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GEOLOGY, COASTAL

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GULLS

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Gulls are the birds perhaps most frequently associated with coastlines, as they soar in coastal updrafts and walk on the shoreline in search of food. Some species also frequent large bodies of water inland. They are relatively large birds in the family Laridae with characteristic white, gray, and black colors, and they feed on a wide range of foods derived both naturally and through human activities. Because of their active lifestyles and relatively high densities, gulls can be important components of food webs along shorelines. As a group, they are fairly tolerant of human presence, which has facilitated many fascinating observations of their behavior, ecology, and life history.

APPEARANCE

Gulls are notable for their generally uniform appearance. They are typically colored white on the underside and on the tail, with their back and wings ranging in shade from white to black. The two major groups of gulls are differentiated by having either an all-white head or a head covered all or in part in black feathers. Black-headed species usually replace most of their black head feathers with white feathers in the nonbreeding season. A few species (e.g., Heerman's gulls and slaty gulls) are exceptional in being colored a fairly uniform gray on the entire body. The beaks of most species are usually some shade of yellow with species-specific black or red markings, although a few species have solid yellow, black, or red beaks. Young gulls lack the distinctive coloration of adults, but instead exhibit dull gray or brown plumages for one to three years in most cases. The often-nondescript juvenile plumage contributes to the difficulty of identifying gull species in the field. Gull identification is further complicated because there are several geographic areas where different species hybridize, creating individuals that look like neither parent species. For example, on the Pacific coast of North America, the glaucous-winged gull *(Larus glaucescens)*, a northern species characterized by a light gray back and wing tips, hybridizes with the Western gull *(Larus occidentalis)*, a southern species characterized by a black back and wingtips, to produce offspring that look superficially like species such as the herring gull *(Larus argentatus)*, that has gray backs with black wing tips. The study of gull hybrid zones provides biologists with an opportunity to better understand the processes of species formation.

The function of the uniformity of adult gull coloration is not well understood. One possibility is countershading, with the white underside making it hard for fish prey or swimming predators to see them from below, whereas darker shading above may make them harder to be seen by aerial predators. Alternatively, the strong contrast between light and dark colors may facilitate long-distance signaling to other gulls that a source of food is present. When fish become locally abundant near the water surface, gulls often congregate in large groups, sometimes referred to as "herring balls." There is evidence that such group feeding may be beneficial to individual gulls by disrupting the defensive schooling behavior of fish, thereby increasing feeding efficiency. Other evidence suggests a role in communication for the color differences. The age-dependent plumage pattern exhibited by gulls indicates that the coloration pattern may play a role in social interactions and dominance. Experiments exposing young birds to elevated levels of testosterone, a hormone often related to maturity and social interactions, have caused early molting into adult plumage patterns in some species.

Aside from coloration, most gulls also have a similar morphology. The beaks of most species tend to be rather robust with a slight hook at the end, well suited

FIGURE 1 An adult herring gull *(Larus argentatus)*, illustrating the coloration and morphology typical of many gulls. Photograph by the author.

to a generalized diet. Gulls also have webbed feet to facilitate swimming on the water surface, but they do not have the streamlined shape to permit underwater swimming or diving, as do some other seabirds. Males and females look very similar, but males tend to be slightly larger.

FEEDING

Most gulls are dietary generalists. Aside from being fairly tolerant of direct human observation when feeding, analysis of feeding is facilitated because gulls regurgitate the indigestible shells, bones, and scales of their prey as pellets, which can be regularly seen both along shorelines and in middens at nesting areas. Fish usually make up the largest component of the diet, but a range of benthic and pelagic invertebrates regularly contributes to the diet of many species. Invertebrate prey includes gastropods, squid, bivalves, crabs, shrimp, goose barnacles, starfish, sea urchins, krill, isopods, polychaete worms, and earthworms. Gulls also opportunistically capture and eat small mammals and birds, particularly burrow-nesting seabirds such as auklets and storm petrels. Additionally, gulls will often consume the eggs and young of other birds, including other gulls, during the nesting season. There is even one report of extensive grazing on algae by herring gulls in Japan. Because they often occur in high densities, gulls can significantly deplete prey resources along shorelines. Aside from capturing live prey, gulls also function as scavengers, feeding on dead fish, sea birds, invertebrates, and marine mammals that accumulate along the drift line of the shore.

As human populations have expanded, some gull species have been observed feeding extensively on garbage at dumps and in plowed fields where invertebrates such as earthworms have been exposed. They are also well known to follow fishing boats, feeding on the excess bait and fisheries by-catch that is dumped back into the ocean. The role that these human-generated food resources contribute to gull population dynamics is a current area of interest. Some studies indicate that garbage dump use is not extensive in relation to other food resources, and they also find that the gulls using garbage resources tend to be males. Several studies report lower reproductive success for gulls that feed on garbage than for those that feed on natural food sources. Hence, the role that garbage feeding plays in gull population dynamics is unclear, as it could either provide a low-quality supplemental food supply that augments populations to some extent, or trigger population reductions if gulls preferentially choose to focus their foraging activity on highly concentrated "junk food" sources.

Gulls also deploy several interesting behaviors to facilitate food capture. First, detailed diet observations reveal individual specialization on particular food types, which may increase foraging efficiency because gulls learn specialized techniques for prey capture. Second, individuals that feed on hard-shelled prey often learn to drop prey from the air onto anvil rocks to crack the shells and gain access to the enclosed meat. Third, some individuals engage in kleptoparasitic behavior, often forcing sea birds or other gulls to drop the prey they have captured. In many cases, adults focus such piracy on young individuals, who are less-skilled fliers and have smaller body sizes.

Many food items of gulls contain high salt concentrations, and freshwater availability can be low in many coastal situations. To deal with the osmoregulatory problems this situation creates, gulls possess in their head specialized salt glands, which actively pump salt out of their blood and into their nasal passages, where it is exuded into the environment.

ENEMIES

As fairly large and agile birds, gulls are at relatively low risk of succumbing to predation. Nevertheless, several groups of animals will feed on gulls and in some circumstances may have a large effect on gull populations. Immature gulls seem particularly vulnerable, probably because of a combination of inexperience in detecting and evading predators and because of their smaller body size relative

to adults. Predators such as sharks and pinnipeds attack from underwater while gulls are floating on the surface. Eagles and other large birds of prey attack gulls while they are either flying or standing on the shore. Some land mammals may also take gulls when the opportunity arises. Such predation effects can be extreme when land mammals are introduced to previously predator-free offshore nesting colonies. Crows and other gulls can also have a substantial impact on survival of gull eggs and nestlings.

FIGURE 2 A recently hatched glaucous-winged gull *(Larus glaucescens)* chick hiding just outside of its nest, illustrating typical nestling coloration. Photograph by the author.

LIFE HISTORY

Gulls typically nest in colonies on offshore islands and on steep cliffs, although some smaller species may nest inland in trees or on buildings. The reasons for usually nesting in dense aggregations are an area of debate, but several explanations may contribute, including preferential nesting in areas with low predation risk, group defense against predators, nesting at densities that facilitate finding acceptable mates, and living in situations where information on food resources can be transmitted socially. For example, gulls actively mob larger animals that enter their breeding colony, including clawing with their feet, pecking with their beaks, and defecating on the intruder, which can be effective at discouraging predation in the colony. On islands, gulls often nest in a range of microhabitats from vegetated edges of the island to cliffs on the sides to drift lines on open sandy beaches. Older, more experienced individuals tend to use vegetated flat areas at the edges of the island, which appear to be beneficial by providing shelter from both flying predators and climate extremes, by giving individuals a better vantage point for spotting feeding aggregations, and by being in locations where nests are least likely to be washed away by waves. Nests are made out of a variety of materials including grasses, forbs (nongrass herbs), and seaweeds. Nest material collection can often have strong local effects on the cover of terrestrial plants and intertidal algae as substantial amounts of plant material are removed. This impact can subsequently affect the species composition of communities of terrestrial plants and sessile intertidal organisms, favoring species that are poor competitors for light or space but are resistant to being removed.

The high-density lifestyle of most gulls often leads to squabbles among neighbors. Perhaps correlated with the regular aggression observed on both nesting and feeding areas, gulls maintain high levels of the hormone testosterone in their bodies throughout the year, which contrasts with the pattern typically exhibited by birds, wherein testosterone levels increase at the onset of the breeding season and then drop back to low baseline levels.

Gulls exhibit a curious pattern of clutch size, with the majority of pairs having three eggs, a moderate number having two eggs, a few having one egg, but virtually none having four or more. The absence of larger clutches is not an absolute energetic constraint, because females will lay a total of four or more eggs if the first egg is experimentally removed from the nest during the egg laying period. Despite this pattern, several lines of evidence indicate a role of food limitation in egg production. Reduced clutch sizes have been observed in low-food (e.g., El Niño) years, and feeding supplementation studies show that the weight of the last egg laid, and hence the size of the chick produced, may depend on food, with runt chicks produced when food is more scarce. The strategy of variably provisioning the final egg is probably advantageous, because a strong size hierarchy among the chicks may ensure that at least one chick receives sufficient food to survive, rather than having all chicks starve on a food supply that could have supported fewer. Gulls also engage in courtship feeding, in which males provide food to females, and so clutch size patterns may be influenced by male decisions on how to allocate courtship feeding relative to other activities such as mate guarding over the course of the breeding season. Although individuals are not known to lay more than three eggs under nonexperimental circumstances, nests with four eggs are occasionally observed. Careful study has revealed that these nests usually result from female–female pairs, which may develop because gull populations often have female-biased sex ratios. Environmental pollutants may be partially to blame for these skewed sex rations, because feminization of gulls exposed to pollutants has been documented. Hence gulls are a useful indicator of environmental impacts that

may be of concern to humans. The existence of successful female–female nests also indicates that gulls will mate outside their social pair bond. The strongly spotted eggs are laid every other day and hatch after 3–4 weeks. Because gulls will start incubating their eggs before the clutch is complete, chicks hatch somewhat asynchronously, which can further contribute to a size hierarchy among chicks. The chicks, which hatch with tan to gray down with heavy dark spots that make them harder to see, can walk after several days, but they are often viciously attacked if they stray away from the nest onto a neighboring territory. Adults feed chicks on the nesting territory for 1–2 months, and the chicks follow adults around for at least several more weeks while being fed by the adults and learning to capture prey through direct observation of their parents and trial-and-error pecking at potential food items.

MOVEMENT PATTERNS

Gulls vary in their migration patterns with the seasons. Adults of many coastal species are relatively sedentary, with only northernmost populations moving south for the winter, presumably because ocean temperatures significantly buffer temperature variation along coastlines. Juveniles are much more nomadic. Species that nest in interior habitats, such as California gulls *(Larus californicus)* and most black-headed species, are much more migratory, typically moving from interior to coastal habitats following the breeding season, with some (e.g., Franklin's gull, *Larus pipixcan*), migrating between the Northern and the Southern Hemisphere. Some unique migratory patterns also exist. For example, Heerman's gulls *(Larus heermanni)* breed in late winter and then migrate north during the summer nonbreeding season.

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