

ECOLOGY AND BEHAVIOR OF SEABIRDS

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Summary

Seabirds are marine predators who occupy the upper trophic level in marine food webs. They are present in all marine ecosystems and oceans of the world, from coastline to pelagic and open seas. Seabirds feed on a wide range of marine organisms, from zooplankton to relatively large fish and squid. They use also a wide range of foraging techniques, from surface feeders to divers, which can feed at more than 200 m deep. Seabirds can forage near the breeding colonies not far from the coastline, or at very long

distances during days or weeks in the open ocean. Morphological and physiological adaptations for their marine style of life are diverse. Seabirds comprise several different families of birds inhabiting marine ecosystems, and each group has its own ecological features. However, all seabirds share several life history traits: high adult survival, high mean generation time, progressive access to reproduction at relatively old ages, low reproductive rate and low number of predators. All these traits determine a rather *k* evolutionary strategy based on the high residual reproductive value established on the high number of reproductive chances in the life of an individual. Dynamics of seabird local population are not only determined by birth-death processes, but also by emigration-immigration phenomenon, which connect populations in a metapopulation scale. Seabirds compete with other marine predators, especially with human fisheries. The relationships between both groups are complex and represent a host of interactions, some of them beneficial and other detrimental for seabirds. Conservation of seabirds is essential and must be part of sound policy-oriented progress towards sustainable world development.

1. Prologue

Consider a small Mediterranean archipelago at the beginning of March. The first Cory's Shearwaters of the season are homing from their wintering quarters in the waters of the Benguela Current off South Africa and Namibia, several thousand kilometers away. The old couples come to visit their old nesting tunnels as soon as it gets dark and some stay overnight and copulate, protected by the darkness of their burrows. By the beginning of May, the birds that were present in their burrows during the day, start visiting the colony only at night, and during the second fortnight of the month almost all breeding birds in the colony lay one ovate white egg representing some 11% of the weight of the adult female. If the egg is lost, there will be no clutch replacement and the breeding season will end up unsuccessful. As soon as the egg is laid, typically the female will begin incubating and the male will take up the task after a few uninterrupted days. This process goes on and on, day and night, for some fifty days until the egg hatches and a helpless brown-downed nestling comes to life by mid July. The chick will be brooded day and night by the adults over a few days, until homeothermy is attained. Afterwards, the nestling will be fed intermittently (mainly fish and squid) and only at night during three long months. Late in October the young birds will leave their natal colony heading towards their Atlantic wintering quarters. These birds will not recruit as breeding adults until at least age seven. The same adult couple will return to breed next year, at the same colony and the same burrow, unless one of the members of the pair dies during wintertime and a new pair is formed. This cycle can go on and on for several decades...

We could describe the breeding cycle of many other seabird species and we would find some strikingly similar features in their ecology and behavior. Indeed, all marine birds are long-lived species. They make small contributions to their populations every breeding season, although high effort is invested. They take several years to reach maturity and have a high life expectancy. These life-history traits basically reveal the main life strategy of seabirds: maximizing life-time reproductive success. Seabirds (especially pelagic species) usually breed on islands, that is, environments typically free of predators and disease and these factors are selective pressures which favor seabird

species with long-lived individuals. In addition, the sea surrounding colonies is usually either an ecological desert or a rich source of food, but experiencing unpredictable ups and downs. In either case, the advantage is again for long-lived individuals since the currency in use is not how well you do in a given year (in terms of reproductive output) but how long you are able to survive and attempt reproduction annually. Hence, the longer you live the higher your fitness, if you are a seabird. Most seabirds are good examples of some evolutionary trade-offs such as those between current reproduction and survival and current reproduction and future reproduction.

2. Taxonomy and distribution of seabirds

There are over 9000 bird species on our planet of which only a roughly 3% are seabirds. One would say, after considering those figures, that becoming a seabird is not an easy evolutionary enterprise. However, we have to take into consideration that modern bird phylogenies, based on molecular techniques (DNA-DNA hybridization), place all (eight) seabird families (Laridae, Phaethontidae, Sulidae, Phalacrocoracidae, Pelecanidae, Fregatidae, Spheniscidae and Procellariidae) within the order Ciconiiformes, the youngest avian order only after Passeriformes (see Table 1). In total, there are 327 species of seabirds, although certain other birds such as divers, seaducks, phalaropes and grebes are also sometimes classed as seabirds. Classical phylogenies include seabirds in at least four taxonomic orders: Sphenisciformes, Procellariiformes, Pelecaniformes and Charadriiformes and twelve families: Spheniscidae, Diomedidae, Procellariidae, Hydrobatidae, Pelecanoididae, Phaethontidae, Pelecanidae, Phalacrocoracidae, Fregatidae, Stercorariidae, Laridae, Rynchopidae, Alcidae. These old phylogenies (still the most popular ones), based mostly on similarity of phenotypical traits (sharing of traits among related present-day species), used to place marine birds among the oldest bird groups (e.g. penguins were considered the oldest birds only after tinamous and giant flightless birds like kiwis, emus, cassowaries, rheas and ostrich).

Order	Suborder	Family	No. of species	Common names
Ciconiiformes	Charadrii	Laridae	130	jaegers, skuas, skimmers, gulls, terns, noddies, auks, murrees, puffins
		Phaethontidae	3	tropicbirds
	Ciconii	Sulidae	9	boobies, gannets
		Phalacrocoracidae	38	cormorants, shags
		Pelecanidae	9	Pelicans, shoebill
		Fregatidae	5	frigatebirds
		Spheniscidae	17	penguins
		Procellariidae	116	petrels, shearwaters, diving-petrels, albatrosses, storm-petrels

Table 1. Taxonomic groups of seabirds

Obviously, phylogenetic relationships derived from comparative anatomy can be very misleading since similarities could be due to adaptive convergence (analogous characters) and not to common ancestry (homologous characters). The analysis of similarity including ethological, physiological and biochemical clues strongly increases

the chances of deriving a correct phylogenetic classification, although it does not completely remove the confounding effect of adaptive convergence. It seems clear, however, that some morphological characters used traditionally in bird systematics (e.g. relations established among toes by membranes) are not the most appropriate to avoid mistaken analogy and common ancestry. For example, traditional classifications include within Pelecaniformes all groups of seabirds with the four toes joined by membranes (totipalmate feet) whereas new classifications suggest that this feature has been acquired independently by the tropicbirds, pelicans, cormorants, darters, gannets and frigatebirds.

We compare (see Table 2) the most widely accepted traditional classification of the Class Aves (that by Morony, Bock and Farrand published in 1975) with that from Sibley & Monroe based on modern molecular techniques and published in 1988. Orders including seabird families are highlighted in bold type.

TRADITIONAL		MODERN	
ORDER	FAMILIES	ORDER	FAMILIES
STRUTHIONIFORMES	5	STRUTHIONIFORMES	4
TINAMIFORMES	1	TINAMIFORMES	1
SPHENISCIFORMES	1	CRACIFORMES	2
GAVIIFORMES	1	GALLIFORMES	3
PODICIPEDIFORMES	1	ANSERIFORMES	4
PROCELLARIIFORMES	4	TURNICIFORMES	1
PELECANIFORMES	6	PICIFORMES	5
CICONIIFORMES	5	GALBULIFORMES	2
PHOENICOPTERIFORMES	1	BUCEROTIFORMES	2
ANSERIFORMES	2	UPUPIIFORMES	3
FALCONIFORMES	4	TROGONIFORMES	1
GALLIFORMES	4	CORACIIFORMES	9
GRUIFORMES	12	COLIIFORMES	1
CHARADRIIFORMES	16	CUCULIFORMES	6
COLUMBIFORMES	2	PSITTACIFORMES	1
PSITTACIFORMES	3	APODIFORMES	2
CUCULIFORMES	2	TROCHILIFORMES	1
STRIGIFORMES	2	MUSOPHAGIFORMES	1
CAPRIMULGIFORMES	5	STRIGIFORMES	9
APODIFORMES	3	COLUMBIFORMES	1
COLIIFORMES	1	GRUIFORMES	9
TROGONIFORMES	1	CICONIIFORMES	29
CORACIIFORMES	10	PASSERIFORMES	46
PICIFORMES	6		
PASSERIFORMES	60		

Table 2. Classification of the Class Aves

In fact it makes perfect sense that seabirds are not one of the oldest groups of birds since all marine vertebrate animals (except fish) come from terrestrial ancestors and have conquered the world seas necessarily late. Hence, the poor adaptive radiation of seabirds might either be a consequence of the harshness of the marine environment or the youth of its evolutionary history. If the latter is the case, we should expect further diversification of seabird species during millennia to come.

Seabirds tend to be larger than landbirds and are generally much less colorful. Sexual dimorphism both in color and size is small compared to other families of birds.

Some seabird species have breeding populations distributed over wide geographical areas, comprising more than one biogeographical region, e.g. the common tern, which breeds in the Palearctic, Nearctic and Afrotropical regions, whereas some others have minute distributions. For example, only eight breeding colonies are known for Heermann's gull (all in the Nearctic region), and the Amsterdam albatross only breeds on Amsterdam Island in the Indian Ocean. There is normally an association between geographical range and abundance, and in turn conservation status, the Amsterdam albatross once again being a good example: only 5 pairs breed on average every year on Amsterdam Island, and the population is estimated at only ca. 44 to 63 birds (see *Life cycles and Conservation of Seabirds*).

The world ocean covers 70% of the Earth surface. Hence, we should expect a wide distribution of seabird groups throughout the globe, from polar to equatorial regions. However, seabird distribution is influenced by a number of limiting factors. Penguins, for instance, only inhabit the Southern Hemisphere but they are not restricted to Antarctica—indeed the Galapagos penguin lives on the equator. Actually, penguins need to feed in cold waters and their distribution is thus determined partly by water temperature. Species living in warmer climates, like Humboldt penguins living along the coasts of Chile and Peru, are associated with cool marine currents, like the Humboldt Current which flows northwards off the western coast of South America, or to local upwellings (as is the case in the Galapagos Islands). These species (Humboldt and Galapagos penguins) among others are subjected to periodic variations in marine productivity. Complex oceanographic and atmospheric features like the El Niño Southern Oscillation (ENSO) cause the inhibition of upwellings, resulting in a paucity of phytoplankton and depletion of the anchovy population on which many seabird species (as well as Peruvian fisheries) depend. Local and distant seabird colonies can suffer total breeding failures as well as slumps in adult numbers.

The distribution of land and water on the earth's surface is not uniform. In fact, the water-to-land ratio in the southern hemisphere is more than twice that in the northern hemisphere. This fact probably explains why seabirds are more diversified in the southern oceans. After all, pelagic seabirds only need a safe piece of land (a territory as large as an incubating bird can reach by stretching its neck) during the breeding season, located as close as possible to food sources. Whole emblematic groups of seabirds like penguins occur only in the southern hemisphere and some authors believe that petrels may have evolved in the southern hemisphere like the penguins, although their fossil record (from the middle Oligocene) is richer in the northern hemisphere, probably owing to better conditions for fossilization. Migratory movements in the southern

oceans may take place across lines of longitude, where seabirds may travel down the westerly winds.

Some seabird species generally feed in water not far from their colonies and are classed as “inshore feeders”. These include terns, cormorants and most of the gulls,. They normally perform short feeding trips and chicks are fed frequently. Other species feed out of sight of land, and are called “offshore feeders”, e.g. some penguins or some gulls. Among offshore feeders there are the so called “pelagic feeders”—species which do not normally return to land outside of the breeding season and take several days to forage before feeding the chick (see *Feeding Ecology of Seabirds*)

3. Feeding ecology of seabirds

It is not a surprise that seabirds, which spend most of their life at sea, feed mainly on marine organisms. Some terrestrial prey (invertebrates, small mammals, carcasses and garbage for scavenging species, olives and other fruits) may also be present for more opportunistic species, which are commonly inshore feeders. This is not the case with offshore and especially pelagic species such as shearwaters and albatrosses. Size of prey is normally related to the species body size: while storm petrels (weighing ca. 30 g) feed on small zooplankton, albatrosses (weighing up to ca. 12 kg) feed mostly on large squids. The type of prey also influences the foraging behavior: small pelagic fish normally concentrate in shoals and attract flocks of surface feeders (such as gulls) and plunge diver feeders (such as gannets and terns), whereas some other marine organisms like squid may be more solitary and are caught by more solitary feeders (such as some albatrosses). When birds forage in flocks, both visual and auditory cues obtained from feeding individuals attract others (conspecifics or heterospecifics) to the same feeding spot. Foraging techniques and location can also affect seabird diets, which can even differ significantly between populations of the same species in nearby colonies, due to different environmental features around breeding grounds. Seabird mainly feed during the day, although there are several species that forage during the night since they have vision adapted to darkness. Some larids (such as Audouin’s gull or swallow-tailed gull), some sulids and the black skimmer are partly or largely nocturnal foragers, whereas most tubenoses and some alcids attend young and excavate burrows only at night, and some may forage at night.

Surface-shoaling fish are very important to seabirds in large areas of comparatively shallow waters (called neritic waters) over the continental shelf. These fish include herrings, sardines, anchovies and sprats (Clupeidae), sandeels (Ammodytidae), and capelin (Osmeridae). In tropical regions, shoaling fish are less available and most are chased by predators such as dolphins or tunas. In these regions flying-fish and halfbeaks (Exocoetidae) are the main prey of seabirds. Nevertheless, in polar regions fish are much less important to seabirds, squid and crustaceans (especially the Antarctic krill) being the main prey.

Whatever the cause of the poor adaptive radiation of seabirds, it is obvious that feeding and surviving out at sea is not a straightforward task. Remember the case study with which we opened this article. Cory’s Shearwaters are equipped with a pair of long and narrow wings (high aspect ratio wings) and breed at latitudes where marine upwellings

are nearly negligible. Shearwaters need those wings to spend days at sea searching for food. They either scavenge offal and fish discarded from fishing vessels or used as bait (the modern version of the old commensalism between seabirds and whales or schools of predatory fish) or capture squids at night, as they move upwards following the circadian vertical migrations of fish. Razorbills, puffins and guillemots on the other hand, have short wide wings (low aspect ratio wings) appropriate for long dives and short flights, which they need for capitalizing on the abundant resources present at high latitude upwellings. Here, food is extremely abundant, but only during short periods of time. For seabirds that normally catch prey sitting on the water (albatrosses, petrels), cephalopods usually constitute a large proportion of the diet. Most of those that use high energy techniques, like underwater diving (cormorants, auks), or hovering and diving (boobies, terns), eat nothing other than fish, which has a much higher energy content than cephalopods.

3.1. Feeding habitats for seabirds

Seabirds can be divided in two large sets, according to their feeding ecology: inshore feeders (e.g. gulls, terns, cormorants) and offshore feeders (e.g. albatrosses, shearwaters, petrels). The former breed mainly on mainland or islands located close to the mainland coast and feed within sight of land. The latter normally breed on oceanic islands and feed out of sight of land. Inshore feeding is usually associated with seabirds of small size, larger reproductive effort per season (normally more than one egg per clutch), early maturity and shorter life spans. Somehow, a trade-off between present and future reproduction seems to occur so that an energetic fee is paid every time you reproduce and this cost accumulates over time and is paid as increased adult mortality. Inshore feeding would be closer to the r extreme of the r/K *continuum* of population ecology theory, whereas the opposite would be the case for offshore feeders. Inshore feeders inhabit less isolated environments where predation (by foxes, badgers, crows, etc) is an important selective pressure, making their breeding habitats more unpredictable in time. In fact one can tell, just by looking at the pigmentation of seabird eggs, the extent to which they have evolved under the pressure of predation. Ground-nesting gull eggs imitate the background surrounding nests, just like army camouflage clothing. However, the eggs of cliff-nesting gulls, like kittiwakes, are much less pigmented and hence more visible. The white coloration of the eggs of hypogeous species, like shearwaters or storm petrels, are the result of a trade-off between avoiding less likely predation by aerial intruders such as gulls, and the need to be discernible to adults coming into their burrows in complete darkness. In fact, nestlings of these species have dark plumages (that make them less invisible to predators inside dark tunnels) because they do not have the need to advertise their presence by means of light colors, employing other clues like their characteristic strong odor and sound.

Inshore feeders not only have higher offspring mortality but also can get food more readily. That not only influences the number of eggs laid and the number of chicks reared per season, but also the growth rate of the nestlings. Chicks of seabirds like terns and gulls have fairly rapid growth rates that can be sustained by a high number of feeds per day. However, the single chick of oceanic seabirds needs to grow slowly (and have a low metabolic rate) in order to make optimal use of the intermittent feeds it receives. In fact, as a result of their slow growth rate, chicks of petrels, albatrosses, shearwaters

and other offshore feeders can accumulate large quantities of fat as an insurance against periods of food scarcity (see *Life Cycles and Breeding Behavior of Seabirds*). Interestingly enough, this vital feature, extremely important for their ontogeny, has been one of the most significant causes of the recent decline of many seabird populations since, until recently, seabird chicks were collected in big numbers by man (for feathers, down, flesh, fat and oil) (see *Conservation of Seabirds*).

3.3. The role of seabirds in marine ecosystems and nutrient cycling

Seabirds are predators of different marine organisms, mostly animal. Some species feed on zooplankton (which in turn depends on the availability of phytoplankton and nutrients), while others feed on fish (both larval, juvenile and adult phases) and squid. Areas of high productivity resulting from oceanographic phenomena such as upwellings, ocean currents or river mouths, are rich in nutrients and trophic chains are enhanced. Seabirds, along with other marine vertebrates such as some dolphins, sharks and turtles, play the role of predators in the trophic chain, and some of them actually occupy the niche of top predators, e.g. albatrosses, pelicans and shearwaters.

Many offshore feeders are night-dwelling seabirds. Seabirds not depending on nutrient-rich waters (like river deltas, marine fronts and oceanographic or orographic upwellings) are faced very often with a foraging ground resembling an ecological desert, punctuated here and there with patches of food which are fairly unpredictable in time and space. That is why many pelagic seabirds rely on the moon for foraging. Moonlight seems to attract phytoplankton to the surface which, in turn, is followed by zooplankton, zooplanktivorous fish species like sardines and fish-eating animals like squids. This piece of ecology has been known by fishermen since ancient times. All fishing methods that employ more or less powerful lights at night to lure fish rely on this principle. Thus, full-moon nights are bad nights for purse-seine fishing since fish cannot be concentrated locally as the effect of light is very widespread. The fact that many marine creatures (e.g. many cephalopods) show bioluminescent properties may also help detecting prey at night. During daytime very often the most profitable option for seabirds is to follow fishing vessels and take advantage of offal and discarded fish, just like fishermen used to employ seabirds as a cue for the location of fish schools prior to the times of sonar and other modern technologies. Seabirds use visual cues to detect fishing boats but “tubenoses” (i.e. Procellariiformes) also seem to make use of olfactory cues. In fact their complex nostril is very likely an adaptation for a well-developed sense of smell.

Through their faeces, seabirds can increase the amounts of organic matter both in the soil of breeding colonies or in relatively closed marine areas such as bays, estuaries or mangles. This participation in nutrient cycles is of vital importance since some elements such as phosphorous or nitrogen are injected back in the ecosystems. Nevertheless, when seabird local breeding populations increase dramatically as a consequence of the influence of human activities (e.g. refuse dumps, fisheries), the impact on local vegetation can be deleterious through physical disturbance (pulling-up, treading, collecting of nest materials), chemical disturbance (soil manuring, salt deposition) or alteration of competitive processes (dispersal of allochthonous seeds, expansion of annual or ruderal species).

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Biographical Sketches

Daniel Oro

I was born in May 1963 in Barcelona (Catalonia, Spain). At the crèche, a teacher told my mother “animals occupy all his minds...” But it was not until I was 18 that I realized that by observing birds around my house I had the chance (other than documentaries on TV) to observe nature and its processes. After my Bachelor in Biology, I scraped a living working for 4 years as perfumist, salesman and some other temporary jobs. In 1990 I was once again fired and then I decided to go back to Biology. I started to work at the Ebro Delta Natural Park where I developed several projects on waterbird conservation, and by chance I paid attention to Audouin's gull, in spring 1991. I then carried out my PhD thesis at Barcelona University on seabird ecology and its relationship with fisheries and obtained a European Union Diploma for that in 1996. After that, I moved to France (CNRS Montpellier) and Scotland (UK) (Glasgow University) as a post-doc researcher learning mathematical models to study population dynamics and demography and the energetic constraints of avian egg formation. My studies have been carried out in islets and marshes in the western Mediterranean, mostly in the Ebro Delta, where Audouin's gull has been used to study colonization and growth of seabird populations. I am now based as a Permanent Researcher at the Spanish Research Council CSIC (an autonomous, multi-disciplinary public research body) in its branch of Esporles at the Balearic Islands, where there are new challenges to work on population ecology and conservation issues. Here, I lead a group of researchers working on different topics such as ecology of seabird communities, fisheries and seabirds, molecular ecology and demography. More information is available at our web page: <http://www.imedeia.uib.es/Natural/danieloro/index.html>

Alejandro Martínez-Abraín

I was born in Montreal (Quebec, Canada) in June 1966 because my parents moved there from their natal Spain in search of opportunities. We came back to Spain in 1969 and I grew up in the province of Valencia, on the Mediterranean Sea. I started watching birds at the age of fifteen since one of my cousins and my uncle were naturalists. I remember learning with them the first Latin names in the Spanish version of *The Birds of Britain* produced by Reader's Digest during my long summer vacations in Vigo (NW Spain). My first birds were wetland birds (I still recall the flight of my first Grey Heron) and seabirds (Shags, Yellow-legged Gulls and the last Guillemots of the Cies islands). I have always felt a special attraction to wetlands and islands. I had the great luck of joining a passionate group of ornithologists at the Albufera Ornithological Station in 1984 (before any protected area had been yet established in our region). That was my field school and too often I gave priority to my fieldwork rather than to my biology studies at the University of Valencia. That finally led me to move abroad to finish my undergraduate studies, which I did at Acadia University (Nova Scotia, Canada), in 1993. After graduation I came back home and worked for five years in the management of my beloved Albufera Nature Park. Once I felt I needed a break I applied for a Fulbright Grant, got it, and moved to St. Louis (Missouri, EEUU) to complete a graduate certificate in conservation biology in UMSL. I am now a 34 year old Ph.D. student at the Mediterranean Institute for Advanced Studies (CSIC-UIB), working on population dynamics and conservation of western Mediterranean seabirds.