THE AUK

A QUARTERLY JOURNAL OF

ORNITHOLOGY

VOL. 101 JANUARY 1984 No. 1

BREEDING ECOLOGY AND EXTINCTION OF THE GREAT AUK (*PINGUINUS IMPENNIS*): ANECDOTAL EVIDENCE AND CONJECTURES[1]

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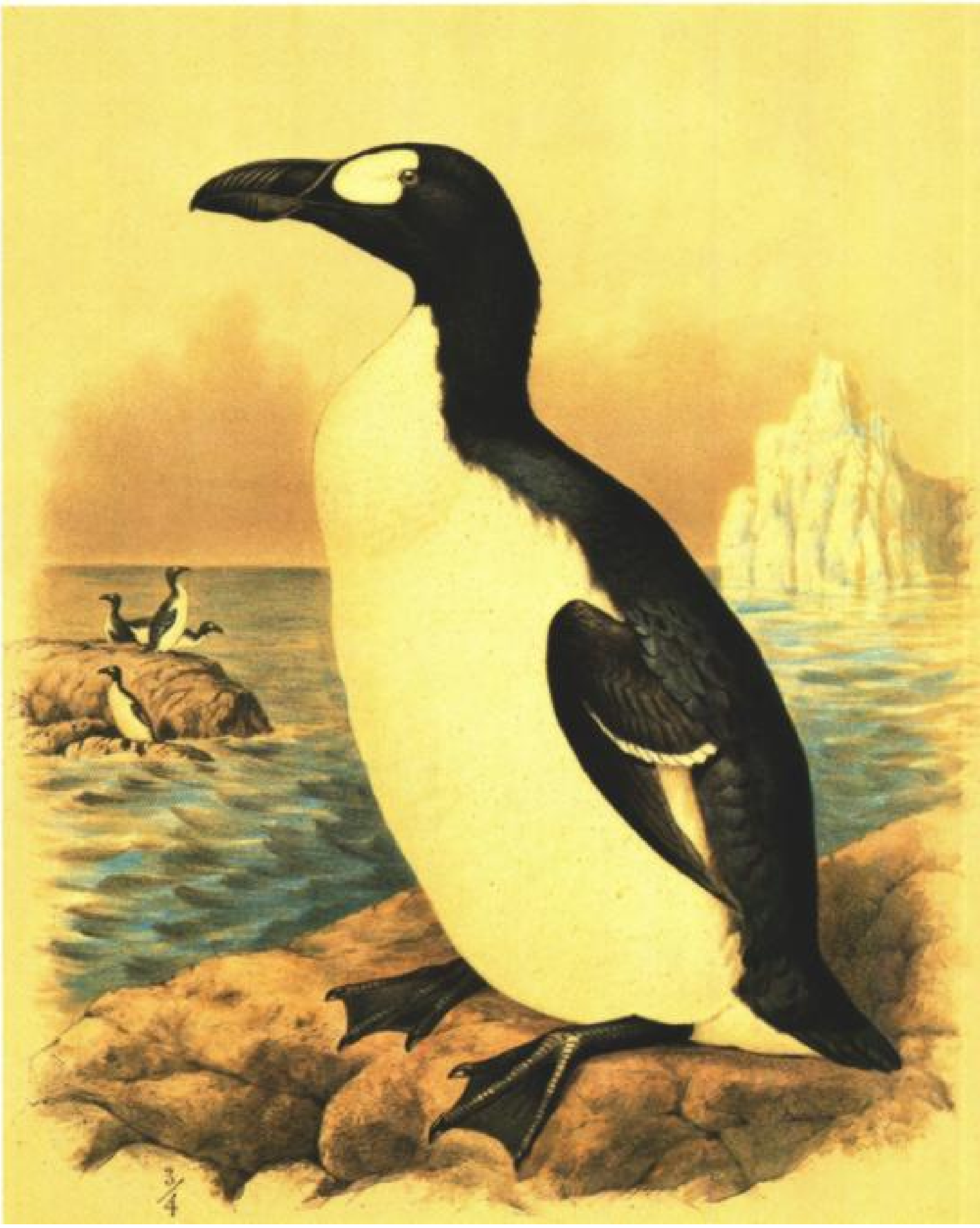
The Garefowl, or Great Auk (*Pinguinus impennis*) (Frontispiece), met its final fate in 1844 (or shortly thereafter), before anyone versed in natural history had endeavoured to study the living bird in the field. In fact, no naturalist ever reported having met with a Great Auk in its natural environment, although specimens were occasionally kept in captivity for short periods of time. For instance, the Danish naturalist Ole Worm (Worm 1655) obtained a live bird from the Faroe Islands and observed it for several months, and Fleming (1824) had the opportunity to study a Great Auk that had been caught on the island of St. Kilda, Outer Hebrides, in 1821.

Notwithstanding the extreme shortage of detailed field observations of living Great Auks, there are numerous published accounts of voyagers having seen and collected the species at sea or on its breeding grounds. Similarly, there is an abundance of fossil records from archeological excavations, and the total literature dealing with the Great Auk is truly impressive. In 1855 Professor Japetus Steenstrup published the first monograph (in Danish), and exactly 30 yr later Symington Grieve's excellent book, "The Great Auk, or Garefowl (*Alca impennis*, Linn.). Its History, Archeology, and Remains," appeared and was dedicated to Steenstrup, "the father of Garefowl history." Another rich source of information is Naumann's (1903) "Naturgeschichte der Vögel Mitteleuropas," which contains hundreds of literature references to the Great Auk.

Thus, the sad history of this grand, flightless auk has received considerable attention and has often been told. Still, the final episode of the epilogue deserves to be repeated. Probably already before the beginning of the 19th century, the Great Auk was gone on the western side of the Atlantic, and in Europe it was on the verge of extinction. The last few pairs were known to breed on some isolated skerries and rocks off the southwestern peninsula of Iceland. One day between 2 and 5 June 1844, a party of Icelanders landed on Eldey, a stack of volcanic tuff with precipitous cliffs and a flat top, now harbouring one of the largests gannetries in the world. The men went ashore on a sloping ledge and, in Newton's (1861) narration, the following took place: "As the men clambered up they saw two Garefowls sitting among numberless other rock-birds (*Uria troile* and *Alca torda*), and at once gave chase. The Garefowls showed not the slightest disposition to repel the invaders, but immediately ran along under the high cliff, their heads erect, their little wings somewhat extended. They uttered no cry of alarm, and moved, with their short steps, about as quickly as man could walk. Jon (Brandsson), with outstretched arms, drove one into a corner, where he soon had it fast. Sigurdr (Islefsson) and Ketil pursued the second, and the former seized it close to the edge of the rock, here risen to a percipice some fathoms high, the water being directly below it. Ketil (Ketilson) then returned to the sloping shelf whence the birds had started, and saw an egg lying on the lava slab, which he knew to be a Garefowl's. He took it up, but finding it was

[1] An invited review.—J.A.W.



FRONTISPIECE. Great Auk (*Alca impennis*). From an engraving in C. B. Cory's "Beautiful and Curious Birds of the World" Part II, February 1881. This engraving was presented to the American Ornithologists' Union by the Nuttall Ornithological Club to commemorate the latter's centennial celebration in October 1973.

broken, he put it down again. Whether there was not another egg is uncertain. All this took place in much less time than it takes to tell it." These were the last living members of the Great Auk ever heard of; later reports of sightings, on both sides of the North Atlantic, could never be sufficiently documented. The two Eldey birds were turned over to a dealer, but the ultimate destiny of the skins is unknown. Their bodies were also saved, and some of the organs are still preserved in the collections of the Museum of Zoology at the University of Copenhagen, the only pickled specimens in existence.

Most writers have, quite understandably, been preoccupied by the decline and disappearance of the Great Auk. This paper focuses on bits and pieces of information that can be used in an effort to draw a picture of its ecology. There is not much reliable first-hand information to be found in the literature on any aspect of its life history (often none at all), so some speculation is an unavoidable necessity. Naturally, many of my conjectures concerning the Great Auk's ecology are strongly influenced by what we know to be true of the ecology of the extant species of the family Alcidae. In the final section of the paper, I discuss the reasons for the extinction of the Great Auk, suggesting major environmental changes as an alternative, or at a least contributing factor, to the commonly held opinion that man alone was responsible.

DISTRIBUTION

The early published accounts frequently (and erroneously) referred to the Great Auk as breeding in "the arctic seas of both continents where it is almost constantly resident" (Bonaparte 1828; see also Temminck 1820, Dumont 1826, Thienemann 1838; all cited in Steenstrup 1855). Steenstrup (1855) disposed of this misunderstanding and made it quite clear that it was a species of the cold-temperate parts of the North Atlantic, in historical times mainly occurring on the western side of the Atlantic. The distribution seems to have been roughly the same as that of the Northern Gannet (*Sula bassanus*). In historical times, however, the western breeding range of the Great Auk may have been very restricted. Many of the accounts given by voyagers and fishermen, who reported mass slaughter of breeding Great Auks in the 16th and 17th centuries, probably refer to the colony on Funk Island off the east coast of Newfoundland (see Grieve 1885). Quite possibly it may also have bred on other islands along the east coast of North America (although see Peters and Burleigh 1951), as birds were frequently encountered on the fishing banks and bones have been found as far south as Florida, although nowhere in such quantities as on Funk Island (for a review see Greenway 1958). Undoubtedly the prehistoric distribution was at times much wider (Salmomonsen 1945), but the exact range is difficult to evaluate solely on the basis of findings of bones in subfossil deposits; being a primarily sea-living bird, the Great Auk surely strayed over large areas outside the breeding season.

Whether or not the Great Auk bred in Greenland cannot be determined, although it is claimed to have done so in the 16th century on skerries in the Angmagssalik District (Salmonsen 1967). However, Salmonsen (1950–1951, 1967) may well be correct in suggesting (on the basis of various evidence) that the Great Auk was a regular visitor along the low-arctic parts of western Greenland between September and January, when mostly younger birds migrated northward from the breeding grounds near Newfoundland.

In Iceland the Great Auk bred on a few isolated skerries and rock islands off the southwestern coast and possibly also in a few other places. It also seems certain that it bred at least occasionally on the island of St. Kilda, in the Orkneys, and possibly also on Shetland and the Faroe Islands. It was certainly regularly observed around these groups of islands, and on the Faroes there are place names that indicate that the sites were used for driving the flightless Great Auks ashore.

It must be taken for a fact that, at the time when the Funk Island colony still flourished (i.e. in the 16th and 17th centuries), the Great Auk had a very limited distribution on the eastern side of the North Atlantic and that the numbers must have been relatively small. In prehistoric times the European distribution was much wider and the subfossil records are extensive (see Greenway 1958). Numerous bones of the Great Auk have been found in kitchen middens from northernmost Norway (the Varanger District; see Olsen 1967) and southward through western Europe into the Mediterranean (Pleistocene deposits in Italy; see Violani

1974). Along the Norwegian coast alone there are about 40 sites where postglacial deposits (2,000–13,000 yr old) contain remains of the Great Auk, often in large quantities and including young birds (see Greenway 1958, Olsen 1967, Hufthammer 1982). A recent morphometric study of Scandinavian bones revealed distinct geographical variation in some osteological characters, and also some variation in time (Hufthammer 1982). This indicates that separate populations of the Great Auk existed in Europe in prehistoric times and that some northward migrations occurred, as it seems unlikely that the species bred in northernmost Norway, despite its rich representation in kitchen middens.

Feeding Habits and Food

The Great Auk was the largest (ca. 70 cm tall) member of the contemporary alcid community, and the only flightless one. It was reported to be an expert swimmer ("left a six-oared boat far behind"; Grieve 1885) and diver. The wings were reduced to a size smaller than those of the allied, but much smaller, Razorbill (*Alca torda*), and they were used for subaqueous flight. The flightlessness of the Great Auk and of the penguins (Spheniscidae) of the southern seas is often given as an example of evolutionary convergence. In this context it may be recalled that the smaller extinct Pliocene Lucas auks (*Mancalla californiensis* and *M. diegense*) had even more flipper-like wings than those of the Great Auk and thus were even more penguin-like (Miller and Howard 1948).

The family Alcidae includes species that feed almost exclusively on plankton (e.g. the murrelets *Synthliboramphus*), fish-eaters (*Uria* and *Alca*), and intermediates (e.g. *Fratercula*). The plankton-feeders have a relatively small body weight and a large ratio of bill-width to gape (gape being the distance from the commissural point to the tip of the culmen), whereas the fish-feeders may be small or large in size but have a small bill-width/gape ratio, the Great Auk being at the extreme end of the scale (Bédard 1969). In fact, the Great Auk was so specialized as a fish-feeder that it sacrificed its ability to fly to become even more adapted to pursue its prey under water.

The old literature records, however, do not contain much reference to the specific food choice (or feeding habits) of the species. In his "Fauna Groenlandica," Fabricius (1780) mentioned *Cottus scorpius*, *Cyclopterus lumpus*, and other fishes of the same size as being taken. The two species mentioned by name undoubtedly occurred in the shallow waters near where the auks bred, but Grieve (1885) was probably correct in assuming that the "other species" were more important. The Icelandic zoologist Saemundsson (1936: 655) stated that the Great Auk was feeding on herring, other small fishes or spawn, and probably also crustaceans. These and other scattered remarks are not of much help in understanding the feeding ecology or the Great Auk—they could apply to any fish-eating alcid. In a recent and very fascinating study, however, Olson et al. (1979) attempted to assess the food of the Great Auk on Funk Island. They assumed that the carcasses of auks slaughtered and eaten on the island had been discarded and left there to decay among the heaps of bones that were later found on the island. Thus, by analyzing soil samples from sites where large quantities of Great Auk bones were accumulated, they hoped to find fish remains originating from the digestive tracts of the birds. In the National Museum of Natural History they found a crate containing a field sample of Great Auk bones, collected by F. A. Lucas on Funk Island in 1887, and from the soil attached to the bones a number of fish remains could be retrieved and identified to species. Most of the remains came from 140–190-mm-long specimens of the menhaden (*Brevoortia* cf. *tyrannus*; Clupeidae), but there were also remains of shad (*Alosa*; sp. Clupeidae), capelin (*Mallotus villosus*; Osmeridae), three-spined stickleback (*Gasterosteus aculeatus*; Gasterosteidae), *Morone* cf. *saxatilis* (Percichthyidae), a flatfish (Pleuronectidae), and some indeterminable teleosts. This list of prey species and ecological and distributional information on the fish species led Olson and his colleagues to make some tentative suggestions about the feeding habits of the Great Auk: While on the breeding grounds at Funk Island it was usually feeding in shallow waters (max. 18 m) and within 2 km of the shore. Moreover, it selected relatively large prey (70–190 mm long; max. about 300 mm) of fat species with a high caloric value; the latter is typical for alcids in general (Harris and Hislop 1978).

In the North Atlantic the large species of alcids overlap considerably in their choice of food, but they select different size-classes of prey in relation to their respective body sizes (Harris 1970, Swennen and Duiven 1977). It seems that the GreatAuk fitted this pattern very well, taking the same species of fish as the other fish-feeding alcids, but with a preference for large prey individuals.

BREEDING BIOLOGY

There are exceedingly few details available concerning the breeding habits of the Great Auk. Here, I have compiled what little information there is in an attempt to reconstruct, in broad and conventional terms, the breeding strategy or ecology of the species. The discussion is largely molded upon modern studies of other species of alcids but is limited by the few "facts" about the Great Auk. Thus, I have good excuses both for speculating and for not doing so.

Behavior.—Auks are decidedly gregarious in their habits, some species more than others. Sightings of Great Auk frequently referred to more than one bird, or small parties in coastal waters. Their behavior was described by Newton (1861) as follows: "they swam with their heads much lifted up, but their necks drawn in . . . [they] never tried to flap along the water, but dived as soon as alarmed . . . [they] sometimes uttered a few low croaks." He also added that "the colour of their mouths is said to have been yellow, as in the allied species." Several other writers briefly remarked that the species was often seen bobbing, or vigorously shaking its head. Head movements, the yellow mouth, and the large oval white patch on either side of the head between the beak and the eye, as well as the markings on the beak, suggest that the Great Auk may have indulged in social and courtship displays similar to those described for other, related species of auks (see Conder 1950, Fisher and Lockley 1954).

Breeding sites.—As stated before, there are only a few known breeding places. Funk Island is a flat and low (14-m) granite rock island about 800 m long and 400 m wide, where today dense colonies of other species of seabirds breed (see Tuck 1961, who also presents habitat photographs). In contrast, Eldey, off southwestern Iceland, is a high (ca. 80-m) basalt rock where the Great Auk bred on a broad ledge sloping into the sea below the northern cliffs of the island (see Fisher and Lockley 1954). The flightlessness of the species clearly put constraints on its choice of nesting sites. The breeding skerries or islands had to provide suitable landing places, where the birds could scramble up a gently sloping ledge or where they could get ashore by riding on the surf. Once on land the Great Auk was reported to move awkwardly, but, topography permitting, it seemed quite prepared to move away from the shoreline and nest some distance from the water, as on Funk Island. When leaving the breeding ledge it "has been known to drop down some two fathoms off the rock into the water" (Newton 1861). Although it has been suggested several times that the Great Auk may have nested also in some mainland sites, it seems more likely that it was confined to outlying, more-or-less isolated, and inaccessible skerries and islands.

The records from Funk Island convincingly testify to the gregariousness of breeding Great Auks; the colony must surely at one time have been both large and dense (see Grieve 1885). Compared with Funk Island, the population around Iceland was probably small (Steenstrup 1855 and others), although there, also, the species bred in colonies: they "had their nests and eggs in common" (Ólafsson and Pálsson 1772). At least in historical times the situation on Funk Island was exceptional, perhaps also in prehistoric times. It has been suggested that the colony size of different seabird species is positively correlated with foraging distance (Diamond 1978; see also Lack 1968, Gaston and Nettleship 1981). This would be consistent with small colonies in the flightless Great Auk. Only where the conditions were exceptionally favorable [i.e. island topography suitable, protection from predators (including man) sufficient, and available inshore food resources abundant], could a breeding place support a large colony.

Time of laying.—The only reference to what might be called the date of land-coming is that of Martin (1698), who visited St. Kilda in 1697 and who stated that the Great Auk "appears the first of May, and goes away about the middle of June." Now it should be remembered that these dates are 11 days later by our present calender. Moreover, it is not clear whether the dates refer to the birds coming on land or just to birds observed around the island. If the latter is true, the Great Auk arrived much later and departed earlier than did the other species of auks breeding there. Assuming that the statement refers to observations of birds on land, it implies that the Great Auk must have accomplished egg-laying, incubation, and fledging (i.e. sea-going of the young) in a period of 6–7 weeks, starting around 12 May. This would mean that laying commenced slightly earlier or at about the same time as in the Razorbill, Common Murre (*Uria aalge*), and Atlantic Puffin (*Fratercula arctica*). However, one should perhaps not put too much confidence in the information from St. Kilda, where the Great Auk probably was not even a regular breeder, and certainly occurred in very small numbers at the time of the statement. According to the old annals, the Icelandic seabird fowlers traditionally visited the skerries and islands where the Great Auk bred about 24 June to collect eggs and birds. We know that the last pair breeding on Eldey had an egg in the first week of June 1844. When the crew of a vessel visited the nearby Geirfuglasker (a skerry destroyed by a series of volcanic eruptions in 1830), however, they raided the Great Auk colony for several days at the end of July and in the first week of August in 1808, and the men are reported to have killed many birds and collected both eggs and young (Newton 1861). A certain spread in the date of laying (within and between years) has commonly been found in most alcid species and colonies. Some of this variation is thought to be due to extrinsic factors (weather) and some to age differences of the birds involved. It is also a general habit of auks to replace an egg that is lost (Kartaschew 1960), which extends the laying period. In this context it is interesting to record that, according to Martin (1698), the Great Auk is said to have been the only seabird species on St. Kilda that did not lay a second egg when the first was lost. Although the data from Iceland are far too scanty to permit any conclusion, I am inclined to agree with Saemundsson (1936), who suggested that laying started at about the same time as in the Razorbill. In southern Iceland the Razorbill, Common Murre, and Atlantic Puffin begin egg-laying at the end of May (Timmermann 1938–1949).

The egg.—The Great Auk laid a clutch of one, the shape of the egg was ovate pyriform, and the ground-color and markings on the shell varied in the same manner as in eggs of the Razorbill. The average size was about 124 × 76 mm, although size varied greatly [length 110–140 mm, breadth 71–84 mm (Bent 1946, Witherby et al. 1958; there are some 80 eggs known from museum collections)]. Individual and seasonal variation in egg size is a typical feature of Alcidae and may be an adaptive response to changes in environmental conditions (Birkhead and Nettleship 1982). The volume of the egg was ca. 300 cm^3 (calculated from Worth 1940), which is considerably more than for the eggs of the Razorbill (ca. 81–83 cm^3; Lloyd 1979) and the Common Murre (ca. 96 cm^3; Mahoney and Threlfall 1981). No wonder that the eggs of the Great Auk were frequently collected for consumption, especially as they were probably also, like eggs of murres, rich in yolk and had high calorific contents (see Tyrova 1939, Kuroda 1963). Steenstrup (1855) quoted Baron Lahotant, who spoke about large birds called "moyacks" (presumably Great Auks) that bred along the northeastern coast of North America and laid eggs "half as big again as a swan's, and yet they are all yolk, and so thick, that they must be diluted with water before they can be used in pancakes."

Incubation.—Presumably both sexes participated in incubation, as they both had one brood-spot each (Faber 1826), just like the murres but unlike the Razorbill and Atlantic Puffin, which have two brood-spots, although they also lay one-egg clutches. The incubation period has been estimated to be 39 ± 5 days, but was probably around 44 (Worth 1940). For comparison, the Razorbill's egg takes about 35 days to hatch (Lloyd 1979) and the Common and Thick-billed (*Uria lomvia*) murres about 30–34 days (Mahoney and Threlfall 1981, Gaston and Nettleship 1981).

Fledging.—Fisher and Lockley (1954) suggested that the fledging period of the Great Auk may have been as short as 9 days; in *Uria* and *Alca* the chicks leave the nesting ledges at an age of about 3 weeks. The estimated fledging time is based on Martin's statement (see above) that the Great Auk on St. Kilda completed the land-based reproductive activities in 6–7 weeks and that incubation lasted about 40 days (see Worth 1940). No other information is available, but a relatively short fledging period is not unlikely, as I will argue below. It also provides an explanation (not necessarily a good one) for the fact that nobody ever gave a detailed and convincing description of a Great Auk chick, and none is known to be preserved in museum collections (although there are ca. 80 skins of full-grown birds)—the chicks spent but a few days on land, and, while at sea, they may have been difficult to catch.

Discussion.—Auk ecology is, for obvious reasons, mostly concerned with events that take place at the breeding sites; the life at sea is far more difficult to study. Often the breeding strategies of alcid species are described and compared in terms of an interplay between feeding habits [food choice, feeding range, food resources, parents' capacity to carry food to the chick(s), etc.], fledging period (growth-rate patterns), and nest-site selection (protection against predation, adverse weather, etc.). When the Great Auk still existed six other species of the family Alcidae also occurred in the North Atlantic [*viz.* Atlantic Puffin, Common Murre, Thick-billed Murre, Black Guillemot (*Cepphus grylle*), Dovekie (*Alle alle*), and Razorbill], although their breeding ranges were only partially overlapping. In several respects the Great Auk was the odd member of the assemblage, and not only because it eventually went extinct. It was the most highly specialized of all for a marine life, being the largest (ca. 5,000 g; estimated by Bédard 1969) and the only flightless one. This probably made it a very efficient fish-feeder (like the penguins), but also imposed certain constraints on breeding performance. For instance, its foraging radius was limited as long as the central place was the egg or the chick on land, and suitable nesting sites that provided both plenty of food at the right time and safety from predators may not have been that common. Because of its body size, the Great Auk may have been able to bring quite large meals to the chick each time one of the parents take the trouble to climb ashore. A full-grown bird, however, usually selected large prey (p. 3), whereas the small chick probably required smaller-sized food items, which may have been more costly to collect. Moreover, a full-grown Great Auk may have required about 1,000 g of fish per day for its own maintenance; an adult murre that weights about ⅕ the weight of a Great Auk needs about 200 g (Sanford and Harris 1967, Marsault 1975). All this taken together suggests that the Great Auk ought to have minimized the amount of time spent on incubation and fledging of the chick. The total energetic costs of producing the offspring cannot be negotiated, only the time pattern of the expenditures. By getting the chick sea-borne the parents could have fed it more easily (although they may not have done so; chicks of some other species are independent when fledged) and the family could have followed the movements of the prey species,which may often have been migratory pelagic fishes.

The scanty records available are reconcilable with the fledging strategy outlined above. It appears that the Great Auk may not have come ashore until shortly before egg-laying started (Martin 1698), which is in sharp contrast to the most closely related species. The combined incubation and fledging period may have been somewhere between 43 and 53 days (p. 5), or about the same as for the much smaller Razorbill (ca. 55 days) and murres (ca. 50–54 days); for the smallest species, the Dovekie, it is 52 days (Evans 1981). Among species of the family Alcidae, the fledging period varies considerably, not only between species, but also to some extent between individuals of the same species. Chicks of *Synthliboramphus* are truly precocial and leave their nests within 2 days of hatching (Sealy 1973), whereas for *Alca* and *Uria* the fledging time is about 20 days (Birkhead 1977a), for the Dovekie 27 days (Norderhaug 1970), for the Black Guillemot 36 days (Kartaschew 1960), and for the Atlantic Puffin about 36–40 days (Ashcroft 1979).

It has been suggested that the length of the fledging period is positively correlated with the degree of protection of the nest site, species breeding on exposed ledges, such as murres, having a shorter fledging time than those nesting in crevices and burrows, such as puffins, Black Guillemots, and Dovekies (Fisher and Lockley 1954: 252, Cody 1973; but see Lack 1968). It remains to be demonstrated, however, that the chicks are more vulnerable to such factors as predation and hard weather on land than at sea. More recently, the length of the fledging period has been discussed in terms of the parents ability to bring provisions and the type and abundance of available food (Sealy 1973, and a number of later authors). Providing food both for themselves and for young in the nest may place a considerable strain on the parents; for instance, the energy expenditures of House Martins (*Delichon urbica*) rearing young are 3.59 times the basal metabolic rate, or about twice as much as for other stages (Bryant and Westerterp 1980). So the parents should (it would seem) carefully "consider" the implications of central-place foraging theory (Andersson 1978, Orians and Perason 1979, Schoener 1979). For alcids that feed on unpredictable food resources or that must fly long distances to collect food for the chick, an early departure to sea seems advantageous (Sealy 1973). The problem facing the flightless Great Auk was that it could not cover any large distances to collect food and at the same time maintain a sufficiently high feeding rate of the chick on land. Moreover, it was a large-sized species and required a lot of food. An early fledging, so that the chick could follow the parents to the food, would thus be a good strategy to adopt, especially if the chick also quickly became independent and aquired its own food. The suggested fledging period of 9–10 days seems short, but may nevertheless have been true.

To produce an "advanced" chick, a relatively large and/or nutritionally rich egg is a prerequisite. Among alcids, the precocial species lay the relatively largest eggs, weighing about 20% of adult body weight in the murrelets (Sealy 1975), 12–14% in *Uria* and *Alca* (Birkhead 1977a), and 13 and 19% in Atlantic Puffin and Dovekie, respectively (Kartaschew 1960). In the Great Auk the egg may have weighed about 325 g, or about 6–7% of adult weight. The newly hatched chick may have weighed around 200 g, compared with 62 g in the Razorbill (Lloyd 1979) and 82 g in the Thick-billed Murre (Gaston and Nettleship 1981). Chicks of *Uria* and *Alca* approximately double their weights during the first 8–10 days posthatching. Assuming that this held true also for the Great Auk, its chick weighed 8–10% of adult weight when it supposedly fledged. This would place the Great Auk very close to the murrelets (*Synthliboramphus*), which have precocial chicks, as the chicks of the semi-precocial species (e.g. auklets, puffins, and small guillemots) fledge at 65–90% of adult weight, and the intermediate species (*Uria* and *Alca*) weigh 20–25% of adult weight (Sealy 1973). It should be noted, however, that there is usually a great deal of variation in fledging weight with date of hatching, between years, and between colonies (see Gaston and Nettleship 1981).

There is a general, positive relationship between the yolk content of an egg and developmental maturity at hatching (Heinroth 1922, Nice 1962), and an increase in proportion of yolk and yolk lipid level, solids, and caloric content and a decrease in water content are claimed to be correlated with degree of precocity (Ricklefs 1977, Carey et al. 1980; but see Williams et al. 1982). This is true also for alcids, although we should not take Lahotant's statement about the yolk in Great Auk eggs (p. 5) too seriously. The Great Auk did lay a large egg, however, ensuring a large total amount of calories. Chicks of alcids depend on the yolk sac for a few days after hatching, and chicks of *Uria* do not achieve homeothermy until 9–10 days of age (Johnson and West 1975). Once their own metabolism is in full working order there is also a metabolic increase. If this can be extrapolated to apply also to the Great Auk, it adds another arguement in favor of a 9–10-day fledging period; the chick left the nesting ledge very soon after it achieved adequate thermoregulation, but before its energy demands increased markedly.

Why did the Great Auk not provide even more for the newly hatched chick by producing an even larger egg? The simplest answer would be that it could not, that it would impose too much strain on the female. The size of an egg is determined by both intrinsic and environmental factors—the quality of the female and the amount of food and time available. In alcids (as in many other, possibly all, birds) egg size declines with season, which can be interpreted as an adaptive trade-off between egg size and laying date, as discussed for the Thick-billed Murre (Birkhead and Nettleship 1982). If the female had been capable of producing a larger egg, she would have had to build up a larger energy reserve, which probably would have delayed the laying date and certainly would have lengthened the incubation period, but would not necessarily have shortened the fledging period. The date of hatching was probably critical to breeding success; starvation among alcid chicks is frequently invoked in explaining breeding failure. From the meagre records it seems that the Great Auk commenced egg laying at about the same time as, for instance, the Razorbill and the murres. Because of its slightly longer incubation period, it hatched a week or 10 days later than the other species mentioned, but, assuming that it adopted the fast fledging strategy suggested, the Great Auk chick may have been feeding by itself a few days before the bulk of chicks of other species left the nesting ledges. That an early laying and fledging may have been crucial is also indicated by the statement (Martin 1698) that the Great Auk did not replace the egg if it was lost, although other alcids do replace lost eggs. Being a large-sized and presumably long-lived bird, the Great Auk could probably afford not to invest too much in a year that did not turn out as it should. Although nothing is known about its longevity and rate of reproduction, it is not unreasonable to assume that the Great Auk may have taken 4-7 yr to reach maturity and that survival rate was high. For instance, the Razorbill does not breed for the first time until 4-5 yr old, and, although only 0.13 of the young reach breeding age, adult annual survival is 0.90 or more (Lloyd and Perrins 1977). Very similar results have been obtained for the Common Murre and Atlantic Puffin (Birkhead and Hudson 1977, Harris 1983). Individual Great Auks may often have reached an age of 20-25 yr and possibly did not breed every year. In contrast to the other North Atlantic alcids, the species did not breed in the northernmost regions, which may indicate that it was more sensitive to late and cold seasons than the others. Like the closely related species (Razorbill and murres; Southern et al. 1965, Birkhead 1977b, Lloyd 1979), the Great Auk probably exhibited a high degree of nest-site and mate fidelity.

DECLINE AND DISAPPEARANCE

When the Great Auk was finally exterminated off Iceland during the first half of the 19th century (in North America probably before 1800), its fate had long been sealed. Most of the literature consists of records of subfossil bones found in kitchen middens, "last observations," and mass slaughters and ruthless collecting of the species on its breeding grounds. It is therefore not surprising that almost every writer maintains that the Great Auk was exterminated by man. When the Europeans (re-)discovered Newfoundland in 1497, a period of intensive exploitation of the rich fishing grounds there started, and each year an armada of 300-400 French, Spanish, Portuguese, and British vessels visited the area. It became customary to call in at rich seabird colonies to reinforce the supplies with fresh meat. On what must have been Funk Island, the fishing crews collected Great Auks by the thousands, and the birds were salted and barreled or boiled and eaten on the spot, using the fat from some of the birds for fuel (see accounts in Steenstrup 1855, Grieve 1885). On Funk Island there are still remains of huts and pounds made of stones, into which the flightless birds were driven to be slaughtered. Sometimes, when the weather so permitted, the crews would "draue a great number of the fowles into their boats upon their sayles," or "driue them on a plank." Grieve (1885) quotes one early visitor, who in about half an hour loaded his two vessels with 4 or 5 tons of dead "Penguins," not counting those that the crews had consumed fresh; i.e. about 1,000 birds. No matter how large the population was, the numbers taken must have implied that the population was being overexploited. The same was undoubtedly true, although on a smaller scale, at the few European breeding sites known from historical records. On the breeding islands off Cape Reykjanes, southwestern Iceland, the total population of Great Auk possibly only numbered a few hundred birds (or less) at the end of the 18th century, but between 1813 and 1844 at least about 75 birds are known to have been killed. Despite the comparatively moderate numbers killed, the species was probably already beyond the point of rescue, although not until 1835 do we meet with an author who explicitly expressed concern for the species' survival (Nilsson 1835).

For convenience we may separate prehistoric and historic times when considering man's role in the decline of the Great Auk. Setting the time-boundary at about year 1500 (though there are some older historical records), we have already seen that the species was rare in Europe and had a very limited breeding distribution on the western side of the Atlantic. This in itself made the Great Auk highly vulnerable to extinction, and the records unequivocally point in the direction of over-exploitation by man. In prehistoric times the species in all probability had a much wider distribution on both sides of the North Atlantic (pp. 2-3), and the fossil records testify that it was hunted by Indians and Eskimos in North America (Salomonsen 1945) and by Scandinavians, Icelanders, Faroese, and others in Europe. The question is, did the prehistoric hunters also over-exploit the Great Auk and thereby cause (or contribute to) its decline, which must have taken place prior to 1500? For them the situation was different from that of the voyagers raiding the colony on Funk Island, because the hunters had to rely on the Great Auk (and other seabirds) for subsistence, and prudence in exploitation seemed a necessity (although admittedly some sailors may have saved their lives by collecting Great Auks). For instance, in the Faroes the collecting of seabirds has been of economic importance even in the present century, but there are no indications that this extensive fowling by modern hunters has had any negative effects on the number of birds or has been responsible for any marked population fluctuations (Nörrevang 1977, pers. comm.). The Faroese fowlers knew their birds from experience and "monitored" their numbers, imposed regulations when needed, and only rarely and accidentally did they take too many birds on a certain ledge or part of a colony. One may, perhaps, argue that the suggested prudence of the prehistoric hunters only applied to the most abundant, and consequently most important, prey species. The Great Auk was probably nearly always outnumbered by other species of alcids, and being so large and rare, it may in fact have suffered a sort of "negative" apostatic selection; i.e. being taken in preference to the smaller species. The Great Auk did not suddenly disappear when man entered the arena and began to hunt for it. Rather, for thousands of years man and bird lived together, and the total number of prehistoric hunters was probably not fewer than those people killing the bird in historic times. For instance, in Norway, where there are numerous archeological finds of Great Auk remains in kitchen middens, the earliest deposits date 12,000–13,000 yr B.P. and the youngest are about 1,500–1,800 yr old (Olsen 1967, Hufthammer 1982). It is noteworthy, however, that the rich deposits from Medieval time in Norway (ca. 1050–1550) do not contain any bones of the Great Auk. In my opinion, the decline of the Great Auk commenced long before man is known to have caused havoc in breeding colonies in the mid-16th century and onwards.

Remarkably few alternative explanations for the decline and extinction of the Great Auk have been advanced. Several writers have pointed out that the species frequently nested at sites that were vulnerable to geological destruction (e.g. Steenstrup 1885). This is certainly what happened to the rock Geirfuglasker in Iceland (p. 5), but it only made the breeding birds move over to the adjacent Eldey, and the consequences were, of course, negligible compared with those of major ecological changes. For instance, even a rather small change in sea temperature may have profound effects on the abundance and distribution of prey species. As a case in point, Olson et al. (1979) note that some of the fish species presumably eaten by Great Auks breeding on Funk Island have changed their distribution since then. Tuck (1961: 24) suggests that the Great Auk was possibly more vulnerable to meteorological disasters, less tolerant of low temperatures, and less catholic in its choice of food than murres.

What evidence is there for major environmental changes that could conceivably have affected the abundance of the Great Auk? Climatic fluctuations in the North Atlantic region manifest themselves in the amount of sea ice drifting southward from the polar seas, and cold periods seem to occur about every 2,500 yr. The latest cold period, known as the "Little Ice Age," started in the 13th century or slightly earlier, and lasted at least until the beginning of the present century. It was characterized by cold summers, harvest failures, famines, and local human extinctions or at least changes in the distribution of settlements (see John 1977). Scandinavian Vikings colonized the Faroes, Iceland, and parts of Greenland between 800 and 1000 and established settlements also on the coasts of Labrador and Newfoundland. Already at the beginning of the 1400's the westernmost settlements were gone, presumably as a result of a climatic deterioration. In northern Europe the climatic conditions also caused declines in human populations.

By far the best historical records of weather conditions in the North Atlantic come from the Old Icelandic sagas, annals, and chronicles, going back for about 1,000 yr. The amount of sea ice around the coasts of Iceland seems to have increased in the 12th century as the climate deteriorated. Apart from a period of improved conditions in the first half of the 15th century, a major improvement did not occur until the late 1800's (Bergthorsson 1969). From 1200 to 1600 there are fairly frequent reports of severe sea-ice conditions, and from then on the records are more detailed and indicate even worse conditions (several papers in Einarsson 1969; see also Eythorsson and Sigtryggsson 1971). In some years the ice also reached the southernmost parts of Iceland, and the Great Auks breeding islands were undoubtedly completely surrounded and blocked by pack ice. The old records contain many references to failures of the grass harvest, and also mention that some species of birds were unable to "bring out their broods." There were also more frequent visits by polar bears (*Thalassarctos maritimus*), and the harp seal (*Pagophilus groenlan-*

dicus), which does not occur in these waters today, was abundant in some years, to the benefit of the hunting islanders.

Thus, there is good evidence that a climatically severe period preceded and coincided with the period when man was dogging the Great Auk. In the absence of more detailed information about the rate of decline of the bird populations, hunting pressure, and the environmental changes, we cannot separate the effect of hunting and that of climate. There is good evidence that climatic changes directly or indirectly affect alcid populations (e.g. Tuck 1961). One such example is Tuck's account of the history of Common Murres and Northern Gannets on Funk Island. The former species was apparently abundant during Cartier's visit to the island in 1534 and also in 1874, although insignificant numbers were reported a few years later (1887). Since about 1885, and particularly since 1920, the rise in temperature has caused the amount of Arctic sea ice to decrease and the cold surface layer of the sea to diminish. From 1936 to 1959 the number of breeding Common Murres on Funk Island increased from about 10,000 to 500,000, and Tuck (1961) argued that this dramatic increase as well as previous declines were responses to climatic changes and ecological phenomena associated with them. Similarly, the abundance of Northern Gannets has changed on Funk Island from large numbers in 1534, none in the 19th century, 7 pairs in 1936, nearly 2,800 pairs in 1959, to 4,051 pairs in 1972, according to recent counts (Tuck 1961, Nelson 1978). The changes of the Northern Gannet, and of its main prey, the mackerel (*Scomber scombrus*), are also paralleled by changes of the marine environment. Many more examples from both sides of the North Atlantic could be cited to show that alcids and other species of seabirds have responded to climatic ameliorations in recent times. The point I wish to make is that ups and downs in late-Pleistocene climate very probably had effects on the distribution and abundance of prehistoric populations of alcids; possibly the effects were more pronounced on the large and specialized Great Auk than on the other species.

Alcid population numbers are ultimately determined and regulated by the abundance of available food (Ashmole 1963, Rowan 1965), and even very small changes in sea-water temperature may have large effects on the abundance and distribution of prey organisms. In the eastern North Atlantic, the fluctuations in time and space of the herring (*Clupea harrengus*) stock is a good example. Alcids may respond to deteriorating conditions (cooler climate and less food) by not breeding or by laying eggs and hatching chicks that then often die from starvation. Recently, for example, changes in the food situation of the large puffin colonies on Lofoten, northern Norway (believed to be at least partly due to overfishing by man) have caused mass starvation among newly hatched chicks for a long run of years (Mills 1981, 1983). Many alcids are, however, long-lived birds, and a given colony can probably take a number of nonbreeding years without experiencing any marked population decline. Besides, common and widely distributed species are probably successful in some parts of their breeding range and, therefore, are more likely to recover from hard times. The Great Auk was possibly never very numerous and was restricted to a relatively narrow climatic zone, not breeding in the Arctic regions. Moreover, the colonies were possibly often rather small, and, being a large but flightless bird, the Great Auk probably required a combination of a safe breeding place surrounded by rich supplies of food to reproduce successfully. These traits in the life history of the Great Auk probably made it more vulnerable to climatic changes (expressing themselves in various ecological phenomena) than are other species of North Atlantic Alcidae. Of course, it also became more vulnerable to the destructive activities of man.

I wish to end this paper by re-emphasizing that my discussion of the ecology of the Great Auk is based on very few indisputable facts. Also, the final section is not intended to acquit man of his guilt in the extermination of the Great Auk, but to point to other possible contributory reasons for the decline and extinction of the species.

ACKNOWLEDGMENTS

I am grateful to Mrs. Ulla Holmberg, who assisted in the literature search, to Dr. Pehr H. Enckell for encouraging discussions, and to Dr. Anne Karin Hufthammer, who allowed me to cite her unpublished thesis. I also thank Dr. John A. Wiens for the invitation to write this paper and for patience and linguistic scrutiny.

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