ALCIDAE

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Introduction

The auks are seabirds of the northern hemisphere. They form a family (Alcidae) or subfamily (Alcinae) of the order Charadriiformes, which includes the gulls, terns, jaegers, sandpipers, and plovers. They are often considered the northern hemisphere equivalents of the penguins, being well-adapted to underwater swimming. However, all extant species retain the power of flight. They are almost entirely confined to Arctic, Subarctic and Boreal waters and are marine throughout the year, being most common in waters of the continental shelf and slope. Twenty-three species are currently recognized and one other became extinct in historic times (great auk *Pinguinus impennis*). Six species of five genera occur in the North Atlantic and 20, of 10 genera in the North Pacific, south of the Chukchi Sea. Two murres (*Uria* spp.), the dovekie (*Alle alle*) and the black guillemot (*Cepphus grylle*) are circumpolar in distribution.

Many species of auks are extrememly abundant, with common and thick-billed murres (*Uria aalge*, *U. lomvia*), least and crested auklets (*Aethia pusilla*, *A. cristatella*), dovekies and Atlantic puffins (*Fratercula arctica*) all having world populations of >10 million individuals. They form the dominant avian biomass over large areas of Arctic and Subarctic waters throughout the year and may be significant predators on large zooplankton and small fishes in areas around their breeding colonies.

Evolution and Systematics

Recent work on mitochondrial DNA and allozymes divides the family Alcidae into 5 tribes and 12 genera (**Table 1**), with the puffins (Fraterculini) and auklets (Aethiini) being sister tribes, more closely related to one another than to the other auks. Otherwise, the molecular data suggest that the tribes originated from an initial rapid divergence among early members of the family, possibly about 10–12 million years ago.

There is extensive fossil material on the family. The first definite records of auks are from the middle Miocene, about 15 million years ago (Ma), although putative proto-auks have been described from as far back as the Eocene. A subfamily of flightless auks, the Mancallinae, was present in the Pacific during the late Miocene (7–4 Ma). Deposits from California have yielded at least five species of the flightless *Mancalla*, ranging in size from about 1 to 4 kg.

Auks probably originated in the Pacific, where all but two (*Alca, Alle*) of the extant genera are widely distributed, colonizing the Atlantic soon after. Since then, Pacific and Atlantic auks evolved largely in isolation. The Pliocene auk fauna from California was similar in diversity to the recent fauna, but the diversity of auks represented in the Pliocene sediments of eastern North America suggests that the current, relatively small, community of auks in the Atlantic (six species, including the great auk) is not a historical consequence of the lack of connections with the Pacific. Instead, it is a consequence of extinctions during the Pleistocene, presumably as a result, directly or indirectly, of the ice ages.

Characteristics and Adaptations

Auks are well-adapted to underwater swimming. They have compact, streamlined bodies, short wings and very short tails. The feet are placed far back on the body, webbed, with no hind toe; claws are narrow and the tarsus is laterally compressed. The bill is variable in shape and may be highly ornamented in the breeding season. There are 11

Table 1 Tribes and genera of the Alcidae (after Gaston and Jones 1998)

Tribe	*Genus*
Fraterculini	Fratercula
	Cerorhinca
Aethiini	Aethia
	Cyclorhynchus
	Ptychoramphus
Brachyramphini	Brachyramphus
Cepphini	Cepphus
	Synthliboramphus
Alcini	Alle
	Pinguinus
	Alca
	Uria

primary wing feathers and 16–21 secondaries, the outermost primary being very small and the longest being, usually, the tenth. The feather tracts of the back and belly are continuous and, beneath the contour feathers, down feathers are present and dense all over the body. There are 6–8, occasionally 9, pairs of tail feathers.

The fusiform body, with the feet set far back, is common to all underwater swimming birds. Other characters that are common to underwater swimmers, but absent in Charadriiformes that do not dive, are the presence of strongly developed vertebral hypophyses on the last cervical vertebra, and the enlarged number of thoracic vertebrae (8–10 compared to 5–7 in other Charadriiformes). An increase in the number of vertebrae allows for a longer body, while retaining flexibility of movement.

Auks fly with rapid wing-beats and without gliding or soaring, using the spread feet for steering and braking. They generally take off from land with difficulty and use the feet to taxi when taking off from water. Underwater, they swim using the wings as paddles, like penguins. Maneuvering underwater is achieved mainly by asymmetrical strokes of the wings. Air is released from plumage before diving by forcing it from the breast feathers using subcutaneous muscles. On land, the Alcini and Brachyramphini rest on the belly, or on the tarsi, rising to their feet only in walking, whereas Aethiini and Fraterculini are more agile and normally stand with the tarsus erect, rather than horizontal.

The anatomy of the auks is similar to that of other Charadriiformes, except for their specializations towards underwater swimming. They have shorter wings and legs than gulls and shore birds, and the relative length of the humerus is reduced. The covert feathers are stiffer and more extensive, both above and below the wing, an arrangement that reinforces the trailing edge of the wing and closes gaps between adjacent flight feathers. Primaries 6–10 form a closely knit unit with little independent movement, making the wing more effective as an underwater paddle. The rigidity is caused by a greater development of connective tissue, compared to other Charadriiformes. Despite the fact that the primary feathers are very stiff, the leading edge of the wing is very curved on the downstroke, presumably because of water resistance.

The articulating surface of the humerus is much larger in auks than in other Charadriiformes, allowing greater force to be transmitted in swimming. However, like other flighted birds, but unlike penguins, the auks retain considerable flexibility of movement at the articulation of the humerus. The supracoracoideus muscle, which raises the wing during the recovery stroke (2–3% of body mass) is larger than in shore birds and gulls (1.5%) and the pectoralis muscles, the main source of power on the downstroke, although similar in size to those of gulls and shorebirds, are more elongated, with the supracoracoideus lying directly below them. This arrangement improves streamlining, and also improves insulation by distributing stored fat in a thin subcutaneous layer over most of the body, rather than depositing it in discrete pockets, as occurs in many birds.

Underwater, auks swim very jerkily, with a rapid acceleration at each downstroke. Hence, forward propulsion on the upstroke, if any, is relatively small. The wings are held sharply bent at the wrist, reducing the functional surface area to slightly less than half that when spread in flight. The fact that the whole wing area is unnecessary for effective underwater propulsion is emphasized by the fact that all genera except *Aethia* and *Cyclorhynchus* lose their flight feathers simultaneously during the annual postbreeding moult, becoming flightless for a month or more.

The auks have developed many physiological adaptations for prolonged diving, including high blood volume and high levels of myoglobin ($>1\%$ body mass), both of which enhance the bird's ability to store oxygen. Despite these enhancements, many long dives undertaken by thick-billed murres, and probably other auks, exceed the estimated limit for aerobic respiration, requiring the birds to respire anaerobically for a portion of the time underwater. Heart rate and peripheral blood flow also may be restricted.

The digestive system includes a well-developed proventriculus, a muscular stomach and a relatively short intestine. A functional crop is present only in auklets, although there is some croplike development of the lower proventriculus in the puffins. Auklets and dovekies develop diverticulae in the throat while breeding, in which they transport food for their young. Nasal glands, which are used to excrete salt and maintain ion balance, are very well developed.

The dominant plumage color of auks is black above and white below, but *Cepphus* species are mainly black in summer, mainly white in winter, and *Brachyramphus* species are mottled brown in summer (**Figure 1**). Temporary nuptial ornaments, including ornamental plumes on the head and deciduous, brightly colored, horny plates on the bill, are present in the Aethiini and Fraterculini. Sexual dimorphism is very small: males of most species are slightly larger in some dimensions, especially bill

Figure 1 Examples of the Alcidae. (1) Razorbill (*Alca torda*). Adult breeding plumage. Length: 42 cm; approximate body mass: 710 g. Range: North Atlantic Ocean. (2) Brunnich's guillemot (*Uria lomvia*). Other name: thick-billed murre. (a) Adult breeding plumage; (b) adult non-breeding plumage; (c) transitional plumage. Length: 40 cm; approximate body mass: 950 g. Range: North Pacific, North Atlantic and Arctic Oceans. (3) Least auklet (*Aethia pusilla*). Length: 15 cm; approximate body mass: 85 g. Range: North Pacific Ocean. (4) Marbled murrelet (*Brachyramphus marmoratus*). Adult breeding plumage. Length: 25 cm; approximate body mass: 235 g. Range: eastern North Pacific Ocean. (5) Crested auklet (*Aethia cristatella*). (a) adult breeding plumage; (b) adult, non-breeding plumage. Length: 25 cm; approximate body mass: 260 g. Range: North Pacific Ocean. (6) Atlantic puffin (*Fratercula arctica*). Other name: puffin. Adult, breeding plumage. Length: 35 cm; approximate body mass: 470 g. Range: North Atlantic Ocean. (7) Little auk (*Alle alle*). Other name: dovekie. Adult breeding plumage. Length: 20 cm; approximate body mass: 165 g. Range: North Pacific and North Atlantic Oceans, Arctic Ocean. Illustrations from Harrison P (1985) *Seabirds, an identification guide. Revised edition*. Boston, Massachusetts: Houghton Mifflin.

depth. There is no plumage dimorphism and no distinctive immature plumage. First-winter birds generally appear similar to winter-plumage adults, although young *Cepphus* are readily distinguished by their greater mottling.

Diet and Foraging Ecology

The diet of the smaller auks consists largely of zooplankton, especially copepods and euphausiids and larval fishes, although the parakeet auklet *Cyclorhynchus psittacula* takes substantial quantities of jellyfish medusae. The larger auks take a mixture of zooplankton and small fishes and squid, with common murres and *Cepphus* spp., and possibly *Brachyramphus* spp., being mainly piscivorous. Nestling *Uria*, *Alca*, *Brachyramphus*, *Cepphus*, *Cerorhinca*, and *Fratercula* species are all fed predominantly on fish.

Auks that feed mainly on fish tend to have narrower, more pointed bills (low width/gape ratio), and narrower, more cornified, tongues than those that feed on plankton. Planktivorous auks, apart from having broader, shorter bills, have large numbers of fleshy denticles on the palate and the upper surface of the tongue. The convergence of these characters for auks feeding exclusively on plankton is dramatically demonstrated by the parallels between the auklets and the dovekie. These adaptations are also shown within the genus *Uria*, with the predominantly fish-eating common murre having a narrower tongue and fewer palatal denticles than the thick-billed murre, which feeds on a greater variety of prey. Bill depth seems to be unrelated to diet, suggesting that the very deep bills of puffins and auklets may have evolved for secondary sexual purposes, rather than as feeding adaptations.

Auks feed predominantly in continental shelf waters, with species of *Brachyramphus* and *Cepphus* feeding entirely in inshore waters and most other genera occurring mainly within 50–100 km of land. However, *Fratercula* species are found far offshore in winter, including waters beyond the continental shelf. All species feed entirely underwater, with the smaller species diving to maximum depths of 30–40 m and the larger species to over 100 m. The deepest dives are achieved by *Uria* species, which may reach 200 m on occasions. Normal foraging depths for smaller auks are 10–30 m and for larger auks 30–60 m.

Many species take advantage of prey aggregations caused by oceanographic fronts and tidally induced upwellings. Striking examples occur in the passes among Aleutian Islands and other complex archipelagos, where feeding auklets may reach great densities. The prey involved are usually slow-swimming zooplankton such as pteropod mollusks, copepods, euphausiids, and amphipods.

Reproduction

Breeding sites are coastal, except in the marbled and Kittlitz's murrelets, which are also the only solitary nesters, and in the dovekie. Most auks breed on islands, and some species breed exclusively on remote islands well offshore, because islands offer refuge from terrestrial predators and at the same time may be close to foraging areas. Hence, the distribution of breeding auks is much influenced by the distribution of suitable breeding islands.

Most species are highly social while breeding, with a prolonged prebreeding period and extensive courtship activity in which both vocal and visual displays are prominent. All species are socially monogamous and the sexes play equal roles in incubation and in rearing chicks to the age when they leave the colony. Most show a strong tendency to return to the colony where they were reared.

Auks are highly variable in the type of nesting site that they use. None builds a nest: the *Aethia* auklets and some *Synthliboramphus* murrelets use crevices under boulders or among scree, and murres lay their eggs on open cliff ledges or on flat rocky islets (common murre), while puffins, ancient murrelet, and Cassin's auklet often dig extensive burrows in soil. Most of the smaller auks make use of sites that protect them from surface predators, such as gulls and crows: only the largest, the murres, nest in the open in colonies, where their densely packed ranks form a defense against nest predators. Cliffs are frequently used, especially in the Arctic. The other open nesters, the *Brachyramphus* murrelets, are solitary nesters, either on the horizontal limbs of mature trees (marbled murrelet *Brachyramphus marmoratus*, commonly) or on the ground on remote mountain tops (Kittlitz's murrelet *B. brevirostris*).

Like many other small seabirds, some of the auks are nocturnal in their coming and goings to their breeding sites. The *Synthliboramphus* murrelets and whiskered and Cassin's auklets (*Aethia pygmaea*, *Ptychoramphus aleuticus*) are invariably nocturnal, and the rhinoceros auklet (*Cerorhinca monocerata*) is largely nocturnal, but diurnal or crepuscular in some parts of its range. *Brachyramphus* species are normally crepuscular. Everything about the breeding strategies of the auks suggest the dominant influences of predation and kleptoparasitism.

Egg formation is a lengthy process and females spend most of their time away from the colony during the last 10 days before they lay. Clutches consist of one or two eggs and only one brood is reared annually (California populations of Cassin's auklet sometimes rear two). Eggs are thick-shelled and either white, buff, tan, or bluish in ground colour, sometimes with prominent black or brown markings. After clutch completion, the sexes alternate incubation duty, taking equal shares. Laying, in practically all populations, is confined to a span of about 6 weeks, with most eggs being laid within 2–3 weeks. Incubation periods range from 29 to 45 days. The time from the start of incubation to chick departure varies from a minimum of 35 days in the precocial *Synthliboramphus* species to a maximum of more than 80 days in the *Cerorhinca*.

Most species, including the puffins, auklets and razorbill (*Alca torda*) that lay only a single egg, have two lateral brood patches. The murres and the dovekie have a single, central patch, set far back on the belly. Brood patches are a potential site of heat loss. They defeather rapidly at the start of incubation, refeather as soon as hatching occurs, and are small relative to the size of the eggs, so that during incubation only part of the egg's surface is in contact with the patch. Nonbreeders either do not form brood patches or develop only partial patches.

Notwithstanding these adaptations, the insulation of the auks appears to be relatively poor, considering the climates in which they live. To maintain normal avian body temperature, they rely principally on a very high rate of metabolism: basal metabolic rates (the metabolic rate of resting, nondigesting birds) among auks are exceptionally high, compared to those of other birds of similar size.

Hatchlings are covered with a dense, woolly, down plumage. They are active within 1–2 days after hatching and capable of thermoregulation either immediately (*Synthliboramphus*) or within a few days (the rest). All genera except *Synthliboramphus* are semiprecocial and chicks are reared at the nest site for a minimum of 2 weeks. There is no postfledging parental care except in the dovekie, although in *Synthliboramphus*, *Uria*, and *Alca* the young are cared for until some time after departing the colony, which they leave when only partly grown and incapable of sustained flight. Most breeders leave the colony either with their chicks (Alcini and *Synthliboramphus* spp., where there is parental care after departure), or within 1–2 weeks following chick departure. Juveniles, family parties, and postbreeding adults disperse rapidly from the colony area (except young whiskered auklets).

Postbreeding and Wintering

A complete prebasic molt (except in the puffins, where it involves the body plumage only) follows rapidly on the termination of breeding and involves the shedding of nuptial ornaments and the adoption of a generally distinctive nonbreeding (winter) plumage (no change in Craveri's and Xantus' murrelets). In the auklets, primary molt is sequential and begins during chick-rearing, but in other species the primaries are dropped simultaneously, making flight impossible for a period. Most species remain scattered offshore while molting.

Following the annual prebasic molt, most species disperse or shift toward distant wintering areas. However, some populations of common murres and black guillemots return to the area of the breeding colony and commence periodic attendance at the breeding site. This also applies to some populations of marbled murrelets. These birds feed in the same areas practially year-round. However, among most species breeding in Arctic and Subarctic waters, the bulk of the population moves substantially farther south. Young birds tend to disperse farthest and there is usually a disproportionately high representation of first-year birds in 'wrecks'; – the periodic casting ashore of large numbers of weakened birds, often during prolonged storms. Wintering areas and the behavior of auks on the wintering grounds have been less studied than their activities during the breeding season. Detailed studies of feeding ecology in winter have mostly been carried out on species and populations that occur in inshore waters and the winter ecology of many is essentially unknown. Movement toward the breeding colonies begins in February–April, depending on latitude.

Population Dynamics

Annual survival of adult auks is generally greater than 85%, and greater than 95% in some populations of common murres and Atlantic puffins (*Fratercula arctica*), making them among the longest-lived birds. In the longer-lived species, average age at first breeding is 5 years or more, whereas Cassin's auklets, ancient murrelets, and probably some *Aethia* spp. may begin to breed at 2, many at 3 years. Populations contain substantial numbers of nonbreeders. Those in their second summer or older often attend the breeding colony to select mates and breeding sites. Reproductive success increases with age for the first few years of breeding. Comparisons of reproductive success are complicated by the fact that different species depart from the colony at different stages of development. The maximum

productivity is about 1.5 young/pair per year and most average < 1.

Auks and People

Auks and their eggs have been harvested by people from the earliest times and their bones are frequent constituents of middens throughout the coastal areas of the northern hemisphere. The remains of the great auk have been discovered in 40 middens in Norway alone, as well as some in Britain, Iceland, Greenland, and the United States. Excavations in Newfoundland dating to 4000 BP contain many Great Auk bones and they are also found in middens in Florida dating to 3000 BP. All major colonies of thick-billed murres in the eastern Canadian Arctic show traces of Eskimo occupation nearby, usually with associated remains of thick-billed murres. In areas surrounding the Straits of Georgia, British Columbia, common murre remains are widespread in Indian middens dating from the pre-European period, while middens in the Aleutians, some dating to 4000 BP, contain the remains of auklets and puffins, as well as murres.

A variety of techniques were developed for catching auks. One of the most widespread, used by Bering Sea Inuit, Icelanders, and Faeroese to catch puffins, and by the Inuit of north-west Greenland to catch dovekies, was a net at the end of a long pole. The hunter sheltered behind a stone wall, or depression in the ground, and suddenly raised the net in the path of low-flying birds, which were unable to turn in time to avoid it. In Iceland, snares placed on rafts floating offshore were also used to good effect, trapping murres, puffins, and razorbills.

The technique of netting birds flying over the colony is a very efficient way to harvest auks, as the prebreeding component of the population often circles constantly, making them much more vulnerable than the breeders. Similarly, snares placed on boulders or floating rafts used by displaying birds, a method used on St. Lawrence Island to capture least and crested auklets, and in Thule, Greenland, to capture dovekies, select mainly prebreeders. The removal of these birds has much less effect on the population than the killing of breeders and may partly explain how early societies managed to coexist successfully with their prey. It has been estimated that 150 000–200 000 Atlantic puffins were taken annually in Iceland, without any apparent effect on population levels. In contrast, the shooting of breeding birds at colonies that became widespread in Greenland in this century has been the main cause of the drastic decline suffered by thick-billed murre populations there over the past 50 years.

The harvesting of auk eggs has been very common throughout their range and may well have been a factor controlling their distribution on inshore islands accessible to permanent human settlements. On St. Kilda, harvesting of puffin and murre eggs was a regular activity, while in the Queen Charlotte Islands, and throughout the Alaskan islands, the excavation of ancient murrelet and auklet burrows for eggs was a routine spring harvest. Thick-billed murre eggs are harvested in Greenland, Canada, the Pribilof Islands, and Russia.

In addition to their use as food, the skins and ornaments of certain auks were valued for clothing and decoration. Inuit on St. Lawrence Island and Aleuts in the Aleutian chain sewed parkas out of auk skins, especially crested auklets and horned puffins. Elsewhere, puffin and dovekie skins were sewn into inner garments, to be worn under furs. In north-west Greenland, dovekie skins were made into undershirts, while farther south, in Upernavik District, murre skins were made into capes. Dovekie skins had to be softened by chewing; only elderly women did this, as their teeth were worn smooth enough not to damage the delicate skins. The spectacular beaks of puffins and auklets were also used as ornaments by the Aleuts and Inuit of the Bering Sea region, hundreds sometimes being sewn on the outside of a garment, along with the golden crests of tufted puffins.

Commercial exploitation of auk colonies by postindustrial societies resulted in substantial declines. In the Gulf of St. Lawrence, the huge auk colonies visited by Audubon in 1827 were reduced to a mere remnant by the late nineteenth century, while at Funk Island, Newfoundland, the great auk was exterminated largely for its feathers. The common murre population at the Farallon Islands, California, and several large thick-billed murre populations in the Russian Far East and Novaya Zemlya were decimated by egg harvesting.

Substantial harvesting of auks still occurs in several areas. Traditional harvests of murres and puffins continue in Iceland and the Faroes, although reduced from former levels. Relatively small numbers of thick-billed murres are taken by Inuit in the Canadian Arctic, although they form important components of the summer diet at a few settlements. Much larger numbers are taken in West Greenland, where regulations prohibiting the shooting of birds at their colonies were introduced only in 1978 and were still more or less unenforced in 1987. Shooting away from the colonies is still permitted throughout the year in some districts, although subject to seasonal limits in the more populated areas.

The same populations are hunted more heavily off Newfoundland and Labrador in winter, with the annual kill estimated at about 200 000 since 1993. Although it is only legal to kill murres, some razorbills and dovekies, and a few puffins, are also shot.

Although direct harvests have affected several auk species and were responsible for the extermination of the great auk, the effects of mammalian predators, introduced either deliberately, or accidentally, have probably had a much greater impact on auk populations worldwide. The main agents of destruction were foxes, introduced throughout the Alaskan islands for fur farming. Rats have also caused many declines and extirpations. Raccoons and mink have an important impact in some areas, and rabbits, through their effects on vegetation and soil, may also have caused problems for some burrowing species.

Japanese, Craveri's, Xantus' and marbled murrelets are all considered endangered or threatened in one way or another. It is certain that the majority of auk populations are smaller, in many cases much smaller, than they would have been a few centuries ago. Probably, we will see little change in that situation, although programs to eliminate introduced predators from certain important Pacific islands may improve the situation for some species. All auks are very susceptible to contamination by oil and they have formed the majority of seabirds killed in oil spills off Europe and North America. Unlike gulls, they have not profited at all from fisheries wastes. Protection from egging has led to increases of some species in the twentieth century. However, overall, the auks remain precariously dependent on human goodwill for their future survival.

See also

Fish Predation and Mortality. Laridae, Sternidae and Rynchopidae. Network Analysis of Food Webs. Plankton. Seabird Conservation. Seabird Foraging Ecology. Seabird Migration. Seabird Population Dynamics. Seabirds and Fisheries Interactions. Seabirds as Indicators of Ocean Pollution.

Further Reading

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ANTARCTIC CIRCUMPOLAR CURRENT

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The Antarctic Circumpolar Current (ACC) flows eastward around the globe in the Southern Ocean, driven by the strong eastward winds characteristic of southern polar latitudes. Direct and indirect measurements of the total transport of this current are consistent with the idea that average winds drive the average flow. However, abrupt changes in transport do not correspond to changes in local winds, nor do changes occur consistently around the globe. The path of the ACC is controlled by ocean depth through the tendency for large-scale ocean flow to be along lines of constant planetary vorticity (Coriolis parameter divided by depth). Drake Passage is the narrowest constriction to this flow (about 700 km in width). Strong current extends throughout the water column related to an upward tilt of the constant density, temperature, and salinity surfaces to the south. The strongly tilted property surfaces in the ACC allow deep (3–4 km deep) water, originating in the polar North Atlantic, to reach the surface where it is driven northward by the winds, thus completing the circuit. The ACC is composed of three circumpolar, frontal jets, each having about three times the speed of the flow between the fronts. Dynamic instability