

Sherman K, Okemwa EN and Ntiba MJ (eds) (1998) *Large Marine Ecosystems of the Indian Ocean: Assessment, Sustainability, and Management*. Malden, MA: Blackwell Science.

Sherman K and Tang Q (eds) (1999) *Large Marine Ecosystems of the Pacific Rim: Assessment, Sustainability, and Management*. Malden, MA: Blackwell Science.

Tang Q (1993) Effects of long-term physical and biological perturbations on the contemporary biomass yields of the Yellow Sea ecosystem. In: Sherman K, Alexander LM and Gold BD (eds) *Large Marine Ecosystems: Stress, Mitigation, and Sustainability*. Washington DC, AAAS Press, pp. 79–93.

LARIDAE, STERNIDAE AND RYNCHOPIDAE

J. Burger, Rutgers University, Piscataway, NJ, USA

M. Gochfeld, Environmental and Community Medicine, Piscataway, NJ, USA

Copyright © 2001 Academic Press

doi:10.1006/rwos.2001.0231

Introduction

Gulls belong to the family Laridae and terns to the family Sternidae, although many authorities treat them as subfamilies (Larinae, Sterninae) of a single family, the Laridae. Skimmers belong to the Rynchopidae. Gulls, terns, and skimmers, all members of the order Charadriiformes, are similar in many respects, but they differ significantly in many morphological, behavioral, and ecological ways.

Gulls and terns are generally diurnal species that perform most of their breeding, foraging, and migrating activities during the day, while skimmers are largely nocturnal, and forage and court mostly at night. The only gulls that are primarily nocturnal during the breeding season are the swallow-tailed gull of the Galapagos Islands and the gray gull that breeds in the deserts of northern Chile.

Of all seabirds, gulls are among the least specialized, and occupy a wide variety of habitats from the high Arctic and subAntarctic islands, to tropical sea coasts, and even to interior marshes and deserts. In both breeding and feeding, gulls are generalists, and their overall body shape reflects their lack of specialization to any one foraging method, food type, or nesting habitat. Gulls are highly gregarious birds that breed, roost, feed, and migrate in large colonies or flocks.

Terns and skimmers are more specialized than gulls, both in their breeding habitat and in their foraging behavior, and skimmers have a highly specialized morphology and feeding behavior. While individual species of gulls, such as herring gull, may breed in many different habitats, ranging from dry land to cliffs, species of terns and skimmers breed

in fewer habitats, and some are quite stereotypic in their habitat selection. Gulls feed in more different habitats on many different foods, while terns feed mainly over water by plunge-diving or dipping. Skimmers have one of the most unique feeding methods, skimming the water surface.

Taxonomy

The gulls are a worldwide group of about 51 currently recognized species with the main diversity occurring in both north and south temperate latitudes. Terns are also a worldwide group of about 44 species, with the main diversity occurring in tropical as well as temperate latitudes, while each of the three species of skimmers has a more limited distribution, one each in the Americas, Africa, and Asia (scientific names given in **Tables 1** and **2**). There is a tendency for taxonomists working at higher categories to lump genera and families together, where specialists on particular groups are more likely to emphasize differences within the group, by generic splitting – the approach followed here.

Gulls

There are several natural subgroups among the gulls, most of which can be assigned either to the large white-headed or the small dark-hooded tribes. On behavioral grounds, emphasizing the commonality of display patterns, Moynihan treated all gulls in the genus *Larus*. Most taxonomists, however, separate some relatively unique gulls into their own genera, including the swallow-tailed gull (*Creagrus*), of the Galapagos, and several Arctic species, including Ross's gull (*Rhodostethia*), ivory gull (*Pagophila*), kittiwakes (*Rissa*) and Sabine's gull (*Xema*). Less often two south temperate species, the dolphin gull (*Leucophaeus*) and occasionally the Pacific gull (*Gabianus*) are separated as well.

Terns

The main groups of terns include the black-capped terns (mostly in the genus *Sterna*), marsh terns

Table 1 Gulls of the world with general breeding range

Gull	Scientific name	General breeding range (winter range)
Dolphin gull	<i>Leucophaeus scoresbii</i>	Southern South America
Pacific gull	<i>Larus^a pacificus</i>	Southern Australia
Band-tailed gull	<i>Larus belcheri</i>	Pacific Coast of South America
Olrog's gull	<i>Larus atlanticus</i>	Uruguay to Argentina
Black-tailed gull	<i>Larus crassirostris</i>	Siberia to Japan (east China)
Gray gull	<i>Larus modestus</i>	Western South America (coastal)
Heermann's gull	<i>Larus heermanni</i>	West Mexico (California)
White-eyed gull	<i>Larus leucophthalmus</i>	Red Sea
Sooty gull	<i>Larus hemprichii</i>	Middle East (East Africa and Pakistan)
Mew gull	<i>Larus canus</i>	Eurasia and western North America (Africa, east Asia)
Audouin's gull	<i>Larus audouinii</i>	Western Mediterranean and West Africa
Ring-billed gull	<i>Larus delawarensis</i>	Central and eastern North America (to northern South America)
California gull	<i>Larus californicus</i>	Central North America (Pacific Coast to west Mexico)
Great black-backed gull	<i>Larus marinus</i>	Holarctic (south-eastern US, western Europe)
Kelp gull	<i>Larus dominicanus</i>	Southern South America, Australia, Africa
Glaucous-winged gull	<i>Larus glaucescens</i>	Eastern Asia to western North America
Western gull	<i>Larus occidentalis</i>	Pacific Coast of North America
Yellow-footed gull	<i>Larus livens</i>	Gulf of California
Glaucous gull	<i>Larus hyperboreus</i>	Holarctic
Iceland gull	<i>Larus glaucoides</i>	Eastern Canadian Arctic and Greenland (North America and Europe)
Thayer's gull	<i>Larus thayeri^b</i>	Arctic Canada (Pacific Coast of North America)
Herring gull	<i>Larus argentatus</i>	Holarctic (to northern South America and South-east Asia)
Yellow-legged gull	<i>Larus cachinnans</i>	Eurasia (North Africa, Middle East to Western India)
Armenian gull	<i>Larus armenicus^b</i>	Armenia, Turkey (Middle East)
Slaty-backed gull	<i>Larus schistisagus</i>	Siberia to Japan (south to Taiwan, few in Alaska)
Lesser black-backed gull	<i>Larus fuscus</i>	Eurasia (Africa, Arabia, south-western Asia)
Greater black-headed gull	<i>Larus ichtyaetus</i>	Central Asia (southern and south-east Asia)
Brown-headed gull	<i>Larus brunnecephalus</i>	Central Asia (southern and south-east Asia)
Gray-headed gull	<i>Larus cirrocephalus</i>	Southern South America, Africa
Hartlaub's gull	<i>Larus hartlaubii</i>	South Africa
Silver gull	<i>Larus novaehollandiae</i>	Australia, New Caledonia
Red-billed gull	<i>Larus scopulinus</i>	New Zealand
Black-billed gull	<i>Larus bulleri</i>	New Zealand
Brown-hooded gull	<i>Larus maculipennis</i>	Southern South America (northward along coasts)
Black-headed gull	<i>Larus ridibundus</i>	Eurasia (Africa, southern Asia) few in North America
Slender-billed gull	<i>Larus genei</i>	Southern Europe to western Asia (Middle East)
Bonaparte's gull	<i>Larus philadelphia</i>	Alaska–Canada (North American coasts to Caribbean)
Saunders's gull	<i>Larus saundersi</i>	North-eastern China (China to Japan)
Andean gull	<i>Larus serranus</i>	Andes (Pacific Coast of South America)
Mediterranean gull	<i>Larus melanocephalus</i>	Southern Europe (north Africa)
Relict gull	<i>Larus relictus</i>	Central Asia (unknown)
Lava gull	<i>Larus fuliginosus</i>	Galapagos endemic
Laughing gull	<i>Larus atricilla</i>	Eastern US, Caribbean to South America
Franklin's gull	<i>Larus pipixcan</i>	Central North America (South America)
Little gull	<i>Larus minutus</i>	Eurasia (Europe, North Africa)
Ivory gull	<i>Pagophila eburnea</i>	Holarctic
Ross's gull	<i>Rhodostethia rosea</i>	Siberia to Alaska
Sabine's gull	<i>Xema sabini</i>	Holarctic
Swallow-tailed gull	<i>Creagrus furcatus</i>	Galapagos and Malpelo I (Colombia) (South America)
Black-legged kittiwake	<i>Rissa tridactyla</i>	Holarctic
Red-legged kittiwake	<i>Rissa brevirostris</i>	Bering Sea endemic

^aOften placed in the monotypic genus *Gabianus*.^bThe status of this as a species is in question.

(*Chlidonias*), noddies (*Anous*, *Procelsterna*, *Gygis*), and the Inca tern (*Larosterna*). The capped terns include small and medium sized birds in the genus

Sterna and the distinctive, large, crested terns (appropriately considered a separate genus *Thalasseus*, although often placed into *Sterna*). Some unique

Table 2 Terns and skimmers of the world with general breeding range

<i>Tern/skimmer</i>	<i>Scientific name</i>	<i>General breeding range (winter range)</i>
Gull-billed tern	<i>Gelochelidon^a nilotica</i>	Old and New World
Caspian tern	<i>Hydroprogne^a caspia</i>	Old and New World
Elegant tern	<i>Thalasseus^a elegans</i>	Pacific Coast of North America (to South America)
Lesser crested tern	<i>Thalasseus bengalensis</i>	Old World tropics
Sandwich tern	<i>Thalasseus sandvicensis</i>	American tropics and Europe (Africa)
Chinese crested tern	<i>Thalasseus bernsteini</i>	China: Taiwan; nearly extinct (Indonesia)
Royal tern	<i>Thalasseus maximus</i>	American tropics and West Africa
Greater crested tern	<i>Thalasseus bergii</i>	Old World tropics
Large-billed tern	<i>Phaetusa simplex</i>	South American rivers (coastal South America)
River tern	<i>Sterna aurantia</i>	India and south-east Asia
Roseate tern	<i>Sterna dougallii</i>	Pan-tropical
Black-naped tern	<i>Sterna sumatrana</i>	Old World tropics
White-fronted tern	<i>Sterna striata</i>	New Zealand (south-east Australia)
South American tern	<i>Sterna hirundinacea</i>	South American coasts
Arctic tern	<i>Sterna paradisaea</i>	Holarctic (subAntarctic)
Antarctic tern	<i>Sterna vittata</i>	Subantarctic (southern Africa)
Kerguelen tern	<i>Sterna virgata</i>	Crozets, Prince Edward, Marion, Kerguelen
Forster's tern	<i>Sterna forsteri</i>	North America (Central America)
Trudeau's tern	<i>Sterna trudeaui</i>	Southern South America
Little tern	<i>Sterna albifrons</i>	Eurasia, Africa, Australasia
Saunders's tern	<i>Sterna saundersi</i>	Indian Ocean (Africa)
Least tern	<i>Sterna antillarum</i>	North America (northern South America)
Yellow-billed tern	<i>Sterna superciliiaris</i>	South American rivers (coastal South America)
Peruvian tern	<i>Sterna lorata</i>	Pacific Coast of South America
Fairy tern	<i>Sterna nereis</i>	Western and southern Australia
Damara tern	<i>Sterna balaenarum</i>	South Africa (to West Africa)
White-cheeked tern	<i>Sterna repressa</i>	Indian Ocean and Middle East
Black-bellied tern	<i>Sterna acuticauda</i>	India and south-east Asia
Aleutian tern	<i>Sterna aleutica</i>	Siberia and Alaska
Gray-backed tern	<i>Sterna lunata</i>	Central and western Pacific
Bridled tern	<i>Sterna anaethetus</i>	Pan-tropical
Sooty tern	<i>Sterna fuscata</i>	Pan-tropical
Black-fronted tern	<i>Sterna albistriata</i>	New Zealand rivers (New Zealand coast)
Whiskered tern	<i>Chlidonias hybridus</i>	Eurasia, Africa, Australasia
White-winged tern	<i>Chlidonias leucopterus</i>	Eurasia (Africa, Australasia)
Black tern	<i>Chlidonias niger</i>	North America and Europe (South America, Africa)
Brown noddy	<i>Anous stolidus</i>	Pan-tropical
Black noddy	<i>Anous minutus</i>	West Indies, Australia, south-west Pacific
Lesser noddy	<i>Anous tenuirostris</i>	Indian Ocean to western Australia
Blue noddy	<i>Procelsterna caerulea^b</i>	Tropical western Pacific
Gray noddy	<i>Procelsterna albivitta^b</i>	Temperate Pacific
White tern	<i>Gygis alba</i>	Pan-tropical
Inca tern	<i>Larosterna inca</i>	Pacific coast of South America
Black skimmer	<i>Rynchops niger</i>	North American coasts and South America inland
Africa skimmer	<i>Rynchops flavirostris</i>	West, central, and East Africa (Egypt)
Indian skimmer	<i>Rynchops albicollis</i>	North Indian subcontinent to Cambodia

^aThese genera are often placed in the genus *Sterna*.

^bThese two species have until recently been considered a single species.

capped terns are the gull-billed (*Gelochelidon*), Caspian (*Hydroprogne*), and large-billed (*Phaetusa*) terns. *Sterna* is a relatively homogenous assemblage. Noddies are uniformly colored, either all dark (black, brown, blue and gray noddies) or all white (white tern), while the unique Inca tern is all dark with dramatic yellow wattles at the gape.

Skimmers

The three species of skimmers are closely related and form a superspecies. The Indian skimmer breeds in southern Asia from Pakistan to Cambodia; the African skimmer breeds along rivers in Africa, and the black skimmers breeds in North and South America.

Physical Appearance

In all species of these families, males and females are indistinguishable on the basis of plumage. Moreover in gulls and terns there is very little sexual size dimorphism, while skimmers are among the most sexually dimorphic in size of any bird. The skimmers are heavy-bodied, with very long narrow wings, and large, narrowly compressed or knife-like bills for skimming the water. Adult gulls, terns, and skimmers of most species have the coloration of plunge-diving sea birds. They are generally white below, which is believed to serve as camouflage against the pale sky, reducing their conspicuousness to their underwater prey. Young birds are generally spotted or blotched or streaked, affording camouflage on the various substrates they occupy, particularly during the critical pre-fledging period when they rely on cryptic coloration to avoid predation (Figure 1).

Gulls

As a group gulls are generally heavy-bodied, long-winged birds with intermediate length necks and tarsi, webbed feet, and heavy, slightly-hooked bills. Gulls range in weight from as little as 100 g for a little gull to 2000 g for some great black-backed gulls. Gulls exhibit no sexual dimorphism in plumage patterns, but females are slightly smaller than males and in some species show more slender necks and beaks. All species have 12 rectrices and the tails are rounded in all but a few species (Sabine's gull, swallow-tailed gull).

Gulls are generally white-bodied, with a darker mantle varying from pale silvery-gray to black (except for the all-white ivory gull). Several of the smaller species exhibit a pale pink or cream-colored bloom on their breast early in the breeding season. In the Ross's gull (not roseate tern) this is very pronounced and persistent. Gulls have either a dark hood (nearly obscure in some species), dark mask, or all white head during the breeding season. Generally the larger gulls are white-headed, although the great black-headed gull, one of the largest species, is an exception. The smaller gulls are generally either dark-masked or dark-headed. In almost all species the wingtips are black, the melanin pigment offering resistance to wear. Most species have a complex pattern of white 'windows' on the black outer primaries which may differ among closely related species. Several Arctic species (glaucous, Iceland, ivory gulls), have white wing tips.

Some species of gulls reach adult plumage in 2 years (the smaller hooded and masked gulls), while the larger species have 3–4 distinct plumage

year classes. Some do not reach fully adult plumage until their fifth year. Most gulls molt their flight feathers twice a year, and their body feathers once a year. Franklin's gull, which migrates farther than any other gull from its breeding range in the prairies of North America to South America, undergoes two complete molts each year. However, Sabine's gull migrates almost as far, but has only one complete molt each year.

Terns

Terns have narrower, more elongated bodies than gulls and proportionately longer, more slender and pointed wings. Their beaks are generally slender and sharply pointed. Most species of terns forage at least occasionally, by plunge-diving for fish, and accordingly their body is stream-lined. Most terns are white below and gray above, with a black crown in nuptial plumage, although a few species are all dark or all white. The roseate tern has a pale pinkish 'bloom' on the breast early in the breeding season. This is quickly lost by wear. There are no sexual differences in plumage patterns.

The plumage patterns of the gull-billed tern, crested terns, typical black-capped, and large-billed tern are similar: mainly white below, gray above, with a black cap during the breeding season. During the nonbreeding season most species lose part or all of the black crown. Terns have one complete molt and one body molt each year.

Skimmers

Skimmers are the size of the large terns, and are black above and pure white below, although there is a pale cream-colored tinge particularly on the flanks, early in the nesting season. The Indian skimmer has a broad white collar and the other two species gain such a collar in their post-breeding molt. The beak is bright reddish-orange with a yellow tip in the African and Indian skimmers and is red at the base with the distal half black in the black skimmer. The knife-like bill is adapted for slicing through the water surface when the birds are skimming to catch fish. A most unusual feature of skimmers is that the upper mandible is shorter than the lower. Skimmers have two molts a year, including a complete molt and a body molt.

Habitat

Gulls and terns are quite variable in their habitat preference, although almost all species feed and nest in association with water. Gulls forage in a wider range of terrestrial and aquatic habitats, while terns



Figure 1 Examples of gulls, terns and skimmers. (1) Common tern (*Sterna hirundo*) Adult, breeding plumage. Length: 36 cm; wingspan: 80 cm; approximate body mass 120 g. Range: Widely distributed in Northern Hemisphere during breeding season, and coastal oceans of the world during the non-breeding season. (2) Sooty tern (*Sterna fuscata*). Other names: Wideawake. (a) Adult; (b) juvenile. Length: 44 cm; wingspan: 90 cm; approximate body mass: 195 g. Range: Tropical Oceans. (3) Black skimmer (*Rynchops niger*). Adult, breeding. Length: 45 cm; wingspan: 117 cm; Range: Coastal waters and some rivers of North and South America. (4) Herring gull (*Larus argentatus*). Adult, breeding plumage. Length: 61 cm; wingspan: 139 cm; approximate body mass: 1160 g. Range: Widespread in coastal waters of North Pacific and North Atlantic Oceans. Also along coasts of Mediterranean Sea and Indian Ocean. (5) Great black-backed gull (*Larus marinus*). Adult breeding plumage. Length: 75 cm; wingspan: 160 cm; approximate body mass: 1680 g. Range: North Atlantic Ocean. (6) Kittiwake (*Rissa tridactyla*). Other name: black-legged kittiwake. Adult breeding plumage. Length: 41 cm; wingspan: 91 cm; approximate body mass: 385 g. Range: North Pacific, North Atlantic and Arctic Oceans. Illustrations from Harrison P (1985) *Seabirds, an identification guide. Revised edition*. (Boston, Massachusetts: Houghton Mifflin).

and skimmers forage almost exclusively over water. Exceptions include the gull-billed tern which feeds extensively on insects obtained by plunging to the surface or hover-dipping over grasslands.

Gulls

Gulls use a wide variety of habitats; for any single species the range may be narrow or broad. In the breeding season, colonies of nesting gulls can be found in coastal and estuarine habitats, as well as inland. Most species of gulls nest along the continental coasts or on large inland lakes, showing a strong preference for islands or inaccessible sites. A few (brown-hooded, Franklin's, relict) nest mainly on inland lakes or marshes, while two, the lava and swallow-tailed gulls nest on remote oceanic islands, the Galapagos. Franklin's gulls breed on inland freshwater marshes but winter on South American sea coasts.

Gulls occupy a wide variety of nesting habitats, including sandy or rocky islets or beaches, with or without vegetation, marshes, riverine or lake sand bars, wind-swept sand dunes and cliffs, trees, and even buildings. The unique gray gull breeds in the barren, montane deserts of Chile, flying each day over the Andes to the Pacific Coast to obtain food for their young. Gull colonies are generally located in habitats removed from mammalian predators, but some gulls will breed on terrestrial habitats where both avian and mammalian predators are threats.

During migration gulls fly to coastal and estuarine habitats, and in winter, they generally remain along coasts or on large lakes. Although they can be found out to the continental shelf, most are not truly pelagic.

During the winter, their distribution is a function of food availability. Since they eat a wide variety of foods, they can be found in nearly all aquatic habitats. Outside the breeding season, gulls are found at virtually all latitudes where open water is available.

Terns

Terns occur throughout the world, and breed on all continents, including Antarctica (Antarctic tern). Although individual tern species are less variable in their breeding habitats than gulls, overall, terns occupy a wide range of breeding habitats, including inland and coastal marshes, islands in rivers, lakes and estuaries, sandy or rocky beaches, cliffs, and oceanic islands. Since most terns nest on the ground, they seek remote or inaccessible places as an anti-predator strategy against mammalian predators. Several of the noddy species nest on trees.

During the nonbreeding season, most species of terns migrate to coastal estuaries and the open

ocean, although some never leave their inland marshes and rivers. Some species are truly pelagic during most of the nonbreeding season. Sooty tern, the most oceanic tern species, maintains a pelagic existence from the time of fledging until returning to land to breed for the first time at several years of age. Arctic terns wintering in Antarctica often roam through the loose pack ice along the edge of the ice pack.

Skimmers

The skimmers in South America, Africa, and Asia are largely restricted to nesting on riverine sand bars and islands in lakes. The black skimmers of North America are mainly coastal, nesting on beaches and islands, although small numbers breed inland. Except in North America, the nesting of skimmers is influenced by rains, for they must wait until water levels fall and their islands are exposed. Skimmers are the least pelagic members of this family, and rarely are observed far from land.

Breeding Ecology and Behavior

Gulls, terns, and skimmers normally breed in colonies, either in monospecific colonies, or in monospecific groups within colonies that include other species. Terns are the most gregarious and they generally breed, forage, and migrate in flocks that can range from a few individuals to many thousands or even millions (sooty tern).

Most gulls and terns in temperate zones breed at the same time of year, breed once a year, and breed every year. While North American skimmers do likewise, skimmers that are dependent on the formation of sand bars and sandy islands in rivers must wait until such sand bars are exposed. Some tropical terns have shorter breeding seasons, and can breed every 8 months.

Territory size generally increases with body size for gulls, and decreases with body size for terns (Figures 2 and 3). Based on an examination of 49 species of gulls and terns nesting in aquatic and terrestrial habitats, variability in density was accounted for by colony size, body length, and wingspan, and variability in nearest neighbor distance was accounted for by body size.

Gulls and terns of several species, such as common tern, can be very aggressive at mobbing potential predators, including human intruders into their colony. Such mobbing behavior can deter avian predators, but is less effective in discouraging mammalian predators. Small species often nest in colonies with larger species to take advantage of the larger size and antipredator behavior of these

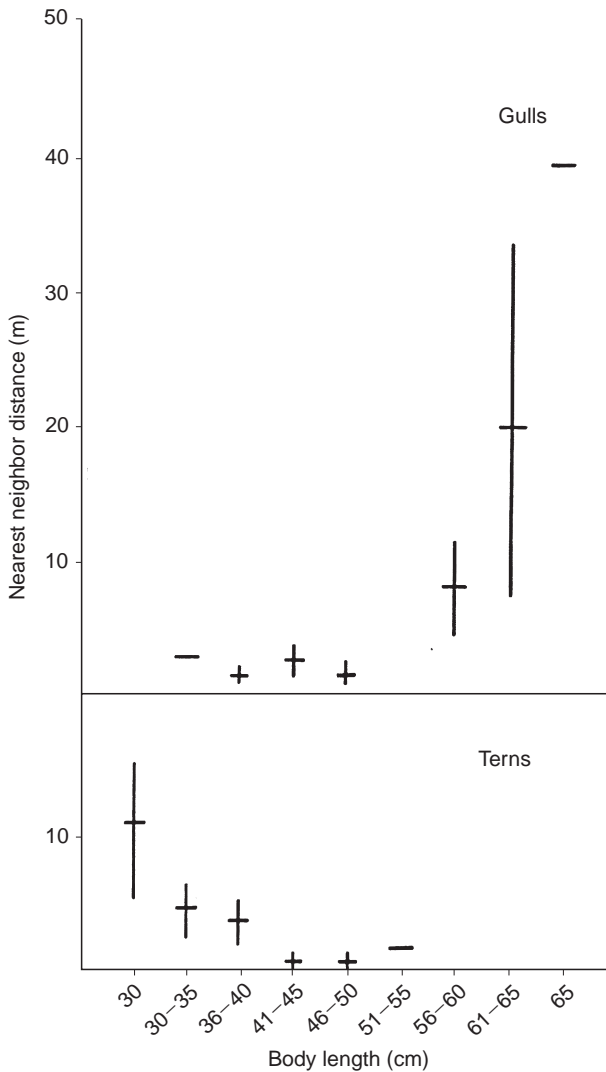


Figure 2 Relationship between body size and territory size (nearest neighbor distance) showing that smaller gulls and larger terns tend to nest more densely.

species, and skimmers often nest in colonies with other species to take advantage of their mobbing behavior, because they do not normally do so.

Both members of the pair engage in territory defense, incubating, and protection and feeding of the young. The eggs of most gulls and terns are brown with dark splotches, while the base color of skimmer eggs is white. Clutch size in most gulls and terns is two or three, while in skimmers it is more variable, ranging from two to four or occasionally five. Since incubation begins after laying the second egg in skimmers, there is asynchronous hatching, and the young can be very variable in size. The first two chicks may hatch only a day apart, while the fourth may not hatch until 5 days later. Pairs that lose eggs or chicks may initiate a repeat nesting

attempt. Following the breeding season, young skimmers and gulls may remain with their parents for a few days or weeks while they improve foraging skills, however, young terns remain with their parents for weeks or months, perfecting the difficult task of plunge-diving. Some terns migrate with their parents and remain with them much of the winter.

In a normal breeding season the phenology includes (1) arrival in the colony vicinity a few weeks

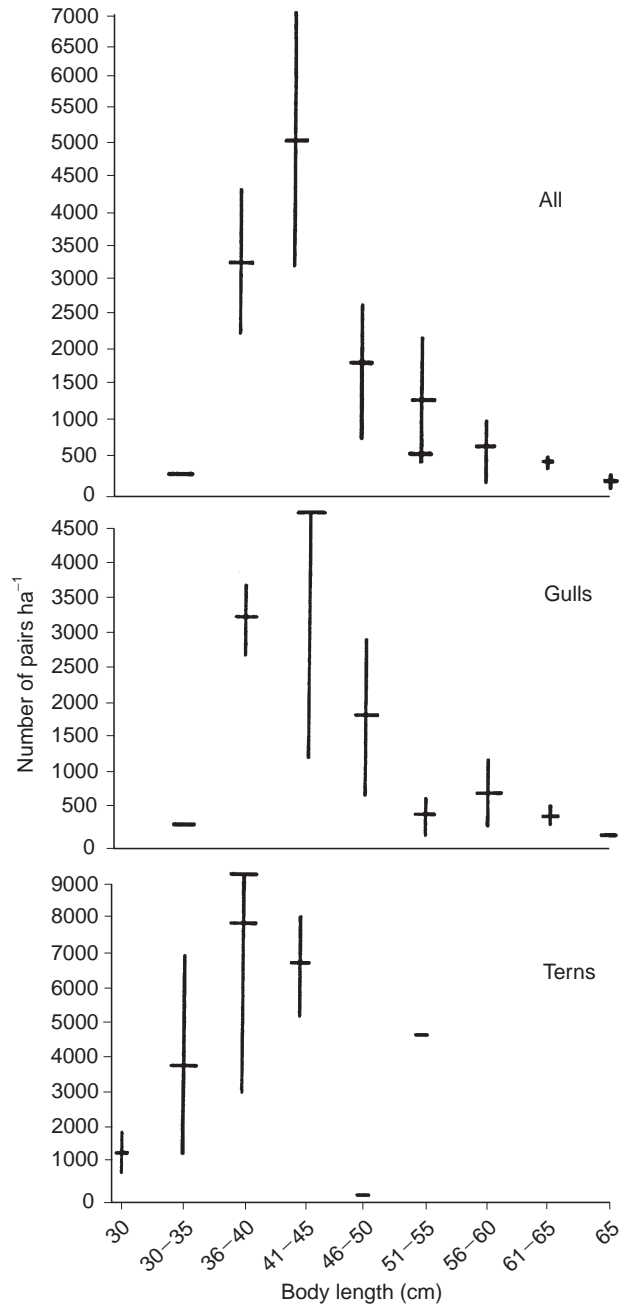


Figure 3 Relationship between body size and colony size showing that smaller gulls tend to nest in larger colonies while smaller terns tend to nest in smaller colonies.

before occupation, (2) colony occupation for a few weeks before initiation of nest-building and egg-laying, (3) territorial defense and courtship during this period, (4) courtship feeding of the female by the male and selection of a nest site and nest construction, (5) a copulation period of a few days to 2 weeks, (6) an egg-laying period of 1–3 weeks, (7) an incubation period of 20–30 days resulting in incubation activities in the colony over about 6 weeks, and (8) a brooding or pre-fledging phase of 4–6 weeks. These time periods are slightly less for the small gulls, and slightly more for the large gulls. Environmental constraints such as low food supply or bad weather impose synchrony on the breeding cycle.

Gulls

Most species of gulls nest in a wide range of habitats, although some species are specialists, nesting only in one habitat (Franklin's and brown-hooded gulls nest only in marshes, kittiwakes nest on cliff ledges or buildings, and Bonaparte's gulls normally nest in trees).

Most gulls breed in colonies of few to several hundred pairs, although some species will occasionally breed solitarily (herring gull, Bonaparte's gull), and others will breed in colonies of several thousand pairs (Figure 3). The small gulls generally nest in more dense colonies than do the larger gulls. The large gulls nest in more open colonies, which is partly the result of cannibalism.

Species nesting in or adjacent to gull colonies include: grebes, ducks, cormorants, herons and egrets, gannets, alcids, and even penguins. Some of these apparently do so because they derive early warning and antipredator advantages from the gulls, although they also risk predation by the gulls.

The nesting period usually lasts from 3 months for the smaller gulls, and up to 5 months for the larger species. A prominent exception to the annual cycle is the swallow-tailed gull of the Galapagos which breeds in all months of the year, and even within a colony there is breeding asynchrony among pairs.

The age of first breeding in gulls varies from 2 (for some smaller species) to 5 years of age (for some large species). Females are likely to start breeding at a younger age than males. Factors that influence age of breeding within a species include availability of mates, nesting sites, food, and weather conditions. Reproductive success usually increases over the first few years as birds gain breeding experience; success remains relatively high for a number of years, and decreases only in very old gulls.

A typical cycle is exemplified by the widespread herring gull. Early in the breeding cycle, gulls begin to gather on 'clubs' on their nesting colonies, where they solicit for mates or re-establish pair bonds. Gradually the gulls spread out over the nesting colony to delineate and defend nesting territories. Unmated males defend territories while courting potential mates; mated pairs defend the territory together and engage in pair-bond maintenance. Once pairs have formed, display frequency increases, and pairs may spend hours every day engaging in 'mew calls', mutual 'long-calling', and 'head-tossing'. Within a few days, the pair begins to select a nest site, and each member shows the other its choice for a nest site with a 'choking' display. Nest building is an integral part of pair formation and pair maintenance for some species, and is less important for others, depending upon physical constraints. All gulls construct a nest, and use vegetation to form a nest cup. In most species males courtship-feed their mates in the pre-egg-laying period, although the level of courtship feeding is less than it is for terns. Copulation is always accompanied by a staccato, repetitive 'copulatory call' that is accompanied by 'wing-flagging' which is visible far across the colony. This leads to contagious copulation by neighboring pairs, and is believed to lead to greater breeding synchrony.

Most gulls have a modal clutch size of three eggs, although some species such as Hartlaub's, black-billed, silver gulls, and kittiwakes usually lay only two eggs, and swallow-tailed gulls only one. Both members of the pair engage in incubation, which lasts an average of 24–26 days. Incubation bouts usually range from 1 to 4 h during daylight, with one member of the pair remaining on the nest at night. The first two chicks usually hatch within a few hours of one another, but the third chick may hatch a day or two later, giving it a distinct disadvantage when competing with siblings for food. The cryptic downy chicks are usually a pale gray or pale tan with dark splotches. The chicks are brooded until they are 1–2 weeks old, and usually are guarded until they fledge.

Both parents feed chicks, although during the first week the male performs more provisioning, while the female remains on the territory and broods the chicks. After the first week or two, both members of the pair take turns with foraging trips and guarding the chicks. Unless disturbed by storms, floods or humans, they use the nest throughout the brooding period. The pre-fledging period in gulls ranges from 4 to 7 weeks, depending on the size of the species. The full extent of post-fledging parental care has not

been established for gulls, but for some it clearly extends for a few weeks post-fledging.

In all species of gulls studied, pair-bonds are monogamous, with a relatively high degree of mate fidelity from year to year. Pairing for life is characteristic of gulls that have been studied. However, divorce occurs when pairs are unable to work out incubation and brooding activities, or when they are unsuccessful at raising offspring. Pairs that remain together lay earlier, and raise more young than pairs that have found new mates.

Study of the mating systems of gulls has been stimulated because of the relatively recent reports of female-female pairs in ring-billed, herring, western, red-billed, and California Gulls. Female-female pairs constitute at least 10% of the pairs of western gulls in some colonies and 6% of the pairs in red-billed gulls. Female-female pairs apparently result from a shortage of breeding males, which may be a consequence of differential survival rates. Laboratory experimentation with western gull eggs indicated DDT-induced feminization of genetically male gull embryos. The levels of DDT that caused feminization were of the same magnitude as those found in seabird eggs in Southern California in the early 1970s. Developmental feminization of males may be associated with inability to breed as adults, and may explain the highly skewed sex ratios and reduced number of male gulls in some populations. Some promiscuity occurs in gulls, with both sexes copulating with birds other than their mates.

Males and females invest approximately equivalent effort, averaged over the entire season, although males often provide more of the initial territory defense, perform all of the courtship feeding, and may perform the bulk of territorial defense, as occurs in western gulls and ring-billed gulls. Females sometimes perform more of the incubation duties and chick defense than males. Moreover, in territorial clashes, males tend to defend against males, and females defend against females when both are present on the territory.

Terns

Although terns have a worldwide distribution, some individual species have a very restricted range. Terns breed in colonies that may be used for several years or decades, and are abandoned when the breeding site becomes unsuitable because of increased predation, human disturbance, habitat changes, or weather stresses such as severe storms or floods. Philopatry varies as a function of habitat stability, and species that nest on remote oceanic islands or on cliffs occupy the same colony site for years. Changing habitats, such as freshwater marshes,

riverine sand bars, and coastal sandspits, may be used for only a few years or even only 1 year. In some species individual terns are known to return to their previous site, assess its suitability, and then either occupy the site or move elsewhere.

The breeding season may last only 2 months for Arctic species, 3–4 months for temperate species, and 3–5 months for tropical species. Terns usually spend only 2–3 weeks in the vicinity of the colony before they begin to settle on the colony for another breeding attempt. Temperate species of terns typically leave the breeding grounds with their chicks, and disperse before migrating to wintering grounds. The chicks may remain with their parents for many weeks or months, slowly decreasing their dependence on their parents for food. Post-fledging parental care has been documented only in those species that migrate and overwinter near land where parents can land to feed their chicks.

Nesting colonies range in size from a few widely dispersed pairs (e.g. Damara and Inca terns) to colonies of a million or more (sooty terns). Intermediate-sized terns, such as the common tern, usually nest in colonies of tens to hundreds of pairs (with a few colonies exceeding a thousand). The large terns usually nest in colonies on the order hundreds of pairs (Figure 3).

All species of terns are territorial, although the size of the territory varies from 40 cm to a few meters. Unlike gulls, the inter-nest distance decreases as the size of the tern increases (Figure 2). That is, the larger species (royal, Caspian, crested, and sandwich terns) nest in very dense colonies where an incubating bird can almost reach its neighbor, the intermediate-sized terns (common, roseate, Arctic, Forster's, noddies) nest in fairly dense colonies where inter-nest distances may range from 1 to 3 m, and the small terns often nest in fairly dispersed colonies where inter-nest distances may be 5 m or more. The larger species rely on their dense nesting pattern to prevent any ground or aerial predators from getting within the colony, while the smaller species rely on dispersion and cryptic coloration to reduce predation, and they rely on antipredator behaviors such as mobbing and aerial attacks to repel predators.

Although some species of terns nest in monospecific colonies, many species nest with other species of terns, gulls, skimmers, boobies, alcids, and ducks, and with sea turtles. Some terns (Forster's black) choose to nest with other species, and they select the colony site after the other species is already nesting. These terns are smaller than the gulls, and derive antipredator protection from the larger gulls that mob and attack aerial predators such as

hawks. Terns also nest in colonies that are adjacent to colonies of other species, such as albatrosses, boobies, and cormorants.

The normal breeding phenology is to select territories, defend territories, solicit mates or reestablish pair-bonds with former mates, engage in courtship and courtship feeding for a few days or weeks, to have an egg-laying period of a few days to 2 or 3 weeks, to have an incubation period of 22–26 days, and to have a brooding and pre-fledging phase of about 4 weeks. After fledging birds may linger at the colony or depart, resulting in a colony breeding phase of up to 6–10 weeks. Smaller terns require somewhat shorter and larger terns longer, breeding times. Within a colony breeding is generally much more synchronous among Arctic species and can be much less synchronous among tropical species. The former are constrained by short breeding season and the latter by less abundant food supplies.

During courtship both mated and unmated birds engage in 'fish flights', which begin when a mated male brings back a fish to a female. After he lands on the territory, both take off and fly high in the air, often joined by one or two other birds. They glide and circle on stiffly bowed wings, uttering unique flight calls. Once pairs have formed, courtship displays continue, with the addition of courtship feeding. During this period the female often remains on the territory, defending it against intruders, while the male spends all day bringing back fish to courtship feed her. This is said to offer the female the opportunity to assess the prospective paternal qualities of her mate.

Nest site selection occurs when both members of the pair agree on a given location. Most terns do not construct a nest, but merely make a scrape in the sand or roll a few pebbles or shells around a scrape, or find a suitable cup-shaped place in the coral or rock for their eggs. Terns nesting in marshes (for example Forster's terns and black terns), construct a nest of vegetation, on which eggs can float up if flooding occurs. Tree-nesting species such as some noddies must select a branch or shelf where they can build a nest of twigs and feathers cemented by their excreta. Cliff or ledge-nesting species such as brown noddies often move the small coral rubble to the edge of the cliff, providing a smooth surface for the eggs and chicks, and a slight lip to prevent the egg from rolling off. The white tern makes no nest at all, but places its egg on a branch, or ledge, or artificial object, where it is hardly protected from falling.

Clutch size in terns varies from one egg (royal, elegant, white-fronted, black-naped, sooty, noddies,

white tern), to two eggs (Caspian, roseate, Arctic, sandwich, least), to three eggs (gull-billed, common). For species that normally lay two or three eggs, clutch size is dependent on food supply. In low food years, terns can reduce the average clutch size, delay breeding, or forego breeding. Members of pairs share incubation duties and chick care, although early in the brooding phase males may bring back more food and females may incubate them more often.

The birds leave their overnight roost or breeding colony to search for food at dawn. These feeding flights may involve large flocks (particularly of non-breeding birds), or prolonged streams of individuals and small groups. During the breeding season, terns that are not incubating often rest on their territory with their mates. Terns are often more active in the early morning and late afternoon. The daily activity patterns of coastal-nesting species of terns are often influenced by tidal cycles.

Skimmers

The breeding behavior of skimmers is similar, except for the following: (1) they shift colony sites more often because of the changing nature of their nesting habitat, (2) colonies may consist of only a few pairs, (3) males defend the territory more than females, (4) a male will usually bring back a fish prior to copulation, pass it to his mate, and she may hold it while they copulate, (5) clutch size is more variable, and may range from two to five, depending upon food supply, (6) since clutch size is larger than in gulls and terns, and the parents may start incubating almost immediately, there can be greater size disparity between the offspring, and a pair rarely raises more than two young, even when food is not especially scarce, (7) males provision the chicks more often during the first 2 weeks of their lives, and (8) if disturbed, they move the chicks soon after hatching. Once chicks are more than a week old, the parents may not brood them, and they continue to be vulnerable to prolonged chilling rains, which can produce high mortality among chicks in the 1–2 week age range. At the same time the parents may be brooding the much smaller, last-hatched chicks, which may, under these circumstances, survive.

Foraging

Gulls have the most diverse foraging behavior and feed on the greatest variety of foods, while terns primarily plunge-dive or hover-dip for fish, and skimmers skim the surface of the water for fish. Both terns and skimmers are limited to feeding over

Table 3 Conservation status of selected gulls, terns and skimmers^a

<i>Species</i>	<i>Status</i>
Pacific gull	Near-threatened. Nowhere common; is declining probably due to kelp gull pressure.
Olrog's gull	Vulnerable , and probably endangered. Only 1200 pairs known in six colonies, none secure. Competition from increased fishing; vulnerable to oil exploration.
Heermann's gull	At least vulnerable with only eight colonies, and most of its large population in one colony.
White-eyed gull	Vulnerable . Poorly known, with fewer than 7500 pairs. Vulnerable to eggging, oiling, exploitation, tourism.
Audouin's gull	Formerly endangered , but increasing under intense protection. Still fewer than 20 000 pairs, but now in about 30 colonies. Fishing competition potentially severe.
Yellow-footed gull	Vulnerable due to very low numbers and small range. Probably < 5000 pairs in less than a dozen colonies.
Armenian gull	Vulnerable. Low numbers and very small range in Arnebua to north-western Iran. Formerly considered a race of herring gull.
Hartlaub's gull	Probably vulnerable. About 30 known breeding colonies, and over 25% of population in one colony (albeit protected).
Saunder's gull	Endangered . Fewer than 2500 pairs (probably < 1500 pairs). All seven known colony sites are being developed or slated for development. Intense management and protection urgently required.
Relict gull	Probably endangered. Small range, few colonies, small population. Fewer than 2000 pairs and declining.
Lava gull	Vulnerable and probably threatened. The world's rarest gull. Although there are fewer than 400 pairs, most of the habitat is currently well-protected. Increased tourism and fishing jeopardize its survival.
Red-legged kittiwake	Vulnerable . A Bering Sea endemic that is declining. Only seven known colony sites. Although population is still large, it has declined precipitously through the 1990s.
Chinese crested tern	Critically endangered , breeding area unknown, often listed as extinct, but a few recent sight records on wintering grounds.
River tern	Status poorly known, vulnerable
Roseate tern	Not globally threatened (c. 50 000 pairs), but North American and European populations are endangered , Caribbean population is threatened .
Kerguelen tern	Vulnerable and probably threatened. No truly secure colony. Total population < 2500 pairs, mostly in Kerguelen where cat predation is a continuing problem.
Saunder's tern	Status unknown, not known to be common anywhere. No secure colonies documented.
Least tern	Not globally threatened, but all races vulnerable, and California race is endangered .
Peruvian tern	Status uncertain, a vulnerable species. World population probably around 5000 pairs.
Fairy tern	Vulnerable . About 5000 pairs in Australia. New Zealand population is endangered with fewer than 10 pairs.
Damara tern	Near-threatened with fewer than 10 000 pairs. Breeding areas are neither protected nor heavily disturbed at this time.
Black-bellied tern	Vulnerable . Fewer than 10 000 pairs and continually declining.
Black-fronted tern	Vulnerable . Fewer than 10 000 pairs, mostly in small colonies on braided rivers being invaded by lupine.
Lesser noddy	Not globally threatened, but status poorly known. Only a few colonies known.
Gray noddy	Not globally threatened, but eastern colonies on Desadventuras and Easter Island are at least threatened if not endangered.
African skimmer	Not globally threatened, but fewer than 10 000 pairs, breeding in many very small colonies.
Indian skimmer	Vulnerable . Declining, but poorly documented over most of its range.

^aOfficial global or regional status is given in boldface. The list provides both official and unofficial status of tern and gull species that are in trouble. For many of the remaining species that are globally secure, there may be many colonies, populations, or regions where it is declining or in danger of disappearance. The hallmark of security is having many colonies, including those in protected areas. The consequence of having many colonies is that not all can be protected.

water, while gulls feed on land, along the shore, and over water. Both gulls and terns engage in piracy, although terns generally pirate from conspecifics or other terns, while gulls pirate from a range of species. Foraging efficiency increases with age in gulls, terns, and skimmers.

Gulls forage in a variety of natural habitats including the open ocean, the surf zone, intertidal

mudflats, rivers and rivermouths, rocks and jetties, estuaries, bays, lakes, reservoirs and rivers, wet meadows and farm fields, sewage outfalls, refuse dumps, and even in the air. Gulls are an integral part of coastal and estuarine habitats, and many species feed along the shore on a variety of fish and invertebrates. Gulls are particularly characteristic of the intertidal zones. They also feed in a variety of

man-influenced situations, including on landfills, behind ploughs or boats, and by pan-handling from people at fast-food places or along the shore. They forage using a wide range of techniques, including walking on the ground, swimming in the water and dipping for food, and plunge-diving. They also drop invertebrates from some distance to crack open their shells, a behavior shared only with Corvids. In some species, individuals have specialized diets or foraging techniques when compared with their populations as a whole.

Conservation

Of the 99 species of gulls, terns and skimmers, world population estimates range from a few hundred pairs (lava gull) to several million pairs (herring gull) and several tens of millions (sooty tern). Saunder's gull and Chinese crested tern are endangered. Ten species are considered 'threatened', and one skimmer is considered 'vulnerable' (see Table 3).

Although eggging, hunting, and exploitation for the millinery trade resulted in sharp declines for many species in the last two centuries, human persecution has ceased in many (but not all) parts of the world. 'Egging', the collection of bird eggs for food, continues to be a major threat in tropical regions, (e.g. roseate terns in the Caribbean). Current threats to species in this family include habitat loss, habitat degradation, increased predation (often caused by predators, such as cats, introduced and maintained by humans), and overfishing by humans that reduces food supplies. Populations can also be threatened by pollution, particularly oil spills that occur near nesting colonies or in favorite foraging grounds. In the 1960s and 1970s eggshell thinning due to DDT was a problem, and in the 1980s in the Great Lakes of North America, organochlorides contributed to decreased hatching rates, lowered parental attendance, and lower reproductive success.

Gulls, terns, and skimmers suffer heavy and increased predation from predators introduced by man, including cats, dogs, and by predators that have profited by man's activities, such as foxes. In addition, many species of terns and smaller gulls have been negatively impacted by competition with larger gulls. In many temperate regions, the large white-headed gulls (e.g. herring gulls, ring-billed gulls) expanded their numbers and ranges dramati-

cally during the twentieth century, abetted by the availability of human refuse in uncontrolled garbage dumps. This new food source greatly increased the survival of juvenile gulls. The large gulls displaced smaller gulls and terns from their traditional nesting sites. They also preyed on the eggs and chicks of these species. New landfill practices and alternative refuse management have reduced this food source in many urban areas; the populations of some gulls have begun to decline.

Conservation measures include protecting colonies from direct exploitation (hunting of adults, eggging), creation of suitable nesting space, stabilization of ephemeral nesting habitats, construction of artificial nesting islands or platforms, removal of predators (feral cats, large gulls, foxes), protection from other predators, and reduction of human disturbance at colony sites through sign-posting, fencing, or even wardening. More difficult, but equally important, is the protection of foraging sites and the prey base, which may involve fisheries management.

See also

Beaches, Physical Processes Affecting. Network Analysis of Food Webs. Oil Pollution. Seabird Conservation. Seabird Foraging Ecology. Seabird Migration. Seabird Reproductive Ecology. Seabirds and Fisheries Interactions. Seabirds as Indicators of Ocean Pollution. Sea Level Change.

Further Reading

- Burger J and Gochfeld M (1996). Laridae (gulls). In: delHoyo J, Elliot A and Sargatal J (eds) *Handbook of the Birds of the World*, pp. 572–623. Barcelona, Spain: Lynx Ed.
- Gochfeld M and Burger J (1996) Sternidae (terns). In: del Hoyo J, Elliott A and Sargatal J (eds) *Handbook of the Birds of the World*, pp. 624–667. Barcelona, Spain: Lynx Ed.
- Grant PJ (1997). *Gulls: A Guide to Identification*. Vermillion, South Dakota: Buteo Books.
- Olsen KM and Larsson H (1995). *Terns of Europe and North America*. Princeton, NJ: Princeton University Press.
- Tinbergen N (1960). *The Herring Gulls World*. New York: Basic Books.
- Zusi RL (1996). Rynchopidae (skimmers). In: del Hoyo J, Elliott A and Sargatal J (eds) *Handbook of the Birds of the World*, pp. 668–677. Barcelona, Spain: Lynx Ed.