zealand Protected Natural Areas: a review for the Department of Conservation*. Science and Research Series No. 14, Department of Conservation, Wellington, New Zealand, 114 pp.
- Williams, P.H. 1982. The distribution and decline of British bumble bees (*Bombus* Latr.). *Journal of Apicultural Research* 21: 236–245.
- Williams, P.H. 1985a. A preliminary cladistic investigation of relationships among the bumble bees (Hymenoptera, Apidae). *Systematic Entomology* 10: 239–255.
- Williams, P.H. 1985b. On the distribution of bumble bees (Hymenoptera, Apidae), with particular regard to patterns within the British Isles. PhD thesis, University of Cambridge, UK. 180 pp.
- Williams, P.H. 1986. Environmental change and the distribution of British bumble bees (*Bombus* Latr.). *Bee World* 67: 50–61.
- Williams, P.H. 1988. Habitat use by bumble bees (*Bombus* spp.). *Ecological Entomology* 13: 223–237.
- Williams, P.H. 1989a. *Bumble Bees—And Their Decline in Britain*. Central Association of Beekeepers, Ilford.
- Williams, P.H. 1989b. Why are there so many species of bumble bees at Dungeness? *Botanical Journal of the Linnean Society* 101: 31–44.
- Williams, P.H. 1991. The bumble bees of the Kashmir Himalaya (Hymenoptera: Apidae, Bombini). *Bulletin of the British Museum (Natural History) (Entomology)* 60: 1–204.
- Williams, P.H. 1994. Phylogenetic relationships among bumble bees (*Bombus* Latr.): a reappraisal of morphological evidence. *Systematic Entomology* 19: 327–344.
- Williams, P.H. 1998. An annotated checklist of bumble bees with an analysis of patterns of description (Hymenoptera: Apidae, Bombini). *Bulletin of the Natural History Museum, London (Entomology)* 67: 79–152.

- Williams, P.H. 2005. Does specialization explain rarity and decline among British bumblebees? A response to Goulson et al. *Biological Conservation* 122: 33–43.
- Williams, P.H. 2007. The distribution of bumblebee colour patterns worldwide: possible significance for thermoregulation, crypsis, and warning mimicry. *Biological Journal of the Linnean Society* 92: 97–118.
- Williams, P.H., Araujo, M.B. and Rasmont, P. 2007. Can vulnerability among British bumblebee (*Bombus*) species be explained by niche position and breadth? *Biological Conservation* 138: 493–505.
- Williams, P.H., Cameron, S.A., Hines, H.M., Cederberg, P. and Rasmont, P. 2008. A simplified sub-generic classification of the bumblebees (genus *Bombus*). *Apidologie* 39: 46–74.
- Williams, P.H. and Osborne, J.L. 2009. Bumblebee vulnerability and conservation world-wide. *Apidologie* in press.
- Williams, P.H., Tang, Y., Yao, J. and Cameron, S.A. 2009. The bumblebees of Sichuan (Hymenoptera: Apidae, Bombini). *Systematics and Biodiversity* 7, in press.
- Willmer, P.G., Bataw, A.A.M. and Highes, J.P. 1994. The superiority of bumblebees to honeybees as pollinators: insect visits to raspberry flowers. *Ecological Entomology* 19: 271–284.
- Wills, R.T., Lyons, M.N. and Bell, D.T. 1990. The European honey bee in Western Australian kwongan: foraging preferences and some implications for management. *Proceedings of the Ecological Society of Australia* 16: 167–176.
- Willson, M.F. and Ågren, J. 1989. Differential floral rewards and pollination by deceit in unisexual flowers. *Oikos* 55: 23–29.
- Wilms, J. and Eltz, T. 2008. Foraging scent marks of bumblebees: footprint cues rather than signals. *Naturwissenschaften* 95: 149–153.
- Wilms, W., ImperatrizFonseca, V.L. and Engels, W. 1996. Resource partitioning between highly eusocial bees and possible impact of the introduced Africanized honey bee on native stingless bees in the Brazilian Atlantic Rainforest. *Studies on Neotropical Fauna And Environment* 31: 137–151.
- Wilms, W. and Wiechers, B. 1997. Floral resource partitioning between native *Melipona* bees and the introduced Africanized honey bee in the Brazilian Atlantic rain forest. *Apidologie* 28: 339–355.
- Wilson, E.O. 1971. *The Insect Societies*. Harvard University Press, Cambridge, MA.
- Wilson, E.O. 1990. *Success and Dominance in Ecosystems: The Case of the Social Insects*. Ecology Institute, Oldendorf/Luhe, Germany, pp. 104.
- Wilson, P. and Stine, M. 1996. Floral constancy in bumble bees—handling efficiency or perceptual conditioning. *Oecologia* 106: 493–499.
- Wilson, P. and Thomson, J.D. 1991. Heterogeneity among floral visitors leads to discordance between removal and deposition of pollen. *Ecology* 72: 1503–1507.
- Wilson, P., Thomson, J.D., Stanton, M.L. and Rigney, L.P. 1994. Beyond floral Batemanian—gender biases in selection for pollination success. *American Naturalist* 143: 283–296.
- Wiltschko, W. and Wiltschko, R. (1988) Magnetic orientation in birds. In: *Current Ornithology* (ed. R.F. Johnston), Vol 5, pp. 67–121. Plenum Press, London, New York.
- Winston, M.L. 1987. *The Biology of the Honey Bee*. Harvard University Press, Cambridge, MA.
- Winston, M.L. and Graf, L.H. 1982. Native bee pollinators of berry crops in the Fraser Valley of British Columbia. *Journal of the Entomological Society of British Columbia* 79: 14–20.
- Winston, M.L. and Scott, C.D. 1984. The value of bee pollination to Canadian apiculture. *Canadian Beekeeping* 11: 134.



- Winter, K., Adams, L., Thorp, R., Inouye, D., Day, L., Ascher, J. and Buchmann, S. 2006. Importation of non-native bumble bees into North America: potential consequences of using *Bombus terrestris* and other non-native bumble bees for greenhouse crop pollination in Canada, Mexico and the United States. A white paper of the North American Pollinator Protection Campaign (NAPPC).
- Witjes, S. and Eltz, T. 2007. Influence of scent deposits on flower choice: experiments in an artificial flower array with bumblebees. *Apidologie* 38: 12–18.
- Witte, G.R., Segre, J. and Häfner, N. 1989. Spatial vision in arthropods. In: *Handbook of Sensory Physiology* (eds H. Autrum, R. Jury, W.R. Loewenstein, D.M. Mackay, H.L. Teuber), Vol VII/6C. Springer Verlag, 1981, pp. 98–201. Hummelschauanlagen. Veröffentl. des Schulbiologiezentrums, Hannover.
- Wojtowski, F. and Majewski, J. 1964. Observations and experiments on the settlement of bumble bees in nest boxes. *Roczniki Wyższej Szkoły Rolniczej w Poznaniu* 19: 185–196.
- Wolda, H. and Roubik, D.W. 1986. Nocturnal bee abundance and seasonal bee activity in a Panamanian forest. *Ecology* 67: 426–433.
- Wolf, S. and Moritz, R.F.A. 2008. Foraging distance in *Bombus terrestris* L. (Hymenoptera: Apidae). *Apidologie* 39: 419–427.
- Wolf, T.J., Ellington, C.P., Davis, S. and Fletham, M.J. 1996. Validation of the doubly labelled water technique for bumblebees *Bombus terrestris* (L.) *Journal of Experimental Biology* 199: 959–972.
- Wolf, T.J., Ellington, C.P. and Begley, I.S. 1999. Foraging costs in bumblebees: field conditions cause large individual differences. *Insectes Sociaux* 46: 291–295.
- Wolf, T.J. and Schmid-Hempel, P. 1989. Extra loads and foraging life span in honeybee workers. *Journal of Animal Ecology* 58: 943–954.
- Woodward, D.R. 1990. Food demand for colony development, crop preference and food availability for *Bombus terrestris* (L.) (Hymenoptera: Apidae). PhD thesis, Massey University, Palmerston North, New Zealand.
- Woodward, D.R. 1996. Monitoring for impact of the introduced leafcutting bee, *Megachile rotundata* (F) (Hymenoptera: Megachilidae), near release sites in South Australia. *Australian Journal of Entomology* 35: 187–191.
- Woodward, G.L. and Laverty, T.M. 1992. Recall of flower handling skills by bumblebees: a test of Darwin's interference hypothesis. *Animal Behaviour* 44: 1045–1051.
- Worden, B.D. and Papaj, D.R. 2005. Flower choice copying in bumblebees. *Biology Letters* 1: 504–507.
- Woyke, J. 1963. Drone larvae from fertilized eggs of the honeybee. *Journal of Apicultural Research* 2: 19–24.
- Woyke, J. 1979. Sex determination in *Apis cerana indica*. *Journal of Apicultural Research* 18: 122–127.
- Wratt, E.C. 1968. The pollinating activities of bumble bees and honey bees in relation to temperature, competing forage plants, and competition from other foragers. *Journal of Apicultural Research* 7: 61–66.
- Xie, Z.H., Williams, P.H. and Tang, Y. 2008. The effect of grazing on bumblebees in the high rangelands of the Eastern Tibetan Plateau of Sichuan. *Journal of Insect Conservation* 12: 695–703.
- Yarrow, I.H.H. 1970. Is *Bombus inexpectatus* (Tkalcu) a workerless obligate parasite? (Hym. Apidae). *Insectes Sociaux* 17: 95–112.
- Yazgan, M.Y., Leckman, J.F. and Wexler, B.E. 1996. A direct observational measure of whole body turning bias. *Cortex* 32: 173–176.
- Yokoi, T. and Fujisaki, K. 2007. Repellent scent-marking behaviour of the sweat bee *Halictus (Seladonia) aerarius* during flower foraging. *Apidologie* 38: 474–481.

- Yokoi, T., Goulson, D. and Fujisaki, K. 2007. The use of heterospecific scent marks by the sweat bee *Halictus aerarius*. *Naturwissenschaften* 94: 1021–1024.
- Yoneda, M., Furuta, H., Tsuchida, K., Okabe, K. and Goka, K. 2008. Commercial colonies of *Bombus terrestris* (Hymenoptera: Apidae) are reservoirs of the tracheal mite *Locustacarus buchneri* (Acari: Podapolipidae). *Applied Entomology and Zoology* 43: 73–76.
- Young, A., Boyle, T. and Brown, T. 1996. The population genetic consequences of habitat fragmentation for plants. *Trends in Ecology and Evolution* 11: 413–418.
- Yourth, C.P., Brown, M.J.F. and Schmid-Hempel, P. 2008. Effects of natal and novel *Crithidia bombi* (Trypanosomatidae) infections on *Bombus terrestris* hosts. *Insectes Sociaux* 55: 86–90.
- Yourth, C.P. and Schmid-Hempel, P. 2006. Serial passage of the parasite *Crithidia bombi* within a colony of its host, *Bombus terrestris*, reduces success in unrelated hosts. *Proceedings of the Royal Society of London B* 273: 655–659.
- Zayed, A. and Packer, L. 2001. High levels of diploid male production in a primitively eusocial bee (Hymenoptera: Halictidae). *Heredity* 87: 631–636.
- Zayed, A. and Packer, L. 2005. Complementary sex determination substantially increases extinction proneness of haplodiploid populations. *Proceedings of the National Academy of Sciences USA* 102: 10742–10746.
- Zayed, A., Roubik, D.W. and Packer, L. 2004. Use of diploid male frequency data as an indicator of pollinator decline. *Proceedings of the Royal Society of London* 271: S9–S12.
- Zeuner, F.E. and Manning, F.J. 1976. A monograph of fossil bees (Hymenoptera: Apoidea). Bulletin of the British Museum (Natural History). *Geology* 27: 151–268.
- Zimmerman, J.K. and Aide, T.M. 1989. Patterns of fruit production in a neotropical orchid: pollinator vs. resource limitation. *American Journal of Botany* 76: 67–73.
- Zimmerman, M.L. 1979. Optimal foraging: a case for random movement. *Oecologia* 43: 261–267.
- Zimmerman, M.L. 1981a. Nectar dispersion patterns in a population of *Impatiens capensis*. *Virginia Journal of Science* 32: 150–152.
- Zimmerman, M.L. 1981b. Patchiness in the dispersion of nectar resources: probable causes. *Oecologia* 49: 154–157.
- Zimmerman, M.L. 1981c. Optimal foraging, plant density and the marginal value theorem. *Oecologia* 49: 148–153.
- Zimmerman, M.L. 1982. Optimal foraging: random movement by pollen collecting bumblebees. *Oecologia* 53: 394–398.
- Zimmerman, M.L. 1983. Plant reproduction and optimal foraging: experimental nectar manipulations in *Delphinium nelsonii*. *Oikos* 41: 57–63.
- Zimmerman, M. and Cook, S. 1985. Pollinator foraging, experimental nectar-robbing and plant fitness in *Impatiens capensis*. *American Midlands Naturalist* 113: 84–91.
- Zimmerman, M.L. and Pyke, G.H. 1986. Reproduction in *Polemonium*: patterns and implications of floral nectar production and standing crop. *American Journal of Botany* 73: 1405–1415.

*This page intentionally left blank*

# Index

- Acarina 71–73  
*Aconitum* 113, 117, 152, 158, 200  
*Aconitum columbianum* 152  
*Aconitum napellus* 117  
*Aconitum septentrionale* 113, 200  
*Aconitum variegatum* 117  
*Acrostalagmus* 67  
*Actinidia deliciosa* 162, 166  
*Aeropetes tulbhagia* 113  
Aggression, see conflict  
Alfalfa, see *Medicago sativa*  
*Allium schoenoprasum* 125  
Alloethism 16, 21, 26, 28, 32  
Allozymes 48, 194  
Amino acids 127–128  
*Anacamptis morio* 125  
*Anacardium occidentale* 231  
*Anchusa officinalis* 106  
*Anodontobombus* 3  
*Antherophagus nigricornis* 73  
*Anthidium manicatum* 143, 148, 149  
*Anthophora* 1, 67, 89, 103, 132, 148  
*Anthophora abrupta* 89  
*Anthophora pilipes* 132  
*Anthophora plumipes* 148  
Anthophoridae 1, 142  
*Aphomia sociella* 61, 214  
Apiaceae 113, 158  
*Apicystis bombi* 69  
*Apis mellifera*: 25, 26, 85, 144, 163, 189, 221, 224, 235;  
africanized 205, 222, 223, 226  
*Apodemus sylvaticus* 61  
Apple, see *Pyrus malus*  
Argentina 171, 220, 225  
*Argiope aurantia* 59  
Artificial insemination 55, 56, 69, 70  
*Ascospaera aggregata* 230  
*Ascospaera apis* 229  
Asia 2–3, 12, 45, 195, 220  
Asilidae 59  
*Aspergillus candidus* 67  
Australia 162, 171, 191, 219, 220, 222, 224, 226–227, 231,  
232, 235, 236, 237  
Bacterial pathogens 66  
Badger; see *Meles meles*  
*Banksia ornata* 231  
Barberry shrub, see *Berberis darwinii*  
*Beauveria* 67  
Bee-eater, see *Merops apiaster*  
Behavioural changes, following parasitisation 63, 68  
*Berberis darwinii* 234  
*Bettsia alvei* 230  
Blueberry, see *Vaccinium*  
*Boettcharia litorosa* 65  
*Bombias* 3, 4  
*Bombus alpinus* 14  
*Bombus americanorum* 60  
*Bombus appositus* 152, 175  
*Bombus armeniacus* 180  
*Bombus ashtoni* 181  
*Bombus atratus* 12, 14, 31, 50  
*Bombus balteatus* 14  
*Bombus bifarius* 50, 51  
*Bombus bimaculatus* 64  
*Bombus bohemicus* 49, 78  
*Bombus borealis* 180  
*Bombus brodmannicus* 113  
*Bombus californicus* 46, 51, 185  
*Bombus campestris* 158  
*Bombus confusus* 45, 51  
*Bombus consobrinus* 113, 117, 200  
*Bombus crotchii* 46  
*Bombus cryptarum* 5, 117  
*Bombus cullumanus* 117, 177, 180  
*Bombus dahlbomii* 4, 14, 232  
*Bombus distinguendus* 156, 177, 179, 184, 192, 193, 195,  
196, 198, 200, 203, 215  
*Bombus diversus* 31, 140, 151, 194  
*Bombus edwardsii* 16, 32  
*Bombus fervidus* 35, 46, 64, 66, 117  
*Bombus flavifrons* 64, 86, 112, 152, 157, 158  
*Bombus florilegus* 196, 199  
*Bombus franklini* 180, 188, 229  
*Bombus frigidus* 5, 11, 50, 51  
*Bombus gerstaeckeri* 113  
*Bombus griseocollis* 45  
*Bombus hortorum* 8, 11, 14, 47–49, 71–73, 97, 126, 134,  
141, 142, 151, 154–156, 158, 164, 169, 173, 199, 201, 202,  
205, 209, 219, 220, 227  
*Bombus humilis* 126, 155, 158, 177, 201  
*Bombus huntii* 11, 14, 28

- Bombus hyperboreus* 5, 76  
*Bombus hypnorum* 5, 10, 11, 27, 41, 42, 51, 53, 55, 56, 62, 71, 76, 158, 177, 196, 197, 200, 220  
*Bombus hypocrita* 48, 151, 227, 228  
*Bombus ignitus* 41, 103, 151, 195, 196, 229  
*Bombus imitator* 4  
*Bombus impatiens* 15, 66, 67, 103, 116, 118, 123, 124, 137, 140, 164, 167, 182, 188, 191, 231, 236  
*Bombus incarum* 12  
*Bombus inexpectatus* 76  
*Bombus jonellus* 11, 14, 175, 196, 197, 201  
*Bombus kashmirensis* 58  
*Bombus lapidarius* 11, 14, 29, 33, 35, 48, 54, 64, 72, 73, 78, 95–96, 97, 99, 105, 108, 110, 111, 112, 142–144, 146, 154, 156, 158, 173, 190, 196, 199, 201, 202, 203, 204  
*Bombus lapponicus* 14, 48, 51  
*Bombus lucorum* 3, 5, 8, 27, 35, 36, 41, 42, 46, 47, 48, 63, 64, 65, 72, 74, 76, 78, 87, 105, 152, 154, 155, 156, 157, 158, 159, 169, 173, 175, 190, 193, 194, 196, 199, 201, 202  
*Bombus magnus* 201  
*Bombus mastrucatus* 173  
*Bombus medius* 14  
*Bombus melanopygus* 10, 41  
*Bombus mendax* 45  
*Bombus mexicanus* 14  
*Bombus monticola* 48, 180, 194, 197  
*Bombus morio* 8, 31  
*Bombus morrisoni* 46  
*Bombus muscorum* 46, 51, 62, 95, 177, 195, 196, 197, 199, 201, 204  
*Bombus nevadensis* 45  
*Bombus niveatus* 6, 46  
*Bombus occidentalis* 173, 175, 180, 188–189, 191, 226, 229  
*Bombus pascuorum* 8, 10, 23, 33, 50, 54, 62, 63, 64, 65, 66, 72, 95, 97, 98, 99, 105, 106, 121, 122, 142, 143, 145, 154, 156, 157, 158, 164, 169, 173, 174, 175, 183, 185, 190, 191, 195, 196, 199, 201, 202, 204, 205, 209, 229, 230  
*Bombus pennsylvanicus* 33, 66, 117  
*Bombus perplexus* 23  
*Bombus polaris* 5, 8, 16, 18, 76  
*Bombus pomorum* 177  
*Bombus pratorum* 5, 8, 11, 35, 62, 65, 72, 78, 96, 97, 99, 126, 142, 152, 154, 156, 157, 158, 159, 173, 196, 197, 199, 201  
*Bombus pyrenaeus* 158  
*Bombus regeli* 46  
*Bombus ruderarius* 46, 76, 95, 158, 180, 201, 204  
*Bombus ruderatus* 57, 151, 158, 164, 171, 180, 201, 219, 220, 227, 232  
*Bombus rufocinctus* 4, 15, 45, 51, 76, 157, 158  
*Bombus rufofasciatus* 58  
*Bombus rupestris* 78  
*Bombus serratissima* 180  
*Bombus sidemii* 180  
*Bombus sonorus* 46  
*Bombus soroensis* 97, 158, 177, 201, 202  
*Bombus subterraneus* 46, 57, 126, 156, 177, 184, 192, 197, 199, 200, 201, 203, 212, 215, 219, 220, 227  
*Bombus sylvarum* 5, 95, 158, 177, 178, 184, 192, 193, 195, 196, 198, 199, 200, 201, 202, 204, 212, 215  
*Bombus sylvestris* 46, 48, 78  
*Bombus ternarius* 23, 33, 154, 180, 182  
*Bombus terrestris* 5, 7, 8, 11, 12, 19, 22, 23, 24, 25, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 39, 40, 41, 42, 47, 48, 50, 51, 52, 53, 54, 55, 56, 57, 61, 62, 63, 64, 65, 66, 68, 69, 70, 72, 74, 76, 77, 78, 83, 84, 87, 89, 91, 92, 93, 94, 95, 96, 97, 98, 99, 104, 105, 120, 121, 123, 124, 125, 126, 135, 136, 137, 138, 140, 142, 143, 144, 145, 147, 148, 151, 152, 154, 155, 156, 157, 158, 152, 164, 165, 167, 169, 170, 171, 173, 174, 175, 183, 185, 186, 188, 190, 191, 194, 195, 196, 199, 200, 201, 202, 203, 204, 208, 214, 219, 220, 221, 222, 223, 224, 225, 227, 228, 229, 230, 232, 233, 234, 235, 236  
*Bombus terricola* 8, 23, 31, 41, 42, 154, 180–181, 188, 229, 231  
*Bombus transversalis* 6, 62  
*Bombus vagans* 29, 31  
*Bombus variabilis* 180  
*Bombus vestalis* 50, 65, 77, 78  
*Bombus veteranus* 158  
*Bombus vosnesenskii* 16, 19, 32, 185, 186, 203  
*Bombus wilmattae* 16  
*Bombus wurflenii* 158  
*Borago officinalis* 154  
*Brachicoma devia* 64  
*Brachicoma sarcophagina* 64  
Braconidae 65  
*Brassica campestris* 166  
*Brassica juncea* 162  
*Brassica napus* 98, 162, 166  
Brood care 6–10, 12, 15, 18, 19, 25, 27–28, 76  
Brood clump 6, 7, 9, 18, 23  
Broom, see *Cytisus scoparius*  
Buzz pollination 163, 164  
  
California 185, 186, 208, 226  
*Calluna vulgaris* 213  
*Camelina sativa* 168  
Canada 62, 63, 64, 67, 152, 162, 167, 169, 187, 216, 230  
*Candida* 67  
*Capsicum* 166  
*Carduus* 79  
*Carduus acanthoides* 133  
Carpenter bees, see *Xylocopa*  
Caste determination 21, 22–25  
*Centaurea* 79, 128, 154, 210, 233  
*Centaurea solstitialis* 233–234  
*Cephalosporium* 67  
*Cerceris tuberculata* 88

- Cerinth* 113  
*Chalicodoma muraria* 88  
 Chalkbrood, see *Ascospaera apis*  
 Chile 171, 220  
*Chilopsis linearis* 175  
*Cimicifuga simplex* 135  
*Cirsium* 79, 128, 208  
*Cirsium arvense* 233  
*Citrullus lanatus* 165, 166  
*Citrus* 166  
*Clethrionomys* 61  
 Climate 2, 8, 12, 14, 17, 18, 32, 163, 171, 172, 219, 222  
 Coat length 14, 18, 156, 165, 222  
 Coexistence 151–154, 159, 222, 227  
 Colorado 152, 153, 173, 223  
 Commensals 11, 20, 66, 73, 205  
 Commercial rearing 7, 66, 165–167, 188–191, 216, 220, 230, 237  
 Communication 2, 21, 137–139, 148, 223  
 Compass: magnetic 104; sun 90  
 Competition: among parasitoids 64; for flower 103, 123, 140, 221; for mates 43; for nest sites 227–228; for pollination services 114; interspecific 20, 148, 151–159, 188, 190, 191, 199, 200, 221, 222–227, 231, 237; intra-colony 33, 38, 39, 94, 95  
 Competition point 36–39  
 Conflict, intra-colony 21–40, 53, 56, 70, 77  
 Conopidae 31, 62–64  
*Conops* 62  
 Conservation 168, 170, 177–218  
 Conservation headlands 168, 206, 207, 212  
 Copulation 45, 52, 54–55  
*Cordyceps* 67  
 Corolla depth 33, 151–153, 155, 173, 202, 209, 215, 232, 233  
*Corydalis caseana* 175  
*Cosmea maritima* 168  
 Cranberry, see *Vaccinium macrocarpon*  
 Creeping thistle, see *Cirsium arvense*  
*Crithidia bombii* 53, 66, 67–70, 188, 191  
 Cuckoo bumblebees; see *Psithyrus*  
 Cucumber, see *Cucumis sativus*  
*Cucumis melo* 162, 166  
*Cucumis sativus* 165, 166, 205  
*Cucurbita* 166, 167  
*Cucurbita pepo* 167  
*Cuphea* 168  
*Cynoglossum officinale* 106  
*Cytisus scoparius* 29, 82, 235  
  
 Dandelion, see *Taraxacum officinale*  
 Darwin's interference hypothesis 115, 116, 120, 122  
 Declines: in bumblebee populations 152, 164, 167, 171, 177–199, 203, 204–205, 216, 225, 228, 229; in floral diversity 172, 181–186  
 Defence, of nest 26, 62, 65, 77  
 Deformed wing virus 66, 191, 230  
*Delphinium* 151  
*Delphinium barbeyi* 152  
 Denmark 59, 68, 72  
 Departure rules from flower patches 104, 107, 111, 112  
 Development time of immature stages 7, 22–24  
 Diet breadth 123, 126, 129, 159, 201, 202–204, 221, 223  
*Digitalis purpurea* 133  
 Diploid males 34, 50, 74, 198–199  
 Dispersal 193–195, 197, 198, 204  
 Distribution, geographic 2, 32, 151, 152, 156, 177–180, 182, 184, 192, 197, 217, 220, 221, 229, 230, 233  
 Division of labour 25, 75  
  
*Echium vulgare* 106, 133, 141, 154, 213  
 Egg-eating 35  
*Eichhornia crassipes* 219  
 Ellington, Charles 82, 83  
 Encapsulation response 31, 73, 74, 136, 198  
*Endrosia sarcitrella* 73  
 Energetics of flight 31, 82, 83, 87–88, 94, 99, 224  
*Ephestia kühniella* 73  
*Erica cinerea* 213  
*Erica tetralix* 213  
 Euglossinae 89, 103  
*Euplusia surinamensis* 89  
 Europe 2, 3, 5, 8, 11, 15, 19, 45, 50, 53, 58, 59, 62, 63, 67, 68, 95, 98, 142, 152, 153, 156, 159, 162, 165, 167, 168, 171, 173, 177, 180, 181, 182, 184, 185, 189, 190, 191, 194, 195, 196, 197, 199, 200, 202, 204, 206, 209, 210, 211, 212, 216, 220, 222, 228, 229, 230, 233, 237  
 Eusociality 1, 2, 21, 26, 52  
 Evolution of bumblebees 1–2  
*Exoneura* 226, 227  
*Exoneura xanthoclypeata* 224  
 Extinction 30, 57, 177, 180, 183, 184, 192, 193, 197–198, 199, 200, 202, 215, 216, 220, 229, 236  
  
 Fabre, Jean-Henri 88  
*Fannia canicularis* 73  
 Fat reserves 10, 11, 22, 69  
*Ficus* 113  
 Fidelity to foraging sites 98, 103, 132  
 Field bean, see *Vicia faba*  
 Field margins 168, 183, 185, 206–211, 216  
 Flight: energetics of 31, 82, 83, 87–88, 94, 99, 224; mechanics of 82; speed 31, 82–83, 87, 89  
 Floral complexity 27, 29, 63, 82, 116, 122, 131, 146, 147–148  
 Floral rewards, assessment of 131–136  
 Floral scent 135, 137  
 Floral symmetry 134–135  
 Flower age 132–133  
 Flower constancy 72, 114–124  
 Flower recognition 120, 134

- Fluctuating asymmetry, of flowers 134–135
- Foraging: also see under nectar or pollen; central place 84, 86; efficiency 29–30, 33, 81, 83, 84, 120, 121, 131, 141, 148, 187, 223, 224, 232; range 31, 84–99, 171, 204, 214, 216, 224, 226
- Formica neorubifibarus* 173
- Fossil bumblebees 2
- Foulbrood, see *Paenibacillus larvae*
- Fox, see *Vulpes vulpes*
- Fragaria x ananassa* 162
- French Guiana 226
- Fructose biphosphatase 14, 15, 155–156
- Gardens 5, 11, 12, 47, 49, 54, 59, 61, 151, 180, 202, 203–204, 213–214, 215
- Genetically modified crops 81, 85
- Gland: Dufour's 141, 142; hypopharyngeal 23; labial 45, 47, 48, 51, 142; mandibular 52, 141; tarsal 142
- Glycine max* 166
- Gorse, see *Ulex europeaus*
- Gossypium* 166
- Grazing 181, 184, 211, 213
- Great grey shrike, see *Lanius excubitor*
- Grevillea X gaudichaudii* 231
- Guard bees 27
- Guizotia abyssinica* 168
- Habitat management 85, 97, 168, 170, 185, 206–215
- Haemolymph 17, 18, 62, 67, 72
- Halictidae 1, 141, 220, 226
- Halictus aerarius* 149
- Handedness 105–106
- Handling, of flowers 27, 29, 82, 91, 108, 110, 113, 115–117, 120, 121, 122, 134, 141, 147, 224
- Haplodiploidy 21, 35, 52, 69, 95, 192
- Hay meadows 181, 185
- Hedgerows 5, 47, 168, 181, 182, 183, 185, 206, 210, 211
- Heinrich, Bernd 13, 88, 82, 83, 87
- Helianthus annuus* 162, 166
- Helicobia morionella* 65
- Hibernation 5, 11, 12, 24, 41, 42, 43, 56, 62, 67, 70, 72, 75, 77, 78, 79, 157, 158, 186, 193, 198, 203, 211
- Hirsutella* 67
- Homing ability 88–91
- Honey stomach 22, 31, 63, 87, 88
- Honeybee, see *Apis mellifera*
- Host range (of parasites and pathogens), 57, 64, 230
- Host selection, by parasitoids 63–64
- Hoverflies, see Syrphidae
- Hypericum perforatum* 213
- Hypoaspis* 72
- Ideal free distribution 102, 106
- Immune response 68, 73–75, 198
- Impatiens capensis* 231
- Inbreeding 50, 193, 197, 198–199, 215, 216
- Inbreeding avoidance 50–51
- Inbreeding in plants 172, 204
- Incubation 6, 7, 9, 18–19, 25, 27
- Innate preferences 114, 134
- Inquilines, see *Psithyrus*
- Intensive farming 87, 99, 153, 168, 169, 170, 181, 182, 185, 192, 204, 206, 212, 216, 224
- Introductions of bumblebees 57, 170–171, 188–191, 194, 199, 219–237
- Israel 220, 225
- Italy 194, 195
- Jamaica 231
- Japan 48, 151, 165, 167, 171, 181, 194, 196, 199, 220, 227, 229, 232, 237
- Juvenile hormone 24
- Kin selection 40, 52
- Kiwifruit, see *Actinidia deliciosa*
- Kuzinia laevis* 72
- Lamiastrum galeobdolon* 33
- Lamium album* 33, 169, 209, 210
- Landmarks 45, 47, 90, 91, 97, 103–104
- Lanius excubitor* 58
- Lathyrus vernus* 171
- Lavandula stoechas* 133
- Leaf-cutter ants, see *Atta*
- Learning 27, 49, 58, 59, 68, 75, 81, 82, 103, 114, 115–117, 119, 123, 124–125, 132, 133, 134, 135, 140, 143, 145–149, 158
- Life cycle of bumblebees 5–12, 76, 79
- Linaria vulgaris* 104, 175
- Locustacarus buchneri* 72, 188, 229
- Lolium perenne* 181
- Longevity 8, 31–32, 136
- Lotus corniculatus* 121, 146, 185, 213, 215
- Lupinus* 162, 166, 168
- Lupinus arboreus* 213, 234
- Lycopersicon esculentum* 162, 163, 164, 165, 166, 167, 168, 171, 186, 188, 220, 236, 237
- Lysandra bellargus* 191
- Lythrum salicaria* 234
- Mallophora bomboides* 60
- Marginal value theorem 102, 107–112
- Mark-recapture 31, 86, 89, 96, 193
- Mate location 10, 12, 43, 45–56
- Matricide 39–40
- Medicago sativa* 162, 166
- Megachile pugnata* 230
- Megachile relativa* 230
- Megachile rotundata* 220
- Megachilidae 163, 220

- Melastoma affine* 231  
*Meles meles* 8, 60, 62  
*Melilotus* 154, 213  
*Melipona fasciata* 85, 223  
 Meliponinae 1, 2, 223, 226  
*Melissococcus pluton* 67  
 Melon, see *Cucumis melo*  
 Memory 68, 81, 115, 116, 119, 123, 124–125  
*Mendacibombus* 3, 4  
*Mephitis mephitis* 60  
*Merops apiaster* 58  
 Microsatellites 39, 41, 46, 76, 77, 95, 195, 196  
*Microtus* 61  
 Mimicry; Batesian 60; Müllerian 3, 58, 77  
*Mimosa pudica* 231  
 Mink, see *Mustela vison*  
 Minoing 123, 139  
*Misumenia vatia* 59  
 Mites, see Acarina  
 Mitochondrial markers 3, 195  
 Models: foraging range 31, 87–88; marginal mosaic 200; optimality 81, 86, 101, 102–112  
 Mole, see *Talpa europea*  
 Monogamy 40, 52, 53, 56, 95, 193  
 Mouse, field, see *Apodemus sylvaticus*  
 Multiple generations 11, 12  
*Muscicapa striata* 58  
 Musk melon, see *Cucumis melo*  
*Mustela nivalis* 60  
*Mustela vison* 61  
 Mutilidae 65–66  
*Mutilla europaea* 65  
*Myopa* 62  
  
 Navigation 88, 90, 97, 99, 103  
 Nectar: as food for larvae 1, 6, 23, 26, 81; as fuel for incubation 7; competition for 140, 148, 151–159, 223, 224, 225, 232; concentration 16, 87, 88, 124, 126, 136; gathering 1, 22, 26, 27, 29, 30, 31, 63, 68, 81, 87–88, 94, 101, 104, 106, 113, 114, 115, 124, 131, 133, 136, 141–149, 157; pesticides in 187; rewards in flowers 16, 20, 33, 104, 126, 131, 133, 134, 137, 140, 141–149, 151, 161, 207, 208, 215, 233; robbing 152, 161, 172–176; storage 6, 8, 9, 136  
 Nematode 66, 70–71, 229  
*Nepeta cataria* 107  
 Nest searching 5, 75, 97, 193  
 Nest sites: 5, 19, 75, 97, 139, 157, 168, 169, 170, 185, 186, 203, 204, 221, 227, 228; artificial 169–170, 211–212  
 Nest size 10, 94, 95  
 Netherlands 165, 172, 229  
 New Zealand 12, 56, 68, 71, 165, 167, 168, 169, 170, 174, 184, 194, 199, 201, 212, 213, 215–216, 219–221, 227, 229, 230, 233, 234, 235  
 Niche differentiation 151–159, 221, 222, 227  
  
 Niger, see *Guizotia abyssinica*  
*Nomia melanderi* 220  
 North America 2, 3, 13, 15, 45, 53, 58, 59, 60, 62, 64, 65, 66, 76, 153, 157, 163, 165, 167, 168, 171, 173, 177, 180, 181, 182, 188, 191, 206, 210, 216, 217, 220, 221, 228, 229, 230, 231, 233, 236  
*Nosema apis* 229  
*Nosema bombi* 67, 68, 188, 230, 237  
  
 Odontobombus 3, 25  
*Odontites verna* 213  
 Oilseed rape, see *Brassica napus*  
*Onobrychis viciifolia* 105, 154, 213  
 Ontario 153, 168, 180, 181, 233  
*Ophrys speculum* 113  
 Orchidaceae 113, 125, 171  
 Organic farming 212–213  
*Osmia cornifrons* 67  
*Osmia rufa* 205  
 Outcrossing, of plants 172, 175, 204  
 Ovarian development: of *Psithyrus* 77; of queens 18, 65; of workers 35, 36, 37, 38, 77, 78  
 Overheating 17, 18, 19, 32, 224  
  
*Paecilomyces farinosus* 67  
*Paenibacillus larvae* 67, 229  
 Panama 223, 226  
*Papaver rhoeas* 98, 210, 213  
 Parasite 21, 41, 53, 56, 62–73, 74–79, 94, 181, 188, 191, 215, 216, 221, 228–231  
*Parasitellus* 71, 72, 73  
*Parasitellus fucorum* 72  
 Parasitoid 31, 35, 62–66, 73, 74, 136, 205  
*Parus caeruleus* 59  
*Parus major* 58, 59, 119  
 Patch use when foraging 85, 87, 88, 94, 98, 102–112, 155, 158  
 Pathogens 53, 55, 67, 68, 69, 73, 74, 188–189, 191, 221, 228–231  
 Pathogen spillover 188–189  
 Patrolling 10, 11, 47–50, 51  
*Pedicularis palustris* 175  
 Pesticides 168, 182, 186–188, 205, 212, 216, 231  
 Petiole 17, 18  
*Phacelia tanacetifolia* 207, 208  
*Phaseolus coccineus* 175  
*Phaseolus lunatus* 166  
*Phaseolus multifloris* 166  
 Phenology 5, 11, 12, 67, 125, 157, 158, 203  
 Pheromones: male-produced 10, 11, 47–50; queen-produced 23–24, 36, 37, 38, 39, 51–52; worker-produced 137, 139  
 Phoresis 71–73  
*Phylidonyris novaehollandiae* 226  
*Physocephala* 62, 63, 64



- Physocephala rufipes* 64  
*Physocephala texana* 62  
*Phyteuma nigrum* 172  
*Pneumolaelaps* 72, 73  
 Pocket makers; see *Odontobombus*  
*Polemonium viscosum* 135, 171  
 Pollen: as food for larvae 1, 6, 7, 9, 23, 25–26, 81, 83; as food for young queens 8; gathering 1, 8, 16, 26, 27, 29, 30, 33, 63, 77, 83–84, 88, 93, 98, 113, 126–130, 131, 133, 134, 157, 158, 190, 201–203; protein content 81, 83, 88, 127–129, 203; quality 126–130  
 Pollen storers; see *Anodontobombus*  
 Pollination 60, 81, 85, 97, 98, 112, 113, 114, 125, 133, 134, 161–176, 204, 205, 208, 216, 219, 220–221, 231, 232, 233–235  
 Pollination syndrome 161, 171  
 Polyandry 10, 21, 41, 52–53, 55, 70  
 Polyethism 26  
 Population structure: of bumblebees 191–199; of plants 98, 231, 232  
*Potentilla erecta* 213  
 Predation 31, 33, 57–62, 69, 94–95, 136, 182  
 Prevalence of infection by parasites 63, 66, 67, 68, 69, 70, 72, 189, 231  
*Proctacanthus hinei* 60  
 Protandry 41, 43, 133  
*Prunus avium* 166  
*Prunus cerasus* 166  
*Prunus communis* 166  
*Prunus domestica* 166  
*Psithyrus* 3, 4, 12, 36, 43, 47, 48, 50, 58, 62, 65, 70, 76, 77–78, 79, 94  
*Pulmonaria* 132  
 Purple loosestrife, see *Lythrum salicaria*  
*Pyrobombus* 4, 155, 197  
*Pyrus malus* 165, 166  
  
 Radar, harmonic 87, 89, 91–93  
 Range expansions 5, 191, 195, 205, 220, 232  
 Recruitment of foragers 96, 106–107, 137–140  
 Relatedness, within nests 22, 35, 52, 53, 148  
 Reintroduction 215–216  
 Resource partitioning 151, 153, 154  
*Rhinanthus* 210, 211, 213  
*Ribes* 166  
*Ribes grossularia* 166  
 Risk aversion 33, 124  
 Robber fly, see *Asilidae*  
*Rubus ideaus* 166  
*Rubus fruticosus* 151, 154, 166, 213  
  
*Salix* 59, 210  
*Salvia splendens* 215  
  
*Sarcophaga* 65  
 Sarcophagidae 64–65  
 Scent-marks 45, 47–51, 140–149  
*Scutacarus* 72, 73  
*Scutacarus acarorum* 72  
 Search image 119–122  
 Search times, for flowers 30, 109–112, 121–122  
 Seed set 232–233, 235–236  
 Selective attention 119  
*Senotainia tricuspsis* 65  
 Set-aside 211, 214  
 Sex determination 34, 35, 52, 198  
 Sex determining locus 34, 198  
 Sex ratios 40–43, 53, 63  
 Shrew, see *Sorex*  
*Sicus* 62  
*Sicus ferrugineus* 31, 63  
 Size variation of workers 25–26, 31, 33, 99, 154  
 Skunks, see *Mephitis mephitis*  
 Social behaviour, evolution of 1  
 Social parasitism 75–79  
*Solanum melongena* 166  
*Solidago canadensis* 154  
*Sorex* 61  
 South Africa 113, 171, 220, 236  
 South America 2, 3, 12, 219, 227, 231, 232  
 Spain 194, 195  
 Specialisation, behavioural 26, 28, 123, 208, 212  
 Species richness 2, 185, 205  
 Sperm competition 53  
 Sperm plugs 54, 55, 56  
*Sphaerularia bombi* 66, 70, 71  
 Sphingidae 13  
 Sphecoidea 2  
 Spiders 31, 58, 59, 60  
*Spiroplasma melliferum* 67  
 Spiroplasmataceae 67  
 Spotted flycatcher, see *Muscicapa striata*  
 Strawberry, see *Fragaria x ananassa*  
 Sunflower, see *Helianthus annuus*  
 Swarming 1, 12  
 Sweden 47, 65, 169, 171, 185, 195, 196, 212  
 Sweet pepper, see *Capsicum*  
 Switching between flower species 111, 115–116, 120, 123–124  
*Symphytum officinale* 114, 145, 154  
*Syntretus* 65  
*Syntretus splendidus* 65  
 Syrphidae 73, 115, 143, 206  
 Systematic searching 90, 103, 104–109, 112  
  
*Talpa europea* 60  
*Taraxacum officinale* 126, 213

- Tasmania 56, 170, 174, 194, 199, 220, 221, 222, 223, 225, 227, 232, 233, 235, 236, 237
- Taxonomy 3, 5, 48
- Territoriality 45–46, 51, 148
- Thermogenesis 13, 14, 15, 16, 155, 156
- Thermoregulation: of bumblebees 13–18, 32, 159; of nest 18–20, 28
- Thoracobombus* 3, 4, 5, 95, 155, 190, 197, 204
- Thresholds, behavioural 19–20, 27, 145–146, 156
- Tineidae 73
- Tomato, see *Lycopersicon esculentum*
- Tongue length 29, 33, 129, 151–153, 155, 159, 164, 173, 201–202, 204
- Translocation 215–216
- Transmission, of pathogens 67, 68, 191, 221, 228–231
- Trap-lining 103
- Tree lupin, see *Lupinus arboreus*
- Trifolium* 105, 162, 166, 182, 185
- Trifolium medium* 212
- Trifolium pratense* 163, 184, 213, 216, 219
- Trifolium repens* 108, 129, 154, 203, 213
- Trigona* 141
- Trigona fulviventris* 149
- Trigona prisca* 2
- Trigonini 86, 223
- Tropaeolum majus* 134
- Tropical bumblebees 1, 2, 12, 18, 31, 55, 62
- Ulex europeus* 235
- Unimproved grassland 181, 182, 183, 184, 185, 201, 203, 204, 213, 216
- United Kingdom 5, 6, 11, 29, 48, 50, 57, 60, 64, 65, 77, 78, 95, 99, 126, 151, 153, 156, 157, 163, 168, 170, 173, 177, 180, 181, 182, 183, 184, 185, 187, 190–194, 197–198, 200, 201, 202, 203, 206, 209, 210, 211, 212, 213, 214, 215, 216, 220, 222, 229
- United States of America 162, 167, 168, 180, 187, 205, 213, 216, 220
- Urban areas 186, 203, 204, 213–215
- Urtica dioica* 208
- Usurpation of nests 75–76, 77, 94, 227
- Vaccinium* 164, 165, 187
- Vaccinium angustifolium* 166
- Vaccinium ashei* 166, 231
- Vaccinium corymbosum* 166, 173
- Vaccinium macrocarpon* 166
- Varroa destructor* 163, 229
- Verticillium lecanii* 67
- Vicia* 155
- Vicia cracca* 29, 121, 201, 213
- Vicia faba* 154, 162, 166
- Vicia villosa* 166
- Virus, entomopox 66
- Visual acuity 30, 120, 190
- Vitula edmandsii* 73
- Vole 61, 62, 185
- Volucella bombylans* 73
- Vulpes vulpes* 60
- Wahlenbergia* 227
- Water hyacinth, see *Eichhornia crassipes*
- Watermelon, see *Citrullus lanatus*
- Wax 6, 9, 19, 25, 26, 61, 71, 73
- Wax moth, see *Aphomia sociella*
- Weasel, see *Mustela nivalis*
- Weeds 175, 182, 185, 186, 199, 206–207, 208, 210, 220, 221, 233–235
- Wildflower seed mixes 206, 208, 209, 210
- Xylocopa* 141, 236
- Xylocopa californica* 230
- Xylocopa varipuncta* 46
- Xylocopa virginica* 142
- Yellow star thistle, see *Centaurea solstitialis*
- Yucca* 113