

Biology *of* MARINE BIRDS

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1 Seabirds in the Marine Environment

E. A. Schreiber and Joanna Burger

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1.1 INTRODUCTION

Marine birds are equally at home on land, in the air, and in the water. While many organisms can go from land to water (amphibians, some reptiles, some insects), others generally live in only one medium during their lives. Marine birds switch from one to the other, often daily. Such flexibility requires unique physiological and morphological adaptations to the environment, a medium that has also exerted selective forces on the behavior, ecology, and demography of these birds. Amazingly, marine birds have adapted to essentially all environments on the earth, from those able to survive winters in Antarctica to those who can sit for days incubating their eggs in the tropical sun. Trying to learn about and explain this diversity may be why we find the study of them so fascinating: How does their structure and function interact with the marine environment to produce their particular life histories?

There is no one definition of marine birds or seabirds. For this book, we define marine birds as those living in and making their living from the marine environment, which includes coastal areas, islands, estuaries, wetlands, and oceanic islands (Table 1.1). But many Charadriiformes (shorebirds) and Ciconiiformes (erons, egrets, ibises) that feed near shore or along the coastlines are generally not considered to be true seabirds. Seabirds are a subset of the birds in Table 1.1, those that feed at sea, either nearshore or offshore; this excludes all the Ciconiiformes and the shorebirds from the Charadriiformes. The one common characteristic that all seabirds share is that they feed in saltwater, but, as seems to be true with any statement in biology, some do not.

In this book we have attempted to provide a thorough examination of the biology of seabirds: all the Sphenisciformes and Procellariiformes, all the Pelecaniformes except anhingas, and all the Charadriiformes except shorebirds (Figure 1.1). Because we felt the book should be useful to land managers, public policy-makers, and conservationists (who must knowledgeably manage our quickly disappearing wetlands and estuaries), we have included gulls as seabirds (although few go to sea) and also summary chapters on wading birds (Ciconiiformes) and shorebirds. These birds are particularly dependent on nearshore habitat for both feeding and nesting.

Seabirds exemplify one of the reasons for man's fascination with birds — the ability to fly and live so far from the mainland. They are among the most aerial of birds, able to spend weeks,

TABLE 1.1
Marine Birds Include Birds in the Following Orders

Order	Types of Birds
Sphenisciformes	Penguins
Procellariiformes	Albatrosses, petrels, storm-petrels, fulmars, shearwaters
Ciconiiformes	Herons, egrets, storks, ibis, spoonbills
Pelecaniiformes	Pelicans, frigatebirds, gannets, boobies, cormorants, anhingas
Charadriiformes	Shorebirds, skuas, jaegers, gulls, terns, skimmers, auks, guillemots, puffins

Note: The Ciconiiformes, anhingas, shorebirds, and skimmers are not considered to be seabirds.

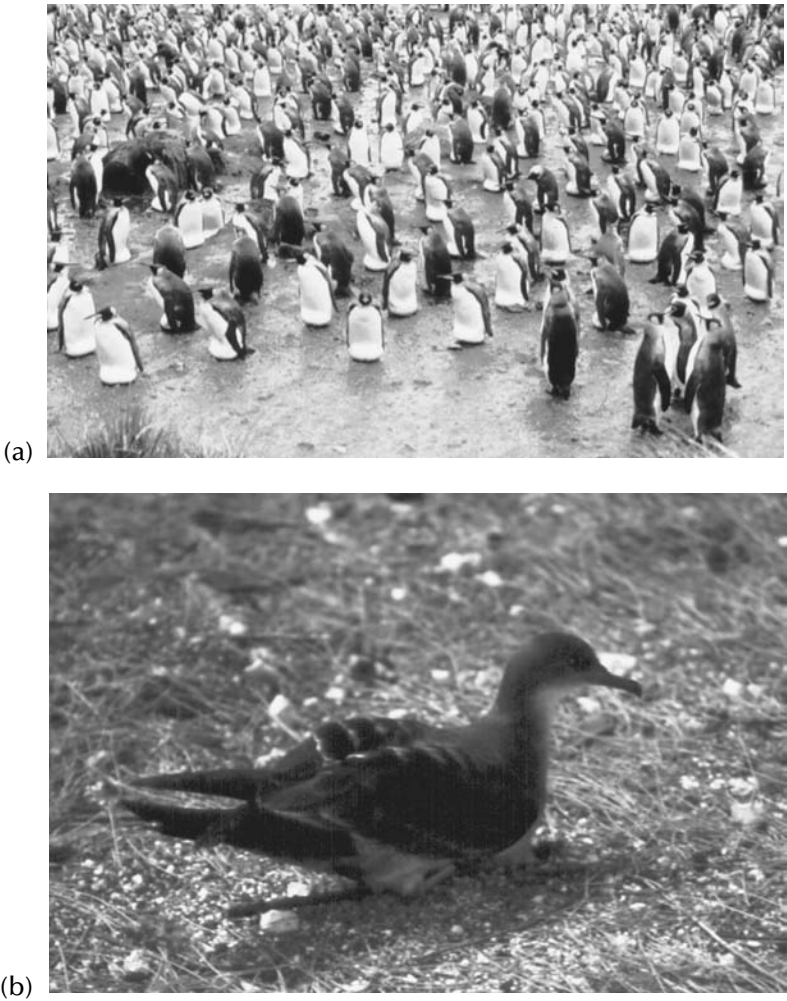


FIGURE 1.1 Representatives of the four major seabird orders: (a) Sphenisciformes: King Penguins incubating their eggs on their feet; (b) Procellariiformes: a Wedge-tailed Shearwater on Midway Island; (c) Pelecani-formes: a Brown Pelican incubates its three eggs; (d) Charadriiformes: a Blue Noddy on Christmas Island. (Photos a and b by J. Burger; c and d by E. A. Schreiber.)

(c)



(d)



FIGURE 1.1 *Continued.*

months, and, in some cases, even years at sea. This habit of spending long periods at sea, out of sight of land, has also made them among the most difficult of bird species to study and understand. Much of their life is spent where we cannot observe or study them, although this is changing with advances in technology such as satellite transmitters that are light enough to be carried by a bird.

Although the open ocean seems to us to be a uniform environment, a tremendous diversity of seabirds has evolved to feed in this environment in a great variety of ways. Such diversity suggests that the marine environment is not as homogeneous as we once thought, at least to the organisms that live there. The apparent uniformity was reflected in our inability to detect and measure the heterogeneity. We now know that the seas vary on seasonal cycles as well as stochastically and spatially (see Chapters 6 and 7). We are not as at home on the ocean as seabirds and have learned to take lessons from birds. Mariners often relied on seabirds to tell them they were near land, while fishermen today still rely on feeding flocks to help locate schools of fish. Mutiny on Columbus' voyage to the New World was thwarted by seabirds: when the crew finally saw feeding flocks of seabirds, they knew they were close to land (Couper-Johnston 2000).

TABLE 1.2
Comparison of Characteristics of Seabirds and Passerines

Life History Characteristic	Seabirds	Passerines
Age of first breeding	2–9 years	1–2 years
Clutch size	1–5	4–8
Incubation period	20–69 days	12–18 days
Nestling/fledging period	30–280 days	20–35 days
Maximum life span	12–60 years	5–15 years

1.2 WHY ARE SEABIRDS DIFFERENT?

Seabirds have dramatically different life-history characteristics, or demography, from most land birds, such as members of the order Passeriformes (Table 1.2). In fact, their life history characteristics are often referred to as extreme: long life (20 to 60 years), deferred maturity (breeding age delayed to up to 10 years of age), small clutch size (in many cases one egg), and extended chick-rearing periods (often up to 6 months). Passerine birds, in comparison, have shorter lives and larger clutches of eggs, and chicks grow to fledging age much faster. Seabirds also tend to be larger than land birds, less colorful in plumage, and sexually monomorphic. Plumage colors of seabirds are mainly white, gray, black, or brown, or some combination thereof, another area that needs research.

Basically the two life styles exemplified by seabirds and passerines represent two different ways to accomplish the same end: leave enough offspring to replace yourself in the population. Red-footed Boobies (*Sula sula*) commonly live 16 years, begin reproducing (one young per year) at 3 years of age, and 35 to 40% of their young survive to reproduce (Schreiber et al. 1996). A pair thus has the potential to produce about five breeding offspring (birds), although there are generally a few failed breeding seasons owing to the occurrence of El Niño events (see Chapter 7). More coastal species, such as Black Skimmers (*Rynchops niger*), live for about the same time and are capable of raising two or three young a season, but colonies can also fail completely in some years due to heavy rains and thermal stress (Burger and Gochfeld 1991; see Chapter 7). Robins (*Turdus migratorius*), a typical passerine, commonly live 3 years, first lay at 1 year of age (lay an average of four eggs), and can raise two broods in some years; about 20% of their young survive to reproduce (Sallabanks and James 1999). So in a lifetime they can raise about five young that survive to reproduce. They also can have failed years when no young are produced, but it is less likely to occur throughout a whole region as it does in seabirds.

Why have these two very different lifestyles evolved? They may reflect conditions imposed on seabirds by living in the marine environment (Ashmole 1963, Lack 1968), and also conditions imposed on land birds by predation (Slagsvold 1982). Seabirds may not have been exposed to predation historically, although the human introduction of mammalian predators to both coastal and oceanic islands has been a major source of mortality for seabirds that did not evolve with this threat (Moors and Atkinson 1984, Burger and Gochfeld 1994).

Early hypotheses on the reasons for the life-history characteristics of seabirds have come to be called the “energy-limitation hypotheses.” David Lack (1968) proposed that seabirds’ unusual demography evolved owing to energetic constraints on adults’ ability to supply food to chicks. Birds feeding at sea were viewed as randomly searching a vast area for patchily distributed food that then had to be caught and carried long distances back to a colony. Philip Ashmole (1963) also suggested that dense aggregations of birds in one area, such as in seabird colonies, depressed local food resources, causing density-dependent limitations on breeding and nest success (Figure 1.2). He proposed that seabirds were perhaps over-fishing the area around colonies and adults could not find enough food to raise more young or faster-growing young. Specifically then, small clutch sizes and slow growth of young were considered to be adaptations to an imposed low rate of food delivery



FIGURE 1.2 Cape Gannets (South Africa) are one of the most densely nesting seabirds. Neighbors can easily peck each other if they have a disagreement and thus much signaling of intentions (behavioral posturing) goes on to forestall any misunderstanding. Shown is Michael Gochfeld. (Photo by J. Burger.)

to chicks. Additionally, seabird chicks (particularly Procellariiformes) lay down large amounts of fat during development, which, presumably, was necessary to carry them through periods when adults could not find enough food (Lack 1968, Ashmole 1971).

These hypotheses have been the driving force behind many studies on seabirds over the past 35 years and, interestingly, they are hypotheses for which it is hard to find support. Their role in the development of seabird biology was critical. However, as with any discipline, hypotheses change as we gather more information, and the energy-limitation hypothesis proved particularly difficult to validate. Some studies do not support the hypotheses, and other studies show that they could be true. We believe that biologists will never prove one way or the other why seabirds are different from land birds. It is undoubtedly a combination of selective factors. Indeed, it may be more of a continuum than we had believed. The discussion that follows is intended to highlight some issues for future study. It is also necessary to note that marine birds may appear food limited today because of the rapidly intensifying competition with fisheries and increasing human pressure.

Potential support for the energy-limitation hypothesis comes from clutch size, colony size, and foraging area comparisons. Seabirds that feed offshore generally have smaller clutches than those that feed nearshore (Nelson 1983; see Chapter 8). Pelicans, cormorants, gulls, and skimmers feed primarily nearshore and have average clutches of two to four eggs (see Appendix 2), presumably because they feed close by, making use of highly productive nearshore and estuarine resources. Offshore-feeding seabirds, such as albatrosses, petrels, boobies, and some terns, have clutches of one. Lower clutch size in itself does not prove offshore feeders are energy limited, however.

If there were a correlation between colony size and productivity of local waters, one might expect the smallest colonies to be in tropical waters away from cold water upwelling areas such as in the Humboldt Current where food is abundant. There certainly are some very large colonies in the Humboldt and Benguela Current areas, but there are also large concentrations of breeding birds in tropical non-upwelling areas such as on Midway Island (approximately one million seabirds; U.S. Fish and Wildlife Service 1996) and on Christmas Island (an estimated 12 million seabirds; Schreiber and Schreiber 1989), both in the central Pacific.

If adults are energy limited, you might expect to see populations with high mortality rates of growing chicks when feeding conditions deteriorate at all. There is little evidence for this occurring. Nest success rates in seabird colonies on oceanic islands are frequently on the order of 75% or greater, and failed nests are often those of young, inexperienced birds (see Chapter 8). Years with



FIGURE 1.3 Multispecies assemblages of breeding seabirds often have overlapping diets, foraging zones, and foraging methods, raising the question of the significance of competition in their evolution. Least Auklets (left) and Parakeet Auklets often nest in colonies (around the Alaskan coast) with several other species. (Photo by J. Burger.)

high chick mortality occur infrequently, and are generally associated with an unusual weather occurrence such as an El Niño event, when starvation of chicks occurs because of a disappearance of, or great reduction in, the food source (see Chapter 7; Schreiber and Schreiber 1989).

If adults are limited in their ability to provide food to chicks because of an irregular or unpredictable food supply, daily feeding rates of young should be sporadic and irregular. As you might expect, with the great diversity of seabird species, there is some evidence on both sides of this prediction. Some studies of feeding rates of chicks found that chicks are fed on a more regular basis than expected by chance alone and that fat stores are not needed for periods of fasting (Taylor and Konarzewski 1989, Navarro 1992, Hamer 1994, Hamer and Hill 1994, Cook and Hamer 1997, Schreiber 1994, Reid et al. 2000). Other studies have found a degree of unpredictability in food delivery which indicates fat reserves may be useful in carrying a chick through lean times (Hamer et al. 2000). Reid et al. (2000) suggested that fat stores in albatross chicks may have evolved to carry chicks through fledging while they learn to feed themselves.

Dense aggregations of breeding seabirds trying to raise hungry young might be expected to over-fish an area, but there is little evidence for this happening, and it would be difficult to prove. With high nest success rates (in non-El Niño years) in some very huge seabird colonies, such as that on Christmas Island (Central Pacific Ocean), it appears that birds may not over-fish an area (Schreiber and Schreiber 1989). Birt et al. (1987) found some inconclusive evidence for prey depletion around a colony of Double-crested Cormorants (*Hypoleucos auritus*).

A possible indication that food supply is an energy-limiting factor would be the evolution of the reliance on separate food sources in sympatrically breeding species as a way to avoid competition for the resource (Figure 1.3). Ornithologists have reconciled the discrepancy between high reproductive success and limited food resources by claiming that seabirds are partitioning the food resource by either taking different prey species, foraging in different areas, or breeding at different times of the year. However, there is little direct support for this. Ashmole and Ashmole (1967) found a large degree of overlap in the species and sizes of fish and squid taken by eight tropical seabird species breeding on Christmas Island (central Pacific). There is also extensive overlap in the size of fish and squid taken by the Pelecaniform species nesting on Johnston Atoll (central Pacific; E. A. Schreiber unpublished). In both locations, breeding seasons of the nesting seabirds overlap extensively. Large overlap in the prey base has been found in other studies (Whittam and

Siegel-Causey 1981, Ainley 1990). Thus, diet differences may be important in some colonies, but they are far from the rule. Conversely, reliance on different types of food may have been a pre-adaptation to cohabitation, but which came first?

Studies on seabird populations of the Farallon Islands, off northern California, found that feeding-niche segregation mainly occurred during difficult times such as an El Niño event (Ainley and Boekelheide 1990). Ainley's (1990) suggestion that Farallon seabird communities appeared to be operating much like grassland shrub-steppe communities of birds with regards to food (foraging opportunistically on a highly variable, but nonlimiting resource with no evident competition) brings to mind the question: Are seabirds any more energy limited than land birds? The biological importance of differences that are detected should be examined: When differences are small, but statistically significant, was there actually selection pressure to avoid competition?

The diets of the six main seabird species breeding on Bird Island, South Georgia, show extensive overlap in krill size taken (Croxall and Prince 1980, Croxall et al. 1988, Croxall et al. 1997). However, Croxall et al. (1997, see Figure 1.2) report significant differences in the *mean* sizes of krill taken, implying dietary segregation in spite of the large degree of overlap in sizes. To seabirds, the statistical differences may not be biologically relevant, and more studies are needed to examine the significance of such differences.

Several authors have examined feeding-niche separation in species nesting and foraging in coastal habitats. The question of niche separation has been examined extensively in Common (*Sterna hirundo*) and Roseate Terns (*Sterna dougallii*) along the east coast of North America. Duffy (1986) suggested that the two species appeared to partition food on the basis of patchiness, with Common Terns being more successful over larger patches of prey than were Roseate Terns. He made the important point that it is essential to examine foraging behavior at sea, and not rely only on the traditional methods of examining diet, and identifying prey species and prey size at the colony. However, he did not measure prey availability, nor examine the foods parents brought back to their young. Safina and Burger (1985), working in the same general area, used sonar to demonstrate that terns fished in areas with high concentrations of prey fish (usually with predatory fish), but there was no correlation between number of feeding terns and prey density, as one would expect if prey were limited.

In Australia, Hulsman (1987, 1988) similarly found that the niches of several tern species varied, and that the size and type of prey in a bird's diet were a function of the bird's morphology, foraging method, foraging zones, and interactions with other birds and predatory fish. Even so, most species of terns fed solitarily (except for Black Noddy, *Anous minutus*) and fed near the colony (except for Lesser Crested Tern, *Sterna bengalensis*), and there was overlap in the sizes of prey taken (Hulsman 1988). The data suggested that the guilds are dynamic, and that terns exhibit a wide range of foraging habitats and foraging methods and take a variety of prey sizes and types (Hulsman 1988).

Tests of the energy-limitation hypotheses have also included experiments designed to determine whether adult seabirds are bringing the maximum amount of food to chicks that they can. If birds can be induced to work harder, this would prove they are not normally working at full capacity (Figure 1.4). Doubling experiments have been conducted where two chicks are put in a nest of species that normally raise only one to see if increased demand causes adults to supply more food. This also implies that adults feeding young respond to the amount of food demanded and are not just bringing the maximum amount they can. In many cases parents were able to successfully provision these enlarged broods (Harris 1970 [Swallow-tailed Gull, *Creagrus furcatus*], Nelson 1978 [Northern Gannets, *Morus bassanus*], Navarro 1991 [Cape Gannets, *Morus capensis*], Schreiber 1996 [Red-tailed Tropicbirds, *Phaethon rubricauda*]). Experiments on most Procellariiformes have failed, but the reasons why remain unknown; it may not be due to lack of ability to increase effort, but to behavioral limitations (Boersma et al. 1980, Ricklefs et al. 1987).

If the amount of food brought to the chick is somewhat regulated by the chick, mediated by food begging, as many studies have found (Nelson 1964, Henderson 1975, Navarro 1991, Anderson



FIGURE 1.4 It is hypothesized that energy limitation prevents most seabirds from raising more than one young. Brown Boobies lay two eggs but rarely raise more than one chick. However, on Johnston Atoll (Pacific Ocean), about 0.5% of nesting pairs raise two young. (Photo by E. A. Schreiber.)

and Ricklefs 1992, Schreiber 1996, Cook and Hamer 1997), then food limitation may not account for the slow growth and long fledging period of seabird chicks. Adults are simply responding to chick needs, not bringing the maximum amount of food possible. There may be physiological or genetic constraints on growth rate in chicks as found in some studies (Place et al. 1989 [Leach's Storm-petrel, *Oceanodroma leucorhoa*], Konarzewski et al. 1990 [several species of altricial and precocial birds], Ricklefs 1992 [Leach's Storm-petrel]). Or the nutritional content of food may be the limiting factor (Prince and Ricketts 1981 [Grey-headed Albatross, *Thalassarche chrysostoma*, and Black-browed Albatross, *T. melanophris*]).

Parent seabirds appear to have flexible time budgets that allow them to increase feeding effort in years of poor food availability (Drent and Daan 1980, Burger and Piatt 1990, Schreiber 1996). Spare time is notably present in many seabirds, such as boobies, gulls, terns, and alcids where both members of a pair often have time to loaf together at the nest, even during the chick-rearing period (Burger 1984, Schreiber et al. 1996, Norton and Schreiber in press). The presence of spare time in birds' lives would imply that they are not normally energy limited.

Mass loss of adult birds during breeding has often been interpreted to indicate stress or increased effort (Bleopol'skii 1956, Ricklefs 1974, Harris 1979, Gaston and Nettleship 1981). This seems to be a reasonable explanation, and there are some data in support of it (Drent and Daan 1980, Monaghan et al. 1991, Chastel et al. 1995). Yet, an alternative hypothesis proposes that loss of mass is adaptive, resulting in lower wing loading and more efficient flight that enables adults to fly farther in search of food (Blem 1976, Norberg 1981, Croll et al. 1991).

Chick growth rate might be constrained (slow in seabirds) by the inability of tissues to mature at a faster rate. There is some evidence that metabolizable energy is limited simply because the digestive tract cannot assimilate food faster (Ricklefs 1969, Konarzewski et al. 1990, Diamond and Obst 1992). In domestic fowl, the gut capacity of chicks to assimilate nutrients is closely matched to the chick's requirements, suggesting that there are constraints on growth rate (Obst and Diamond 1992). We might expect a difference in growth rate between the altricial chicks of Pelecaniformes (hatching naked and helpless) and the semiprecocial chicks of Charadriiformes (hatching with a full coat of down and able to move about; Ricklefs et al. 1998). In fact, the more mature semiprecocial chicks grow more slowly than altricial chicks, also suggesting that functional maturity of tissues might limit growth rate (Ricklefs et al. 1998). If chicks lacked physiological constraints

on growth, you might also expect to see them exhibit spurts of high growth (compensatory growth) following periods of starvation, which apparently does not happen (Schew and Ricklefs 1998).

Continuing investigations of growth in seabirds, and understanding the effects of constraints on growth, are needed before we can fully understand the evolution of seabird life histories. Experimental studies across phylogenetic lines can provide one of the most fruitful avenues of investigation. We need to know if chicks can make use of extra food and alter growth rates significantly. We do not yet understand how maturation of tissues and growth are controlled. The role of nutrient reserves, in the form of fat, is not fully understood. However, as Ricklefs et al. (1998) acknowledge, "Testing an hypothesis about a growth rate-function is exceedingly difficult because several tissues may assume symorphic relationships to a single most limiting tissue, several tissues may constrain growth simultaneously, and limiting tissues may differ between age or different developmental types."

1.3 COLONIAL LIVING

While this topic is considered in detail in Chapter 4, some mention is warranted here. Lack (1954) thought about birds living in colonies and the potential for competition for space as well as food. Seabirds must be one of the ultimate examples of colonial living! Colonies can consist of several species and millions of individuals, providing a ripe environment for investigations of topics such as competitive exclusion (see Chapter 8). There are few data on population dynamics in most seabird species. And even for those few species on which we have good data, we do not truly understand how populations are regulated or the effect of density-dependent mechanisms.

If large colonies of seabirds deplete the food resource around the colony you might see a decrease in the breeding population size or an effect in some other aspect of reproductive biology (Figure 1.5). This has been documented in a few colonies (Hunt and Butler 1980, Anderson et al. 1982, Piatt 1987, Safina et al. 1988), but not in most others (see discussion in Chapter 4). However, in many cases adults apparently have some spare time in their budget and can compensate for reductions in the food supply (Drent and Daan 1980, Burger and Piatt 1990, Schreiber 1996), implying they are able to cope with potential competition for food.

Over 95% of seabirds are colonial, with colony sizes ranging from a few pairs to many thousands. Some colonies are almost unbelievably large, numbering in the millions of pairs. Living



FIGURE 1.5 The largest Magellanic Penguin colony in the world, at Punta Tombo, Argentina, consumes many tons of fish from local waters during the nesting season. (Photo by P. D. Boersma.)

in colonies makes communication among birds a necessary part of daily life and thus colonies can be exceptionally noisy. Colonies of more densely nesting birds are often noisier and it may be that the proximity of neighbors makes communicating their intentions more important (Figure 1.2; see discussion in Chapter 10).

Understanding population dynamics of seabirds requires long-term studies of individually marked birds. Ideally a study should last at least one generation of a species, if not more, to truly understand what is driving changes in population levels, survival, and demographics. With long-lived species, such as seabirds, this can mean a researcher's entire lifetime of field work spent on one species. Studies such as John Dunnet's on Northern Fulmars (*Fulmaris glacialis*; Dunnet and Ollason 1978, Dunnet et al. 1979), John Coulson's on Black-legged Kittiwakes (*Rissa tridactyla*; Coulson 1966, 1983, 1985, Coulson and Thomas 1983, Coulson and White 1956, 1958), John Mill's on Red-billed Gulls (*Larus scopulinus*; Mills 1973, 1980, Mills et al. 1996), and the British Antarctic Surveys' long-term commitment to Antarctic studies (Croxall 1992, Croxall and Rothery 1991, 1994, Croxall et al. 1988, 1992, 1997, Prince 1985, Prince and Ricketts 1981, Prince et al. 1994) have given us tremendous insights into seabird breeding biology, ecology, physiology, and demography.

1.4 ADAPTATIONS AND LIFESTYLES OF MARINE BIRDS

Life at sea and feeding on marine organisms presents several challenges to seabirds, and it undoubtedly has played an important role in shaping their life histories and physiology. Feeding in the marine environment requires that seabirds deal with high physiological salt loads. One of the methods they use to accomplish this is through their salt glands, an extra-renal kidney located in the orbit of the eye (see Chapter 14). They also limit their ingestion of salt water, getting most of their fluids from the high water content of the food they eat. For instance, seawater contributes about 8.5% of the total water influx in Diving Petrels (*Pelecanoides* spp.; Green and Brothers 1989). Life at sea also involves other challenges, such as dealing with foraging conditions that are greatly impacted by weather (see Chapter 7), with natural and anthropogenic contaminants (see Chapter 15), and with increasing competition from fisheries worldwide (see Chapter 16).

Seabirds have diversified to live in all areas of the globe and to feed by a great variety of means (Chapter 6). Some seabird species fly vast distances to their feeding grounds (albatrosses) and their long, narrow wings make them well adapted for this. The dynamic soaring of albatrosses enables them to fly without flapping, making headway in almost any kind of weather and expending little energy to do so. Smaller birds, such as auks and puffins, flap hard and fast to stay airborne, and feed closer to shore, probably because of the high energy cost of flapping flight (Rahn and Whittow 1984; see discussion in Chapter 11). Feeding methods of seabirds are just as diverse, from piracy and cannibalism (frigatebirds, skuas) to sitting on the ocean surface plucking squid and krill (albatrosses, petrels), to plunge diving (boobies and Brown Pelicans [*Pelecanus occidentalis*]), to deep diving (penguins, see Chapter 6).

Bills, feet, and body shapes also show a myriad of adaptations to the various lifestyles of seabirds. Many of the adaptations are for swimming and diving. Most have webbed feet to aide in propulsion through the water. Frigatebirds are an exception, with greatly reduced webs, but they never enter the water. Bill adaptations for various types of feeding are diverse. They all use their bills to capture and handle food, except for pelicans (*Pelecanus* sp.) who capture fish in their large pouches. For the albatrosses and petrels, a hook on the end of the beak helps hold their food (generally squid and krill). They do not have tremendous closing strength in the bill, possibly because they do not take strong, muscular prey. Frigatebirds (*Fregata* sp.) often take large flying fish, using their hooked bills to pin the fish between the mandibles until they can flip them around and swallow them. The hooked bill of pelicans seems to be used primarily for preening, and rarely serves a purpose in feeding. Boobies, tropicbirds, cormorants, gulls, and terns that feed on fish generally catch them sideways in the bill. Some bills are serrated on the edge, with the teeth angled

toward the throat so that fish cannot wriggle out of their grasp (boobies). Boobies and tropicbirds have a hinge on the upper mandible at the base which allows them to exert greater pressure at the tip, further ensuring that prey do not get away. The lower mandible of skimmers (*Rhynchops* sp.) is compressed laterally and is longer than the upper mandible. They catch fish by flying along at the water surface with the lower mandible slicing through the water, searching for prey by tactile means. The bill is snapped shut as soon as a prey item is encountered. The bill of puffins is impossible to explain in terms of a functional food-catching mechanism, and its evolution may be related to its use in courtship.

Bodies of boobies and gannets are compressed to a bullet shape, making them efficient divers. Most seabirds are black, white, or black and white, and most are basically sexually monomorphic. Given the colorful variety and wonderful sexual differences found within land birds, one wonders why seabirds are so “dull.” Several polar nesting species are white, such as the Ivory Gull (*Pagophila eburnea*), providing cryptic coloration. Yet other Polar species have large amounts of black, like penguins, and even young penguins (supposedly more vulnerable to predators) are not cryptically colored. But predation is a problem for few seabirds that nest on islands or remote cliffs free of predators. White in some birds is considered conspicuous coloration, offering at-sea feeding birds an opportunity to see others who might have found food and head toward the source. White on the belly of seabirds has been considered to provide them with less conspicuous coloring to avoid being seen by the fish for which they are searching (Simmons 1972). Yet, immature birds of several species (such as Brown, *Sula leucogaster*, and Red-footed Boobies) are dark below, presumably putting these amateur fishers at a disadvantage if this theory is true. Indeed immatures are usually less efficient foragers than adults (see Chapter 6). Many aspects of seabird biology are, as yet, unexplained.

1.5 LOOKING TO THE FUTURE

The past 20 years have seen tremendous progress in our knowledge about marine birds and about their relationships with their environment, competitors, predators, and prey. Early scientists observed seabirds, but now we have multiple methodologies to examine them. New developments in technology and techniques are allowing us to examine aspects of birds' lives that were once unknowable. These include physiological studies of energetics, the connection of weather patterns to seabird ecology, DNA studies examining taxonomic relationships and populational relationships, stable isotope studies of diet and trophic level, tracking daily and annual movements at sea with satellite telemetry, and collecting dive depth and frequency data electronically.

As the chapters in this book indicate, answering questions about the biology, ecology, and conservation of marine birds is challenging, and will continue to be so for years to come. There are still many unanswered questions in need of research, particularly by those willing to make a long-term commitment to studying a single species. New improvements in technology now allow us to follow seabirds during the periods they are at sea, a new frontier in seabird research. Changing concepts of the uniformity–heterogeneity of the ocean, and of the scales (both temporal and spatial) on which the oceanic environment operates, have advanced our ability to ask the right questions (see Chapter 6). One of the threads you will find woven throughout this book is that the more we learn about seabirds, the more we find they have adapted and are adaptable to the situation at hand. For instance, the diversity of morphology in seabird families which allows them to exploit a broad range of resources and environments has resulted in differing demographic strategies worldwide (see Chapter 5). We encourage students of seabirds to keep an open mind, think broadly, and question and test what they read. We still have much to learn.

Exciting research directions that need to be taken include: comparisons of coastal- vs. oceanic-nesting species, studies of traditional seabirds in comparison with others heavily using marine environments (marine shorebirds), examinations of conspecifics nesting on oceanic vs. coastal islands, and investigations of “energy limitation” in conspecifics in large vs. small colonies.

Addressing the issue of statistical vs. biological significance to marine birds would make major contributions to the fields of ecology, evolution, and biostatistics. Consideration of the continuum from an oceanic existence to coastal, and finally to a truly land-based life-history strategy within seabirds will also advance our knowledge. While answering these questions, most seabird biologists will admit to the exhilaration of watching these fascinating birds on land or at sea, among urban waterways or amidst some of the most spectacular scenery anywhere on earth. It is an exciting time in marine bird biology.

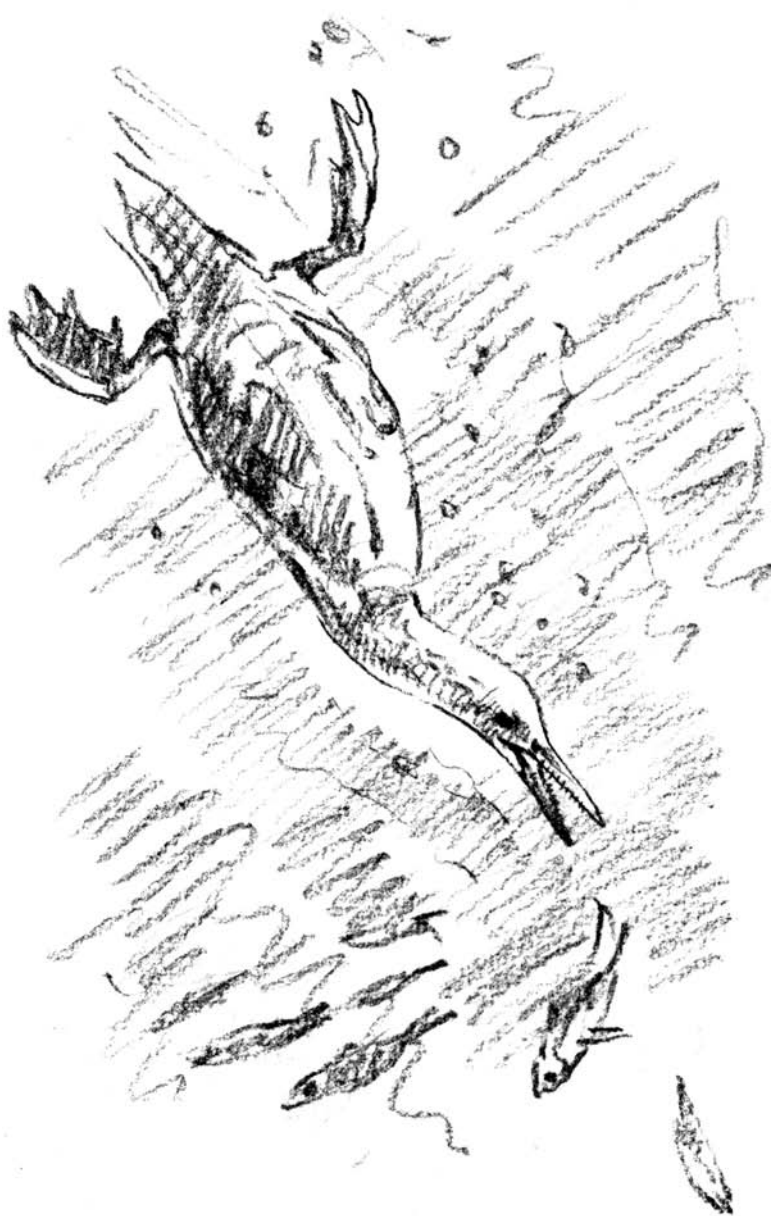
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Hesperonis regalis

3 Seabird Systematics and Distribution: A Review of Current Knowledge

M. de L. Brooke

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3.1 INTRODUCTION

This review of systematics and distribution will be restricted to the groups of birds traditionally considered as seabirds. These groups are the Sphenisciformes, Procellariiformes, Pelecaniformes, and certain families among the Charadriiformes (Table 3.1). And I begin by explaining the significance of the restriction. While all species among the Sphenisciformes (penguins) and Procellariiformes (albatrosses, petrels, shearwaters, fulmars, and allies) are seabirds, this is not universally true for members of the other two orders. Among the Pelecaniformes, tropicbirds, frigatebirds, and boobies are exclusively seabirds. On the other hand, the various species of cormorant, anhinga (= darter), and pelican can be strict seabirds, or freshwater birds, or are able to thrive in both environments. But at least all members of the order are waterbirds. That is not true of the Charadriiformes, an order which comprises some 200 species of shorebirds plus five groups considered to be primarily seabirds, namely, the gulls, terns, skuas, skimmers, and auks. Of these, the auks and skuas are strict seabirds while different species of gull, tern, and skimmer are variously associated with the sea, or with freshwater, or with estuaries.

It is evident already that the distinction between seabirds and other birds is not wholly clear-cut. There are, for example, species of duck, grebe, and loon that may spend a substantial fraction of the year floating on salt water — yet these species are not considered to be seabirds. On the other hand, some species traditionally considered to be seabirds spend much of their lives far from the sea. The Brown-headed Gull (*Larus brunnicephalus*), breeding on the Tibetan Plateau, springs to mind.

In this chapter, the defining characteristics of each of the four orders containing seabirds are outlined. Then the features of the seabird families are described within the orders. This provides an opportunity for considering the relationships among families, and for selectively mentioning certain within-family taxonomic issues that have engendered special debate. At this stage the geographical distributions of the families are sketched. The chapter concludes with a discussion of the broad patterns of seabird distribution. Why, for example, are penguins confined to the southern hemisphere, and how do features of seabird lifestyles influence speciation which, in turn, accounts for the difficulty of drawing species boundaries in some groups?

The broad aim of taxonomic studies is to discover the true (= evolutionary) relationships between lineages. To this end, characters indicative of a common descent from some ancestor are most useful. At a very simple level, birds are considered to be a single lineage marked out by the possession of feathers, a feature not shared with their reptilian ancestors. On the other hand, the possession of feathers, a primitive avian character, is of little use in determining the relationships between orders of birds because it is a character shared by all birds. If, in the future, some birds were to lose feathers, the presence of feathers, a primitive feature, would not allow us to deduce that those birds still feathered were closely related. The risk of relying on shared derived characters is that there may be times when it is difficult to determine whether they are shared because of common descent, and therefore indicative of relationship, or shared because of convergence, and therefore taxonomically irrelevant. The fact that the plumage of so many seabirds is some combination of black, brown, gray, or white, and lacks the vivid colors of land birds, is almost certainly the result of convergence.

By the end of the 19th century bird taxonomists, using a suite of anatomical characters including nostrils, palate, tarsus, syrinx, and certain muscles and arteries, had gained a fair understanding of the relationships between the main bird orders (van Tyne and Berger 1966). The next major advance arrived when Sibley and Ahlquist applied the technique of DNA hybridization. Because it compares the entire genome of species A with that of species B, this technique is relatively crude. Nevertheless the results, culminating in Sibley and Ahlquist's magnum opus (1990), represented a significant taxonomic advance. However, nowadays the technique has largely been superseded by other genetic techniques, especially the sequencing of the individual bases on the genes of the species of interest. Nonetheless, it is important to realize that the modern geneticist and the 19th century anatomist

TABLE 3.1
Two Classifications of Seabirds

A. Traditional Classification of Seabirds

Order Sphenisciformes

Family Spheniscidae: Penguins (6/17)

Order Procellariiformes

Family Diomedidae: Albatrosses (4/21)

Family Procellariidae: Gadfly petrels, shearwaters, fulmars, and allies (14/79)

Family Pelecanoididae: Diving petrels (1/4)

Family Hydrobatidae: Storm petrels (8/21)

Order Pelecaniformes

Suborder Phaethontes

Family Phaethontidae: Tropicbirds (1/3)

Suborder Pelecani

Family Pelecanidae: Pelicans (1/7)

Family Fregatidae: Frigatebirds (1/5)

Family Sulidae: Gannets and boobies (3/10)

Family Phalacrocoracidae

Subfamily Phalacrocoracinae: Cormorants (9/36)

Subfamily Anhinginae: Anhingas or darters (1/4)

Order Charadriiformes

Suborder Charadrii: Various shorebirds (not considered further)

Suborder Lari

Family Stercorariidae: Skuas and jaegers (2/7)

Family Laridae

Subfamily Larinae: Gulls (6/50)

Subfamily Sterninae: Terns (7/45)

Family Rhynchopidae: Skimmers (1/3)

Suborder Alcae

Family Alcidae: Auks (13/23)

B. Sibley–Ahlgquist Classification of Seabirds

Order Ciconiiformes

Suborder Charadrii

Families various, including waders and sandgrouse

Family Laridae

Subfamily Larinae

Tribe Stercorariini: Skuas and jaegers

Tribe Rynchopini: Skimmers

Tribe Larini: Gulls

Tribe Sternini: Terns

Suborder Ciconii

Infraorder Falconides: Birds of Prey

Infraorder Ciconiides

Parvorder Podicipedida: Grebes

Parvorder Phaethontida: Tropicbirds

Parvorder Sulida:

Superfamily Suloidea

Family Sulidae: Boobies, gannets

Family Anhingidae: Anhingas

Superfamily Phalacrocoracoidea

Family Phalacrocoracidae: Cormorants

Parvorder Ciconiida

Superfamilies various including herons, ibises, flamingos, storks, and New World vultures

TABLE 3.1 (*Continued*)
Two Classifications of Seabirds

Superfamily Pelecanoidea
Family Pelecanidae
Subfamily Balaenicipitinae: Shoebill
Subfamily Pelecaninae: Pelicans
Superfamily Procellariodea
Family Fregetidae: Frigatebirds
Family Spheniscidae: Penguins
Family Gaviidae: Loons
Family Procellariidae
Subfamily Procellariinae: Gadfly petrels, shearwaters, fulmars, and diving-petrels
Subfamily Diomedinae: Albatrosses
Subfamily Hydrobatinae: Storm petrels

Note: (A) A “traditional” classification following Peters (1934, 1979). The number of extant genera and species is shown in brackets (genera/species) after each family or subfamily. (B) A classification that follows Sibley and Ahlquist (1990).

employ a similar rationale. Both are comparing the character states of the animals of interest, and proceeding to argue that birds with more similar character states are more closely related. The two are simply using different characters for their studies.

For various reasons, different genes evolve at different rates. Therefore studies of higher level taxonomy preferentially use more slowly evolving genes, while studies at the species level and below use rapidly evolving genes. The cytochrome *b* gene, on the mitochondrial genome, has proved especially useful for species-level studies (Meyer 1994). While there are serious problems with the idea that genes evolve at a steady clock-like rate (e.g., Nunn and Stanley 1998), the idea retains an appeal, not the least because it opens the possibility of ascribing a date to when two lineages separated. Thus if the genetic characters of lineage A and lineage B differ by X units, and Y units of difference are known to accumulate per million years of separation, then the lineages diverged X/Y million years ago. There are examples of the application of this approach both to hybridization and to sequence data later in the chapter.

In this chapter, the classification followed here at the subfamily level and upward will be a “traditional” one, espoused for example by Peters (1934, 1979) and based principally on anatomy. There are significant contrasts between the Peters classification and that suggested by Sibley and Ahlquist (1990) based on DNA hybridization data (Table 3.1). In brief, the Sibley and Ahlquist classification places **all** seabirds in a single order, the Ciconiiformes, which also includes birds of prey, shorebirds, and the long-legged waterbirds such as herons, storks, and ibises. While the validity of this general grouping is beyond the scope of this chapter, it is worth emphasizing that, in a seabird context, the principal impact of the Sibley and Ahlquist scheme is to emphasize the separateness of the various birds placed formerly in the Pelecaniformes. As will be discussed later, these birds form a heterogeneous group whose natural affinities have long been in doubt. Insofar as they relate to other nonpelecaniform seabirds, the contrasts between the two classifications outlined in Table 3.1 generally concern differences over the taxonomic level at which a group is recognized, but do not question the unity of the group. For example, the albatrosses are a family, Diomedidae, under Peters’ classification but a subfamily, Diomedinae, under Sibley and Ahlquist’s scheme. However, the Sibley and Ahlquist scheme allies the diving petrels more closely with the gadfly petrels and shearwaters than is customary in traditional classifications.

While these studies, from a decade or more in the past, provide an adequate higher level taxonomic framework for the chapter, this is not true at lower levels where the pace of taxonomic



FIGURE 3.1 Jackass Penguin pair with their chick — South Africa. (Photo by R.W. and E.A. Schreiber.)

revision is faster. In particular, molecular studies are prompting reassessment of species boundaries. I take the work of Sibley and Monroe (1990) as the starting point for the species list, but frequently deviate from it. Although space does not allow the case for each deviation to be made, at least an attempt will be made to direct the reader to a source that does make the case.

3.2 THE ORDERS OF SEABIRDS

3.2.1 ORDER SPHENISCIFORMES, FAMILY SPHENISCIDAE

Penguins are flightless and easily recognized. On land they stand upright and walk with a shuffling gait, occasionally sliding forward on their bellies. At sea, the legs, set well to the rear, serve as a rudder along with the tail. The forelimbs are modified into stiff flippers which cannot be folded and which lack flight feathers (Figure 3.1). The wing bones are flattened and more or less fused, while the scapula and coracoid are both large. Bones are not pneumatic. Many of these features are evidently adaptations for wing-propelled underwater swimming (Brooke and Birkhead 1991, Sibley and Ahlquist 1990). Penguins, densely covered with three layers of scale-like short feathers, lack the bare areas between feather tracts (apteria) found in most other birds.

While the monophyletic origin of penguins is not in question, it has proved difficult to pinpoint that origin. The earliest possible fossil penguin, from 50 to 60 million years ago (mya), is partial and undescribed. From the late Eocene (40 mya), penguin fossils are more numerous, more specialized, and already highly evolved marine divers (Fordyce and Jones 1990, Williams 1995; see Chapter 2). Thus there are no described fossils truly intermediate between the presumed flying ancestor and extinct species that are broadly similar to extant species (Simpson 1976, Williams 1995). However there are persistent pointers to an ancestry shared with the Procellariiformes.

Such pointers include not only the DNA hybridization data of Sibley and Ahlquist (1990), but also various anatomical features. Features shared by these two groups, and also by the divers (= loons in North America), are these. All have webbed feet and two sets of nestling down. There are two carotid arteries, as opposed to the one found in many birds. More technically, the nostrils are termed holorhinal which means that the posterior margin of the nasal opening is formed by a concave nasal bone. Of the four palate types into which bird palates are sometimes categorized, petrels and penguins have the type known as schizognathous (Sibley and Ahlquist 1990). However,

these shared features are primitive, retained from distant ancestors, and provide suggestive but not conclusive evidence of a more recent relationship for the groups concerned (Brooke in press).

All penguins belong in a single family, the Spheniscidae, containing 6 genera and 17 species (Table 3.1; Williams 1995). Note that here and subsequently, genus and species totals refer to extant taxa only. The penguins are an exclusively southern hemisphere group, concentrated in cooler waters. Judging by the fossil record, the same has always been true in the past. The modern range extends farther north than elsewhere in southern Africa and South America because of cool currents, the Benguela and Humboldt, respectively, sweeping northward. Indeed, the Galapagos Penguin (*Spheniscus mendiculus*) is found at the Equator breeding on the archipelago swept by the Humboldt Current.

3.2.2 ORDER PROCELLARIIFORMES

All procellariiforms have tubular nostrils which are totally characteristic of this group whose monophyly has never been seriously questioned (Figure 3.2). Indeed, this feature provided the now-redundant name of the order, the Tubinares. While the nostrils of albatrosses are separated by the upper ridge of the bill, in the other petrels the left and right nostrils are merged on top of the bill in a single tube divided by a vertical septum. The prominence of the tube varies between species and its function is uncertain. It may serve in olfaction. Thanks in part to well-developed olfactory bulbs, the powers of smell of many procellariiforms are exceptionally good, at least by the standards of birds (Verheyden and Jouventin 1994). It is also possible that the tubes play some part in distributing the secretions of the densely tufted preen gland which may be responsible for the characteristic musky odor of most procellariiforms (Fisher 1952, Warham 1990).

Another unique feature of the petrels is the digestive tract. The gut of petrels does not have a crop. Instead the lower part of the esophagus is a large bag, the proventriculus. In most birds the walls of the proventriculus are smooth. Not so in petrels where the walls are thickened, glandular, and much folded. Morphological reasons for suspecting a common ancestor for penguins and procellariiforms were discussed above. This suspicion has been strengthened by Sibley and Ahlquist's work (Table 3.1B). If correct, it would suggest a southern hemisphere origin for the procellariiforms. Certainly petrels today are most diverse in the southern hemisphere (Figure 3.3). The fact that most fossil petrels have been found in northern deposits (see Chapter 2) does not necessarily argue against the southern case, since the amount of land where fossils might be unearthed is so much greater in the north.



FIGURE 3.2 Laysan Albatross feeding its chick — Midway Island, north Pacific Ocean. (Photo by J. Burger.)

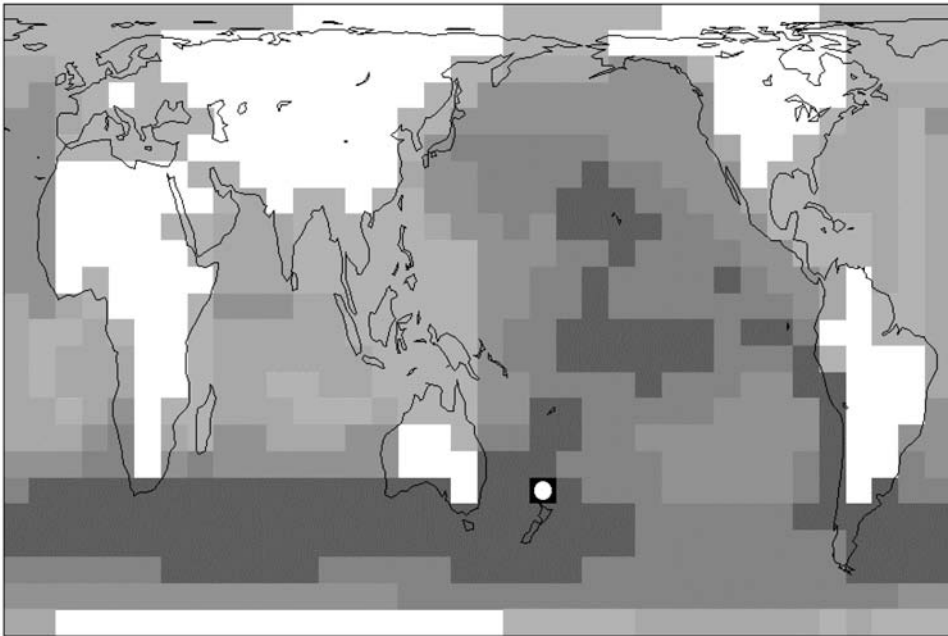


FIGURE 3.3 Map of worldwide species richness of procellariiform species, based on at-sea foraging ranges. Richness is indicated by darkness of the grid cell, and ranges from no records (white) to a maximum of 46 species (black with white circle) in the grid cell immediately north of New Zealand. (After Chown et al. 1998. With permission.)

3.2.2.1 Family Diomedidae

Albatrosses are easily recognized by their large size and, as mentioned, by the separation of the left and right nasal tubes. An interesting feature, shared with the giant petrels (*Macronectes* spp.), is that the extended humerus can be “locked” in place by a fan of tendons that prevents the wing rising above the horizontal. Once the humerus is slightly retracted from the fully forward position, the lock no longer operates, and the wing can be raised. This shoulder lock facilitates the remarkable gliding of albatrosses (Pennycuik 1982).

The taxonomy of albatrosses is in a state of flux. Until recently there were two widely accepted genera: *Phoebetria*, containing the two sooty albatross species of the Southern Ocean, and *Diomedea*, containing all other species. However, molecular work by Nunn et al. (1996) revealed that *Phoebetria* was a sister group to the smaller Southern Ocean species, the “mollymawks,” which were assigned to the genus *Thalassarche*. Meanwhile the North Pacific albatrosses were a sister group to the Southern Ocean’s great albatrosses, such as the Wandering *D. exulans*. Accordingly, Nunn et al. (1996) placed these two groups, respectively, into the genera *Phoebastria* and *Diomedea* (Appendix 1). This generic revision has commanded general support among seabird biologists.

More contentious than the generic revision has been the extensive splitting advocated by Robertson and Nunn (1998), who designated 24 species in place of a former 14. While it may transpire that these splits are justified, this author’s personal view is that the case for all of them is not yet made (Brooke 1999). Accordingly I (Brooke in press), along with BirdLife International (2000), adopt a slightly more conservative 21-species position; *Thalassarche* — 9 species; *Phoebetria* — 2; *Diomedea* — 6; *Phoebastria* — 4 (Appendix 1).

Today’s albatrosses are largely found in higher latitudes ($>20^\circ$), either in the Southern Ocean (17 species) or the North Pacific (3 species). With the exception of the Waved Albatross (*Phoebastria irrorata*) breeding on the Galapagos Islands and off Ecuador, they are absent as breeding birds

from lower latitude stations. This absence has been plausibly related to the dearth, at such low latitudes, of the strong and steady winds on which albatrosses rely for gliding (Pennycuick 1982).

However, the absence of breeding albatrosses from the North Atlantic is more puzzling. Such was not the case in the past. Olson and Rasmussen (in press) report five species in Lower Pliocene marine deposits of North Carolina, dating from about 4 mya (see Chapter 2). They have also been found in Lower Pleistocene, and probably also in underlying Upper Pliocene deposits, of England. This means that albatrosses were common in the Atlantic into the late Tertiary, and disappeared during the Quaternary period (Olson 1985). Presumably Pleistocene climatic fluctuations impinged more severely in the North Atlantic than in the North Pacific. Now it may be that mere chance and the difficulty of crossing Equatorial waters are sufficient explanations of the albatrosses' failure to reestablish in the North Atlantic after the Pleistocene disappearance. The fact that individual Black-browed Albatrosses (*Thalassarche melanophrys*) have survived for over 30 years in the North Atlantic in the 19th and 20th centuries (Rogers 1996, 1998) implies that the ocean is not inimitable to the day-to-day survival of albatrosses.

3.2.2.2 Family Procellariidae

The most diverse and speciose family within the order Procellariiformes is, without question, the Procellariidae, containing 79 species (following Brooke in press). While evidently petrels, these mid-sized species (body weights 90 to 4500 g) are most conveniently defined by an absence of the features characteristic of the other three families. Within the Procellariidae there are 5 more or less distinct groups of species, namely, the fulmars and allies (7 species), the gadfly petrels (39), the prions (7), the shearwaters (21), and the larger petrels (5). Do these groupings reflect evolutionary history? Drawing principally on the cytochrome *b* data of Nunn and Stanley (1998) the answer is a qualified affirmative (Figure 3.4).

The fulmarines are generally medium to large, often scavenging species, represented by six species in the higher latitudes of the southern hemisphere and one, Northern Fulmar *Fulmarus glacialis*, in the north. The six prion species in the genus *Pachyptila* and the Blue Petrel (*Halobaena caerulea*) are united by plumage pattern, myology, and bill structure (Warham 1990). All are confined to the southern hemisphere. Also confined to the southern hemisphere are the five fairly large (700 to 1400 g) species in the genus *Procellaria*. Shearwaters include more aerial species that obtain their food at or close to the surface and those which recent research has revealed to be adept and deep divers. For instance, the mean maximum depth reached by Sooty Shearwaters

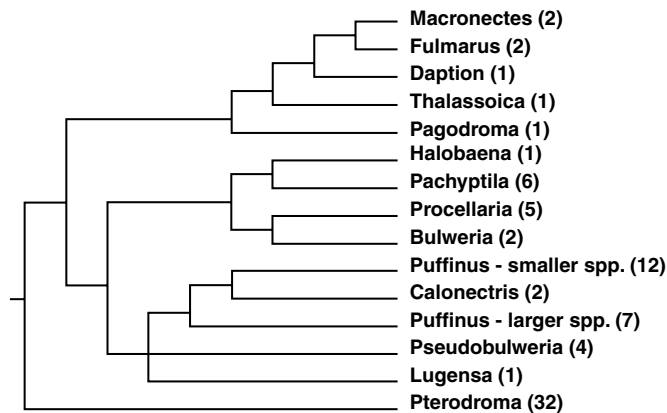


FIGURE 3.4 Possible generic relationships within the Procellariidae based on cytochrome *b* evidence from Nunn and Stanley (1998) and Bretagnolle et al. (1998). After each genus, the number of species within the genus is indicated in brackets.



FIGURE 3.5 Wedge-tailed Shearwater courting group on Johnston Atoll, Pacific Ocean. (Photo by R.W. Schreiber.)

(*Puffinus griseus*) on foraging trips was 39 m, and the greatest depth attained was 67 m (Weimerskirch and Sagar 1996). Shearwaters occur in virtually all oceans, except at the very highest latitudes (Figure 3.5). However, there is one very significant exception. No shearwaters breed in the North Pacific although huge numbers of Sooty and Short-tailed Shearwaters (*Puffinus tenuirostris*) spend the austral winter in this area, having undertaken a transequatorial migration from breeding stations mainly around Australia and New Zealand.

While Mathews and Iredale (1915) placed the two gray-plumaged shearwater species in *Calonectris*, this separation has not been supported by molecular studies. These same molecular studies (Austin 1996) have revealed an unexpectedly deep split within the genus *Puffinus* between the larger species and the smaller species (*nativitatis*, and members of the *puffinus*, *lherminieri*, and *assimilis* species complexes).

Finally the largest and most confusing procellariid group comprises the gadfly petrels, so called because of their helter-skelter flight over the waves. They are found in all oceans, but nowhere breed at high latitudes. The two *Bulweria* species, long recognized as distinct (Bourne 1975), show possible molecular, bill, and skull affinities with *Procellaria* (Imber 1985, Bretagnolle et al. 1998, Nunn and Stanley 1998). Four species in *Pseudobulweria* have in the past been merged with *Pterodroma*. However, various authors, reviewed by Imber (1985), have recognized the case for generic differentiation, and the molecular case for a relationship with shearwaters was made by Bretagnolle et al. (1998). The Kerguelen Petrel (*Lugensa brevirostris*) is widely viewed as an “oddball” species. While Imber (1985) thought it might be allied to the fulmarine species, the molecular evidence places it closer to shearwaters (Nunn and Stanley 1998). This leaves 32 gadfly petrels in the core genus *Pterodroma*. This total (following Brooke in press) reflects some judgments about species boundaries that certainly would not be universally accepted. Why species boundaries have proved so very difficult to draw in some seabird groups like *Pterodroma*, but not in others, will be reviewed later in the chapter.

3.2.2.3 Family Pelecanoididae

The four species of diving petrel, all members of the single genus *Pelecanoides*, form a very distinct southern hemisphere group. There is no evidence that their range has ever extended into the northern hemisphere. These birds are characterized by flanges — or paraseptal processes — attached to the central septum dividing the two nostrils. The function of these processes is uncertain, but it may

serve to reduce the ingress of water into the nostrils which face upward. Diving petrels are all small (100 to 130 g) and very similar in plumage, being shiny black above, and white below. Unlike the majority of petrels which often glide, the diving petrels are instantly recognizable by their rapidly whirring flight on short, stubby wings. This flight style is associated with the birds' means of underwater progression, using the half-closed wings as paddles in a manner similar to the auks of the northern hemisphere. Indeed the remarkable convergence between the smaller auks and the diving petrels has been noted for over 200 years (Latham 1785). The convergence extends to many skeletal features (Warham 1990). Interestingly, the convergence may also extend to the molt pattern. Diving petrels, like certain auks, shed the main wing and tail feathers simultaneously (Watson 1968) and become flightless. But given that the full wing area is generally not deployed during swimming underwater, this loss of feathers may be no great impediment.

Cytochrome *b* sequence data confirm that the Pelecanoididae and Procellariidae are sister taxa (Nunn and Stanley 1998). However, given the distinctiveness of the diving petrels, there is a case for retaining them as a separate family rather than merging diving petrels and procellariids into a single taxon (Table 3.1; Sibley and Ahlquist 1990).

3.2.2.4 Family Hydrobatidae

There are 21 species of storm petrel in 8 genera, with a notable concentration of species nesting off western Mexico and California. All are small seabirds, typically less than 100 g, with particularly conspicuous nostrils, often up-tilted at the ends. The 21 species are divided into two subfamilies. Recent molecular work suggests these two subfamilies represent monophyletic but separate radiations from an early petrel stock (Nunn and Stanley 1998). The subfamily Oceanitinae comprises seven southern hemisphere species split into five genera. These birds have relatively short wings with only ten secondaries, squarish tails, and long legs that extend beyond the tail. Carboneras (1992) suggested that these features are associated with the stronger winds of the southern hemisphere, and the fact that the birds feed by slow gliding. As the birds glide, they almost appear to be walking on water since their dangling feet frequently contact the surface. In contrast the 14 species of the northern subfamily Hydrobatinae are split into only three genera, of which two, *Hydrobates* and *Halocystena*, are monotypic. The remaining 12 species belong in the genus *Oceanodroma* whose center of distribution is the Pacific Ocean. Two species breed in the North Atlantic and two visit the Indian Ocean where, however, no species breed — an unexpected gap in the distribution. Compared to the Oceanitinae, the Hydrobatinae have longer, more pointed wings with 12 or more secondary feathers and frequently their tails are forked. In the manner of swallows, they intersperse busy flying with short periods of gliding.

3.2.3 ORDER PELECANIFORMES

Taxonomic relationships within the Pelecaniformes are frankly problematical and unresolved. That in turn makes it difficult to identify with confidence the group's nearest relatives (Table 3.1). That said, features uniting the group are as follows. They are the only birds to have all four toes connected by webs, the condition known as totipalmate. A brood patch is lacking in all groups (Nelson in press). Whereas the salt gland of most seabirds lies in a cavity on top of the skull, that of the pelecaniforms is enclosed completely within the orbit (Nelson in press). All have a bare gular pouch, with the exception of the tropicbirds where the feature is inconspicuous and feathered. External nostrils are slit-like (tropicbirds), nearly closed (cormorants and anhingas), or absent (pelicans, frigatebirds, and sulids; Figure 3.6).

Even this brief account is sufficient to indicate that the relationship of the tropicbirds to other pelecaniform groups is especially uncertain. Frigatebirds also may be distantly related to the rest of the order (Nelson in press, Sibley and Ahlquist 1990). On the other hand, an ancestral relationship between sulids, cormorants, and anhingids seems likely. That said, just how closely related the



FIGURE 3.6 Courting pair of Blue-footed Boobies on the Galapagos Islands. (Photo by J. Burger.)

cormorants and anhingids, the only pelecaniform groups that might be confused in the field, are remains uncertain. Sibley and Ahlquist place the two groups in separate superfamilies (Table 3.1), and Becker (1986) has suggested that they have been separated for over 30 million years.

The general picture so far sketched uses evidence from DNA and morphology. However, the conspicuous displays of Pelecaniformes at their colonies, exhaustively documented by van Tets (1965), provide a further line of evidence. When Kennedy et al. (1996) compared a pelecaniform phylogeny based on van Tets' behavioral data with that derived from molecular and morphological data, the congruence was significantly greater than expected by chance. This suggests, perhaps counter-intuitively, that ritualized behavioral displays, such as gaping the bill during greeting, can remain stable over millions of years and thereby retain significant phylogenetic information (see Chapter 10). Further, the Kennedy et al. (1996) study reinforced the case for supposing that tropicbirds and frigatebirds are distinct from other pelecaniforms.

Siegel-Causey (1997) has discussed why the correspondence between the pelecaniform phylogenies derived from molecular, morphological, and behavioral studies may be so poor. Aside from confirming the likely sulid–cormorant–anhingid grouping, the studies are consistent only in their inconsistency. In particular Siegel-Causey wondered whether morphological characters supposed to unite the group may in fact be independently derived. There is an evident opportunity for further work.

3.2.3.1 Family Phaethontidae

There are three closely related species in the single tropicbird genus *Phaethon*. All are medium-sized, predominantly white seabirds with long (30 to 55 cm) tail streamers (Figure 3.7). While the pectoral region is well developed, allowing remarkably sustained flapping flight, the pelvic region is atrophied. Thus tropicbirds can barely stand. They shuffle on land, their bellies scraping the ground.

While Tertiary fossils showing resemblances to tropicbirds come from higher latitudes (London, England, and Maryland, USA: Olson 1985), today's species are essentially tropical. The Red-tailed Tropicbird (*Phaethon rubricauda*) occurs in waters over 22°C (Enticott and Tipling 1997). While the smallest species, the White-tailed (*P. lepturus*), has a pan-tropical distribution, the distributions of the two larger species, the Red-tailed and the Red-billed (*P. aethereus*), are nearly complementary. The former occurs across the Indo-Pacific as far east as Easter Island. The latter occurs in the



FIGURE 3.7 Red-tailed Tropicbird adult prospecting for a nest site, showing long tail streamers common to all the tropicbirds. (Photo by E.A. Schreiber.)

extreme eastern tropical Pacific, in the Caribbean and the Atlantic, and finally in the Arabian Sea where there is overlap with Red-tailed Tropicbirds.

3.2.3.2 Family Pelecanidae

The huge size and capacious throat pouch of pelicans make them easy to recognize. In fact, pelicans are among the heaviest flying birds (4 to 13 kg, depending on species; Figure 3.8; Elliott 1992; see Appendix 2). The seven species, placed in the single genus *Pelecanus*, are distributed across the world in tropical and warm temperate zones where they feed in coastal or inland waters. Like the anhingas, the status of pelicans as seabirds is open to question, and the treatment here is accordingly brief. The Brown Pelican (*Pelecanus occidentalis*) is the species most often met at sea, and is also the only species that plunge-dives in pursuit of prey.

3.2.3.3 Family Fregatidae

With long pointed wings and deeply forked tail, the frigatebirds are aerial seabirds of the tropics (Figure 3.9). Using their long hooked robust beak, they are capable of snatching prey from the sea surface, or indeed in the case of flying fish, from above the surface, without alighting on the water. In fact, their plumage is not sufficiently waterproofed with preen gland oil to allow safe swimming. The reduced webs between the toes are confined to the basal portion of the toes.

There are five decidedly similar modern species of frigatebird in a single genus *Fregata*. Two species, the Great Frigatebird (*Fregata minor*) and Lesser (*F. ariel*), have generally overlapping distributions in the Indo-Pacific. Both also breed at Trindade and Martin Vaz in the tropical south Atlantic. The Magnificent Frigatebird (*F. magnificens*) is found in the tropical Atlantic plus the eastern tropical Pacific, while two species, the Ascension (*F. aquila*) and Christmas (*F. andrewsi*), are single-island endemics.

3.2.3.4 Family Sulidae

As is true of most Pelecaniform groups, sulids are easily recognized. They are fairly large seabirds, with long, strong, tapering bills. The skull is hinged to allow more pressure to be applied to the tip of the bill, the better to grasp fish. Facial skin, bill, eyes, and feet are usually brightly colored.



FIGURE 3.8 The neck of this Brown Pelican will soon molt to brown and it will move into the nesting colony to begin courtship and pair formation. (Photo by R.W. Schreiber.)



FIGURE 3.9 A male Magnificent Frigatebird inflates its pouch and waits for a potential mate to fly over, at which time he will begin his courtship behaviors to attract her. (Photo by J. Burger.)

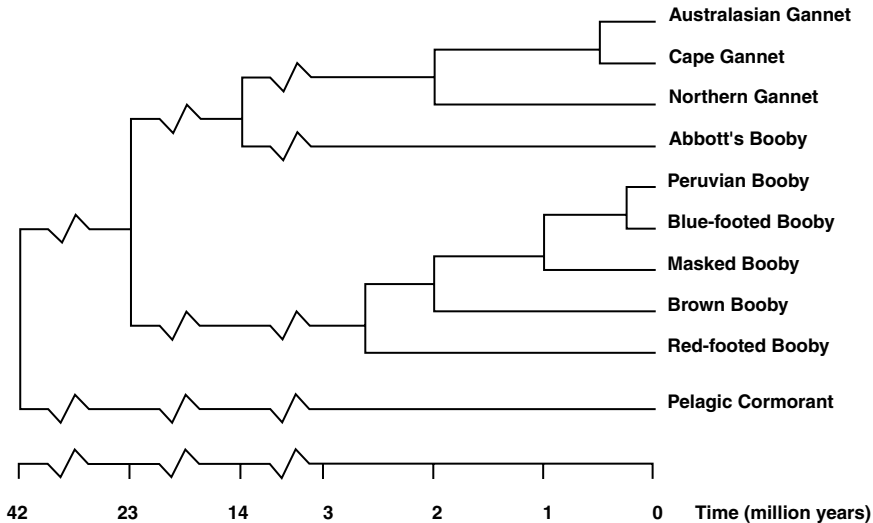


FIGURE 3.10 Approximate time frame for speciation events within the Sulidae (redrawn from Friesen and Anderson 1997). Note that Friesen and Anderson's study was completed before Pitman and Jehl (1998) recommended a split of the Nazca Booby from the Masked Booby.

The wings are long and pointed, and the tail is often diamond-shaped. The preen gland at the base of the tail opens via five apertures (Nelson 1978).

There has been sustained debate over whether the sulids should be divided into two genera, the gannets *Morus* spp. and boobies *Sula* spp. Checklists are divided on the issue. However, using cytochrome *b* evidence, Friesen and Anderson (1997) estimated the booby and gannet lineages diverged about 23 million years ago, about the time when fossils can be clearly recognized as either *Sula* or *Morus* (Nelson in press). Thus the case for the division is strong. Friesen and Anderson's study also lent support to the suggestion of Olson and Warheit (1988) that Abbott's Booby (*Papasula abbotti*) should be placed in a monospecific genus *Papasula*, allied by its long humerus with the gannets, rather than with the boobies characterized by short humeri. In fact, Friesen and Anderson estimated *Papasula* and *Morus* diverged about 14 million years ago. This study therefore proposed the time frame for sulid speciation shown in Figure 3.10. The alliance of Abbott's Booby with the gannets is also supported by behavior; they alone among the sulids have a prolonged face-to-face greeting ceremony using outspread wings (Nelson in press). Since the completion of Friesen and Anderson's study, Pitman and Jehl (1998) have recommended a split of the Nazca Booby (*Sula granti*) from the Masked Booby (*S. dactylatra*). Subsequent cytochrome *b* analysis (Friesen et al. submitted) has confirmed the distinctiveness of the two taxa.

Gannets are plunge-diving birds of productive temperate waters of the North Atlantic and south African and Australian regions. As an adaptation to underwater wing-powered pursuit of prey, the gannets' humeri are long relative to the more distal bones of the wing. On the other hand, the boobies are essentially tropical, species occurring in all tropical oceans. Boobies catch prey on the wing or by dives that are shallower than those of gannets. Accordingly, the humeri are shorter in relation to the distal parts of the wing than in gannets (Warheit 1990).

Implicit within this brief account is the information that today no sulids breed in the temperate North Pacific, an absence which is puzzling given the Miocene and Pliocene records of both *Sula* and *Morus* species from deposits stretching from California to British Columbia (Warheit 1992). There is no evidence to support the idea that the absence represents a major contraction of range resulting from human devastation of colonies. Such contraction has occurred on massive scale in the case of Abbott's Booby which is vulnerable to hunting and habitat destruction. Formerly



FIGURE 3.11 A Flightless Cormorant in the Galapagos, the only cormorant species that cannot fly. (Photo by R.W. and E.A. Schreiber.)

distributed across the entire Indian Ocean and east into the Pacific as far as the Marquesas, the species is now confined to the Indian Ocean's Christmas Island (Steadman et al. 1988).

3.2.3.5 Subfamily Phalacrocoracinae

Cormorants are medium to large aquatic birds that obtain prey underwater by pursuit. Body, neck, head, and bill tend to be elongated (Figure 3.11). The bill is laterally flattened, hooked (c.f. anhingas), and with nostrils nearly closed (Orta 1992). Cormorants occur around most of the world's coasts, with the exception of the high Arctic. Although they breed at certain oceanic islands, such as those of the Southern Ocean and the Galapagos, they are rarely seen in pelagic waters. In addition to the wholly marine species, there are cormorants that occur in both marine and freshwater environments and species which are confined to freshwater. Thus cormorants can be met in the rivers and lakes of all continents, except at the higher northern latitudes.

While cormorants and shags are certainly the most speciose pelecaniform group, deciding just how many genera and species there are has proved exceptionally difficult. For example, Dorst and Mougín (1979) considered that there were 29 species in a single genus *Phalacrocorax*. If species are to be removed from this one genus, the most likely candidates in the past have been the Flightless Cormorant (*Compsohalieu* [= *Nannopterum*] *harrisi*) of the Galapagos and/or the five species of micro-cormorants *Microcarbo* (see Siegel-Causey 1988 for review of past studies). However, Siegel-Causey's own analysis suggested a more drastic revision of the group. He proposed 37 species in nine genera. Excluding one extinct species, his classification is followed in Appendix 1. Relying mainly on osteological characters, Siegel-Causey identified two major groups, the Phalacrocoracinae ("true" cormorants) comprising four genera of all dark littorine species and the Leucocarboninae (shags), five genera of variably plumaged, littorine, or more pelagic species. The increase in the number of species was caused because Siegel-Causey decided to split the blue-eyed shags of the Southern Ocean, often represented by different taxa on different island groups, into more species than recognized by earlier workers. The details of this rearrangement are beyond the scope of this survey, but the general issue of how to deal with subtly different taxa on different islands, an issue also bearing on albatross and petrel taxonomy, will be considered below.

3.2.4 ORDER CHARADRIIFORMES

The alliance of the shorebird families with the skua/gull/tern/skimmer grouping and with the auks was originally based on a shared schizognathous palate, and further anatomical similarities in syrinx and leg tendons (Brooke and Birkhead 1991). It has been supported by Sibley and Ahlquist's (1990) DNA study (Table 3.1) which suggests that these shorebird and seabird lineages diverged at least 25 million years ago.

3.2.4.1 Family Stercorariidae

The skuas form a small, distinctive family of seven species that probably diverged from the gulls about 10 mya (Furness 1996; Figure 3.12). They combine catching their own prey (sometimes on land during the breeding season) with kleptoparasitism. All breed at moderate to high latitudes, and most migrate toward the Equator during the nonbreeding period. The three smaller well-defined species, also known as jaegers, breed in northern high latitudes and are placed in the genus *Stercorarius*. On the other hand, defining species limits in the larger *Catharacta* species has been problematical because of plumage variation within taxa (Dewillers 1978). While the northern hemisphere Great Skua (*Catharacta skua*) is certainly distinct, the southern hemisphere forms are less so. Here the author recognizes the Chilean (*C. chilensis*), Brown (*C. antarctica*), and South Polar Skuas (*C. maccormicki*). While the small (<1%) mitochondrial DNA differences between these three (Cohen et al. 1997) might argue for subspecific status, Dewillers (1978) has made the case for their recognition because, despite considerable overlaps in breeding range, hybridization is avoided.

Relationships among these skuas have yielded one of the most extraordinary and fascinating tales to emerge in seabird systematics in recent years. Mitochondrial DNA sequence data presented by Cohen et al. (1997) suggested that the Great Skua and the Pomarine Jaeger (*Stercorarius pomarinus*) are closely related. Albeit less convincingly, nuclear DNA data supported the close relationship between the Great Skua and the Pomarine Skua. This species pair, in turn, is most closely related to the southern hemisphere skuas and more distantly related to the other northern species, the Parasitic Jaeger (*S. parasiticus*) and Long-tailed (*S. longicaudus*). If this picture is correct, neither of the genera *Catharacta* or *Stercorarius* is monophyletic. Remarkably the feather lice found on Pomarine Skuas are also more akin to those on Great Skuas than those on Parasitic and Long-tailed Jaegers (Cohen et al. 1997).



FIGURE 3.12 A Brown Skua tends its egg and chick in the Falkland Islands. (Photo by P.D. Boersma.)

Cohen et al. (1997) suggested three evolutionary routes to this present-day picture. The first is that the skua ancestor resembled a modern Pomarine Jaeger. From this ancestor, one lineage developed into Parasitic and Long-tailed Jaegers. The other retained the Pomarine Jaeger-like species, and twice budded off *Catharacta* forms. Another idea is that the resemblance of the Pomarine Jaeger to Parasitic and Long-tailed Jaegers is a case of convergence. The third and most intriguing possibility is that interbreeding between a female Great Skua and male Parasitic or Long-tailed Jaeger introduced *Catharacta* mtDNA into the *Stercorarius* lineage, and created the hybrid that was the progenitor of today's Pomarine Jaegers. When Braun and Brumfield (1998) re-analyzed Cohen et al.'s molecular data in a maximum likelihood framework, they concluded that *Catharacta* was, after all, monophyletic. However, Andersson (1999) has supported the hybridization scenario of Cohen et al.

3.2.4.2 Subfamily Larinae

Associated with lakes, wetlands, or marine environments, gulls are fairly small (100 g) to fairly large (2 kg) birds with stout bills and webbed feet. They are long winged and, typically, some shade of gray or black above and white below. There is broad agreement that gulls and terns (Sterninae) are closely related. Gulls have a cosmopolitan distribution. They are normally absent only from deserts, high mountains, extensive tracts of forest (especially tropical rainforest), and from ice sheets. While gulls are invariably encountered on temperate coastlines, they may be absent from tropical coasts, especially from tropical oceanic islands. This absence is not because any other group of birds obviously replaces the gulls as a scavenger/predator, nor is it easily explained on the grounds that tropical coastal zones are less productive than their temperate counterparts. Therefore the explanation offered here is that gulls are relatively scarce on tropical coasts because their scavenging role is undertaken by crabs which can attain great densities on tropical shores. In the warmth of the tropics crabs are not metabolically disadvantaged, compared to homeothermic gulls, as they perhaps are in temperate regions.

For reasons that will be addressed in the discussion (Section 3.3) below, drawing species boundaries has often been problematical. However, most modern lists (e.g., Sibley and Monroe 1990, Burger and Gochfeld 1996) recognize about 50 species in 6 to 7 genera. The overwhelming majority of species are placed in the genus *Larus*, while separated into other genera are the Swallow-tailed Gull (*Creagrurus furcatus*) of the Galapagos, the two Kittiwake *Rissa* species, and the high Arctic trio of Sabine's Gull (*Xema sabini*), Ivory Gull (*Pagophila eburnea*), and Ross's Gull (*Rhodostethia rosea*).

Several studies have attempted to clarify relationships between species. Dwight (1925) emphasized plumage differences, separating the large white-headed species from the smaller dark-headed species. Moynihan (1959) followed Tinbergen (1959) in arguing that behavioral patterns of gulls could reflect relationships as accurately as plumage which might be adapted to current ecology. A similar argument was adduced above in respect to sulids. However, Moynihan's work still recognized the white-headed group of gulls identified by Dwight, but split the dark-headed species into two sister groups. Using 117 skeletal and 64 integument characters, Chu (1998) constructed a gull phylogeny that indicated the dark hood was ancestral, and therefore not necessarily indicative of a relationship. This seems a reasonable conclusion given that the sister groups of the gulls (terns, skimmers, and skuas) are also characteristically dark capped. It is a conclusion supported by the recent study on the topic by Crochet et al. (2000) who used sequence data from the mitochondrial control region and cytochrome *b* gene to assess relationships among 32 gull species.

The principal conclusions of Crochet et al.'s (2000) study were as follows. Dark-headed species are not a single clade, but broadly split into two groups, one of which is allied to the large white-headed species. The several dark tropical gull species are not closely related. Their similarity in plumage is therefore interpreted as convergence, specifically the dark feathers being more resistant



FIGURE 3.13 A White Tern pair courting — Christmas Island, Pacific. (Photo by R.W. and E.A. Schreiber.)

to bleaching. The Arctic Sabine's and Ivory Gulls are sister taxa, despite their strikingly different plumages. Ross's Gull was not available for sequencing.

Noting that Sibley and Ahlquist provide a $\Delta T_{50}H$ of value of 4.5 between *Larus* and *Sterna*, and following Moum et al.'s (1994) estimate that one unit of $\Delta T_{50}H$ corresponds to 3 million years of independent evolution, Crochet et al. date the gull-tern split at 13.5 mya. If molecular evolution has proceeded at a constant rate thereafter, then the divisions within the extant gull lineages date back no farther than 6 mya. This sits thoroughly uncomfortably with possible fossil gulls from the middle Oligocene (30 mya) and more certain gulls from the Lower Miocene (Burger and Gochfeld 1996).

3.2.4.3 Subfamily Sterninae

Terns are invariably associated with water, most frequently coasts, but also freshwater wetlands and rivers or pelagic environments (Figure 3.13). They are small to medium birds with a sharp pointed bill and more or less forked tail. Many species have a black cap. Their distribution is cosmopolitan. Species breeding at higher latitudes are mostly migratory.

Most modern lists (e.g., Sibley and Monroe 1990, Gochfeld and Burger 1996) recognize about 45 species in 7 to 10 genera. Following Sibley and Monroe (7 genera, 45 species), the majority of species (32) are placed in the genus *Sterna*. This genus here includes the relatively large crested terns, sometimes split off into the genus *Thalasseus*. The four so-called marsh terns are placed in the genus *Chlidonias*, while the highly distinctive Large-billed Tern (*Phaetusa simplex*) of South American rivers and the Inca Tern (*Larosterna inca*) of the coasts of Peru and Chile belong to monospecific genera. This leaves seven species in three related genera of the noddy group, *Anous* (3), *Gygis* (2), and *Procelsterna* (2). Because some of the forms in this group (for example, the Black Noddy [*A. tenuirostris minutus*] and White-capped Noddy [*A. tenuirostris tenuirostris*]) have allopatric distributions, they may or may not be conspecific.

3.2.4.4 Family Rhynchopidae

The skimmers belong to a single genus *Rhynchops* where the lower jaw is markedly longer than the upper and where, uniquely among birds, the eye pupil is not round but closes to a vertical cat-like slit. The three species live on the coasts and large rivers of southeast Asia, tropical Africa, eastern Northern America, and much of Central and South America.

While most authors consider that the terns and gulls are more closely related to each other than either is to the skimmers, the possibility that the noddies are a sister group to the skimmers rather than other terns has been aired by Zusi (1996).

3.2.4.5 Family Alcidae

The auks, comprising 23 extant species and the much-lamented extinct Great Auk (*Pinguinnis impennis*), are a distinct group of diving seabirds confined to the northern hemisphere. Following Gaston and Jones (1998), the auks have a compact body, short wings (very short in the flightless Great Auk), and short tail. Because the webbed feet are set far back on the body, the auks frequently rest on their bellies when ashore. There are 11 primaries and 16 to 21 secondaries on the wings which beat hectically in flight and, slightly bent, provide most of the underwater propulsion. To increase the birds' overall density and thereby facilitate diving, the long bones and breast bone are not pneumatized. Nearly all of the features above reflect compromises imposed on birds which combine the power of flight and active underwater pursuit of prey. The bill is very variable in shape and, in some species, highly ornamented during the breeding season.

Recent studies of relationships among the auk species have principally used anatomy (Strauch 1985), protein polymorphism (Watada et al. 1987), and allozymes in combination with mtDNA data (Friesen et al. 1996). While the results of these studies were not identical, there was substantial agreement, and here Friesen et al.'s phylogeny (Figure 3.14) which identifies six lineages is presented:

1. The Dovekie (*Alle alle*) is grouped with Razorbill (*Alca torda*) and murrelets *Uria* spp. Had the Great Auk been included in the study, there is little doubt it would have fallen into this group.
2. The puffins are grouped with the Rhinoceros Auklet (*Cerorhinca monocerata*).
3. The planktivorous Pacific auklets form a distinct group.
4. Among the brachyramphine murrelets, the Long-billed (*Brachyramphus perdix*) of the Pacific coasts of Asia was the most divergent, strengthening the case that it should be recognized as a full species, distinct from the Marbled Murrelet (*B. marmoratus*) of the American Pacific (see also Friesen et al. 1996b).
- 5/6. The synthliboramphine murrelets and guillemots form the two final groups. Whether they are closely related is less certain.

Friesen et al.'s (1996a) study failed to resolve some of the relationships between and within tribes, suggesting periods of "starburst" adaptive radiation during the auks' history. This history was certainly underway 15 mya, for there are unequivocal mid-Miocene fossils. The identity of possible auk fossils from more than 10 million years prior to that is less certain (Olson 1985). Following the early radiation, many of today's auk genera evolved and are represented in the fossil record from 5 mya onward (Gaston and Jones 1998).

Auks today are most richly represented in the Pacific: 17 species confined to that ocean, 2 to the Atlantic, and 4 whose distribution spans both. While it seems likely that the auks originated in the Pacific, the subsequent history of radiation of the various groups in the two oceans is certainly complicated and discussed in some detail by Gaston and Jones (1998). But the modern paucity of Atlantic auk species appears to be a consequence of Pleistocene extinctions, rather than any failure of auk stocks to penetrate to the Atlantic. Thus Olson and Rasmussen (in press) record at least nine auk species from Lower Pliocene deposits of North Carolina (see Chapter 2). There is clearly a parallel between the scarcity of auk species in the North Atlantic today and the absence of albatrosses which likewise disappeared in the Pleistocene (see above). Furthermore, the North Atlantic supports three breeding phalacrocoracids, as compared to six in the North Pacific.

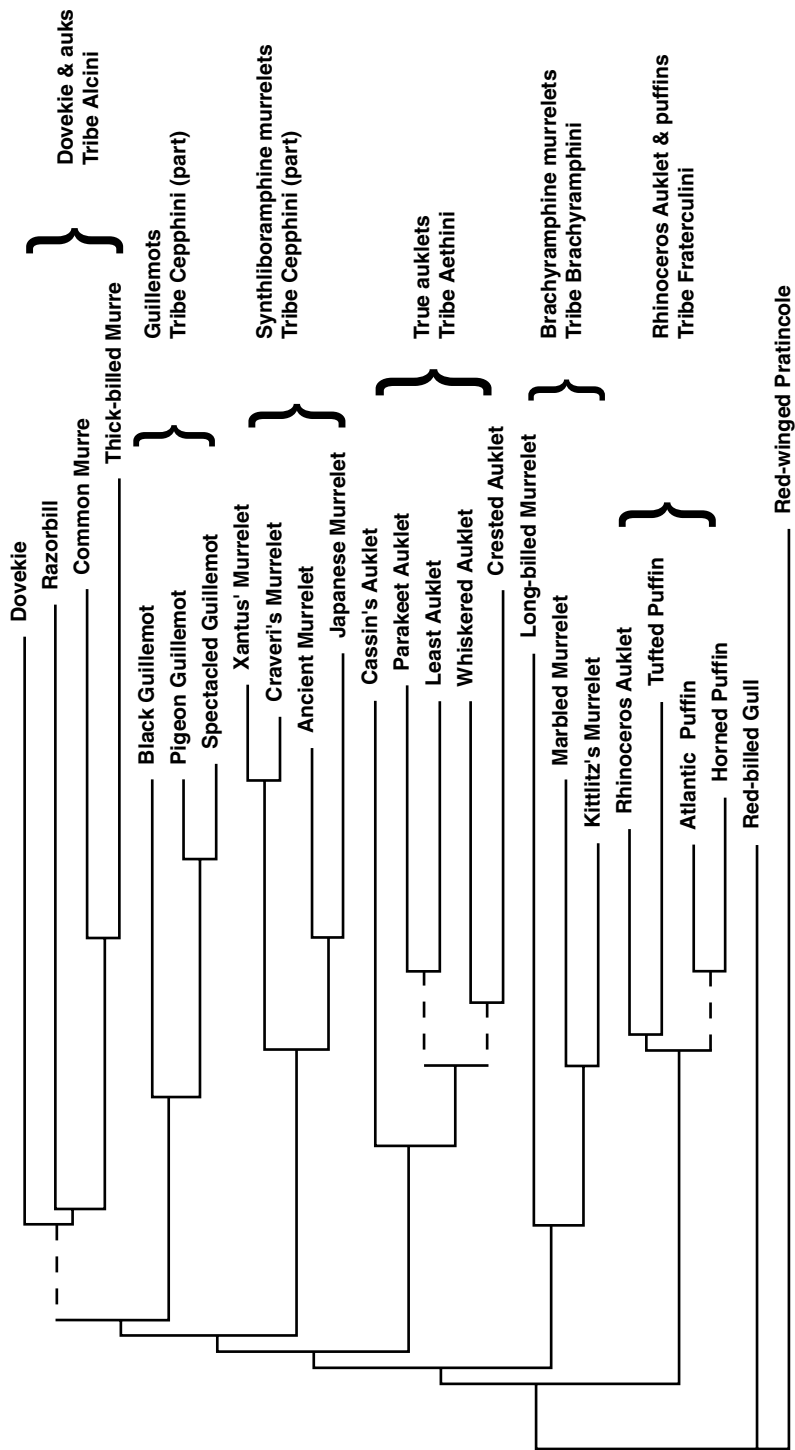


FIGURE 3.14 A phylogeny of the auks redrawn from Friesen et al. (1996a,b). Dashed lines indicate branches with <95% support.

3.3 DISCUSSION

This broad-brush account of seabird systematics and distribution has highlighted many instances of uncertainty, for example, unresolved questions surrounding relationships within the Pelecaniformes. There is not space to discuss them all. Instead two particular issues are considered here, namely, why the species-level taxonomy of some groups, but not others, has proved and continues to prove so contentious, and whether some interesting general patterns of seabird distribution can be discerned.

3.3.1 SPECIES BOUNDARIES

There are four groups of seabirds where species boundaries are difficult to define and conspicuously in a state of flux: the albatrosses, gadfly petrels, southern shags, and larger northern gulls. While this state of affairs could simply represent the fact that it is unreasonable to expect natural diversity always to slot into the constructs of biologists, I suspect the observation may be revealing something more interesting about these groups, and am quite prepared to be criticized for that suspicion.

Let us consider first the albatrosses, gadfly petrels, and southern shags. These birds characteristically nest on islands. Moreover, a significant fraction (3/21 albatrosses, c. 11/39 gadfly petrels, 7/36 cormorants/shags) breeds at just a single island or archipelago (Brooke in press, Enticott and Tipling 1997). In those species breeding at a single island, it must be the case that all individuals return to breed at the island where they themselves were hatched. In more technical terms, natal philopatry is extremely high (Brooke in press). By extension it is also likely to be high in those species breeding at only a few sites.

If, over many generations, seabirds at different stations have evolved slightly different genotypes in response to different conditions, then there might be selection against intermingling of the genotypes, against hybridization between immigrants and those faithful to the natal colony. One way of achieving that is for birds to develop isolating mechanisms, such as divergent plumage, that prevent reproduction and reinforce slight differences already evolved. This is a familiar argument with respect to the evolution of new species (Mayr 1963). However, with high philopatry, few birds will disperse to other colonies. This could reduce selection for plumage divergence. In time the upshot would be birds in widely separated colonies with similar but not identical plumage and structure. But that external similarity need not indicate recent separation of the two populations, or indeed genetic similarity. In summary, an effect of extreme philopatry could be a reduction in the tendency for populations of different colonies to diverge in external appearance. Plumage and morphology would then be a poorer guide than usual to the independent evolutionary history of the birds. Only molecular studies would reveal the extent of independent history and the possible need for redrawing of species boundaries (e.g., Robertson and Nunn 1998).

While many of the difficulties in drawing species boundaries discussed with respect to albatrosses, petrels, and shags arise because the taxa of interest are isolated on remote islands and do not interbreed, the situation is different with respect to gulls. Here the taxa do frequently interbreed and often produce viable hybrids. However, the general observation is that the hybrids are not spreading at the expense of the original taxa. This suggests that some degree of reproductive isolation does exist, and/or that there is selection against the hybrids.

These vexing taxonomic problems at the specific level most acutely affect the larger gull species of the northern temperate regions (Barth 1968, Snell 1991a,b). For example, relationships between the Herring (*Larus argentatus*), Lesser Black-backed (*L. fuscus*), Yellow-legged (*L. cachinnans*), Armenian (*L. armenicus*), and Slaty-backed Gulls (*L. schistisagus*) remain uncertain. Any profound understanding will certainly also take account of the North American cluster of Iceland (*L. glaucooides*), Thayer's (*L. [glaucooides] thayeri*), Kumlien's (*L. [glaucooides] kumlieni*), and Glaucous-winged Gulls (*L. glaucescens*). However, I suggest that the fact that the problems largely involve

temperate species and do not extend at the specific level to the tropics gives a clue to the root of the problem. It is that the larid populations became fragmented during the Pleistocene glaciation. When the ice last retreated some 12,000 years ago, the populations re-established contact, allowing the possibility of interbreeding. But, as mentioned above, the evidence is that some degree of reproductive isolation has developed.

Why then are other seabirds characteristic of the northern boreal and temperate zones, for example, the Northern Fulmar and the auks, not bedeviled by similarly confusing species complexes? It would be difficult to make any case that the Fulmar, auks, and gulls differ fundamentally in philopatry. All are known from modern studies to show significant natal dispersal (Birt-Friesen et al. 1992, Dunnet et al. 1979, Harris 1984, Monaghan and Coulson 1977). Indeed significant post-Pleistocene dispersal must have been involved in the expansion of such northern species into their modern ranges.

Various factors such as generation time, population size, and metabolic rate may affect the rate of molecular evolution (Nunn and Stanley 1998 and references therein). If molecular evolution proceeded more rapidly in gulls than the other northern seabirds when their populations were fragmented by the advance of Pleistocene ice, then the gulls might have proceeded further toward reproductive isolation that would become evident when the ice retreated. While gull populations may be smaller than auk populations by roughly half an order of magnitude (Furness 1996, Nettleship 1996), it is not evident that gulls do differ sufficiently in these factors from the other seabirds to explain the matter.

The suggestion offered here is that this difference in species-level taxonomic uncertainty between the gulls and other north temperate seabirds arises because the two groups are more or less strictly associated with offshore waters. Those strictly associated (e.g., Northern Fulmar, auks) will have been pushed south along the essentially north-south axes offered by the east and west coasts of the Pacific and the Atlantic during glacial advances. They will have moved back north during interglacial periods, but, within each ocean, populations will not have been greatly fragmented. On the other hand, the more coastal large gulls will have experienced a complicated history of population fragmentation as the colonies, broadly strung along an east-west axis encompassing inter alia the North Pacific, Great Lakes, North Atlantic, Mediterranean, Black Sea, and Sea of Okhotsk, moved south and north as ice advanced and retreated.

Interestingly, the more marine northern gull species such as the kittiwakes, Ivory Gull, Ross's Gull, and Sabine's Gull present clearly defined species. So do the terns, which, while coastal inhabitants like the large gulls, differ in being long-distance migrants. Such migration may incidentally enhance population homogeneity.

3.3.2 PATTERNS OF SEABIRD DISTRIBUTION

3.3.2.1 Family Level Patterns

No seabird family is found exclusively in the Atlantic or Indian or Pacific Oceans. All seabird families except three are found in both northern and southern hemispheres. The three exceptions are the penguins, diving petrels, and auks which are largely confined to the higher latitudes of their respective hemispheres. The fact that they are also the seabirds most adapted to underwater pursuit of prey is almost certainly not a coincidence. Partly because birds adapted for underwater pursuit of prey may have sacrificed flight efficiency, thereby making the costs of travel between prey patches higher, and partly because underwater pursuit of prey is itself energetically expensive, underwater pursuit of prey is only a viable way of life when prey density is high, which is most likely where marine productivity is high. With the exception of upwelling zones, marine primary productivity is higher at higher latitudes than near the Equator (Begon et al. 1996, Robertson and Gales 1998). Thus this argument is that the penguins, diving petrels, and auks have been confined to their respective hemispheres by an inability to cross the unproductive waters of the tropics. It is

tempting also to relate the lower species richness of the most speciose seabird order, the Procellariiformes, at lower latitudes to generally lower productivity there (Figure 3.3).

3.3.2.2 Contrasts between the North Pacific and North Atlantic

While the southern seabird communities either of the Antarctic or the sub-Antarctic are broadly similar wherever around Antarctica they are found, there are much more striking contrasts between the communities of the North Atlantic and North Pacific, especially between about 40 and 60°N. These contrasts include:

1. The absence of breeding shearwaters in the North Pacific.
2. The absence of albatrosses in the North Atlantic.
3. The absence of sulids in the North Pacific.
4. The far greater species (and generic) richness of auks in the North Pacific.

As has been indicated in the family accounts, points 2 to 4 appear historical accidents. The seabird family was represented in the ocean concerned until the Pliocene, and it then disappeared or dwindled during the Pleistocene. Today there are major continental barriers to seabird dispersal at the northern temperate latitudes in question and unproductive tropical waters to the south. Together these constraints have presumably impeded the restoration of the pre-Pleistocene pattern.

The situation with respect to point 1 is different. Shearwaters breed in the Hawaiian archipelago and also in Japanese waters (Streaked Shearwater [*Calonectris leucomelas*]), but none are to be found breeding in the Pacific farther north and east. As argued elsewhere (Brooke in press), this could be related to two non-exclusive factors. The first is the greater species richness of auks in the North Pacific which, like most temperate shearwaters, catch prey underwater. The second is the huge numbers of Short-tailed and Sooty Shearwaters which migrate from the Antipodes into the North Pacific during the northern summer. The second argument is given strength by the fact that North Atlantic breeding shearwaters are mostly found in the northeast Atlantic, and in puny numbers in the northwest Atlantic where transequatorial migrants (especially Greater Shearwaters, *Puffinus gravis*) are concentrated. Both the rich auk community and the huge influx of nonbreeding shearwaters to the North Pacific will reduce prey stocks, and therefore may have contributed to the absence of breeding shearwaters.

3.3.2.3 The Influence of Foraging Technique on Abundance and Distribution

It is intriguing to consider the seabird species with the largest global populations (>10 million individuals; data from del Hoyo et al. 1992, 1996). These species are Chinstrap Penguin (*Pygoscelis antarctica*), Macaroni Penguin (*Eudyptes chrysolophus*), Northern Fulmar, Short-tailed and Greater Shearwater, Antarctic Prion (*Pachyptila desolata*), Salvin's Prion (*P. salvini*), Leach's Storm Petrel (*Oceanodroma leucorhoa*), Common Diving-petrel (*Pelecanoides urinatrix*), Guanay Cormorant (*Leucocarbo bougainvilli*; before recent declines), Black-legged Kittiwake (*Rissa tridactyla*), Sooty Tern (*Sterna fuscata*), Dovekie, Common Murre (*Uria aalge*), Thick-billed Murre (*U. lomvia*), Least Auklet (*Aethia pusilla*), and Atlantic Puffin (*Fratercula arctica*).

While population numbers, of course, provide only a crude index of a species' impact on the ecosystem and may have been reduced in historical times, two points stand out. First, reflecting the higher productivity of higher latitudes, all but two (Guanay Cormorant, Sooty Tern) of the species listed are higher latitude species. Second, the majority of the species obtain their food by underwater pursuit of prey. It appears that, where prey density is high enough to render the underwater pursuit lifestyle viable, then species adopting this lifestyle can become very numerous. They are essentially harvesting prey in three dimensions while the surface feeders are restricted to two. The numerical and biomass dominance in polar or subpolar regions of seabirds feeding by

underwater pursuit, using feet or wings for propulsion, is detailed in several studies (Ainley 1977). Where they breed, auks form from 28 to 97% of the breeding seabird biomass (Gaston and Jones 1998). Penguins at South Georgia form 76% of the seabird biomass (Croxall and Prince 1987).

If these arguments have any worth, then we would expect underwater pursuit specialists to be less prominent in the seabird community where productivity was lower. Precisely this argument has already been used to explain the failure of penguins, diving petrels, and auks to cross the Equator. And we might predict that, where a productivity gradient existed at a single latitude, species feeding underwater would form a greater part of the community where productivity was higher.

Among species obtaining food at the surface of the sea, those feeding offshore have potentially a greater area available in which to search for food, because of straightforward geometrical considerations, than do those feeding close to shore. They might therefore have larger populations. Diamond (1978) found support for this idea at several tropical seabird colonies. It is also notable that surface-feeding species with populations in excess of 10 million (Northern Fulmar, Antarctic and Salvin's Prions, Leach's Storm Petrel, Black-legged Kittiwake, Sooty Tern) are all offshore species.

While higher productivity may be one factor contributing to the concentration of certain seabird species or groups, especially the underwater pursuit specialists, to higher latitudes, another factor may be water temperature. As the water becomes warmer nearer the Equator, poikilothermic prey will become more mobile and more difficult to catch. This will further militate against the occurrence of underwater pursuit specialists in warmer waters.

3.3.2.4 Species Level Patterns

While no seabird family is confined by longitude to a single ocean, various species are so confined. In the northern hemisphere this is most evident in the different suite of seabirds found in the North Atlantic and North Pacific. In some cases the species of one ocean are represented by sister taxa in the other. For example, related members of the *Puffinus puffinus* complex breed in the North Atlantic and North Pacific. Similarly, the large *Larus* gulls breeding on the east and west coasts of the lower 48 states of the United States are different but closely related: the Herring and Great Black-backed Gulls (*L. marinus*) in the east, vs. the Western (*L. occidentalis*) and Glaucous-winged Gulls in the west. In other cases the replacement is by less closely related species, for example, the puffins.

Land barriers that might divide seabird species are less manifest in the southern hemisphere than in the northern. Nonetheless, there remain examples of closely related taxa occupying different oceans. Such examples can be from low latitudes (e.g., Red-tailed and Red-billed Tropicbird). However, there are comparable examples from higher southern latitudes where barriers to longitudinal dispersal appear slight. Thus the Greater and Short-tailed Shearwaters are confined, respectively, to the Atlantic and Pacific (Marchant and Higgins 1990). Since allopatric speciation caused by extrinsic barriers to gene flow seems unlikely, I have argued above that philopatry has contributed to genetic divergence in some groups (see also Friesen and Anderson 1997 for a discussion of sulids).

Species distributions are limited not only longitudinally but also latitudinally. As a result one species may replace another along a latitudinal cline, and/or at a temperature discontinuity. Thus the Grey-headed Albatross (*Thalassarche chrysostoma*) tends to have the most southerly distribution of the Southern Ocean mollymawks, and is the species most likely to be met south of the Antarctic Polar Front. Hornby's Storm Petrel (*Oceanodroma hornbyi*) is associated with the cool Humboldt upwelling off Peru and Chile (Murphy 1936). Alternatively, the replacement of one species by another may be associated with salinity differences. In the northern Indian Ocean, Jouanin's Petrel (*Bulweria fallax*) is associated with more saline waters than its congener, Bulwer's Petrel (*B. bulwerii*; Pocklington 1979).

As yet we have limited understanding of what underlies this association between seabirds and particular water bodies. Two examples of studies that indicate the sort of understanding that may emerge can be cited. At the largest possible spatial scale, the body characteristics of nine medium-sized procellariids from the Eastern Tropical Pacific were compared with those of seven species

from the Southern Ocean south of 55°S by Spear and Ainley (1998). It emerged that the tropical species had longer wings and tails, bigger bills, and less fat than their polar counterparts. This was interpreted as enabling tropical species to forage economically over large expanses of ocean, catching sparse and often mobile prey. In contrast, the polar species had smaller wings to cope with stronger winds, smaller bills, to catch abundant and not very mobile prey; and larger fat deposits to weather stormy periods. Presumably this relationship between seabird morphology, prey mobility, and climate has arisen as natural selection has acted over very many thousands of years.

At the scale of a species pair with partly nonoverlapping distributions, Thick-billed Murres have a more northerly distribution than Common Murres. They also have shorter, thicker bills that are presumably more efficient for catching a diet that contains more zooplankton than the more fishy diet consumed by the relatively slender-billed Common Murre (Gaston and Jones 1998). This, in turn, raises the possibility that Thick-billed Murres tend to be more planktivorous because food chains tend to be shorter in the Arctic (Briand and Cohen 1987).

In conclusion, the large-scale patterns of seabird distribution are fairly well documented. At a smaller scale, radio-tracking, and more especially satellite-tracking, are allowing researchers to follow individual birds as they search for prey at sea. But the reasons why seabirds of one species should “choose” to forage in a different sea area to a similar, related species often remain obscure. It is such choices, made by the individual, which generate the observed species distribution. Presumably the choice is made in that individual’s best interest and reflects the ability to secure prey efficiently, either at or below the sea surface. While ornithologists studying land birds have established links between morphology, habitat chosen, diet, and foraging efficiency (e.g., Partridge 1976, Winkler and Leisler 1985, Grant 1986), comparable studies on seabirds are generally less developed.

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Lesser Frigatebird Males Court Females Flying Overhead