

factor that increases adult mortality is potentially detrimental to the conservation of seabirds. Thus, the loss of adult birds in fishery bycatch is of great concern. Breeding adults caught in gill nets and/or on long lines result in the loss not only of the adult, but also the chick for which it was caring. The loss of a breeding adult may also result in lower subsequent reproductive output by the surviving parent because it will likely have lower reproductive success during the first year with a new partner. The group most vulnerable to bycatch on long lines appears to be the Procellariiformes, which make shallow dives to grab baited hooks as they enter or leave the water. These are amongst the longest-lived of seabirds, and the curtailment of their breeding lives has a severe impact on their populations. Indeed, the populations of many species of albatross are declining at an alarming rate. A second major threat to seabirds is the presence of introduced predators on the islands where the birds breed. Rats, cats, foxes, and even snakes kill both chicks and attending adults. Again, loss of adult breeding birds has the most potentially serious impact on the future stability of the population. Reduction of anthropogenic sources of adult mortality in seabirds must be one of the most urgent imperatives for conservation biologists and managers.

See also

Alcidae. Procellariiformes. Seabird Conservation. Seabird Reproductive Ecology. Seabird Responses to Climate Change. Seabirds and Fisheries Interactions.

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SEABIRD REPRODUCTIVE ECOLOGY

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Introduction

Finding the food necessary to produce and raise offspring is a fundamental problem that animals face. The oceans, despite being a productive and rich environment, rarely provide a steady or reliable source of food; instead, feeding opportunities are patchily distributed in both time and space. As a consequence, seabirds, from 20g least petrels

(*Halocyptena microsoma*) up to 37kg emperor penguins (*Aptenodytes patagonicus*), have had their life history strategies shaped by the need to cope with this ebb and flow of resources.

The British ornithologist David Lack published two landmark books in 1954 and 1968 that influenced the way that we think about reproduction in birds. Lack hypothesized that the clutch size of birds has evolved so that it represents the maximum number of chicks that can be reared. His logic suggested that food is most constraining when parents have chicks (i.e., the period when they need to both feed themselves and provide enough food for their chicks to grow) and this must inevitably limit how many chicks parents can care for adequately. It

was an attractive idea, linking reproductive effort to food supply. For marine birds, which by definition must feed in a different place from where they breed, this seemed particularly relevant.

However, more recent theoretical developments suggest that it is not so simple. Most seabirds are long-lived and, in the face of many potential breeding opportunities over a lifetime, there are likely to be trade-offs between reproductive effort and adult survival. The advantages of investing in a reproductive attempt must be weighed against the costs in terms of the breeder's survival and future reproductive potential. In essence, natural selection acts as the scales. The birds do not need to make conscious choices: over time, those animals with the best strategies for balancing survival and reproduction – known as life history strategies – will leave more offspring and the genes controlling their behavior will become more prevalent.

Inshore and Offshore Strategies

Seabirds, by the nature of their prey and their requirements for a solid substrate upon which to lay their eggs, are forced to have a dichotomy between the place where they breed and the place where they feed. As such, the distance of their feeding grounds from the colony will potentially have major implications for their reproductive ecology. David Lack noted that seabirds can be divided into two broad categories: inshore foragers and offshore foragers. The amount of food that can be brought back to the nest by those birds that must travel a long way to reach their prey will be limited by transport costs and logistics. As a consequence, Lack observed that offshore foragers tend to have lower rates of reproduction and take longer to fledge their chicks (Table 1). To offset this, offshore foragers tend to be longer-lived, with higher rates of annual survival.

Lack saw inshore and offshore foraging as strategies to deal with a suite of issues that seabirds must face with respect to breeding: at what age to begin breeding, the best time to breed, whether to breed or not, how much to invest in breeding, and whether to abandon a breeding attempt. One way or another, the solutions all involve a relationship

between the reproductive behavior of the birds and their feeding ecology.

At What Age to Begin Breeding?

To maximize lifetime reproductive output in a Darwinian world it might seem obvious that animals should begin breeding as soon as they are able to do so. Paradoxically, this is not always the case, and especially for seabirds. In some species, at least, breeding exacts a toll on the breeder and this cost tends to be disproportionately high for young, inexperienced breeders. Relatively few (17%) Adelle penguins (*Pygoscelis adeliae*) that begin breeding as 4-year-olds survive to see their 12th birthday, whereas those that do not start breeding until 7 years of age almost invariably get to 12 years and beyond. Female fulmars (*Fulmarus glacialis*) that put great effort into breeding in their first few years lead shorter lives and overall produce fewer offspring than those that do not do so.

In addition, young breeders also tend to be less successful in their breeding attempts. Natural selection, rather than simply maximizing the number of offspring produced, gives a competitive edge to those strategies that maximize the number of offspring produced over a lifetime that go on to breed successfully themselves. Just partaking in a breeding attempt will not be advantageous unless the offspring produced are likely to survive and breed. Fulmars that begin breeding later than the modal age for first-time breeders are much more likely to fledge offspring at their first attempt.

Potential young breeders, then, are faced with a double dose of reality: they are less likely to be successful and they are likely to reduce the number of future breeding opportunities available to them. Consequently, many sea birds delay the onset of breeding until well after they are physiologically capable of breeding. For example, fulmars reach adult size at one year of age, but usually they do not begin breeding until males are 8 years old and females are 12 years old. Gray-headed albatross (*Diomedea chrysostoma*) wait even longer and on average begin breeding when they are 13 years old.

Of course, such wait-and-see strategies only make sense in long-lived birds where they can be reasonably certain that they will live to breed another day. In situations where life spans are short and/or interannual survival rates are low (e.g., owing to annual migrations), birds should be inclined to breed at younger ages when the opportunity arises. Common diving-petrels (*Pelecanoides urinatrix*), the most pelagic of all the diving-petrels, begin breeding as 2-year-olds. Mean age of first breeding of

Table 1 Life-history characteristics of inshore and offshore foraging seabirds

Characteristics	Inshore	Offshore
Clutch size	2-3	1
Breeding attempts in season	1-2	1
Relay eggs	Yes	No
Annual survival	High	Very high

penguins (excluding crested penguins) is correlated with their annual survival rates: those species with the shortest expected life spans begin breeding earlier. (The crested penguins are a law unto themselves, not initiating breeding until 7 or 8 years of age, even though their annual survival rates are not high by penguin standards, suggesting that there are other costs to breeding in these species that mitigate the potential advantage to be gained from breeding earlier.)

When Is the Best Time to Breed?

As well as the age at which birds begin breeding, natural selection also influences the timing of breeding within each season. In an environment where resources fluctuate greatly, it will be highly advantageous to breed when resources are abundant. David Lack suggested that, as the chick-rearing period is the period of greatest food demand, breeding should be initiated so that the chick-rearing period coincides with the period when food is most abundant. Evidence for this comes from many seabird studies, which show that those chicks that hatch late in the breeding season are less likely to fledge, or, if they do, they will be smaller and in poorer condition (which will detrimentally affect their survival prospects). (While prey availability is one factor that has shaped the timing of breeding, other factors are also likely to be important. Amongst alcid, for example, late breeders are more susceptible to predation.)

Selection for the timing of breeding to coincide with peaks in seasonal food abundance has resulted in some species of sea birds being highly synchronous in their laying. In roseate terns (*Sterna dougallii*) and short-tailed shearwaters (*Puffinus tenuirostris*) almost all eggs in a colony are laid within the space of 2–3 days. In the short-tailed shearwater, not only is the laying date highly synchronous, but it is also very constant. In this species, breeding off Tasmania, the mean laying date of 25–26 November has not altered in over 100 years, a fact that is well known by the local people who harvest the eggs for food.

The timing of breeding is most likely to be important for those sea birds breeding in high latitudes, where food supply is more variable owing to the more pronounced seasonality and where other environmental factors – such as the brief break-up of pack ice in the polar summer – are often critical for successful breeding. In contrast, sea birds breeding in the tropics experience a more stable environment with a more constant and steady food supply. The lack of clearly defined seasons in the tropics

has enabled some species to forsake the seasonal concept altogether. Audubon's shearwater (*Puffinus lherminieri*) and the Christmas shearwater (*Puffinus nativitatis*) have no defined breeding season and there is little synchrony in laying. One breeding cycle takes about 6 months and, after a 2-month postnuptial molt, pairs begin breeding again.

Whether to Breed or Not?

Individuals face an important decision at the start of every season: whether to breed or not. If a bird is in poor condition or if feeding resources are poor, then a strategy of skipping a breeding attempt, rather than risking its survival and prospects of breeding in subsequent years, may be more profitable.

The occurrence of nonbreeding or 'sabbatical' years was first recognized in the 1930s, and has since been found to occur commonly in many groups of sea birds, including cormorants, gulls, terns, petrels, and penguins. In a detailed 15-year study on Cory's shearwater (*Calonectris diomedea*), it was found that on average around 10% of the breeding population failed to breed in any given year and, while most birds were absent for just a single year, some birds took sabbaticals of up to 7 years' duration. While there are presently few comparative data on the rate at which seabirds skip breeding attempts, the strategy of taking sabbaticals is likely to be most beneficial in long-lived birds. The exact mechanism by which birds 'decide' whether to breed is unknown, but it is likely to involve a physiological response to the body condition of the bird reaching some minimum threshold. As body condition will be influenced by the availability of food, it can essentially function as an indicator for resource abundance.

Other seabirds are constrained from breeding in every year simply because of the duration of their breeding cycle. Among these are some of the largest representatives of both the flying and flightless sea birds; the wandering and royal albatrosses and the king penguin. (The largest of the penguin species, the emperor penguin, gets around the difficulty of managing to fledge a very large chick and still maintain an annual breeding cycle, by initiating breeding during the heart of the Antarctic winter.) Breeding in these species – from the arrival of adults at the very start of the season to the fledging of the chick – takes around 14 months. Hence, successful breeders (those that fledge chicks) are able to breed only in every other year (albatross) or twice in every three years (king penguins).

How Much to Invest in Breeding?

As there will be trade-offs between reproductive effort and adult survival in their effects on lifetime reproductive success, it behoves long-lived species not to invest too much in any given breeding attempt. Resources should be invested in ways that maximize lifetime reproductive success.

For many species of sea bird, evidence suggests that the body condition of individuals (usually measured as the mass of a bird after scaling for body size) is the proximate factor that regulates the level of investment of resources. Experimental and observational studies have shown that individuals will continue to feed a chick or incubate an egg until they reach a low threshold of body condition. At this point, birds will then either desert the egg or feed the chick at a lower rate so as to maintain their own body condition and enhance their survival prospects. Evidence for this comes from the Antarctic petrel (*Thalassoica antarctica*), a long-lived offshore forager. In an experiment where the costs of provisioning the chick were raised, the extra costs were passed onto the chick (by feeding the chick smaller meals and less often) rather than onto the parents (whose body condition remained constant). Relatively few comparable studies have been performed on inshore foraging seabirds but, because of their lower life expectancy and faster rate of reproduction, they could be expected to more readily deplete their body condition (at the risk of their own survival) to ensure the success of a breeding attempt.

While supplying chicks with enough food may be a constraint for many species of seabird, increasing evidence suggests that the availability of food at other periods of the season – courtship, egg production, and incubation – may also affect the level of resources invested into a breeding attempt. In lesser black-backed gulls (*Larus fuscus*), the body condition of females during the prelaying period is an important factor determining both the number of eggs laid and the size of eggs that are produced (egg size is related to the hatching and survival prospects of chicks). A similar relationship between body condition and egg size is found in Hutton's shearwater (*Puffinus huttoni*) (Figure 1), which breeds at altitudes of 1200–1800m in the mountains of New Zealand. In this species the number of available breeding burrows is limited and adults must regularly fly into the breeding colonies to compete for burrows. As a result of this activity, parents lose body condition during the courtship period, and this subsequently affects the amount of resources that females can invest into the egg.

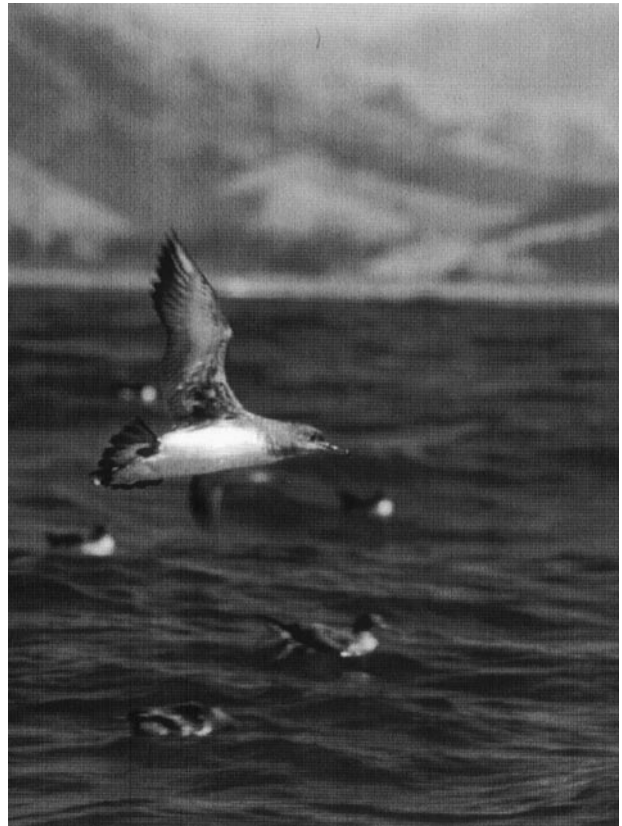


Figure 1 Hutton's shearwaters (*Puffinus huttoni*) exemplify the dichotomy that seabirds face in their need to breed on land and forage on distant marine resources. In this species the breeding colonies are located inland at 1200–1800m in the Seaward Kaikoura Mountains, South Island, New Zealand. (Photo: R. Cuthbert.)

Whether to Abandon a Breeding Attempt?

Having embarked on a breeding attempt, it need not pay a parent to persist with it come hell or high water. Natural selection is not a romantic. Reproductive strategies that enhance lifetime reproductive output will be favored, even if they involve the abandonment of eggs or cute and fluffy chicks.

Internal development of offspring, similar to that in mammals, was never going to be a likely evolutionary option for flying birds, where there were always advantages to be gained from eschewing weight. But the laying of eggs gives birds the opportunity to adjust their reproductive investment early in a breeding attempt, before the costs incurred are too high. When will it pay parents, then, to terminate investment?

When Resources are Low

Parental investment theory predicts that parents should be more inclined to terminate investment

when resources are low, especially if the survival or future reproductive potential of the parent is threatened by persisting with a breeding opportunity in the face of inadequate resources. Seabirds are typically monogamous and have eggs that require a long period of incubation. This necessitates both parents sharing the incubation duties, usually with one bird sitting on the nest while the other is at sea feeding. The sitting bird is unable to eat and, inevitably, there must be a limit to how long it can sustain itself from its fat reserves. Eventually an incubating bird will abandon the nest and eggs.

It is difficult to quantify the proportion of nests lost because of desertion by an unrelieved incubating bird. Frequent surveillance is required to establish causes of loss (very often researchers are faced with just an empty nest, making it hard to ascribe a cause of loss with any certainty) and, compounding this, disturbance caused by frequent surveillance can itself precipitate desertions. Nevertheless, it is clear from those detailed studies that have been carried out on Procellariiformes (petrels and albatross) and Sphenisciformes (penguins), that desertions by unrelieved birds can constitute a major form of egg loss. This is particularly so in poor food years, when increases in the duration of foraging trips are associated with a greater likelihood that the foraging bird's partner will have abandoned the nest by the time it returns.

Early in a Breeding Attempt

Parental investment theory also predicts that parents should be more inclined to abandon their investment early in a breeding attempt (when reproductive costs are low). It is not at all clear how well this prediction is supported, or even how relevant it is for seabirds. In a broad sense, abandonment of the nest may be more likely to occur during incubation rather than during chick rearing in some seabirds; but drawing any definitive support for the prediction from this is complicated because a chick offers a very different stimulus from that of an egg and, as chicks need to be fed, nest reliefs are typically more frequent during chick rearing, reducing the probability that the attending bird will exhaust its energy reserves. Further, although parental investment theory predicts that the sex that has invested least in a breeding attempt should be the one most inclined to terminate investment (because it has the least to lose), this is not always the case (e.g., often at the time of desertion in Adelie penguins (*Pygoscelis adeliae*), it is the abandoning bird that has invested the most). When there is only one breeding opportunity each year, the costs of termination are potentially very high and should not be undertaken

lightly, so seabirds often tend to stick at it until the point where their own survival comes under threat. Hence, ecological constraints, reflected in food supply and foraging times, dictate when seabirds are likely to abandon breeding opportunities rather than levels of relative expenditure.

When Young

Theoretically, young breeders have less to lose from terminating investment in a breeding attempt, because they have more future reproductive opportunities ahead of them than do older breeders. While hazard functions, which display the risk to eggs of being abandoned by parents, do show a heightened risk of abandonment from young breeders in species such as Adelie penguins, it is difficult to separate out the effects of experience from this. That is: Are young breeders more inclined to abandon the breeding attempt because of a lack of experience or because of a strategy to enhance lifetime reproductive output?

There is also controversy about whether the level of investment by seabirds increases with age. One classic study of California gulls (*Larus californicus*) has revealed that the reproductive success of older breeders is greater than for other breeders. The authors put this down to increased effort on the part of the older parents as they had fewer future breeding opportunities. While this explanation sits nicely with parental investment theory, it is also possible that the higher than average breeding success of older breeders simply reflects the effect of experience.

In kittiwakes (*Rissa tridactyla*), reproductive success improves with experience and it has been argued that, even from a theoretical perspective, differences in age-related investment should only occur if annual survival decreases with age. The problem with this last argument is twofold: (1) given a finite maximum life span, even if annual survival rates do not change dramatically until very near the end, birds will have fewer potential breeding opportunities the closer they get to that maximum, and (2) it is very difficult to detect changes in annual survival rates in old birds because there are relatively few studies with the longitudinal data needed to follow annual survival of long-lived seabirds and, even where they exist, sample sizes involving the very oldest birds tend to be very low.

In fulmars, breeding success increases with experience, but only until their 10th year of breeding. Thereafter it remains constant. Data from a 20-year study of little penguins (*Eudyptula minor*) reveals that breeding performance increases with breeding experience up to the 7th year of breeding, but

declines from then on. What is emerging from many of these long-term studies of seabirds is that the quality of individual breeders may override theoretical arguments about age or experience. That is, certain 'high-quality' breeders consistently rear more offspring successfully, they are able to do so more readily in the face of environmental perturbations, and they have better survival. If this is generally the case, as evidenced by kittiwakes, yellow-eyed penguins (*Megadyptes antipodes*) and shags (*Phalacrocorax aristotelis*), then it could also explain the apparent higher productivity of older breeders: that is, those surviving to an older age may be the most successful breeders anyway. Certainly, the one factor that consistently emerges from these studies as explaining most variation in lifetime reproductive output is breeding life span: you have to live to breed.

Inshore and Offshore Strategies Revisited

While it is useful to think of sea bird species as either inshore or offshore foragers, it is important to note that there is a continuum between these extremes. Moreover, studies on several albatross and petrels have shown that some species adopt a strategy of mixing long and short foraging trips that enables them to exploit both inshore and offshore resources. For example, sooty shearwaters (*Puffinus griseus*) breeding on the Snares Islands south of New Zealand make several short and frequent feeding trips, which are good for enhancing chick growth. However, parents use up body reserves during short trips and, when their condition reaches a certain threshold, they embark on a long foraging trip to Antarctic waters that enables them to replenish their own body condition.

Rearing only one chick is a characteristic of offshore foragers, but some researchers have claimed that they are not working to full capacity and could potentially feed more than one chick. Twinning experiments carried out on gannets (*Sula* sp.) and Manx shearwaters (*Puffinus puffinus*) show that, at least in some cases, offshore foragers are capable of providing enough food to rear two chicks. However, these experiments fail to take into account limits at other stages of the breeding cycle and, in particular, impacts on the future reproductive opportunities of the parents.

It is also important to note that the concept of being an inshore or offshore forager has little relevance for some species of seabirds. For example, some skuas (Stercorariidae) and frigate-birds (Fregatidae) obtain much of their food through

Table 2 Reproductive tendencies of inshore and offshore foraging seabirds

Breeding decision	Inshore	Offshore
Age at which to begin breeding	Younger	Older
Best time to breed	Not so critical	Critical
Whether to breed	More inclined	Less inclined
How much to invest	More	Less
Whether to abandon	Less inclined	More inclined

chasing and harassing individuals of other seabird species until they drop or regurgitate their prey (a behavior known as kleptoparasitism), and giant petrels (*Macronectes giganteus*) specialize in scavenging on carcasses.

These species are the exceptions, however, and for most sea birds the concept of an inshore-offshore foraging continuum provides a useful framework for assessing their reproductive tendencies (Table 2).

Coloniality

A discussion of reproductive ecology in seabirds would not be complete without mention of coloniality. Ninety-eight percent of seabirds nest in colonies: groups of nests that can range from a few to a few hundred thousand or more. It has been suggested that seabirds nest together because of habitat constraints, but there are many species where areas suitable for breeding are not limiting and yet the birds are still colonial. Other hypotheses suggest that the colony benefits reproductive behavior through social stimulation, enhanced opportunities for extra-pair matings, allowing assessment of the suitability of a habitat for breeding, and reducing losses due to predation. However, many authors maintain that the main advantage of coloniality is the enhanced foraging efficiency that it promotes. A colony may act as an information centre, whereby birds in the colony learn the location of food by observing or following successful foragers. Alternatively, it may be more efficient to forage in groups and recruitment of members to a foraging group may be facilitated by living together.

Whatever the advantages of colonial living, given the widespread occurrence of colonial breeding in seabirds, they would appear to apply equally well to both inshore and offshore foragers.

Global Effects on Reproductive Strategies

Finally, when considering reproductive strategies of seabirds, large-scale effects need to be borne

in mind. Marine resources vary spatially and temporally. While seasonal patterns occur with a certain level of predictability, environmental stochasticity means that from the breeding seabird's perspective there will be good years and poor years. Population viability analyses reveal that populations of sea birds can be particularly susceptible to catastrophic events. One such cause of reduced breeding performance can be El Niño and La Niña events, which often result in a reduction of available prey or necessitate a switch to poorer-quality alternative prey.

Such environmental uncertainty could be expected to impact upon reproductive life histories. Increases in foraging distances and conservation of breeding life span may be expected. That is, selection should favor offshore foraging strategies that enlarge the potential feeding zone and maximize life span to take advantage of as many good years as possible. Hence, in determining the efficacy of offshore foragers in particular, data from single-season studies are unlikely to be sufficient. Conversely, inshore foragers, which tend to rely on a locally abundant and predictable food supply, are the species most likely to be affected by human activities (e.g., emission of greenhouse gases) that increase environmental stochasticity.

Conclusions

The breeding of seabirds is dictated by life history strategies that have evolved principally in response to food supply. In that sense, David Lack was

correct. However, the situation is more complex than he envisaged. At opposite ends of a continuum there are two broad strategies adopted by seabirds: the James Bond strategy of the inshore foragers (breed fast, die young, and have a good-looking corpse) and the more conservative strategy of the offshore foragers that seeks to maximize lifetime reproductive output by withholding and adjusting investment as necessary to maximize breeding life span. As we learn more about seabirds, we discover that their reproductive behavior is not fixed but can be relatively plastic, adjusting just where they are on that continuum in response to environmental conditions and food availability.

See also

Laridae, Sternidae and Rynchopidae. Seabird Foraging Ecology. Seabird Overview.

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SEABIRD RESPONSES TO CLIMATE CHANGE

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Introduction

This article reviews examples showing how seabirds have responded to changes in atmospheric and marine climate. Direct and indirect responses take the form of expansions or contractions of range; increases or decreases in populations or densities within existing ranges; and changes in annual cycle, i.e., timing of reproduction. Direct responses are

those related to environmental factors that affect the physical suitability of a habitat, e.g., warmer or colder temperatures exceeding the physiological tolerances of a given species. Other factors that can affect seabirds directly include: presence/absence of sea ice, temperature, rain and snowfall rates, wind, and sea level. Indirect responses are those mediated through the availability or abundance of resources such as food or nest sites, both of which are also affected by climate change.

Seabird response to climate change may be most apparent in polar regions and eastern boundary currents, where cooler waters exist in the place of the warm waters that otherwise would be present. In analyses of terrestrial systems, where data are in much greater supply than marine systems, it has been found that range expansion to higher (cooler