Larus argentatus

FRENCH:
Goéland argenté
SPANISH:
Gaviota plateada, Apipizca

Herring Gull

The Herring Gull, perhaps the most common and familiar gull of the northeastern United States and western Europe, is a large white-headed gull that inhabits shorelines of oceans, seas, lakes, and large rivers. Its circumboreal breeding range includes much of Europe and Central Asia. In North America it breeds along the Atlantic Coast from Cape Hatteras north to Davis Strait and Baffin Island and throughout arctic Canada into eastern Alaska. In winter, North American Herring Gulls may be found throughout their breeding range and south into tropical waters, primarily along coastlines in southern and Baja California and the Gulf of Mexico.

This species been divided into at least nine subspecies, of which only one, *L. a. smithsonianus*, breeds in North America. Several Asiatic subspecies have recently been accorded tentative species status. Herring Gulls hybridize in zones of sympatry with several other large white-headed gulls, including Glaucous-winged (*L. glaucescens)* and Lesser Black-backed *(L.fuscus)* gulls, and new species may have arisen through hybridization in this group in Asia.

The behavior and ecology of the Herring Gull are well studied, especially in Europe and Canada. Although this species is an opportunistic feeder, most individuals feed primarily on natural prey such as marine fishes and invertebrates. Studies from Europe and North America indicate that individual gulls specialize in their

The Birds of North America
Life Histories for the 21st Century

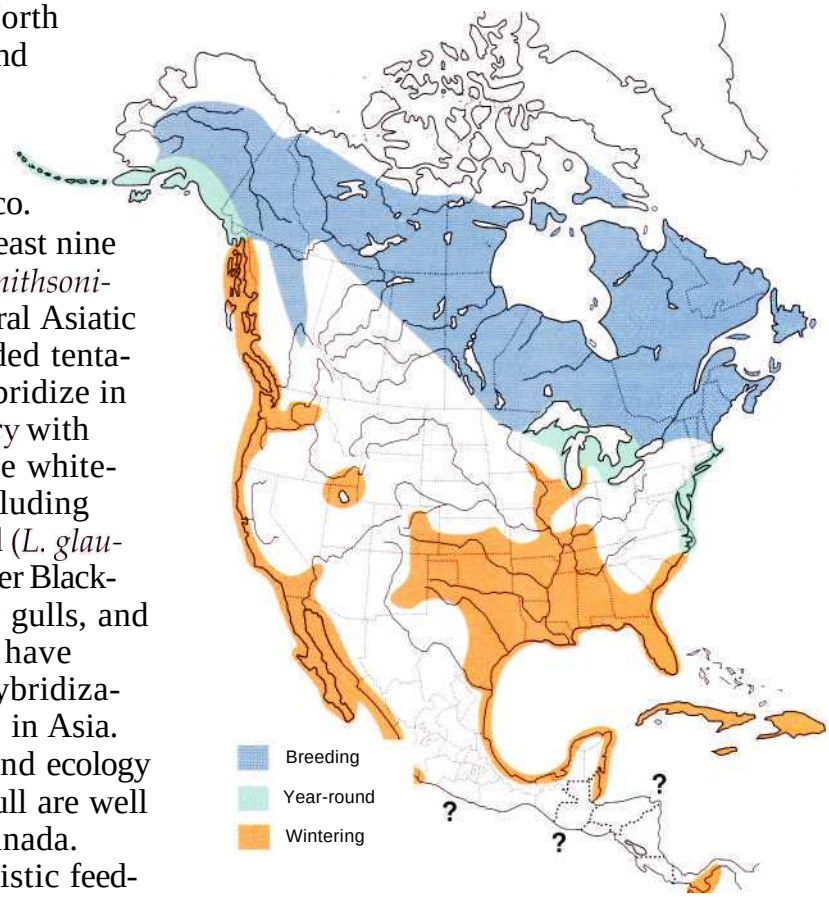

Figure 1.
Distribution of the Herring Gull in North America. This species also breeds in Europe and Asia; see text for details.

foraging and that choice of diet influences breeding performance. This species generally nests in colonies, often large ones; successful nesting appears to require sites near water and safe from terrestrial predation, sites such as islands, offshore rocks, or abandoned piers. This gull typically lays three-egg clutches in May, which generate fledged offspring by mid- to late July.

Nearly extirpated by plumage hunters and eggers in North America during the nineteenth century, the Herring Gull has recovered its numbers owing to protection. By the 1960s, North American populations may even have exceeded historical numbers, possibly the result of plentiful food derived from human refuse. Numbers in New England stabilized during the 1970s. In recent years this species has expanded its range south into Maryland, Virginia, and North Carolina, but it has also been largely displaced from certain breeding habitats in New England by the Great Black-backed Gull (L. *marinus*).

DISTINGUISHING CHARACTERISTICS

Medium-sized gull (male 60-66 cm long, 1050-1250 g; female 56-62 cm, 800-980 g). Adults have white head, neck, and body, with head and sides of breast often streaked dusky in winter. Only gull with light gray back and wings, black wingtips with white spots (mirrors), and pink legs in adult stage. Yellow to light orange bill with subterminal red spot. Iris golden (may be lightly flecked with brown) with yellow or orange orbital ring. Has about 7 plumage stages before adulthood (see Appearance).

Species belongs to large complex of Northern Hemisphere gulls, all of which are somewhat similar and may be confused, especially in immature plumages. Taxonomy of group complicated, especially given frequency of hybridization and possible reticulate evolution in Eurasia (Pierotti 1987b, Panov 1989).

Juvenile Herring Gulls mottled dark gray-brown. Can be confused with juveniles of all species listed below. Subsequent preadult plumage stages also difficult to identify; best characters are combination of mantle (back) color and markings on bill. In North America at least 10 species of white-headed gulls can be mistaken for adult Herring Gulls (species listed below with geographic areas of sympatry).

Pacific Basin: Western Gull (*Larus occidentalis)* similar in size and color of bare parts, has much darker mantle; Glaucous-winged Gull has similar mantle color, slightly larger, with pale gray rather than black wingtips, dark iris with purplish eye-ring (Herring / Glaucous-winged gulls hybridize in se. Alaska; Patten 1980); Mew Gull (L. *canus)* much smaller, has unmarked yellow bill, yellowish legs. Hybrids between Western and Glaucous-winged gulls can appear quite similar to Herring Gulls; these hybrids often have less black in wingtips. In winter along Pacific Coast and in Canadian prairies, California Gull (L. *californicus*) smaller, has yellowish green legs and black spot anterior to red spot on bill.

North Atlantic Coast: Great Black-backed Gull much larger with dark mantle and lighter-colored, heavier bill (rare hybrids reported between Herring and Great Black-backed gulls; Pierotti 1987b); Lesser Black-backed Gull has dark mantle, yellow legs (Herring and Lesser Black-backed gulls hybridize in British Isles and Siberian Arctic; Pierotti 1987b, Panov 1989).

Arctic and North Pacific Coast: Thayer's Gull (L. *thayeri*) almost indistinguishable, best distinguishing characters dark iris, lack of black on undersurface of wing-tips, white tongues proximal to black tips on primaries. Thayer's Gull may not be a true species; possibly a form of Herring or Iceland *(L. glaucoides)* gull.

Winters in North Atlantic: Iceland Gull similar in size and color, has pale, almost white, primaries.

Arctic, North Atlantic, North Pacific, and Great Lakes: Glaucous Gull *(L. hyperboreus)* much larger (size of Great Black-backed Gull), has white primaries (Herring / Glaucous gulls hybridize in Canadian Arctic; Pierotti 1987b, Spear 1987).

Midwestern U.S., Canada (including Great Lakes), and Atlantic Coast: Ring-billed Gull (L. *delawarensis*) smaller, has black ring around bill (nearly always) instead of red spot, yellow legs.

DISTRIBUTION

THE AMERICAS

Breeding range. Year-round resident on Great Lakes and east coast of North America from Newfoundland to North Carolina. Current breeding range (Fig. 1) extends from southern coast of Alaska inland across Canada to Hudson Bay south to North Carolina coast (Harrison 1983). Breeds in Iceland, Europe, and Russia (Grant 1986, Cramp and Simmons 1983).

Winter range. Winter distribution and abundance show strong association with open fresh or salt water; fairly continuous distribution along all Atlantic, Pacific, and Gulf coasts; also

extends north into s. Illinois, W. Virginia, Tennessee, and Alabama along Mississippi, Ohio, and Cumberland Rivers. Gulf Coast distribution extends up Mississippi Valley, without fusing with that of northerly group. Disjunct populations present in Great Plains associated with Pecos, Red, Cimarron, Arkansas, Platte, and Missouri Rivers. Other inland populations associated with small lakes kept open by hot-water discharge from hydroelectric plants (Rocky Mountain foothills), also with Great Salt Lake and Lake Mead, NV. Overall northern limit corresponds to -12°C thermocline (Root 1988). Approximate southern limit of winter range is s. Central America (Grant 1986); recently recorded in Venezuela (Harrison 1983).

OUTSIDE THE AMERICAS

Circumpolar breeding distribution includes Iceland, coastlines of Europe, n. Asia, and n. Africa, and inland lakes of Asia (Cramp and Simmons 1983). Approximate southern limits of winter range extend to n. Africa, along southern coast of Asia (Grant 1986).

HISTORICAL CHANGES

Once bred only as far south as central Maine (Bent 1921); expanded south along Atlantic Coast from 1950 to 1980 (Drury 1973). Atlantic Coast populations decimated in late 1800s; entire Maine coast population down to few thousand pairs (Palmer 1949). Populations at Isles of Shoals (Maine-New Hampshire border) comprised only wintering birds in late 1800s to peak of 7,000 breeding pairs in 1945 (Drury 1973). General southward expansion at expense of Laughing Gull *{Larus atricilla)* (Burger 1979) and possibly in response to southern range expansion of Great Black-backed Gull (McGill-Harelstad 1985, TPG, RJP).

In Newfoundland, recovered from near extirpation to reestablish populations in Witless Bay in late 1940s (L. Tuck pers. comm.).

FOSSIL HISTORY

North American sites of prehistoric findings include Kodiak, Little Kisku, Attu I., Dutch Harbor, and Cape Prince of Wales, AK; Whynacht and Bear River, Nova Scotia ; and Castle Windy, FL. Findings from Green Mound middens in Florida dated to A.D. 550 and A.D. 1200 (Brodkorb 1967). Findings from Holocene Epoch on island of Huar in Yugoslavia, where birds represented 0.26% of fauna uncovered (Malez-Bacic 1983).

Gulls not abundant in fossil record. One early Pliocene (4.5-5.0 million years before present [mybp]) and 2 Pleistocene (0.6-1.8 mybp) North American extinct species named (Brodkorb 1967, Olson 1985). Additional late Neogene records of *Larus* species from Arizona, California, and N. Carolina (Olson 1985, Bickart 1990, Chandler 1990). *Larus argentatus* not closely related to any of these species.

SYSTEMATICS

GEOGRAPHIC VARIATION

Lighter plumage populations in n. Alaska and Mackenzie Delta, Northwest Territories (NWT), once described as Nelson's Gull *(Larus nelsoni),* later considered hybrids with Glaucous Gulls or less melanistic Herring Gulls (Snell 1991). Thayer's Gull may be subspecies of Herring or Iceland Gull (Cramp and Simmons 1983, Harrison 1983).

SUBSPECIES; RELATED SPECIES

L. argentatus smithsonianus only recognized subspecies that breeds in North America. Nine subspecies recognized in Europe and Asia divided into northern or nominate *"argentatus"* group and southern or nominate *"cachinnans"* group (Cramp and Simmons 1983). *L. a. smithsonianus* member of nominate *"argentatus"* group (Grant 1986). Hybrids formed with other large white-headed gulls in regions of overlap (Pierotti 1987b); has interbred with Great Black-backed Gull around Ottawa, Ontario (Pierotti 1987b), with Glaucous-winged Gull on Kenai Peninsula and in se. Alaska (Patten 1980), and with Glaucous Gull in n. Alaska and Northwest Territories (Spear 1987). Glaucous-winged Gull x Herring Gull hybrids also documented in Utah (Fischer 1988). Close genetic similarity among Canadian, Icelandic, and European populations of Herring, Glaucous, Great Black-backed, and Iceland gulls indicated by extremely small Nei's D values (0.000-0.009) and Roger's D distances (0.004-0.032) (Snell 1991).

American Birds records suggest (1) *L. a. vegae* (Asian race) regular visitor to w. Alaska; (2) possible records for L. *a. argentatus* in Newfoundland; (3) birds from s. European *L. (a.) cachinnans* complex recorded at least twice in North America. Yellow legs of *L. cachinnans* probably indicate reproductive isolation from *L. argentatus* (Pierotti 1987, Panov 1989). Evidence from mitochondrial cytochrome b gene indicates that *L. argentatus* and *L. cachinnans* are distinct species with *cachinnans* more closely related to *L.fuscus,* which also has yellow legs (Wink et al. 1994).

The Birds of North America, No. 124, 1994

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

Dispersal begins late Jul, but few individuals leave breeding areas (Moore 1976). Only non-breeding birds appear migratory; most adults remain near breeding grounds throughout year (Drury and Nisbet 1972, Moore 1976). First-year birds winter in southern portions of range, with second- and third-year birds moving intermediate distances. Adults disperse away from breeding colonies in Aug, return to colonies in Apr (Moore 1976). In late fall and winter, apparent major offshore movement of Herring Gulls in ne. U.S., Canadian Maritimes (Powers 1983). Other individuals disperse south to areas of open water in fall. Subadults concentrate along southern Atlantic Coast and Gulf Coast during winter (Moore 1976). Some overwinter in large freshwater reservoirs in Midwest. A few move south along Pacific Coast and overwinter south to California (RJP).

European populations considered nonmigratory, although there is dispersal outside breeding season. Only Baltic populations experience severe winter conditions encountered by North American Herring Gulls in Great Lakes and n. Canada.

MIGRATORY BEHAVIOR

Dispersal away from breeding colonies probably on individual basis. Some young remain with parent(s) for several months postfledging (Burger 1984, RJP). Juvenile and immature birds congregate around areas where food reliably obtained, e.g., intertidal areas, fishing boats, refuse dumps. Adults (and many immatures) found offshore Oct through Mar (Powers 1983, RJP). Great Lakes adults remain near breeding colonies; most immatures disperse southward Oct to Feb (Moore 1976).

CONTROL AND PHYSIOLOGY

Offshore movement related to foraging conditions. Many adults offshore in Mar building reserves forbreeding season. These move onshore in Apr to breed (RJP). Immatures move to milder (less energetically stressful) southern climates when cold weather starts (Oct-Mar).

HABITAT

BREEDING RANGE

Predominantly islands (in broadest sense of word), including major offshore islands, rocky islets, dredge tailings, marshy hummocks, barrier beaches. Adults prefer dry, well-drained

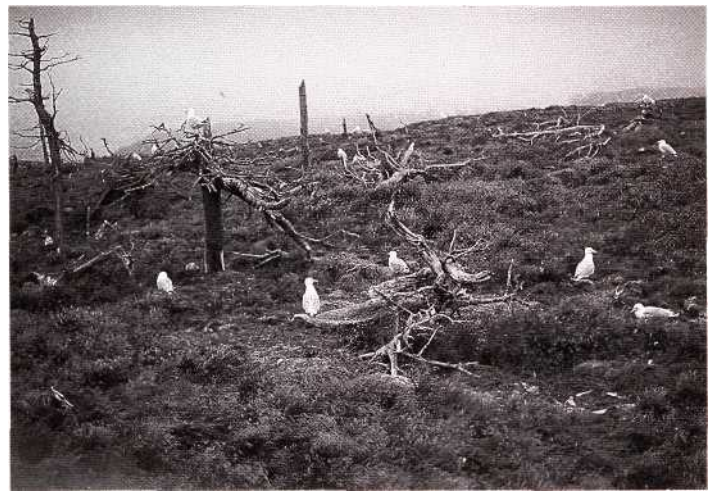

Figure 2. Typical nesting habitat of the Herring Gull in Newfoundland. Photo by RJP.

substrate, e.g., rock or sand, but highest breeding success often achieved in vegetated areas with adequate cover (from both weather and predation) for semiprecocial young (Pierotti 1982, 1987a). Nests in greatest densities on rocky marine terraces in Witless Bay, Newfoundland (Pierotti 1982; also see Fig. 2). Several hundred pairs also nest in cities (e.g., Boston, MA; Portland, ME; Halifax, Nova Scotia; St. John, New Brunswick) on rooftops near water (RJP).

Major requirements appear to be area free of and inaccessible to terrestrial predators and nest sites sheltered from prevailing wind (Pierotti 1982). Typically nests in association with numerous conspecifics. Coloniality appears facultative, since many Herring Gulls nest solitarily on offshore rocks, rooftops, and rocky islets in inland lakes (RJP).

Foraging habitat typically spatially separate from nesting habitat. Forages at sea, in intertidal, on sandy beaches and mudflats, in refuse dumps and ploughed fields, and around picnic areas or fish-processing plants. A few birds forage on breeding colonies by taking eggs and young of conspecifics and other seabirds (Pierotti and Annett 1987, 1991).

Uses open areas as roosting sites, including parking lots, fields, helipads, airport runways.

MIGRATION AND WINTER RANGE

See Migration. Marked differences exist between populations; birds from Nova Scotia and Cape Ann and Boston, MA, remain around breeding colonies throughout year, whereas birds from Maine, Gulf of St. Lawrence, and Newfoundland disperse southward (Drury and Nisbet 1972, RJP, TPG). Outside breeding season, nearly all individuals associated with foraging habitats,

especially during daylight, and roost in areas adjacent to foraging sites.

FOOD HABITS

FEEDING

Main foods taken. As a species, generalist predator on pelagic and intertidal marine invertebrates, fishes, insects, other seabirds, and adults, eggs, and young of congeners. Opportunistic scavenger on fish, carrion, human refuse. Individual specialization common (Pierotti and Annett 1987).

Microhabitat for foraging. Varies with food taken. Along rocky shores, forages primarily in low intertidal and shallow subtidal zones, dives into shallow water to take mussels *(Mytilus* spp.) crabs and urchins (Good 1992b), and crayfish (R. D. Morris pers. comm.). On mudflats, follows retreating tide to capture worms, small bivalves. At sea, congregates around submarine features (mounts, sandbanks, local upwellings) where prey concentrate. Cannot dive below 1-2 m; feeds on prey at or very near surface (Pierotti 1988). Captures crabs in low intertidal and shallow subtidal zones along rocky and sandy shores (Good 1992a).

Food capture and consumption. In intertidal or mudflats, forages alone or in family groups primarily during daylight hours. In coastal areas, captures prey by walking or swimming along shore at low tide, dipping from surface, or shallow plunge-diving. Small prey items swallowed whole; large prey items (gastropods, bivalves, sea urchins, crabs) broken up and eaten in situ or dropped on rock or sand substrates to break open (Tinbergen 1960). Captures small schooling fish and bycatch or discards from stern of fishing vessels by surface-dipping or landing and grabbing. Human refuse obtained by following garbage scows, roosting at refuse tips, waiting downstream of sewage outfalls (Bent 1921). Piracy from gulls and other species (e.g., diving ducks, terns, puffins, murres) used by a few birds, typically males holding territories near other breeders (Pierotti 1980). A few males (< 0.1%; typically only 1-2 per colony) specialize on conspecific chicks (cannibals; Parsons 1971, RJP).

At sea, forages in large, widely scattered groups that coalesce quickly through rapid recruitment when prey concentrations located (Hoffman et al. 1981, Pierotti 1988). Often follows foraging humpback whales (*Megaptera novaeangliae*) or groups of delphinids. Hovers over feeding groups grabbing fish, squid, zooplankton concentrated at surface by mammals, diving birds, or large predatory fishes swimming underneath concentration (Pierotti 1988). Employs similar techniques around fishing boats hauling nets—contemporary functional version of feeding whales.

DIET

Major food items. Direct observation possible year-round; sampling pellets, boli, and prey possible on breeding territories. Observed diets include marine invertebrates, fish, insects, refuse, other seabirds. Sea urchins *(Strongylocentrotus droebachiensis),* jonah and rock crabs *(Cancer borealis* and C. *irroratus),* and green crabs *(Carcinus maenus)* commonly taken along coasts in New England (Good 1992b, Dumas and Witman 1993).

In Newfoundland takes primarily mussels *(Mytilus edulis),* Leach's Storm-Petrel *(Oceanodroma leucorhoa),* and refuse during prelaying and incubation periods. Switches diet to capelin *(Mallotus villosus)* and other small fishes when chicks hatch, followed by secondary switch to squid *(Illex illecebrosus)* in early to mid-Jul (Pierotti and Annett 1987).

In Great Lakes, feeds mostly on small fishes, primarily alewife and smelt *(Pseudoharengus* spp.; *Osmerus* spp.) (Fox et al. 1990, Belant et al. 1993, Chudzik et al. 1994). Large numbers of gulls reported at refuse dumps, but many roosting or loafing; relatively few birds actually feed on refuse (Belant et al. 1993).

On Dutch Frisian I., diet predominantly marine fish and invertebrates during 1960s (Spaans 1971). Increased competition from Lesser Black-backed Gull led to decline in marine fish, increase in garbage and invertebrates by mid 1980s. Decrease in Herring Gull breeding success related to change in diet (Noordhuis and Spaans 1992).

Quantitative analysis. At coastal sites in New England, percent prey taken (occurrences observed year-round): echinoderms 64%, crustaceans 27%, fish 6%, molluscs 3%. Prey remains from "anvils" (areas where prey dropped to break them open) during same time period included echinoderms (37%), crustaceans (44%), and molluscs (19%) (Good 1992b). Pellets, boli, and mate feedings from 1977 to 1978 in Newfoundland showed 79% dietary specialists (47.4% mussels, 20.1% refuse, 11.5% petrels) and 21% dietary generalists (combination of above) (Pierotti and Annett 1991). Pellets and boli of gulls breeding on Great Lakes included 16 species of fish (80% alewife and smelt), 8 orders of insects, and 11 families of birds (Fox et al. 1990, Chudzik et al. 1994). On coastal Maine islands, percent weight of food in stomach contents of young gulls: refuse and fish offal 44-61%, crabs 1-10%,

urchins 1–5%, natural fish 4–14%, squid 1-10%, earthworms 0-30%, tern chicks 0-2%, mussels 1-4%, clams 1-4% (Hunt 1972). On Dutch Frisian I. from 1966 to 1968, pellets: 70% invertebrates, 9% fish, 1.5% garbage; regurgitations: 72% fish, 19% invertebrates; 1985-1987 pellets: >90% invertebrates, 5% fish, 5% garbage; regurgitations: >50% invertebrates, 30-40% fish, 10-50% garbage (Noordhuis and Spaans 1992).

FOOD SELECTION AND STORAGE

Chooses prey easily handled and swallowed; prefers fish over squid; squid over shellfish; small clams, mussels, crabs over large ones (C. A. Annett pers. comm., RJP, TPG). Preferences change in relation to nutritional requirements, e.g., egg formation, feeding offspring (see Nutrition and Energetics) (Pierotti and Annett 1987, 1990, 1991). Prefers red or silver food over other colors (C. A. Annett pers. comm.). No food storage observed.

NUTRITION AND ENERGETICS

Mean daily metabolizable energy intake per day for captive Great Lakes chicks fed marine smelt and vitamin supplement increased almost linearly to 275 Kcal/d during first 30 d after hatching, leveled off until 60 d, declined to 120 Kcal/d by 70 d (Norstrom et al. 1986). Breeding adult birds require approximately 14 kJ/h (males) and 12 kJ/h (females) for normal maintenance, yielding daily requirement of 1,460 kJ/pair/d (Pierotti and Annett 1991). Fresh-caught fish most nutritious food taken (304 Kcal, 30 g protein, 29 g fat/meal), followed by squid (162 Kcal, 23 g protein, 2 g fat/meal), refuse (150 Kcal, 19 g protein, 13 g fat/meal), birds (61 Kcal, 8 g protein, 3 g fat/meal), and intertidal invertebrates (32 Kcal, 5.2 g protein, 1 g fat/meal) (Pierotti and Annett 1987). Despite rankings of last 3 items, most birds specialized on marine invertebrates; these birds had largest, heaviest eggs, highest hatching success (Pierotti and Annett 1987, 1990, 1991).

During mate-feeding, males deplete endogenous fat, females gain fat (Hario et al. 1991). During egg formation, females deplete protein and skeletal calcium reserves (Houston et al. 1983); this may lead to female dietary preference for marine invertebrates or fish, good sources of protein and calcium, during this period (Pierotti and Annett 1987, 1990). Reserves replenished during incubation (Hario et al. 1991). Chick-rearing most demanding period energetically, particularly latter stages when birds must feed each chick up to 200 g of food per day (Morris 1987, Pierotti 1987a). Food demands much lower during nonbreeding season.

METABOLISM AND TEMPERATURE REGULATION

More sensitive to direct solar radiation than to ambient temperature (Lustick et al. 1978). Orients toward sun on hot or sunny days; temperatures under white plumage lower than under dark plumage. Incubating gulls often pant on hot day or in direct sunlight. Most heat loss through bare areas, either through mouth lining during panting or through legs and feet. Gulls with feet exposed pant less in windy conditions (RJP). Gulls in water rarely pant. In cold conditions, use counter-current heat exchanger with thin-walled veins surrounding arteries in legs; unsaturated fats used as lubricants in joints (Scholander 1955 *in* Schmidt-Nielsen 1983).

DRINKING, PELLET-CASTING, AND DEFECATION

Regularly drinks fresh water and visits freshwater sites when possible. When drinking seawater, uses salt glands located over eyes to remove salt from water (Schmidt-Nielsen 1983). Salt glands excrete far more salt than kidneys, generate fluid pure 5% sodium chloride (compared with 3% in seawater). Gland has parallel cylindrical lobes, each containing several thousand branching tubules, which extract salt from blood using counter-current flow and active transport; pump sodium and chloride ions against gradient. Fluid drips out nostrils and off end of bill (Schmidt-Nielsen 1983).

Regurgitates pellets of indigestible material around nests during breeding and on roosting areas. Pellets contain bones, shells, glass, paper; useful for quantification of dietary components (Pierotti and Annett 1987, 1990, 1991). See Food Habits: diet. Defecates on breeding territory and on roosting areas. Defecations can also be used to identify dietary components (Spaans 1971).

SOUNDS

VOCALIZATIONS

Development. First vocalizations, peeping sounds, produced when egg pips prior to hatching. These calls appear identical to Begging Calls produced by newly hatched chicks, which are presumed to elicit regurgitation of food from parents. As chicks grow, Begging Call changes. Small chicks simply sit or stand, and peep with head lifting slightly with each call. By 2-3 wk, chicks thrust head forward with mouth open during calling, which is now more intense. By 4-5 wk, chicks beg with head hunched against body, lifting head each time they emit high-pitched peep. Call appears identical to Begging Call in adults (see Vocal array below).

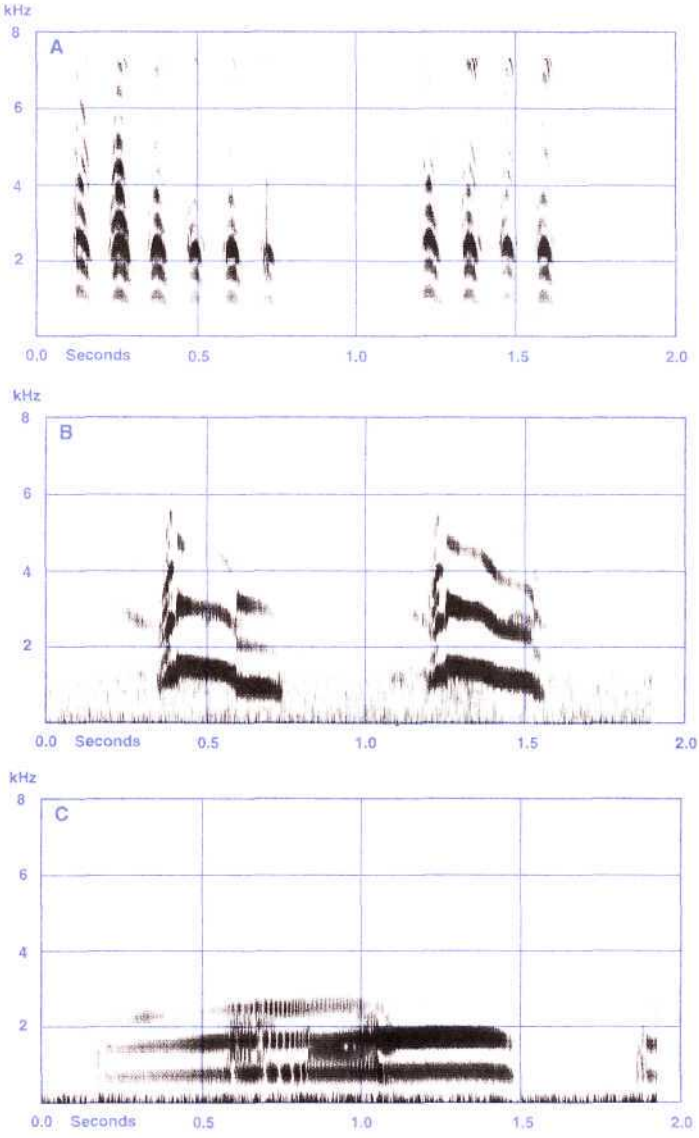

Figure 3. Typical vocalizations of the Herring Gull. A: Long Call; B: Mew Call; C: Alarm Call. From the Borror Laboratory of Bioacoustics (BLB),#5251, 8671,17601. Recorded from coastal Maine.

Another vocalization shown by chicks is Shrill Waver, given when chicks pursued or grabbed, either by predator, conspecific, or investigator. Virtually identical vocalization produced by adults in similar contexts. Tinbergen (1960) suggests that this call is similar to Alarm (gakkering, *hahaha*) Call produced by adults.

During 4-yr transition to adulthood, acquire remaining adult vocal repertoire, although in several cases age of acquisition and ontogeny of specific vocalization unknown. Three-year-old birds show Long-call Note (Keow or Yelp), Long Call (Trumpeting), and Warning Call (Plaintive Yeow) (Tinbergen 1960). Two-year-olds not observed to show these calls (RJP). Calls specifically associated with mating and chick-rearing (Mew Call, Choking, Copulation) only observed in breeding (4- to 5-yr-old) birds.

Vocal array. No "song," but species has complex repertoire of at least 8 (Tinbergen 1960), possibly 12-15, calls. Two of these used by prefledged chicks, 3 others exclusively by adults during breeding (Mew Call, Choking, Copulation). Calls influenced by body posture. Behavior associated with calls described under Behavior. Description of calls follows Moynihan (1955, 1958) and Tinbergen (1959, 1960) except where noted.

LONG CALL. Figure 3A. Also called Trumpeting (Tinbergen 1960). Most elaborate and variable call in repertoire. Almost certainly functions in individual identification in many contexts, e.g., given by both members of pair when 1 returns after absence, first by returning bird, with mate typically responding before first bird has finished. Call consists of several repeated notes produced while bird lowers and then elevates head to Oblique Posture (see Behavior: Agonistic behavior, Communicative interactions; also see Fig. 4). First note(s) longer and lower, probably because of bend in neck and lowered head. Subsequent notes louder and higher pitched (more piercing), show little variation (within an individual) in fundamental frequency, duration, or relative distribution of energy within harmonics (Hand 1979). Final notes flatter and lower pitched, may change into a series of Yelps.

LONG-CALL NOTE. Also called Yelp or Keow. Low intensity, single-note version of Long Call. Highly variable among individuals, may function in individual identification. Often given when predator approaches; also by birds observing other birds fighting, and may function to indicate state of agitation. Heard all times of year, most often during breeding when many individuals are crowded together (Tinbergen 1960).

WARNING CALL. Also called Plaintive Yeow. Simple, clear, slightly descending call, given only by flying birds. Differs among individuals primarily in duration. Tinbergen (1960) considers this call very similar to Long-call Note. Apparent structural differences exist. Warning Call has longer note length, descends markedly in pitch. Difference in structure may result from way in which bird holds neck and head. Flying birds hold neck straight with head and bill in line with neck, in contrast to curve in neck with head perpendicular to neck in Long-call Note. Warning Call is call heard most frequently when visiting (and disturbing) breeding colony.

MEW *CALL.* Figure 3B. Long-drawn, single note invariably linked with distinctive forward bent posture with neck stretched forward and arched.

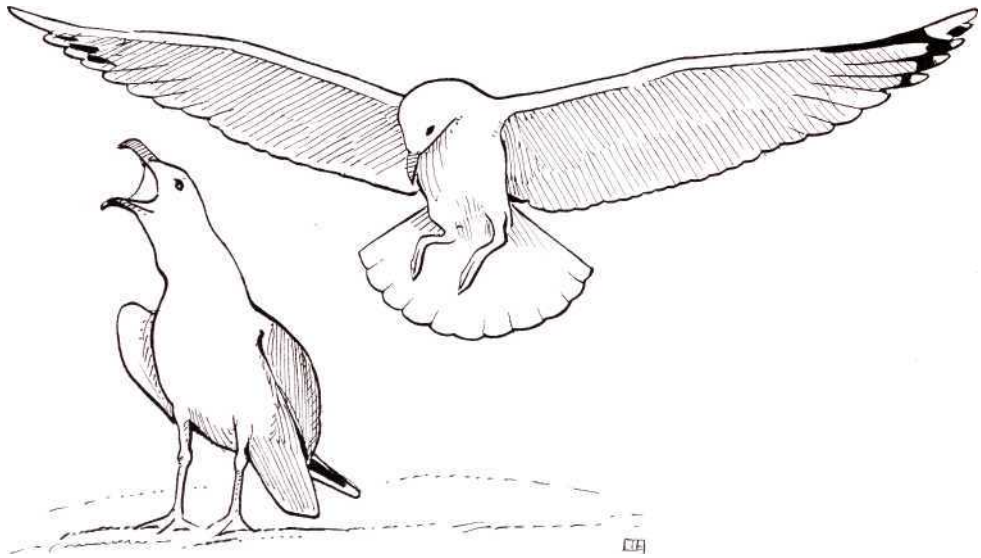

Figure 4. Herring Gull giving its Long Call. Drawing by D. Otte after Tinbergen 1960.

Occurs primarily in four contexts: (1) courtship and precopulation, (2) parent-offspring interactions, (3) nest relief, and (4) aggressive encounters between territorial birds and neighbors. In courtship given primarily by male after returning from absence when about to regurgitate food for mate-feeding; may serve to call mate to be fed. Parents carrying food also use Mew Call to attract offspring; call can be given with beakful of food. In nest relief, given by bird approaching nest, sometimes with nesting material in beak. In these cases appears to function as affiliative call, to get attention of mate or chick. In aggression, given by birds that appear highly agitated; can be last vocalization produced prior to attacking or being attacked.

BEGGING CALL. Simple *Klee-ew* call, accompanied by Head-tossing in which bird assumes a hunched posture and flicks head up sharply while emitting call. Given by female in response to Mew Call by returned male, also given by both male and female prior to mounting. Call virtually identical to food-begging call of chicks (see above, Development) but has softer, less-demanding quality.

COPULATION CALL. Only call produced solely by males. Loud and regular in rhythm, staccato and guttural in quality, with energy concentrated in 1-2 heavy bands. Tinbergen (1960) describes call as more or less intermediate between Choking and Alarm Calls, but Hand (1979) shows low-intensity Copulation Calls not clearly distinguishable from Choking. Call produced by male after mounting, initiated during phase when tail is lowered and cloacal contact begins, continued until completion of copulation. Probably functions to advertise highly motivated state of male and to discourage interruptions.

CHOKING. Named after accompanying visual display (Moynihan 1958, Tinbergen 1959). Usually performed in tandem by mated pair. Birds squat, or crouch, with breasts lowered to ground and tails elevated. Call uttered as head and neck pump with hyoid bone lowered, producing *huoh-huoh-huoh* sound. Occurs in 3 contexts: (1) agonistic encounters, where territorial birds engage neighbors across shared boundary, (2) early stages of courtship, especially during nest-site choice, and (3) during nest exchanges. Appears to indicate tendency to remain in specific physical location (Hand 1979); may explain similarity to Copulation Call, with which males also indicate disinclination toward displacement.

ALARM CALL. Figure 3C. Also called *Eh-Eh, HaHaHa,* or *Kek-Kek* Call. Given in response to predator (observer), especially on breeding colony (Tinbergen 1959, 1960). Given primarily when predator is first seen but does not pose immediate threat. If predator comes closer, birds shift to Yelping or take to air uttering Warning Calls. Call structure has wide frequency distribution with closely spaced harmonics. May indicate tendency to flee (Tinbergen 1959, 1960). Often alternates with Charge Call, so may also indicate conflict between flight and attack.

CHARGE CALL. Given when diving at intruder or predator, or during aerial pursuit of conspecific or predator. Tinbergen (1960) regards this as modified Long-call Note; however, more similar structurally to Mew Call (Hand 1979) and may indicate high state of arousal.

SHRILL WAVER. AS described for chicks (see Development, above), call given when bird is grabbed or attacked unexpectedly, either by

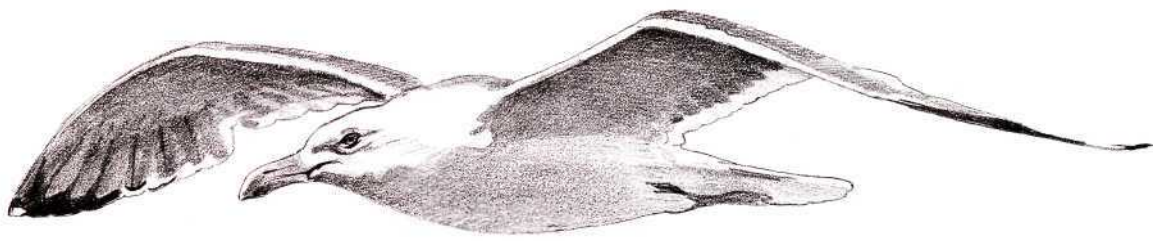

Figure 5. Herring Gull In flight. Drawing by D. Otte, after photo by Arthur and Elaine Morris/VIREO.

predator or conspecific. Structurally related to Begging Call. Females grabbed by mate or male they are courting may Head-toss, give Shrill Waver, or combine the 2. Begging Call and Shrill Waver are first 2 vocalizations developed.

NONVOCAL SOUNDS

None described.

BEHAVIOR

LOCOMOTION

Walking, hopping, climbing. On land, typically walks or runs with legs alternating. Can jump or hop onto perches by opening wings, using single wingbeat for elevation, and pushing off with legs. Also hops down with wings partially spread. In agonistic charges, runs with wings partially upraised. Also runs to take off for flight. Does not use hopping as form of locomotion. Does not climb vertical objects.

Flight. Adjusts wingbeat and orientation to wind to regulate speed. Spends considerable portion of flight time gliding or soaring with outstretched wings (Fig. 5). Dives and swoops by adjusting angle of wings. When joining feeding groups on water, often descends by flapping wings and flying in rapidly diminishing circles (Hoffman et al. 1981). Attacks terrestrial predators using steep dives, strikes at predator with wings, feet, (rarely) beak.

Swimming and diving. Swims on surface of water using paddling motion of legs for propulsion. Can dive either from surface or short distance above water, but cannot reach depths >1-2 m below surface because of high degree of buoyancy (Tinbergen 1960, RJP).

SELF-MAINTENANCE

Preening, head scratching, bathing, anting, etc. Does not ant. Bathes regularly resting on water, ducking head and body parts under water and shaking them. Combines bathing and preening on water. On land, preens using beak on wing, breast, and tail feathers. Rubs head over preen gland, rubs secretion on feathers. Head scratching involved in preening (leg under wing). Preening occupies 6% of 24-h day (Amlaner 1983).

Sunbathing, thermoregulation. See above, Metabolism and Temperature Regulation.

Sleeping and roosting. During breeding season, sleeps or rest-sleeps about 10 h (42% of 24-h day; Amlaner 1983). During daylight, sleeps in 1- to 15-min bouts. At night, sleeps in 45- to 300-min bouts. Sleeps with head resting on breast, legs folded underneath body; some individuals sleep while perching on 1 leg with other leg folded against body. Deeply sleeping birds tuck head under wing along back. Males and females sleep similar amounts of time / d (Amlaner 1983). Birds sleep while incubating or next to incubating mate.

Roosts and loafs in large groups (often mixed species) in open areas that allow large distance between group and approaching predators, including fields, beaches, parking lots, helipads, airport runways, garbage dumps. Sleeps and preens on specific areas, referred to as "clubs," on breeding colonies (Tinbergen 1960).

Daily time budget. Male and female time budgets vary among habitats and between years (Morris 1987, Pierotti 1987a). Males spend more total time on territory and less time incubating than females, who typically spend 85-90% of total time present on nest (Pierotti 1987a). Male present, and incubates, more often in mid-morning and late afternoon. Female present, and incubates, more in early and mid-afternoon and at night. Male typically leaves to forage before dawn, returns mid-morning, when female leaves to forage. Diurnal pattern similar during chick-rearing; male and female present similar amounts of time, except in habitats where Great Black-backed Gulls nest, where males spend more time present guarding chicks from attacks (Pierotti 1987a).

Adults spend most time on territory sleeping or resting. Amount of time spent sleeping and resting varies from 70-75% during incubation to <50% during later stages of chick-rearing (Amlaner 1983, Morris 1987). Outside breeding season, forage 2-3 h/d; rests, sleeps, preens remainder.

AGONISTIC BEHAVIOR

Physical interactions. Inter- and intraspecific intruders chased, both in air and on ground, and may be attacked. Attacks between neighbors begin with jabbing at opponent with beak, grabbing opponent by tail, wing, beak, rarely by neck. Birds gripping each other by beak engage in extended pulling bouts, which may last several minutes (Tinbergen 1960). If individual loses balance during pulling contest, it is struck with wings or pecked. Attacks on intruders usually begin with charge (see below, Communicative interactions). Birds retreating from opponent often give Shrill Waver or Alarm Call (see Vocal array). Birds also pursue retreating opponents by flight, or on ground with wings upraised. Males engage in fights and pursuits much more often than females do (Tinbergen 1960, Pierotti 1987a).

Adults attack chicks running across territory. Chicks typically grabbed by head and shaken. Smaller chicks may be grabbed by body and pummeled or thrown. Intruding conspecific chicks may be killed but are almost never eaten (Pierotti and Murphy 1987, Pierotti 1991). Such infanticidal attacks should not be referred to as "cannibalism," which is engaged in by only a few males (sometimes none) in any single colony. Adults also attack first few chicks to fledge in area. Attacks involve repeated swoops, blows struck with wings, feet, bill; sometimes several adults involved. Behavior strongly resembles attacks directed toward raptors or herons flying over colony and may result from mistaken identity.

Communicative interactions. Complex repertoire, involving at least 11 separate displays. Several displays closely linked with vocalizations after which they are named (see above, Vocal array). Some displays have multiple context-dependent functions (Beer 1975, Hand 1985). Therefore, displays not subdivided into threat and appeasement, although these functions are discussed.

UPRIGHT POSTURE. Approaches slowly in rigid posture with neck stretched upward and forward with head pointed slightly downward (Tinbergen 1960; see Fig. 6). In high-intensity forms, wings lifted so they stand out from body, increasing apparent size. Wings also positioned to strike blows. Given significantly more often by males than females. Directed at neighbors, intruding conspecifics. Often leads to Grass-pulling (see below) or Long Calling with neighbors. With intruder, if opponent does not retreat, displaying bird begins to approach more rapidly, raises wings more prominently, grading into charge.

CHARGE. Also called Attack or Supplant. Bird approaches opponent rapidly, half-running, half-flying, often giving Charge Call. Intruders almost invariably fly in response to Charge. Intruders that persist are often pursued through air. Intruders that do not fly away are attacked (see above). Males more likely to Charge, especially against male opponent. Females Charge primarily female and immature opponents (Pierotti 1987a).

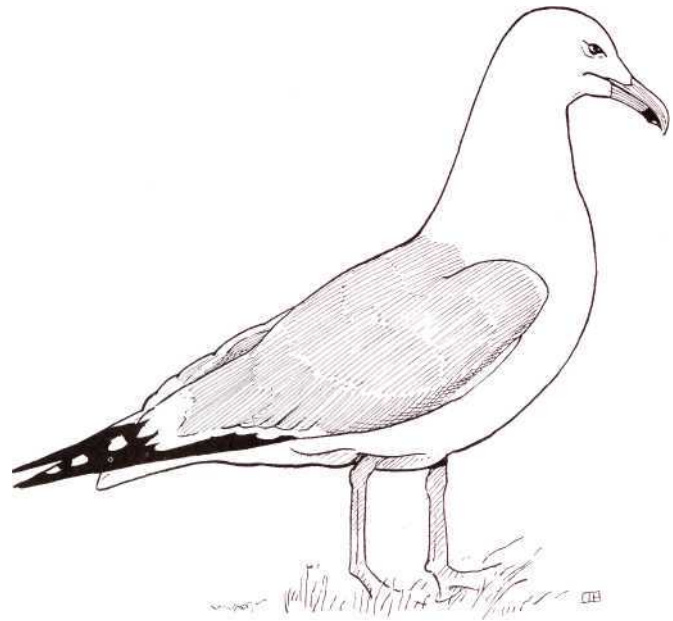

Figure 6. Upright Posture of the Herring Gull. Drawing by D. Otte after Tinbergen 1960.

ALERT *POSTURE.* Like Upright, but neck held back, so appearance less threatening (Tinbergen 1960). Often given by target of Upright. Also shown in presence of predator prior to flight.

OBLIQUE POSTURE. Associated with Long Call. Bird lowers head toward ground (in extreme cases head almost horizontal under breast), produces Long-call Notes. Throws head back over scapulars, stretches neck out fully with mouth wide open (body forms oblique angle with substrate, hence name) while emitting series of call notes (Tinbergen 1959, 1960; also see Fig. 4). Given in several contexts: (1) after bout of aggression over territorial boundary, (2) when mate returns from absence, (3) when neighbor returns from absence, (4) at birds flying over territory. Oblique Posture without Long Call functions as threat when shown by bird stretching neck toward opponent across boundary.

SILENT SQUAT. Bird crouches with breast touching or just above substrate, rear end elevated. Head in position similar to Upright. Often alternates with bill-jabs, Grass-pulling. Directed only at neighbors while face to face. Given more often by males than females (Pierotti 1979).

GRASS-PULLING. During territorial disputes, 1 or both opponents take vegetation in beak, brace feet wide apart, pull vigorously at vegetation (Tinbergen 1960). Usually performed while facing neighbor opponent < 1 m away. Rarely shown by females (Pierotti 1987a). Functions as high-intensity threat. Similar posture taken by bird grasping opponent by wing, tail, or beak during fight (Tinbergen 1960). May be displacement activity.

CHOKING. Display accompanying vocalization. Bird lowers breast, bends legs, points head down, and depresses hyoid bone, giving throat "swollen" look. Bird(s) perform rhythmic jerking movement with head, producing deep *huoh-huoh-huoh* call (Tinbergen 1960). Typically given by pair in tandem during territorial boundary disputes. Only agonistic display performed as often by females as males. Virtually identical display directed at partner when identifying nest scrapes and during nest exchanges. In these cases given by bird on nest or over scrape. Display appears to indicate strong motivation to occupy specific location (Hand 1979). May be derived from incomplete regurgitation (Beer 1975).

MEW-CALL POSTURE. Similar to Upright, except neck more arched and head lowered with mouth open so Mew Call can be produced. Functions to attract mate or chicks when given after returning to territory. In these instances, Mew-call Posture with arched neck often precedes regurgitation of food for mate or offspring. Also shown in territorial disputes, when intruder lands on territory. In these cases appears to function as high-intensity threat.

HEAD-TOSSING. Associated with Begging Call. Bird hunches neck so head drawn close to body (Fig. 7). Head repeatedly flicked upward while Begging Call (*Klee-ew*) given with each toss. Appears to stimulate regurgitation by male when given by female, or by parent when given by chick or juvenile. Given by both members of pair in tandem prior to copulation. May function as agonistic display in juveniles, because adults retreat from Head-tossing juveniles. More likely that adult is unwilling, or unable, to regurgitate and simply moves away from juvenile.

FACING-AWAY. Similar to Upright or Alert Postures, with neck stretched vertically to maximum and head and body horizontal. Individual, or at least head, turned away from other bird, which means weaponry (wings, beak) also turned away. May function in appeasement, allaying opponent's fear, or in cutting off stimuli that might provoke its own flight or attack behavior (Beer 1975). Given during boundary disputes, by mates upon return of partner, and by chicks to parents after parents display at other adults.

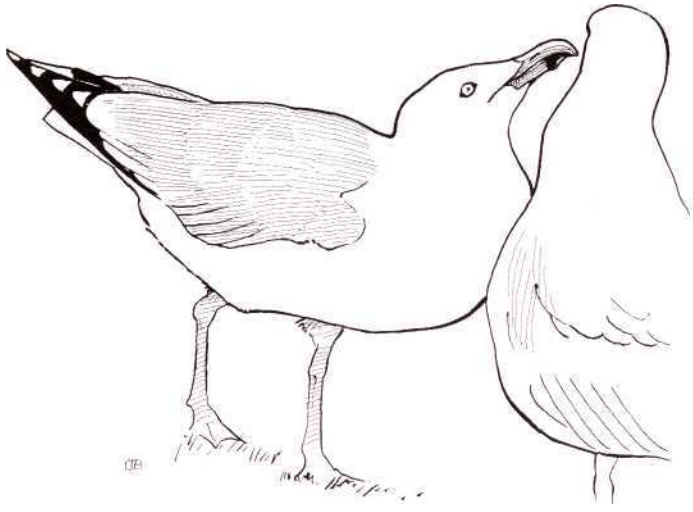

Figure 7. Head-tossing, a begging posture of the Herring Gull. Drawing by D. Otte after Tinbergen 1960.

ANXIETY POSTURE. Like Facing-away, but with wings slightly raised, neck stretched farther forward, body and head oriented away from other bird (Tinbergen 1960). Given by intruder in response to Upright Posture or Charge. Probably preparatory or intention movement for flight.

SPACING

Territoriality. Maintains breeding territory on colony during breeding season; maintains only personal space (< 1 m) on roosting areas during both breeding and nonbreeding seasons. Territory established by male, defended by pair.

NATURE AND EXTENT OF TERRITORY. Breeding territories areas of substrate, defended against conspecifics or congenerics. Territory size depends on nature of substrate and heterogeneity of terrain. Heterogeneous habitats permit smaller areas. On Great I., Newfoundland, internest distances averaged about 4 m in heterogeneous rocky habitats, 6-7 m in tussock meadows with small trees, 8-9 m in open meadows (Pierotti 1982). On Clam I., NJ, nearest-neighbor distance averaged 4.5 to 5.0 m with range 2.3-8.3 m (Burger 1984). Territory size on Clam I. averaged 38.9 ± 14.8 m^2 with range 16.0-72.6 m^2. Size of defended area changes over breeding season: largest during chick-rearing, smallest during incubation, intermediate during prelaying (Burger 1984). Changes relate to value of territory and settling pattern. During earliest stage, fewer pairs settled and defended areas larger. Incubating pairs less aggressive; new pairs can then establish (Burger 1984, Pierotti 1987a). When chicks hatch, parents much more aggressive, attack all intruders in area, strongly defend boundaries against

neighbors (Pierotti 1987a). Territorial boundaries quite flexible, depending on context, with small "unique territory" defended against all birds other than pair and offspring, "primary territory" defended only against neighbors, "secondary territory" defended against intruders (Burger 1984). Last may contain portions of primary, but not unique, territories of other pairs. Males defend all 3 categories of territory; females defend primarily unique territory (Pierotti 1987a).

MANNER *OF ESTABLISHING AND MAINTAINING TERRITORY.* Prior to breeding season, males defend areas of breeding colony. If male already paired, mate helps defend area but does not help establish initial territory. If male not paired, he may be joined by unpaired females, whom he will either court or drive off (Tinbergen 1960). Females defend and maintain territory when male absent (Pierotti 1987a). When male present, he performs most defense and maintenance. Established pairs typically return to same territory as long as they remain paired. If male dies or abandons, female must find new mate and territory. If female dies or abandons, male remains on same territory (Pierotti 1980).

INTERSPECIFIC TERRITORIALITY. Herring Gulls nest in mixed-species colonies with other gulls, terns, skimmers, alcids; rarely with cormorants and gannets. Only defends territories against other gulls: Great Black-backed, Ring-billed, and Laughing gulls along Atlantic Coast and Great Lakes; Glaucous-winged Gull in California; Glaucous Gull in Canadian Arctic or Alaska. Often supplants smaller species, but is supplanted by larger species.

WINTER TERRITORIALITY. Defends feeding areas on beach or intertidal against conspecifics and congenerics (Drury and Smith 1968). Some individuals or pairs defend feeding territories throughout year (I. C. T. Nisbet pers. comm.). In warmer latitudes, some birds may remain on and defend both breeding and feeding territories throughout entire annual cycle.

DOMINANCE HIERARCHIES. Dominance context specific. Adults typically dominant over juveniles or immatures. Males may dominate females during feeding and boundary disputes; females win conflicts over choice of nest site and incubation (Hand 1985).

Individual distance. See Territoriality, above.

SEXUAL BEHAVIOR

Mating system and sex ratio. Almost exclusively monogamous. Rare instances of "polygyny," where 1 male and 2 females occupy territory and incubate either single nest or double nests (Shugart 1980, Fitch and Shugart 1983). Secondary females achieve little or no breeding success. Occasional accounts of multiple females, promiscuous matings, and female-female pairs in gulls probably result from slightly skewed sex ratios favoring females (Pierotti 1980, Burger and Gochfeld 1981). Males losing mates can replace them quickly, whereas females losing mates cannot replace them; suggests more adult females than males in most populations (Pierotti 1980, 1982, Burger and Gochfeld 1981). At least 2 parents necessary to successfully rear offspring because eggs left alone in nests often eaten, and offspring left alone often attacked or killed (Burger 1984, Morris 1987, Pierotti 1987a).

Courtship displays and mate-guarding. No displays specific only to courtship (Tinbergen 1960). Females typically approach males in hunched Head-tossing (begging) posture (Fig. 7), producing Begging Call. Male responds by assuming (1) Upright Posture or (2) Mew-call Posture and Mew-calling. Female circles male, increasing begging intensity if he Mew-calls. Male may either Choke or regurgitate and feed female (Tinbergen 1960). If male regurgitates food and female accepts it by eating, often leads directly to copulation. Mate-guarding reported to be most intense in week prior to laying (Morris and Bidochka 1983).

Copulation. Male and female Head-toss together repeatedly. Male moves behind female, jumps on her back with wings outspread. Female continues Head-tossing while male begins Copulation Call (see Vocal array). After completion, male jumps off, shakes, preens. If female does not eat food regurgitated by male, she may prevent him from mounting by walking away. If male loses balance or takes too long achieving cloacal contact, female may walk out from under him after he begins Copulation Call (RJP).

Duration and maintenance of pair bond. Pair bonds maintained as long as both members of pair remain alive (Tinbergen 1960). Major factor leading to rupture of pair bond is failure to hatch eggs, either because male does not provide adequate food to female during egg formation or because male and female do not synchronize activities so eggs left unattended (often eaten) (Morris 1987, RJP). Only 8 of > 300 pairs on Great I., Newfoundland, broke up (both members of pair observed after breakup) (RJP).

Extra-pair copulations. Males whose mates have completed laying solicit copulation from neighboring females (MacRoberts 1973, RJP). Male may attempt to force copulation on incubating females. No forced copulation attempt ever observed to result in successful transfer of sperm (MacRoberts 1973, RJP).

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Although species nests colonially, most social interactions between neighbors agonistic. Appear to nest as far apart as limited space allows (Pierotti 1979, Coulson 1991). If sufficient habitat available, nest solitarily, breeding success high. Away from breeding colony, loaf and roost together in groups, forage in loose groups that aggregate quickly when prey located (Hoffman et al. 1981, Pierotti 1988). Foraging groups often include other species, including kittiwakes, cormorants, shearwaters, alcids, dolphins, whales (Hoffman et al. 1981, Pierotti 1988).

Play. Occurs in chicks and juveniles. Often pick up objects, run around territory. Other chicks may pursue during these activities, attempt to steal object. Tugs-of-war lasting >1 min may ensue. Practice flights contain elements of play; chicks within brood leap up and down beating wings and chittering (RJP).

Nonpredatory interspecific interactions. Mixed-species foraging, loafing, and roosting groups (see above). Eiders and puffins benefit from Herring Gulls' vigilance and attacks on predators (Pierotti 1983, Gotmark 1989). Interspecific territoriality with other gull species (see above, Spacing: Territoriality).

PREDATION

Kinds of predators. On adults: Bald Eagle *(Haliaetus leucocephalus),* Peregrine Falcon *(Falco peregrinus),* Gyrfalcon *(F. rusticolis),* Great Horned Owl *(Bubo virginianus),* red fox *(Vulpes vulpes),* domestic dog *(Canis lupus familiaris),* harbor seal *(Phoca vitulina),* gray seal *(Halichoerus grypus),* various sharks (e.g., *Charodon).* On chicks: conspecific adults (rare), Great Black-backed Gull (often), other sympatric gulls, Northern Harrier *(Circus cyaeneus),* Great Horned Owl, Short-eared Owl *(Asio flammeus),* Common Raven *(Corvus corax),* Black-crowned Night-Heron *(Nycticorax nycticorax),* Great Blue Heron *(Ardea herodias),* red fox, domestic dog, raccoon *(Procyon lotor),* domestic cat *(Felis catus),* mink *(Mustela vison).* On eggs: conspecifics, other sympatric gulls, ravens and crows *(Corvus* spp.), red fox, mink, raccoon, rats *(Rattus* spp.) (Tinbergen 1960, RJP).

Response to predators. When predator first sighted, Herring Gulls give Alarm Call. If predator approaches, give Warning Call, take off, and circle overhead. Mob flying predators (hawks, ravens) by pursuing through air giving repeated Long-call Notes *(keow),* dive and strike at predator with beak and feet. Dive at terrestrial predators, strike with feet, wings, rarely with beak. Some predators representing threat to adult, e.g., Peregrine Falcon, avoided. More aggressive protecting chicks than eggs. If chick gives Shrill Waver, parents (but not other adults) dive at and strike predator while giving Charge Call while neighbors emit intense Long-call Notes (RJP).

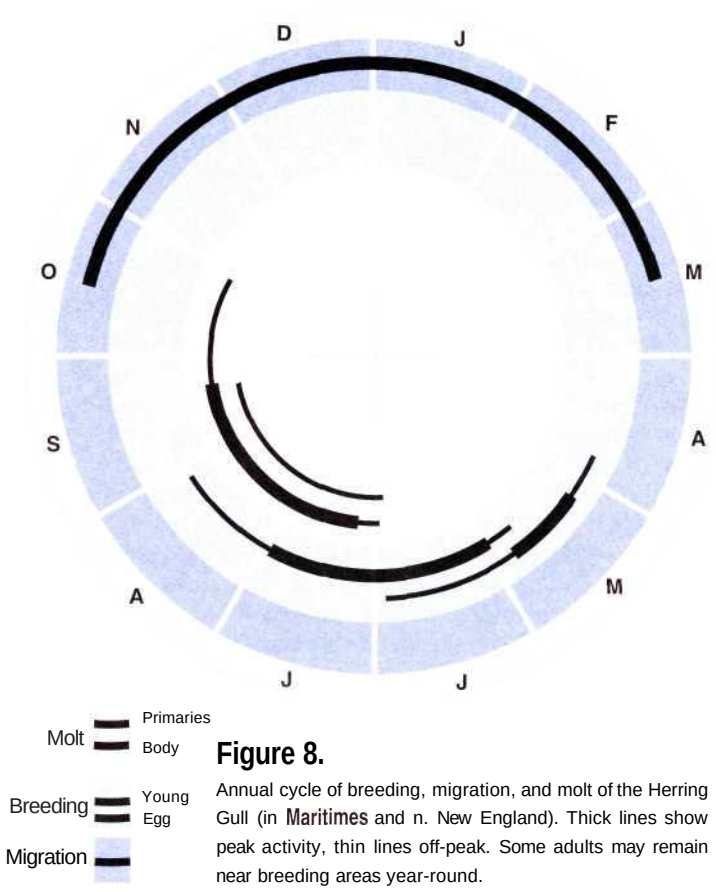

Figure 8.

Annual cycle of breeding, migration, and molt of the Herring Gull (in Maritimes and n. New England). Thick lines show peak activity, thin lines off-peak. Some adults may remain near breeding areas year-round.

BREEDING

PHENOLOGY

Pair formation. At start of breeding season in Mar, Apr (depending on latitude), either on male's territory or loafing areas (Tinbergen 1960). In areas covered by ice, delay nest-building and egg-laying but not territory establishment (Morris and Chardine 1985). Males regurgitate food for females for egg formation, replenishing reserves. Late arrivals pair after onset of breeding of early-nesting pairs and attempt to establish territories among established pairs (Burger 1984).

Nest-building. Male and female choose site and make scrape lined with vegetation, feathers, etc. Nest cup shaped by birds with breast and feet (Tinbergen 1960). Material added throughout incubation (Bent 1921).

First/only brood per season. Figure. 8. One

brood/yr. May lay replacement clutch if first destroyed. Can lay up to 12 eggs if first egg removed before second laid (Pierotti 1979, 1982). Most clutches initiated early through mid-May, can be initiated in late Jun (Pierotti 1982); birds need 4-6 d to lay 3-egg clutch. Incubation begins with second egg, lasts 30-32 d (Drent 1970). Chicks fledge 6-7 wk after hatching, are fed on natal territory until 12-15 wk old (Burger 1984). Parents and chicks abandon territory in early fall. Chicks cared for off territory for up to 6 mo (Drury and Smith 1968, Burger 1984).

NEST SITE

Selection process. Male and female dig various scrapes, fill them with vegetation; up to 3-4/ territory. Both Choke over specific scrapes each has built; if Choke together, site chosen. Ultimate choice is where female lays eggs (Hand 1985).

Microhabitat/site characteristics. Site protected from prevailing wind(s), placed next to large object (log, bush, rock), which acts as visual barrier between nest and closest neighbors (Pierotti 1982, Burger 1984). Nests in rocky areas located in crevices, in depression scraped in sand or soft soil, or pressed down into short vegetation. Located above high tide, splash zone on beaches, marine terraces.

NEST

Construction process. See above, Nest Site: selection process. Built by pair during daylight several days prior to egg-laying. Vegetation added throughout incubation.

Structure and composition matter. Bowl scraped into substrate, lined with vegetation, feathers, plastic, rope, etc. Some nests, especially in sand, have little or no lining (RJP).

Dimensions. Inner cavity averages 15 cm, range 10-20 cm; outer diameter averages 30 cm, range 25-35 cm; depth 5-7 cm (Bent 1921, Cezilly and Quenette 1988).

Microclimate. Protected from prevailing wind. If shelter next to nest removed, nest material blows away (Pierotti 1979, 1982). Shelter lowers windspeed above nest cup, reduces wind chill for incubating adult or uncovered eggs (Pierotti 1979).

Maintenance and reuse of nests, alternate nests. Adults add to nest throughout incubation. Nest not reused, but specific site often reused from year to year. Alternate nests built, not used (Pierotti 1979).

Nonbreeding nests. Alternate nests (indistinguishable from used nests) sometimes built on territory before final nest site chosen. Only final nest (where eggs are laid) is used. Counts of nesting pairs should be conducted during late incubation, otherwise numbers may be overestimated because of counting nonbreeding (alternate) nests.

EGGS

Shape. Variable; most ovoid.

Size. See Appendix 1. Typically 65-75 mm long, 45-55 mm wide (greatest breadth).

Mass. 85-105 g (10-12% of adult female mass; Pierotti 1982). Second egg sometimes heaviest, third egg smallest, although difference reduced in well-nourished females (Drent 1970, Pierotti 1982).

Color and texture. Smooth, nonglossy, with finely granular surface. Usually light olive, buff, or greenish, may vary from pale whitish buff to deep brownish buff. Speckled, spotted, blotched black, dark brown, or dark olive. Terminal egg (usually third) typically scrawled or streaked, especially on wide end (Harrison 1978).

Egg-laying. Nest essentially complete prior to laying first egg. Eggs usually laid in early morning at roughly 2-d intervals (Drent 1970). Male feeds female throughout laying; female rarely leaves territory during laying. Male often absent obtaining food for female, reducing mate-guarding opportunities. Females strongly resist all forced copulation attempts, reducing need for mate-guarding (but see Morris and Bidochka 1983). If first egg lost, females relay for up to 24 d, depending on physiological condition (Pierotti 1979, 1982). If clutch lost, females require 7- to 10-d refractory period to produce new clutch. Replacement clutches often have smaller or fewer eggs than first clutch (Pierotti 1979). Intraspecific nest parasitism and dumping not observed. Chick adoption common (5-10% of pairs), resulting in chick-generated nest parasitism (Pierotti and Murphy 1987, Pierotti 1991).

For detailed account of egg temperature and shift between adult and chick in contribution to egg temperature, see Drent 1970.

INCUBATION

Onset ofbroodiness and incubation in relation to laying. Incubation begins with laying of first egg. Effective incubation begins with laying of second egg; brood patches not fully vascularized, depilated until then (Drent 1970).

Incubation patches. Three incubation patches, 1 on either side of keel, 3 posterior to these. Present in both sexes. Patches larger in female (Drent 1970, RJP).

Incubationperiod. First egg laid day 0, hatches day 30. Second egg laid day 2, hatches day 30. Third egg laid day 4-5, hatches day 31-32 (Drent

1970, Pierotti 1979, 1982). Delayed hatch in third egg, combined with lighter weight of chick, generates "third chick disadvantage," whereby third chick obtains less food, grows more slowly than first- and second-hatched chicks (Pierotti 1982). Can lead to differential mortality (Parsons 1975).

Parental behavior. Incubation shared equally by male and female, especially in successful pairs (Burger 1984, Morris 1987). During good feeding conditions, female spends more time on nest than male does; female also incubates at night (Pierotti 1979, 1987a). Male incubates mostly when female absent, will remain on nest when female returns (Pierotti 1979). Shifts last 3-4 h. Eggs covered about 75% of time until clutch complete, about 98% of time after completion (Drent 1970). Typical change-over occurs when mate returns, pair exchange Long Calls, returning mate approaches nest, may Mew-call or Head-toss. Incubating bird either gets off nest or Chokes, indicating tendency to remain. If incubating bird gets off, arriving bird walks on to nest cup, lowers breast into cup, paddles feet to adjust eggs and feathers. Once settled, preens, adjusts eggs with beak, settles to rest or sleep. If bird on nest Chokes and remains, mate may pick up nesting material, return Mew-calling. If this induces partner to leave nest, bird settles on nest as above, placing nesting material around nest.

Hardiness of eggs. Eggs can be left unattended for several hours without affecting hatchability (Drent 1970, Burger 1984). All eggs lost to predation lost during periods of inattention (Drent 1970, Morris 1987, Pierotti 1987a). Eggs left unattended for extended periods show hatching delay (Drent 1970).

HATCHING

Preliminary events and vocalizations. Five to 6 d prior to hatching, fine webwork of cracks appear at 1 point on shell adjacent to widest egg circumference. After 1-2 d, small "pipping" hole appears in spot, through which tip of chick's beak with egg tooth is visible. Once hole exists, chick produces peeping sounds. Adults respond with Mew Calls. Adults switch own diet to fish when chicks emit first calls within egg (Pierotti and Annett 1987, 1990).

Shell-breaking and emergence. Chicks hatch before midday. First and second chick within 3-4, third chick up to 24 h later. Each egg takes about 2 d from appearance of pipping hole to chick emergence. Shell breaks just above greatest diameter; chicks push out using feet (RJP).

Parental assistance and disposal of eggshells. Parents give no physical assistance, watch over hatching chicks and Mew-call at intervals. Some adults remove shells from nest, others allow shell to be crushed into nest lining (Tinbergen 1960, RJP). Experiments indicate reduced predation by crows if eggshells removed after hatching (Tinbergen 1960), but only on nests unattended by parents. At attended nests, adults cover eggs and hatching chicks throughout hatching process, rendering adaptive function of eggshell removal somewhat problematic (RJP).

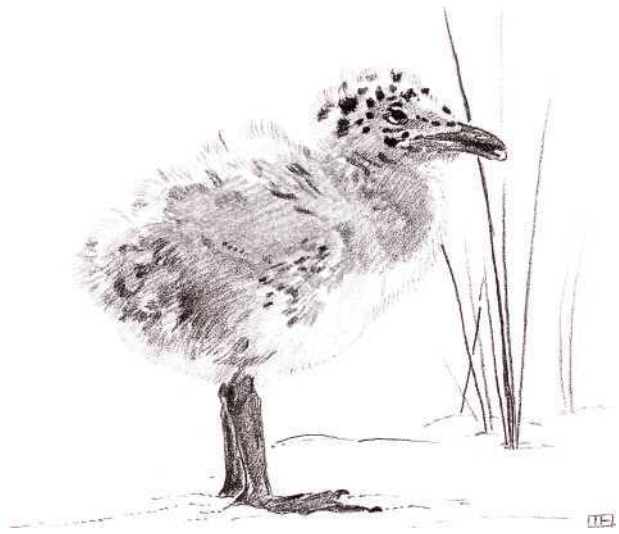

Figure 9. Herring Gull chick, about 7–10 days old. Drawing by D. Otte, after photo by Arthur and Elaine Morris/ VIREO.

YOUNG BIRDS

Condition at hatching. Chicks nidifugous, semiprecocial with open eyes, thick gray down marked with black spots over entire body, weigh 60-75 g. Beak black, except pinkish egg tooth (retained 2-3 d), legs black to dark gray (Bent 1921, Dwight 1925; see Fig. 9). Remain in nest for several hours while drying. First 2-3 d move about nest vicinity; at 1 wk can run about freely, remain on natal territory. Live off yolk reserves first few days, fed by parents within hours of hatching.

Growth and development. On day of hatching: first- and second- hatched chicks weigh 60-75 g (third-hatched chicks slightly smaller); day 5: 100-150 g; day 10: 150–300 g (Fig. 9); day 15: 300-600 g; day 20: 400-800 g; day 25: 500-900 g; day 30: 650-1,100 g (Pierotti 1979, 1982). Chicks weighing < 200 g on day 15 or < 600 g on day 30 unlikely to survive (Pierotti 1979).

Flight feathers emerge between day 15 and 20; primaries and accompanying coverts emerge first, followed by coverts on back and belly; rectrices emerge day 25-30. All feathers fully emerged by fledging, day 40-50. Tarsus about 30 mm long at

hatching, grows steadily to asymptote of 60-70 mm at day 30-35. Culmen about 18-20 mm at hatching, grows steadily to asymptote of 30-35 mm at fledging (about day 50) (Elkowe and Payne 1979, Pierotti 1979).

Young chicks brooded on cold or rainy days until 7-10 d old. Chicks maintain homeothermy within 24 h of hatching, expend about 7% total metabolic costs thermoregulating (Dunn 1976). Chicks ambulatory within 24 h, actively move about by 3-5 d, start stretching wings at 15 d, beating wings about 30 d, jump up and down beating wings between 30 and 40 d, first become airborne about 40-45 d, capable of actual flight by 45-50 d (Pierotti 1979). Chicks have Begging Calls (see Vocal array) at hatching; postural and vocalization changes described above. Chicks peck at, pick up objects, huddle together to sleep or rest. When parent(s) return with food, chicks rush parent and beg actively. If parent regurgitates, chicks scramble to grab food, often pulling fish from parent's mouth. Competition appears to be "scramble"; no obvious aggression among siblings. Larger (earlier-hatched) chicks usually win scrambles. If food provided not adequate for 3 chicks, smallest (youngest) chick may wander off and be attacked or killed (60-70%) or adopted (30-40%) by neighboring adults (Graves and Whiten 1980, Pierotti 1980, 1991, Holley 1984, Pierotti and Murphy 1987).

PARENTAL CARE

Brooding. Both parents brood young, female more in total (Pierotti 1979, 1982). Brooding behavior begins with hatching of first egg and continues until chicks 7-10 d old. Chicks > 5 d brooded only during inclement weather. One adult always present and attending chicks until > 30 d in successful pairs (Burger 1984, Morris 1987).

Feeding. Both parents feed chicks from day of hatching until 11-12 wk. Males feed more often before fledging (0-50 d), females more often after fledging (50-80 d) (Burger 1984, Pierotti 1987a). Adults leave territory to forage, return with food in proventriculus. On return, chicks either rush up and beg, or adult Mew-calls, attracting chicks. Young chicks (<10 d) peck at red spot near gonys, may stimulate regurgitation by adult (Tinbergen 1960), but many adults regurgitate before chicks peck. Major function of red spot may be to orient chick-feeding during early behavioral development. Older chicks (>10 d) do not peck at red spot, but give Begging Call while oriented at base of adult's mouth (RJP). Adult regurgitates food, holds bolus in bill for young chicks (<10 d), regurgitates bolus onto ground for larger chicks. Chicks pick up pieces or entire prey items, swallow whole.

Young chicks (<10 d) fed small prey items (small fishes, euphausiids, copepods, insects, earthworms) or well-digested prey that breaks into pieces small enough to be handled (e.g., fish). Small chicks cannot handle entire large fish or invertebrates (mussels, crabs, squid, urchins) or human refuse. Adults feeding large food items to offspring lose them to death or adoption (Pierotti and Annett 1987, 1990, 1991). Large chicks (>10 d) can handle larger food, swallow entire fish, squid, or refuse. In Newfoundland, chicks fed capelin until 2-3 wk old, squid when chicks > 2 wk old. Chicks fed refuse grow more slowly, survive poorly compared to chicks fed natural diets (Pierotti and Annett 1987, 1990, 1991). In Holland, increase in garbage and invertebrates fed to chicks associated with decrease in breeding success (Noordhuis and Spaans 1992). Chicks fed every 3-4 h by male, every 4 h by female prior to fledging (Pierotti 1987a, Pierotti and Annett 1991). Males fed chicks 160 g capelin or 180 g squid / meal, females 120 g capelin or 100 g squid / meal (Pierotti 1987a, Pierotti and Annett 1987). In Massachusetts and Maine, adults feed chicks small fish, insects, marine invertebrates (RJP). Feeding refuse to small chicks may be cause of low fledging success in some New England colonies (< 1.0 chick / nest in Massachusetts, compared with nearly 2 chick/nest in Newfoundland) (see Kadlec and Drury 1968, Hunt 1972, Pierotti 1982, Pierotti and Annett 1991). Chicks try, but unable to ingest large pieces of refuse, intact mussels, or crabs as food in both Newfoundland and Massachusetts (RJP).

Nest sanitation. Chicks (and adults) defecate on territory but away from nest. Adults also defecate while flying. No parasites observed in nest, but young can become infested with fleas if mammals (rats, rabbits) present on nesting islands.

Parental carrying. Does not occur.

COOPERATIVE BREEDING

A few triads (1 male, 2 females) observed, all of which incubate, brood, and feed offspring (Shugart 1980). These groups typically unsuccessful in fledging offspring.

BROOD PARASITISM

No nest parasitism (eggs) observed. Chicks often adopted when they wander into territories of neighboring pairs (Graves and Whiten 1980, Pierotti 1980, 1991, Holley 1984, Pierotti and Murphy 1987).

FLEDGLING STAGE

Departure from nest. Chicks leave nest within 24 h, remain on nesting territory and around nest 40-plus d. Leave nesting territory initially with first flight at 45-50 d. Chicks fully grown, fully feathered, and at or above adult mass at fledging (Pierotti 1979). Return to nesting territory to rest and be fed up to 12-15 wk of age (Burger 1984).

Growth. Most growth occurs prior to fledging. Mass probably lost while juveniles learn to forage for themselves. Wings and tail may continue to grow after fledging.

Association with parents or other young. Some chicks associate with adults, beg food up to 6 mo postfledging (Drury and Smith 1968, RJP). Newly fledged chicks gather in groups around colony, also concentrate on areas where food predictably obtained, e.g., rocky intertidal, fishing activities, refuse dumps. Large numbers of juveniles associate with feeding humpback whales in Gulf of Maine, off s. Nova Scotia, in fall and winter; feed on fish driven to surface by foraging whales (Pierotti 1988).

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding; intervals between breeding. Males may first breed in fourth year of life, females in fifth (Paynter 1966, Davis 1975). Most breed every year, but some forego breeding during years with poor food supply (Pierotti 1979, 1982).

Clutch. Modal clutch size 3, some birds in poor condition lay 2 or even 1 egg (Tinbergen 1960, Pierotti 1982). Occasional clutches of more than 3 may result from 2 females sharing nest (Shugart 1980) or unusual egg production. Only 1 successful clutch/season, since producing fledged offspring takes minimum 10 wk (typically 15-20 wk; Burger 1984). Up to 2 replacement clutches possible if early clutches destroyed (RJP).

Annual and lifetime reproductive success. Maximum annual fledging success 3, achieved by about 23% of pairs (150/660 pairs in Newfoundland, Pierotti 1979, 1982; 10/43 pairs in New Jersey, Burger 1984). Another 20-30% fledge 2 chicks/yr, 20-30% fledge 1 chick/yr, 15-30% fledge no chicks per year (Pierotti 1979, 1982, Burger 1984). On Great I., Newfoundland, fledging success higher (70-90%) than hatching success (40-85%) (n = 8 subgroups over 2 yr; Pierotti and Annett 1990, 1991). On Clam I., NJ, hatching success (70-80%) slightly higher than fledging success (55-70%) (n = 3 yr; Burger 1984).

Highly variable in lifetime reproductive success, like other birds (Clutton-Brock 1988, Newton 1989); < 50% of fledged chicks survive to breed (Kadlec and Drury 1968). Of these, 30-40% breed only 1-2 times, produce no surviving chicks. Of remaining birds, about half breed 3-4 times, produce 2-4 chicks. Only 10-15% of cohort are highly successful, breeding > 5 yr, producing 10-30 chicks over life span (Paludan 1951, Davis 1975, Pierotti 1979, Coulson and Butterfield 1986). Successful birds in both New England and Atlantic Canada take diet of primarily fish (including fish waste) and marine invertebrates during prelaying and incubation, avoid refuse in diet (Pierotti and Annett 1987, 1990, 1991), and nest in areas without predators (Pierotti 1979, 1982).

LIFE SPAN AND SURVIVORSHIP

Survival of eggs to hatching 70-80%; hatched chicks to fledging 50-70%; fledglings to age of first breeding 50% (Paludan 1951, Paynter 1966, Kadlec and Drury 1968, Pierotti 1979, 1982). Initial breeding attempt crucial step for overall success; probably only 60-70% survive to next breeding season (Paludan 1951, Paynter 1966). In United Kingdom, after second breeding, adult survival about 90%/yr from ages 6 to 18 (Davis 1975, Chabrzyk and Coulson 1976, Coulson and Butterfield 1986), may be as low as 80-85% in North America (Paludan 1951, Paynter 1966, Kadlec 1976), although lower survival rates may represent band loss rather than mortality. Maximum longevity > 30 yr in wild, reportedly > 40 yr in captivity (Terres 1980); 15-20 yr typical in wild (Chabrzyk and Coulson 1976, Coulson and Butterfield 1986).

DISEASE AND BODY PARASITES

Avian tuberculosis, internal parasites (Plotz 1980, Vauk et al. 1980). Some chicks show nasal discharge; harsh breathing often associated with death in Newfoundland (Pierotti 1979). *Salmonella* and botulism implicated as major causes of death in urban colonies. Fleas and ticks (*Ixodes* spp.) on chicks, especially where mammals (e.g., rabbits) present or recently extirpated from colony (RJP).

CAUSES OF MORTALITY

Many adult birds die of injuries (broken wings, beaks, etc.). Others shot, poisoned by fishermen. Almost certainly take in contaminants, e.g., chlorinated hydrocarbons, bacterial toxins, during feeding. Problem especially acute in Great Lakes, where many eggs failed to hatch and chicks showed growth retardation and deformities (Weseloh et al. 1979, Becker et al. 1980). Contamination observed in 1950s became severe

problem in 1960s and 1970s, but has been alleviated during 1980s as contaminant levels declined (Fox 1990). Some contaminants, e.g., o,p' DDT and p,p' DDE, act as estrogen mimics, cause feminization of male embryos, leading to skewed sex ratio in adult population (Fry et al. 1987); results in shortage of adult male gulls and leads to formation of female-female pairs and triads (Pierotti 1981, Fox 1990).

Individuals get tangled in nets and fishing lines. A few taken by predators (owls, raptors, foxes). Most mortality occurs during breeding season (Coulson and Butterfield 1986). Some killed during interspecific territorial conflicts with Great Black-backed Gulls in Newfoundland and Gulf of Maine (Pierotti 1979, McGill-Harelstad 1985).

RANGE

Natal philopatry, dispersal. Natal philopatry high in low-density areas, low in high-density areas. Males much more philopatric than females (Coulson and Butterfield 1986, RJP). At higher latitudes, in colder climates, birds move farther than at lower latitudes (Moore 1976). General southward dispersal responsible for major increases in breeding bird numbers south of Maine since 1900 (Drury and Nisbet 1972, Moore 1976).

Breeding site fidelity, dispersal. Pairs nesting successfully use same breeding territory until male dies or deserts (Tinbergen 1960). Pairs appear to disperse together, possibly accompanied by offspring in late summer and fall; return paired in spring (RJP). Males and females observed together in winter; not known if these are breeding pairs (RJP). Considerable dispersal both southward and offshore in fall and winter (Drury and Nisbet 1972, Moore 1976, Powers 1983).

Home range. Forages up to 100 km from colony; birds breeding at Witless Bay, Newfoundland, observed feeding on Grand Banks (RJP), more typically forage within 20 km (2-h round-trip) of colony (Drury and Nisbet 1972). Home range dependent on location of reliable food sources and dietary proclivities of individuals (Pierotti and Annett 1991).

POPULATION STATUS

Numbers. In 1900, U.S. population only 8,000 pairs, entirely in Maine; around 30,000 in New England by 1935; near 90,000 from Maine to Virginia in mid-1970s (Powers 1983, Andrews 1990); > 100,000 pairs from Maine to Virginia in mid-1980s (Andrews 1990). Last number may represent more accurate censusing rather than actual increase. Current (1990) numbers of pairs break down as follows: Maine 27,000; New Hampshire 350; Massachusetts 35,000; Rhode Island 5,000; Connecticut 3,000; New York 25,000; New Jersey 4,000; Delaware < 100; Maryland 4,000; Virginia 3,000 (Andrews 1990); Gulf of St. Lawrence 11,000 (Chapdelaine and Brousseau 1991). Several thousand pairs breed in Newfoundland and Labrador (Brown et al. 1975). A few thousand pairs breed in Great Lakes (Moore 1976, Blokpoel and Tessier 1991), and a few thousand more pairs probably breed throughout Canadian Arctic south to se. Alaska (Vermeer 1973). Powers (1983) estimated 1 million Herring Gulls offshore from Cape Hatteras to Gulf of Maine in fall. Numbers have stabilized, may even be declining in e. Canada and New England in recent (1980s) years (Hebert 1989). Recent (1980s) increases come mostly from southward range expansion (Andrews 1990).

Trends. See above, and Population Regulation, below.

POPULATION REGULATION

Population growth limited by availability of suitable nesting areas and natural food sources. Historically, low juvenile overwinter survival and persecution on nesting colonies kept numbers low. Cessation of egging and of killing adults for millinery trade allowed recovery (Graham 1975). Recovery probably also spurred by increased overwinter survival of young birds feeding on refuse. Numbers now declining in New Brunswick, Maine, and Massachusetts as result of egging by locals in Canada and incursion of Great Black-backed Gulls from Labrador to Massachusetts (McGill-Harelstad 1985, Hebert 1988, TPG, RJP). In Newfoundland, early 1990s decline has resulted from crash of capelin stocks (J. Chardine pers. comm.); capelin primary food of Herring Gulls and other seabirds in Newfoundland during chick-rearing (Pierotti 1979, Pierotti and Annett 1987, 1990, 1991).

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Breeds in proximity to human habitation. Intentional or unintentional reductions of breeding populations usually local and short-term (Buckley and Buckley 1984, Blodget 1988). Actively hunted for eggs and feathers during nineteenth century, now protected from both forms of exploitation. Exploitation all but stopped in U.S. but continues in Canada. Oil pollution, pesticide contamination, destruction of food

sources through overfishing, and deliberate control measures are human activities most likely to affect populations (Graham 1975, Blodget 1988, Fox 1990).

Herring Gull reached very low numbers during nineteenth century, was considered rare by Audubon. Increase in numbers after turn of century should be viewed in large part as recovery from persecution, especially since we have no good estimates of numbers prior to human impact (Graham 1975). Increased gull population sizes in New England and Great Lakes traditionally attributed to increased food availability from feeding on human refuse, including bycatch and offal from fishing operations (Kadlec and Drury 1968, Hunt 1972, Pons 1992). Actual situation more complex; rapid increase from 1930s through 1960s resulted from combination of factors: (1) serious protection of birds and growth of conservation movement in U.S. (Dunlap 1988), (2) increased fishing activity which (a) generated considerable waste available as food and (b) reduced competition for small to medium-sized fish preferred by gulls by reducing numbers of large fish, e.g., cod, salmon, (3) increasing human population generated large amounts of garbage and proliferation of garbage dumps, which served as foraging areas, especially important in increasing overwinter survival of juveniles, and (4) near extirpation of cetacean and pinniped populations in many areas reduced competition for small fishes (capelin, sandlance *[Ammodytes* sp.]) and pelagic invertebrates (krill, copepods). Herring Gull numbers leveled off in mid-1970s and 1980s as dumps closed and changed, and overfishing destroyed fish stocks; may actually be declining in several areas at present, e.g., Newfoundland, New Brunswick, and Maine.

Numerous studies of use of refuse from dumps *(garbage,* distinguished from fisheries wastes) as food by breeding Herring Gulls do not support idea that garbage dumps were major force driving population increases. In Holland, an increase in garbage as food has been related to decline in Herring Gull breeding success (Noordhuis and Spaans 1992). In Newfoundland and Massachusetts, gulls feeding garbage to chicks showed lower chick growth and survival (Pierotti and Annett 1987, 1990, 1991). In Great Lakes, successful breeding pairs fed primarily on fish; although many gulls were observed on dumps, most were loafing rather than feeding (Belant et al. 1993). Fisheries waste (bycatch and fish offal) much higher in quality as food (Pierotti and Annett 1987). Much confusion over role of "refuse" as a food source resulted from investigators failing to distinguish clearly between fishery-generated wastes and garbage from dumps when using term *refuse* (e.g., Drury and Nisbet 1972, Hunt 1972). Future studies should clearly distinguish between fishery waste and garbage, as these diet categories have different implications for gull nutrition.

MANAGEMENT

Gull culls, egg smashing, and spraying with oil carried out by state agencies and private individuals to provide greater nesting opportunities for other seabirds, including terns, puffins, even other gulls (Drury and Nisbet 1972, Graham 1975, Blodget 1988, Alpers 1991). Efforts ineffective on large scale, although small-scale efforts have been successful in eliminating gulls from small colonies (Blodget 1988, Alpers 1991). In Witless Bay, Newfoundland, Herring Gull supposedly reduced breeding success of Atlantic Puffin (*Fratercula arctica*) through egg and chick predation, and piracy. Cull suggested as solution (Nettleship 1972). Subsequent work showed Herring Gull did not eat puffin eggs and chicks, except when puffins were disturbed by humans or ravens. Piracy on puffins primarily occurred in areas of low puffin density and in years when puffins had low breeding success because of reduced food availability (Pierotti 1983, Rice 1985). Culling Herring Gull on Isle of May, United Kingdom, resulted in 70% decline in number of breeding gulls but only 10% decline in area of island occupied (Coulson 1991). Primary effect was therefore increase in average Herring Gull internest distance; did not make more habitat available for other species.

APPEARANCE

MOLTS AND PLUMAGES

Because of the wide ranging distribution and abundance of Herring Gulls, an enormous amount of basic and applied research has been done on them, including many studies on the molts and plumages of European populations. However, the only stu dies on molts and plumages of North American birds were conducted by Dwight (1901, 1920, 1925). Poor (1946) described individual variation in plumage and soft-part colors in relation to age in Atlantic Coast populations, but he presented few data relevant to molt. These studies mainly presented brief and general descriptions of the extent of each molt and the appearance of each resulting plumage. They were not quantitative or detailed; nor did Dwight describe the sequence of replacement of feathers in each molt or the relative timing of molts (1)

between sexes, (2) among age classes, (3) among different populations, or (4) in relation to ecological factors such as the effect or failed (or unattempted) versus successful breeding. Thus, such studies in North America are warranted.

In European populations, and therefore presumably in North American populations as well, there is tremendous geographic variation in nearly every aspect of the molts and plumages of this species as well as in their morphometrics and bare part colors (e.g., Harris 1971, Verbeek 1977, Walters 1978, Coulson et al. 1983, Ginn and Melville 1983). Therefore, the following discussion is confined to the North American subspecies *smithsonianus*.

The scenario presented below depicts the sequence of molts and plumages for an average individual. Herring Gulls typically do not achieve Definitive plumage until they are > 3 yr old (i.e., during their fourth Prebasic molt), but there is considerable individual variation in the age at which this plumage is attained, some doing so earlier and some later (Poor 1946, Monaghan and Duncan 1979).

Hatchlings. Chicks hatch semi-precocial and downy. Down pale drab-gray with only slight cast of cream-buff or pinkish-buff, particularly on head, grading to pale gray on belly; underparts are palest on chin and throat and unmarked except for spots on sides of chin and an obscure speckling or clouding on the sides, posterior abdomen and undertail coverts. Finely marked on the head with indistinct fuscous-black to deep gray spots that are stellate to polygonal in shape; back, thigh, and undertail coverts diffusely mottled with drab-gray to light clove-brown; this often gives the back a coarsely lined or spotted appearance; dusky spot on the shoulder and two blurred bars across the forearm; a small median spot or line on forehead; very variable spot on anterior crown which diverges into 2 less defined rows of spots in temporal region; a median spot, transverse group of spots or 2 spots one behind the other on occiput; often 2 pairs of large spots on nape, and often an additional large spot to each side of occiput; spots also on lores, relatively smaller spots around eye, and irregular spots on cheek, throat, and side of neck (Dwight 1925, Fjeldså 1977, Cramp and Simmons 1983).

Juvenal plumage. Prejuvenal molt complete; down shed progressively over 30-40 d; lost first on wings, followed by back, underside, neck, and head; Juvenal plumage typically complete by 5-6 wk.

Head and underparts streaked gray-brown with paler face and nape, darker ear coverts and blackish eye-crescent. Mantle and scapulars gray-brown with pale edgings forming scaly pattern. Rump streaked gray-brown with same general tone as mantle and tail, thus contrast usually slight. Wing coverts same color as mantle and scapulars but more barred, less scaly, including outer greater primary coverts. Tertials blackish-brown with obvious pale border and obvious pale notches at sides and subterminal pale bar. Secondaries mainly blackish-brown, forming secondary bar. Primaries and outer wing mainly blackish-brown, but inner primaries pale with dark subterminal marks forming pale window, prominent from above and below. Underwing has prominent pale window; rest of underwing rather uniform pale gray-brown. Base of tail whitish with darker bars, generally gray-brown like rump and underparts; broad blackish-brown subterminal tail band (color plates in Cramp and Simmons 1983, photos and line drawings in Grant 1986, Urban et al. 1986).

Basic I plumage. Partial molt of body plumage, mainly limited to head, neck, many or most mantle feathers, some scapulars, some rump feathers, and the breast and sides. All Juvenal flight feathers retained. Molt begins in Sep, Oct, or Nov (rarely later), typically ending by Dec. Prebasic I and Prealternate I molt overlap in some individuals (Dwight 1925, Cramp and Simmons 1983).

Basic I plumage similar to Juvenal except head (and sometimes underparts) whiter, and new mantle and scapular feathers with more complex pattern of dark bars; scaly Juvenal scapulars often retained (line drawings of primary and rectrix color pattern in Dwight 1920, color plates in Cramp and Simmons 1983, photos and line drawings in Grant 1986, Urban et al. 1986).

Alternate I plumage. Partial molt of body plumage, usually in Mar, Apr, and May, though some may start earlier; chiefly confined to the head, some to most of back, rump, and underparts (Dwight 1925, Cramp and Simmons 1983).

Alternate I plumage similar to Juvenal except head and underparts often extensively whitish. Dark areas of wings and tail often faded to pale brown, and pale areas faded/worn to whitish, giving generally very pale appearance by summer. A few clear gray scapulars may be acquired from Apr onwards (color plates in Cramp and Simmons 1983, photos and line drawings in Grant 1986, Urban et al. 1986).

Basic II plumage. Prebasic II molt complete. Dwight (1925) states that molt occurs from Aug to Oct, i.e., at the same time or later than adults. However, this molt occurs much earlier than in adults, at least in European populations (Coulson et al. 1983, Cramp and Simmons 1983). Whatever

the exact timing may be, it cannot be confined to Aug-Oct as molt takes a minimum of 4 mo and usually as long as 6 mo (see below). Flight feather molt begins with the innermost primary (P1, not P10 as stated by Grant [1986] who followed Dwight's long-abandoned numbering system) and its associated greater covert, and progresses outward to the outermost primary (P10). At any one time, only 2 primaries typically are growing. Secondary molt starts simultaneously from both the outermost (S1) inwards, and from the innermost secondary outwards beginning at about the time P6 and P7 are growing. Secondary molt proceeds much more rapidly than primary molt, many feathers often missing at one time, typically finishing before completion of primary molt. Rectrix molt begins shortly after onset of secondary molt, usually beginning with the central pair and proceeding outward. Some birds replace R6 before R5, and some individuals may lose all rectrices synchronously. Wing coverts other than greater primary coverts are molted just before secondary molt, beginning with the median coverts and progressing to the greater and lesser coverts. Molt of underwing coverts is prolonged and spans the entire molt period. Body molt usually begins on the back (but occasionally on underparts [Harris 1971]), followed shortly thereafter by the humeral and ventral tracts, anterior part of head. Thereafter, body molt progresses outwards in all directions. All subsequent Prebasic molts follow same sequence. At the population level, molt takes about 6 to 7 mo, but individuals complete molt in about 4 to 6 mo (e.g., Harris 1971, Walters 1978). (line drawings of primary and rectrix color pattern in Dwight 1920, color plates in Cramp and Simmons 1983, photos and line drawings in Grant 1986, Urban et al. 1986).

Head white, usually with extensive dusky streaking; underparts and rump mainly white with variable amount of dark streaking; mantle and scapulars sometimes similar to Basic I but usually with extensive gray (contrary to Cramp and Simmons 1983). Outer wing mainly blackish (P10 sometimes with a small white terminal spot), but P1-P4 and their greater primary coverts mainly clear gray; tertials barred black and white or with extensive white internal markings, not mainly dark-centered as in previous plumages. Coverts of inner wing paler, sometimes with much gray color, more uniform than in previous plumages and with variable amount of brown barring; greater coverts vermiculated or finely barred, but not strongly barred as in previous plumages. Underwing generally whiter. Tail extensively whitish at base; broad, mainly solid blackish subterminal band of variable pattern.

Alternate II plumage. Extent and timing of molt same as Prealternate I molt. Plumage same as Basic II except head and underparts mainly white. Mantle and scapulars clear gray, sometimes with a few brown-barred feathers. Dark areas on wings and tail faded, and pale areas faded to whitish (often contrasting with gray mantle and scapulars to give saddle effect) by summer.

Basic III plumage. Extent of molt same as Prebasic II molt; molt probably begins at same time, but finishes about a month earlier (e.g., Dwight 1925, Cramp and Simmons 1983).

Head and body white with extensive dusky streaking especially around eye and on crown, nape, and hindneck; a few streaks on breast-sides and flanks. Mantle and scapulars uniform pale gray. Wings uniform pale gray except for black and white on outer primaries. Extent of black on distal portion of primaries decreases toward more proximal primaries, but is more extensive than in Definitive Basic plumage, i.e., black tips extend to primaries more proximal than P5 (typically innermost primary with a black tip in Definitive Basic plumage). Greater primary coverts and alula also black-tipped. Outer primaries with black also have white tips (mirrors), though smaller, less numerous, and on fewer primaries than in Definitive Basic plumage. Variable amount of brown markings on inner wing, especially on median and lesser coverts, secondaries and their greater coverts, and tertials (which are mainly gray); these brown markings are less than in Basic II plumage. Underwing white (sometimes with some brown marks on coverts) with gray subterminal trailing edge and black tips to outer primaries. Tail white with subterminal markings of highly variable extent and pattern; these markings typically finely barred or freckled (not mainly solidly dark as in Basic II plumage) or often confined to feather centers giving tail dark-and-white striped pattern (line drawings of primary and rectrix color pattern in Dwight 1920, color plates in Cramp and Simmons 1983, photos and line drawings in Grant 1986, Urban et al. 1986).

Alternate III plumage. Extent and timing of molt same as Prealternate I molt. Plumage same as Basic III except head and underparts usually white; freckled brown areas on inner wings worn or faded to whitish; white primary tips reduced or lacking due to wear (Grant 1986).

Definitive Basic plumage. Extent and timing of molt same as Prebasic III molt. Molt typically begins during egg-laying, incubation, or shortly after hatching (e.g., Verbeek 1977, Walters 1978).

Plumage same as Basic III except black primary markings are less extensive and usually terminate with a subterminal spot on P5, forming a clear-cut black wing tip above and below; some individuals also have small blackish marks on outer greater primary coverts. White mirrors larger, more numerous and on more primaries. Mirrors on P9-P10 obvious at long distance. No brown markings on inner wing or underwing; underwing white with gray subterminal trailing edge and black tips to outer primaries. Scapular-crescent small or lacking; tertial crescent prominent when perched. White leading edge to inner wing indistinct, but trailing edge prominent (line drawings of primary and rectrix color pattern in Dwight 1920, color plates in Cramp and Simmons 1983, photos and line drawings in Grant 1986, Urban et al. 1986).

Definitive Alternate plumage. Extent and timing of molt same as Prealternate I molt.

Plumage same as Definitive Basic except head and underparts white; white primary tips reduced or lacking through wear (line drawings of primary and rectrix color pattern in Dwight 1920, color plates in Cramp and Simmons 1983, photos and line drawings in Grant 1986, Urban et al. 1986).

Aberrant plumage coloration. Ross (1963) mentions records of 2 albinistic chicks, one albinistic adult and three other unspecified records of albinistic birds. Albinistic individuals have been reported widely outside of North America. No melanistic birds have been reported in North America, but, again, there are many reports outside of North America.

BARE PARTS

Bare part colors of known age *smithsonianus* and their individual and age-related variation are discussed by Poor (1946).

Hatchlings. Bill described as "horn color with a pink tip" (Dwight 1925) to aniline black, often pinkish at base (especially on lower mandible), and with the distal third pinkish buff in youngest nestlings (Fjeldså 1977, Grant 1986); legs and feet grayish pink becoming brownish drab during nestling period; iris dark brown (Dwight 1925, Fjeldså 1977).

Juvenal. Bill dark, pale at base; gape pale vinaceous or fawn. Iris sepia or dark brown. Legs and feet dark gray with flesh overtones.

Basic I plumage. Bill black diminishing toward base. Iris and feet unchanged. First spring, same.

Basic II plumage. Bill olive-buff, drab, or flesh at base, whitish at extreme tip; gape pinkish white or buff. Iris pale straw, buff, or brown. Legs and feet pale pinkish buff or pinkish white.

Alternate II plumage. Bill more yellowish basally. Iris, legs, and feet unchanged.

Basic III plumage. Bill yellowish olive-buff with black or brown bar or spots behind nostrils; gape pinkish buff. Iris straw yellow or buff. Legs and feet unchanged.

Alternate III plumage. Bar on bill disappears, some of adult red spot appears. Iris brighter yellow. Legs and feet brighter pink.

Definitive Basic plumage. Bill lemon, cream, or other yellows with scarlet or orange-vermilion spot on each side of terminal portion of lower mandible; gape yellow or cream. Iris straw or pale orange-yellow. Legs and feet pale pinkish cinnamon or flesh color.

Definitive Alternate plumage. Bill and gape brighter colored. Iris brighter yellow or orange. Legs and feet unchanged.

MISCELLANEOUS

Norstrom et al. (1986) discuss the energetics of molt in Herring Gulls. The authors conclude that the daily cost of molt is small (about 6 Kcal/d) and may be mostly or entirely offset by reducing other energetic expenditures (e.g., cost of foraging). These conclusions should be viewed critically in light of more recent research on the cost of molting, especially that of Mary Murphy and the late James R. King.

Lustick et al. (1980) showed that as the angle of incidence of solar radiation onto the plumage of Herring Gulls increases, the difference in heat load between light and dark plumages disappears. Thus, by postural adjustment, birds with dark plumage may become thermally white with regard to radiative heat load.

Boss (1943) experimentally induced males and females to acquire Definitive plumage at the age of 1 yr by a series of injections of testosterone beginning at the third day of incubation and continuing periodically for 12 mo. Estradiol, stilbesterol, gonadotropic hormones, and thyroxin had no effect on plumage development. This is noteworthy because it indicates that development of Definitive plumage in both males and females is regulated by testosterone levels.

MEASUREMENTS

LINEAR

See Appendix 2. Males significantly larger than females for all measurements.

MASS

See Appendix 2.

PRIORITIES FOR FUTURE RESEARCH

Most studies of Herring Gull have concentrated on species during recovery and post-recovery periods and have emphasized role of scavenging. Future research should emphasize Herring Gull as component of marine community and focus on species' role (1) in mixed-species foraging aggregations, (2) as intertidal predator, and (3) in offshore fisheries. Much emphasis has been placed on Herring Gull as scavenger around fishing boats, with little emphasis on how fishermen use gulls (or other seabirds) to locate schools of fish or prime areas to set nets. Work in Europe has shown that both Great and Lesser Black-backed gulls outcompete Herring Gull for fisheries waste and for limited marine fish stocks. Good long-term population studies both of colonies and marked individuals needed to learn whether similar factors are at work in New England and Canada. Need to know if Herring Gull is actually increasing in numbers or simply expanding range southward in response to factors making northern parts of range less suitable, e.g., collapse of fish stocks, competition, and predation by Great Black-backed Gulls.

ACKNOWLEDGMENTS

We thank Charles Amlaner, John Chardine, Arthur Borror, and the late Les Tuck for communicating unpublished results. Unpublished data were collected by RJP from 1976 to 1985 with support from Dalhousie University, the Canadian Wildlife Service, and the Ocean Research and Education Society of Gloucester, MA., and by TPG from 1989 to 1993 with support from the University of New Hampshire, Sigma Xi, Scientific Research Society, Frank B. Chapman Fund of the American Museum of Natural History, and Shoals Marine Laboratory. Thanks also to I. C. T. Nisbet and R. Morris for helpful reviews of earlier drafts of this account and to C. Thompson for input on the Appearance section. We dedicate this manuscript to the memories of Les Tuck and William H. Drury. Cover photo © Arthur and Elaine Morris/VIREO.

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Appendix 1. Dimensions of Herring Gull eggs (data from Western Foundation of Vertebrate Zoology and from Pierotti 1982, Table 4).

Western Foundation of Vertebrate Zoology (*n* = 20)

	mean	range
Length (mm)	72.200	64.46-76.47
Breadth (mm)	49.730	47.73-53.08
Shell Weight (g)	6.251	5.166-7.185
Shell Thickness mm)	0.355	0.320-0.389

Great Island, Newfoundland (Pierotti 1982) (data shown as mean ± SD)

	A egg (n = 340)	B egg (*n* = 317)	C egg (n = 233)
Length (mm)	72.3 ±3.0	71.3 ±2.9	69.3 ±2.9
Volume (cm^3)	84.8 ±7.0	82.3 ±6.8	76.1 ±6.8
Mass (g)	96.2 ± 7.4	93.1 ±7.3	87.4+7.8

Appendix 2 Body measurements and mass (mm, g) of male and female Herring Gulls culled at Ram I., Mattapoisett, MA, 15 May 1990. From Evans et al. (in press); *t*-values compare males with females.

	n	mean (±SD, range)	*t*	*P*
CULMEN				
Males	169	66.0 (±2.3, 56-70)	-28.5	0.001
Females	253	57.2 (±1.9, 52-62)		0.001
TARSUS				
Males	169	71.1 (±2.2,65-76)	-24.0	0.001
Females	253	66.0 (±2.0, 60-73)		0.001
WING CHORD				
Males	169	429 (±10.3, 400–460)	-20.8	0.001
Females	253	408 (± 9.6, 384-447)		0.001
MASS				
Males	169	1,147 (±77.7, 973-1,143)	-13.7	0.001
Females	246	1,023 (±106, 718-1,385)		0.001

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The Birds of North America accounts (ISSN 1061–5466) are published bimonthly by The American Ornithologists' Union and The Academy of Natural Sciences, Benjamin Franklin Parkway, Philadelphia, PA 19103-1195. Printed by Smith-Edwards-Dunlap Company, Philadelphia, PA.

The Birds of North America is supported by charitable and governmental organizations including: The Office of Migratory Bird Management (USFWS), National Fish and Wildlife Foundation, The McLean Contributionship, The Geraldine R. Dodge Foundation, The Richardson Foundation, and the American Birding Association. Benefactors of this program include Wallace C. Dayton and Joseph and Helen Taylor.

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RECOMMENDED CITATION
Pierotti, R. J., and T. P. Good. 1994. Herring Gull (*Larus argentatus*). *In* The Birds of North America, No. 124 (A. Poole and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington, D.C.: The American Ornithologists' Union.