

*Stercorarius  
longicaudus*

FRENCH:  
*Labbe à queue longue*  
SPANISH:  
*Estercorario robero (Cuba),  
Salteador cola larga (Mexico)*

# Long-tailed Jaeger



**O**f the three species of *Stercorarius*, the Long-tailed Jaeger is the smallest and most graceful in flight. Transequatorial migration allows this species to forage in regions with high productivity and extended day lengths throughout the year. During the breeding season, it feeds over arctic tundra; as a migrant and throughout the northern winter, it is highly pelagic, spending its time over open seas. Even though this jaeger spends more than three-fourths of its life at sea, nearly all information about its biology comes from its arctic breeding grounds. The species is seldom seen in North America south of Canada and Alaska, and much of the published information not directly related to its breeding biology focuses on vagrancy or identification.

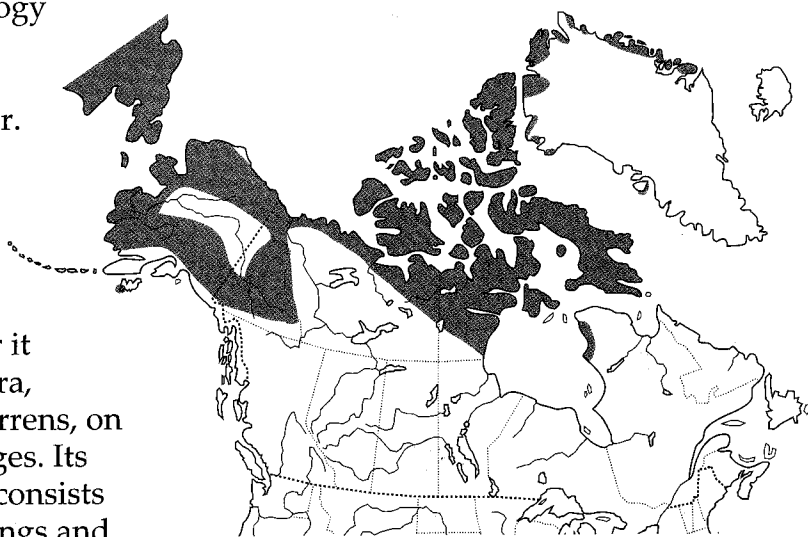
In the Arctic this species is the most widely distributed and abundant jaeger.

## The Birds of North America

Life Histories for  
the 21st Century

Breeding the farthest north of any jaeger, probably as far north as any bird, during the summer it frequents dry tundra, sometimes even barrens, on low slopes and ridges. Its diet in this habitat consists primarily of lemmings and

voles, so this bird is vulnerable to cycles in the densities of these rodents. The Long-tailed Jaeger is supremely adapted for predation on these cyclic rodents. Because it depends on rodents only for breeding, it can survive crashes in rodent numbers without the



**Figure 1.**  
Breeding distribution of the Long-tailed Jaeger in North America. This species winters in South America and also breeds in Europe and Asia. See text for details.

irruptions and high mortality experienced by other arctic predators. In years with low densities of lemmings, the Long-tailed Jaeger simply does not breed and returns to sea. In effect it "skims the cream" from the population cycles of lemmings.

Migrant Long-tailed Jaegers in North America are usually encountered singly. Most individuals migrate over the open ocean; rarely is this species observed near shore. Although some overland migration occurs at high latitudes, in the populated regions of North America inland birds apparently represent vagrants.

Jaegers in general, and the 2 smaller species (Long-tailed and Parasitic [*Stercorarius parasiticus*] jaegers) in particular, are difficult to separate, and much of the literature on these two species and the Pomarine Jaeger (*S. pomarinus*) consists of practical suggestions for identification. The challenges of identification result from the conservative plumages of the genus and from individual, age-related, and polymorphic variation. Many birds seen away from nesting areas are not in the distinctive adult breeding plumage and thus lack characteristic central tail-feathers and other features of this plumage. The problem of separating the 3 jaegers in immature and Basic plumages continues to provide a frustrating challenge.

## DISTINGUISHING CHARACTERISTICS

Smallest member of the subfamily Stercorariine: males about 280 g, females about 310 g.

Adults in Definitive Alternate plumage have grayish upperparts (excluding head), contrasting with blackish remiges and rectrices; head and underparts whitish, with yellowish sides of neck and bold brownish black cap (extending to eye and gape); outermost 2 (occasionally 1–4) primaries have contrasting whitish shafts; and central 2 rectrices are greatly elongated and pointed at tip, extending well beyond rest of tail. Sexes similar, although males somewhat whiter below than females.

In Basic plumage, adults lose their long rectrices and become brown and barred, like subadults (see below). They retain their plain brown underwing-coverts, unlike the barred underwing-coverts of subadults (although some older or dark-morph subadults have plain or nearly plain coverts). This plumage not regularly encountered in North America.

In Juvenal plumage, upperparts brown, with feather tips whitish or buff; brown and white barring on underwing-coverts, flanks, and uppertail- and undertail-coverts; central rectrices only slightly longer than remaining rectrices and with rounded tips. Light morph has pale abdomen, usually barred with brown, and variably whitish, brownish, or grayish head, neck, and breast. Dark morph is similar but has extensively dark underparts. Succeeding immature plumages poorly known, but generally resemble Juvenal and adult Basic plumages. Although dark and light

color morphs occur in Juvenal and immature plumages, adults lack a dark morph like that of other jaegers (see Appearance: molts and plumages, below).

Unmistakable in adult Alternate plumage, with long, flexible central rectrices. Similar in mass to Laughing or Franklin's gull (*Larus atricilla*, *L. pipixcan*). Separated by size alone from larger Pomarine Jaeger, which surpasses Ring-billed Gull (*L. delawarensis*) in mass. Parasitic Jaeger has intermediate mass and overlaps with both congeners. Other features useful for identification of adults in Alternate plumage include absence of breast-band (also true of some adult light-phase Parasitic Jaegers in Alternate plumage), distinct contrast on upper surface between grayish wing-coverts and blackish remiges, absence of white at base of forehead, only 2 (occasionally 3–4) primaries with completely ivory-colored shafts, bluish legs, narrow wings, and buoyant flight like that of a large tern.

Immature and Basic plumages of Long-tailed Jaeger not readily distinguished from corresponding plumages of Parasitic Jaeger. No single character or possibly even combination of characters provides complete separation between these species in immature and adult Basic plumages. Useful distinctions for immature Long-tailed Jaegers include only 2 (occasionally 3–4) primaries with entirely ivory-colored shafts, absence of reddish brown coloration, longer radio-ulnar portion of forelimb (between carpal and humeral joints, with some overlap in immatures), relatively longer distal portion of beak (with some overlap), longer middle toe with claw, and longer tail (even excluding central rectrices; Walter 1962, Melville 1985, Olsen and Larsson 1997). Birds in Juvenal plumage have central rectrices with rounded tips (pointed in Parasitic Jaegers; Løppenthin 1932, Walter 1962) and outer primaries with rounded tips (only in fresh plumage; de Korte 1985, Melville 1985), but they acquire pointed rectrices during first winter while still in brownish, barred plumage (de Korte 1985). Juvenal-plumaged birds also often have contrasting pale band on hindneck and plain gray-brown band across breast (variable in both species). Bluish gray legs (de Korte 1985) and smaller mass (see above) also characteristic. Mensural characters overlap more in immature Long-tailed and Parasitic jaegers than in adults (beak length and width, distal forelimb; Walter 1962), and consequently characteristics of flight, which depend on size, must overlap also.

Upperwing-coverts of adult Basic and immature Long-tailed Jaeger are dark brown. These plumages lack contrast between gray upperwing-coverts and dark remiges like all plumages of Parasitic Jaeger and unlike Alternate plumages of adult Long-tailed Jaeger.

The age at which individuals attain fully adult plumage has never been confirmed with marked birds. Because these birds molt primarily at sea, there are no comprehensive series of specimens. Consequently the progression of immature plumages retains an element

of speculation. Jaegers have probably stimulated more discussion of identification, particularly of immatures, than has any other bird (Walter 1962, Lambert 1981, Melville 1985, Olsen and Jonsson 1989, Kaufman 1990, Olsen 1992, Olsen and Larsson 1997).

## DISTRIBUTION

Holarctic (Fig. 1). Most widespread and numerous jaeger in Arctic. Center of abundance in areas with lemmings (*Lemmus*, *Dicrostonyx*) or voles (*Microtus*, *Clethrionomys*)—all Microtinae. Breeds farther north than either Parasitic Jaeger or Pomarine Jaeger, almost to limit of land in Canada and Greenland, and not so far south as Parasitic Jaeger (see Fig. 1).

### BREEDING RANGE

**The Americas.** In Canada, breeds from w. Hudson Bay (61°N; Godfrey 1986) and Southampton I. (63°N; Sutton 1932, Parker and Ross 1973) northward to n. Ellesmere I. (82°N; Parmelee and MacDonald 1960, Maher 1970). Also widespread throughout coastal plain and major deltas of mainland Mackenzie and Keewatin Districts (Porsild 1943, Hanson et al. 1956, Salter et al. 1980, Martell et al. 1984). In n. Alaska, breeds in passes and valleys of Brooks Range and in foothills extending 50–150 km north. Not a regular breeder on northern coastal plain (no nesting records near Barrow); thus largely allopatric with Pomarine Jaeger (Pitelka et al. 1955, Maher 1974, Pitelka 1974, Sage 1974, Derksen et al. 1981). Nests commonly in w. Alaska southward through Yukon River delta (Brandt 1943, Gabrielson and Lincoln 1959), in Trinity I. group at south end of Kodiak Archipelago, and probably at south end of Kodiak I. itself (R. MacIntosh in litt.). Also breeds in small numbers in mountains of central Alaska (Gabrielson and Lincoln 1959) and sw. Yukon (Price 1969). In foothills of n. Alaska, populations nest in areas where several microtine rodents occur together without marked cycles in density (Maher 1974).

**Outside the Americas.** In Greenland, breeds from 70°N (Scoresby Sound) on eastern coast and from 76°N (Thule) on western coast to at least 83°N on northern coast, but is most abundant between 73 and 78°N in east—the area where lemmings are most abundant (Løppenthin 1943, de Korte 1977, de Korte and Wattel 1988). In ne. Greenland, most nesting occurs below 200 m altitude (highest 350 m) and 0.2–30 km from coast (Manniche 1910, de Korte 1977, 1985). Breeding is sparse in n. Greenland in areas with scant vegetation and few lemmings (Meltofte 1975).

In Siberia, breeds from 70°N along Yenisey River and in w. Taymyr Peninsula and from 72°N in e. Taymyr Peninsula to at least 80°N in Severnaya Zemlya Archipelago (Rogacheva 1992). Also breeds in alpine tundra in Scandinavian mountains above 650 m (Andersson 1976a).

Small populations breed in some arctic areas without lemming populations: Disko Bay, 68°N, w. Greenland (Salomonsen 1950, Kampp 1982); Spitsbergen (Løvenskiold 1964).

### WINTER RANGE

Not completely understood. Large numbers of all ages (shipboard counts >100/d) winter off se. South America (39–45°S), especially near continental shelf break (40–42°S; Wetmore 1926, Murphy 1936, Brown et al. 1975a, Veit 1985), in upwelling region of the Benguela Current off sw. Africa (17–32°S, especially 25–27°S; Lambert 1980, but see Ryan 1989), and farther south along margin of continental shelf of Agulhas Bank and edge of Agulhas Current, where it is widespread north of Subtropical Convergence at 34–44°S and 8–27°E (Ryan 1989). Occasionally reported from coastal waters in South Atlantic (Escalante 1985, Ryan 1986, Vooren and Chiaradia 1989).

Concentrations of wintering birds have so far not been located in Pacific, although regular migrants in North Pacific suggest substantial wintering populations farther south. Regular in small numbers in w. Tasman Sea off se. Australia Oct–Apr (occasionally Sep and May; Barton 1982, Wood 1989, Higgins and Davies 1996), areas where Pomarine and Parasitic jaegers occur in larger numbers. Also regular in Indonesian seas in winter (van Balen 1991) and off coast of Chile (Murphy 1936; 7 specimens, Nov–Dec, American Museum of Natural History [AMNH]). Scarce but regular in winter in central Pacific (King 1970; Panama, Feb, U.S. National Museum [USNM]). Birds off western coast of Middle America in Apr (Jehl 1974) possibly have wintered; edge of continental shelf is not far from coast here. An indication of an undiscovered wintering area was an exceptional "wreck" on New Zealand beaches in Jan–Feb (at least 16 specimens), coinciding with appearance of vagrant seabirds from central Pacific (Melville 1985, Powlesland 1985).

Vagrant in Indian Ocean (Kenya; Urban et al. 1986); fall migrant in small numbers over Elat, Israel (Goodman and Storer 1987). No records from Indian subcontinent (Ali and Ripley 1969, Roberts 1991), and not reported in northern winter in upwelling areas in Arabian Sea (Bailey 1966, Berg et al. 1991) or in w. Indian Ocean (Gill 1967). Not reported in Southern Ocean south of Subtropical Convergence, even in areas frequented by wintering Arctic Terns (*Sterna paradisaea*; Falla 1937, Bierman and Voous 1950).

Reported off S. Carolina in Dec and off Florida in Feb (Wayne 1910); neither season of occurrence confirmed recently. In Gulf Stream off N. Carolina, present until at least 7 Nov (specimen, North Carolina State Museum of Natural Science [NCSM]), with sight records to 20 Dec (Lee 1995), but no reports in midwinter.

#### HISTORICAL CHANGES

No information. No reports that human activities have affected populations either in breeding or in wintering habitats.

#### FOSSIL HISTORY

*Stercorarius schufeldti* recorded from Middle Pleistocene (Fossil Lake, OR; Wetmore 1956). Undescribed species of this genus, including 1 smaller than *S. longicaudus*, occur in Miocene of Europe and North America (Olson 1985). *S. longicaudus* known from several prehistoric sites in Alaska (St. Lawrence, Amaknak, and Kodiak Is.; Brodkorb 1967).

### SYSTEMATICS

#### GEOGRAPHIC VARIATION; SUBSPECIES

Geographic variation in extent of gray on abdomen: Most Scandinavian adults have  $\leq 25\%$  of undersurface gray, most Greenland birds  $\geq 50\%$  (Løppenthin 1932, 1943). No difference between Greenland and North American birds. Nearctic and w. Palearctic populations differ significantly, but range of overlap (25–50% gray below) includes 55% of specimens; no differences in bill or wing length (Manning 1964). Apparently birds in central Siberia (between Lena and Indigirka Rivers and New Siberian Is.) are intermediate in coloration (Løppenthin 1943, Dement'ev and Gladkov 1969, Manning 1964); those from Spitsbergen are on average slightly but not significantly darker than Nearctic birds (Manning 1964). Løppenthin (1943) and Manning (1964) recognized Nearctic populations as separate subspecies, *S. l. pallescens* (accepted by Salomonsen 1950, Dement'ev and Gladkov 1969; rejected by Am. Ornithol. Union 1957). Males have slightly but significantly less gray on abdomen than females (Manning 1964).

#### RELATED SPECIES

Morphological (Schnell 1970), behavioral (Anderson 1971), and molecular (Cohen et al. 1997) comparisons indicate a closer relationship with Parasitic Jaeger than with other Stercorariidae. These 2 species perhaps differentiated during geographic isolation north of continental glaciers during Pleistocene (de Korte and Wattel 1988).

### MIGRATION

#### NATURE OF MIGRATION IN THE SPECIES

Completely migratory, between nesting areas in Arctic and wintering areas in southern temperate oceans (see Distribution, above). Away from vicinity of nesting areas, migrates mostly at sea.

#### TIMING AND ROUTES OF MIGRATION

**Near breeding areas.** Mostly along coasts. In ne. Greenland, migrants arrive in late May and early Jun from south rather than over ice cap from the less ice-bound western coast (de Korte 1984). Migrants begin to fly southward along coasts of Greenland and arctic islands of Canada in late Jul (Parmelee and MacDonald 1960, Hjort 1976, Johnson and Herter 1989). In Siberia, birds migrate along coasts, only exceptionally inland (Rogacheva 1992).

In n. Alaska, migrants fly eastward in spring, westward in fall, along coast or inland parallel to coast (Bee 1958, Maher 1974, Pitelka 1974, Dean et al. 1976). Southbound migrants appear in Beaufort Sea in first half of Aug (Frame 1973); by end of Aug, most have left arctic coast (Johnson and Herter 1989). Northbound migrants occasionally fly through passes in Brooks Range in large numbers (Dean et al. 1976), but birds usually arrive in Brooks Range later than on northern coast and might come from north rather than from south (Irving 1960). The same might apply to birds arriving in Churchill and elsewhere in Manitoba in Jun (Jehl and Smith 1970, Taylor 1993). Birds remain near Churchill in years when rodents are abundant, although nesting is not known there (Jehl and Smith 1970), but they usually disappear by 10 Jul (J. Jehl pers. comm.). Possibly nonbreeding birds in search of rodents move southward into Hudson Bay in Jun and then return northward to join the main migration routes along arctic coasts. Migration across continent is also a possibility (see below).

**South of breeding range.** Migrates mostly far offshore, although strong onshore winds can bring migrants closer to land (Ireland and Scotland [Davenport 1992]; Cape Hatteras, NC [Buckley 1973]). Thousands flew southward along beach at Cape San Antonio, Argentina, 4–7 Nov 1920, during an onshore storm (Wetmore 1926).

In North Atlantic during northward migration, large numbers observed in midocean in late May (Wynne-Edwards 1935 and in Bannerman 1963). In Bermuda, common spring migrant from early Mar to early Jun; most in first half of May (Amos 1991). During southward migration, adults appear in midocean in late Jul and Aug (earliest record 20 Jun; Rankin and Duffey 1948). In Aug this species occurs in midocean in same areas used by migrating Arctic Terns (Wiley 1957). Nearly complete absence of Aug–Sep records for Bermuda (Amos 1991) suggests that southbound routes in North Atlantic differ considerably from northbound routes.

Off ne. U.S., migrates mostly beyond continental shelf (Brown et al. 1975b, Rowlett 1980, Powers 1983). Off N. Carolina, where margin of continental shelf is close to shore, birds in immature plumage occur from Apr to mid-Dec, peaking in late May and late Aug–early Oct; a few adults also appear at these times. Most birds occur over outer continental shelf and

western edge of Gulf Stream (Lee 1995, B. Patteson, N. Brinkley, M. Tove, and T. Hass pers. comm.).

Off sw. Africa (19–20°S), all ages appear by last week of Sep; by mid-Nov, large numbers have arrived (Lambert 1980, Ryan 1989). Most individuals probably leave sw. African waters in Apr; adults and immatures normally absent Jun–early Sep (Lambert 1980).

In North Pacific, migrants likewise far offshore. West of Vancouver I., migrants mostly beyond continental shelf in Aug; few in Sep and May (Morgan et al. 1991). Off California, migrants also mostly beyond continental shelf, mid-Jul–mid-Oct and mid-Apr–early Jun, often coinciding with migration of Arctic Terns (Jehl 1973b, Stallcup 1990). Migrants pass Japan from late Apr through May (Austin and Kuroda 1953).

**Overland migration.** Inland records have suggested migration over interior of North America (Bent 1921, Murphy 1936, Jehl 1974). Because of difficulties identifying this species in immature plumages, it is unclear how frequently it occurs inland; even specimens have been misidentified as Parasitic Jaeger (Lee 1989, Stevenson and Anderson 1994). Nevertheless, the least numerous jaeger inland. Unlike Parasitic Jaeger, rarely reported on Great Lakes (Mlodinow 1984, Kelley 1989, Sherony and Brock 1997) or in Gulf of Mexico (Williams 1965). Small numbers in interior of w. North America, including a few adults in Definitive Alternate plumage, suggest some overland migration, perhaps to and from western coast of Mexico (Jehl 1974, Taylor 1993). In w. Palearctic, also migrates overland in small numbers (Goodman and Storer 1987, Boano 1988). Long migratory movements without feeding appear possible for this species (see Migratory behavior, below), and it takes shortcuts across land regularly within breeding range (Scandinavia [Bell 1965]; Bylot I., Northwest Territories [NWT; Drury 1960]). Nevertheless, inland occurrences remain exceptional, and a case for substantial migration across breadth of northern continents lacks clear support.

#### MIGRATORY BEHAVIOR

Migrants in Arctic often travel in flocks of as many as 20–100 (Manniche 1910, Pedersen 1930, Drury 1960, Parmelee and MacDonald 1960, Jehl and Smith 1970, Maher 1974, Taylor 1974, Hjort 1976). Farther south, flocks more often include 15–25 (Lambert 1980, Davenport 1992), although larger concentrations consisting of many small groups can occur in limited areas (Wetmore 1926, Wynne-Edwards 1935, Davenport 1992). Despite these reports of flocks, migrants at sea often travel singly (Wynne-Edwards 1935, Kuroda 1955, Austin and Kuroda 1953, Wiley 1957). Most migrants near coasts of e. and w. North America are singles, although sometimes several are seen in same day.

Migrants fly as high as 250 m above sea in calm weather (Rankin and Duffey 1948), but usually only

8–20 m. When flying into headwind, stays close to surface (Stallcup 1990). Flight is usually in straight course with steady flapping, but dynamic soaring with banking occurs in strong winds (Olsen and Jonsson 1989). An inland record from N. Carolina includes 1 killed at a TV tower at night (Lee 1989). Some reports suggest prolonged migratory movements without feeding (Wynne-Edwards 1935, Dean et al. 1976, Davenport 1992).

#### CONTROL AND PHYSIOLOGY

No information.

### HABITAT

#### BREEDING RANGE

Arctic and alpine tundra, often far from sea. In ne. Greenland (71°N), nests on tundra dominated by low shrubs, often in areas with scattered ponds and marshes. Dates for 50% snowmelt range from 10 to 30 Jun, often earlier at locations farther inland as result of somewhat higher temperatures and less snowfall (de Korte 1977). In n. Alaska (68–71°N), prefers tussock-heath tundra dominated by cotton sedge (*Eriophorum vaginatum*; Maher 1974). In Canada on Victoria I. (NWT), prefers drier tundra with scant vegetation, such as small ridges, knolls, or exposed areas near marshy tundra (Parmelee et al. 1967). In Perry River delta (67°N), more common in flat coastal tundra than farther inland (Hanson et al. 1956). On n. Ellesmere I. (82°N), nests mostly in marshy places with mountain-avens (*Dryas integrifolia*) near lakes, but also in barren areas with scant vegetation 50–250 m above sea level (Parmelee and MacDonald 1960, Maher 1970).

In central Siberia, inhabits primarily typical tundra zone (dwarf shrubs and sedges, often in tussocks) but extends to polar desert (scant vegetation and much bare ground; Rogacheva 1992); prefers dry tundra near coasts (Dement'ev and Gladkov 1969). On Chukchi Peninsula and Wrangel I., often occurs inland, usually not near rivers, while Pomarine Jaeger occurs primarily near coast, as in Alaska (Portenko 1992). Nests sparsely in larch (*Larix*) forests south of tundra in Siberia (Thayer and Bangs in Bent 1921, Uspenskii 1984, Portenko 1992).

Also nests in alpine tundra in mountains of Scandinavia on exposed ridges with shrubs and sedges (Andersson 1976a). In mountains of sw. Yukon Territory, occupies alpine tundra dominated by shrubs and sedges (Price 1969). Alpine habitats in s. Alaska are presumably similar.

#### MARINE RANGE

Pelagic in nonbreeding season, rarely close to land. As a consequence, little information is available. In upwelling region of Benguela Current off sw. Africa,

follows ships no closer to coast than 2–4 km; usually encountered no closer than 35 km from coast (Lambert 1980), in contrast to Parasitic and Pomarine jaegers, both of which closely approach coast. Off se. Australia, mostly over continental slope, rather than deep ocean or continental shelf (Higgins and Davies 1996). Similarly, off Argentina, most occur over continental shelf break (Veit 1985). Off N. Carolina, usually along outer edge of continental shelf and inner edge of Gulf Stream, where the brown alga *Sargassum* accumulates at oceanic fronts and migrating terns and shearwaters are likely to occur.

## FOOD HABITS

### FEEDING

**Main foods taken.** Successful reproduction usually contingent on availability of lemmings or voles. In high Arctic, reproduction depends mostly on a single species, the collared lemming (*Dicrostonyx groenlandicus*; Løppenthin 1943, Maher 1970, de Korte and Wattel 1988). In low Arctic, other lemmings and voles are also important (Maher 1974, Andersson 1976a, 1981, Portenko 1992). These rodent populations often vary annually by >2 orders of magnitude, with peaks at intervals of 4–5 yr and a year of intermediate rodent abundance often preceding or following a peak (Maher 1974, Andersson 1976a, de Korte and Wattel 1988, Stenseth and Ims 1993). Peaks are sometimes synchronized on a regional scale (100–300 km), but not always (Myrberget 1973, Stenseth and Ims 1993). In Arctic, also takes wide variety of juvenile birds, arthropods, and berries (see Diet, below). In areas with no rodents, depends on kleptoparasitism or scavenging (Kampp 1982).

Little known about diet at sea. Away from breeding areas, takes small fish, invertebrates, and offal, primarily from surface of water (Bent 1921, Manniche 1910). Occasionally feeds on carrion (Witherby et al. 1944); attracted to offal used as chum and to ships' waste (D. Lee pers. obs.). At sea, pursues terns, small gulls, and other birds, but less frequently than other jaegers or skuas (*Catharacta* spp.) do.

**Microhabitat for foraging.** On Bathurst I., NWT, hunts lemmings mostly on tundra barrens, but also in hummock tundra, snowmelt areas (early summer only), and wet meadows (mostly second half of summer); hunts arthropods in wet meadows and on barrens (second half of summer; Taylor 1974). In ne. Greenland, forages along edge of landfast ice in May and early Jun, in leads in fjord ice in Jun, and by wading in intertidal pools in Jul (de Korte and Wattel 1988). In w. Greenland, where lemmings are absent, birds nest only along coast and feed mostly at sea (Salomonsen 1950, Kampp 1982).

During summer, nonbreeders congregate around edges of ponds or swamps where arthropods are

numerous (Taylor 1974, de Korte and Wattel 1988). In Canada, feeds on small fish and larval midges (Chironomidae) in tundra lakes (Hanson et al. 1956, Taylor 1974). Nonbreeders often move to coast to forage along shore and on adjacent tundra (Parmelee and MacDonald 1960, Maher 1974), often near river mouths or along leads in ice (Drury 1960).

**Food capture and consumption.** Collared lemmings become available as snow disappears in early Jun to reveal their winter nests and before they occupy summer burrows (de Korte and Wattel 1988). Long-tailed Jaeger hunts these lemmings by hovering or poising in a headwind at height of 1–10 m (usually about 4 m) above tundra, like a kestrel (*Falco* spp.) and unlike other jaegers, and by watching from perches on small rises or frost mounds (Dement'ev and Gladkov 1969, Maher 1974, Taylor 1974, de Korte and Wattel 1988); also by waiting beside lemming warrens under mats of vegetation (Taylor 1974). Some individuals fly a circuit between perches 50 m or more apart (Taylor 1974). Having detected prey, often pursues it on foot and pecks it until it is dead; never uses feet to capture prey (Andersson 1971). Norway lemming (*Lemmus lemmus*) is not easy for Long-tailed Jaeger to subdue; it has large rump gland that is probably both distasteful and emetic. When given a choice, Long-tailed Jaeger prefers voles over lemmings (Andersson 1976c, Taitt 1993). Unlike Pomarine Jaeger, Long-tailed never digs for lemmings in burrows; unlike Parasitic Jaeger in Alaska, adult Long-tailed with young normally hunts alone (Maher 1974). In n. Sweden (68°N), hunts mostly during hours 02:00–08:00 and 16:00–22:00, times when Rough-legged Hawk (*Buteo lagopus*) and Short-eared Owl (*Asio flammeus*) are less active (Andersson 1971).

During breeding, sexes differ markedly in foraging. Males in ne. Greenland forage in outer parts of their territories or sometimes at sea; females always forage within a few hundred meters of their young (de Korte and Wattel 1988). Males in Scandinavia and Canada capture more lemmings, and females more arthropods; males feed lemmings to their mates (Andersson 1971, Taylor 1974). On Bathurst I., NWT, pairs spend little time hunting before eggs are laid. Thereafter males account for 92% of time spent hunting lemmings and evidently provide a substantial amount of food for their mates (2 pairs, 161 h observation; Taylor 1974). Females spend more than twice as much time as males incubating (see Breeding: incubation, below).

On Bathurst I., males average 1 kill/102 min (range 1 kill/3–319 min) while hunting for lemmings ( $n = 12$  kills). Successful kills occurred in 27% of strikes (range 0–100% at different times of season,  $n = 45$  strikes). These rates suggest that a male kills about 3.5 lemmings/d on average (Taylor 1974).

Eats lemmings either whole (in <3 min) or after eviscerating them (up to 30 min; Taylor 1974, de Korte

and Wattel 1988). Large lemmings are difficult to swallow whole (Maher 1970, 1974). Eviscerates prey by grabbing belly with beak and shaking until skin rips; never holds prey with feet (Andersson 1971, Taylor 1974). Single birds usually eat only viscera and leave remainder; mated pairs often cooperate to dismember prey (Andersson 1971, Maher 1974, Taylor 1974). Pairs can thus consume a large lemming more completely than a single bird can (Andersson 1971).

Less adept at capturing adult birds than Parasitic Jaeger is (Maher 1974); occasionally pursues adult passerines, but no successful chase yet observed (Løppenthin 1943, Drury 1960, Maher 1974, Kampp 1982); does not usually attack adult shorebirds (Parmelee and MacDonald 1960). Pursues fledgling passerines, such as Snow Bunting (*Plectrophenax nivalis*), close to the ground, forcing them to land and killing them; 2–3 wk after fledging, juvenile buntings become too agile to catch (de Korte and Wattel 1988). Kills young sandpipers in flight (Childs 1969). Sometimes groups of immatures in coastal areas chase small shorebirds (Kampp 1982). Captures arthropods by means of quick snaps, dashes, or jumps while walking or running among tundra tussocks (Manniche 1910, Maher 1970, 1974, Taylor 1974, Hansen 1984, de Korte and Wattel 1988). On Bathurst I., NWT, birds hunting arthropods average 8 pecks/min (range 3–20, depending on habitat and time of season,  $n = 2$  pairs, 160 h of observation; Taylor 1974). This species also takes eggs of waterfowl (Taylor 1974) and follows humans searching for waterfowl nests (Strang 1980). Takes berries throughout breeding season: previous year's berries from arrival until Jul, new berries from late Jun (a month before ripening) until departure (de Korte and Wattel 1988).

Over coastal waters in summer, flies slowly or hovers above water, dips to peck at floating debris, occasionally plunges underwater from a height (Drury 1960, Løppenthin 1943). Away from breeding areas, flies like tern above water; often hovers, swoops to peck at floating debris (Bell 1965, Veit 1985). In coastal areas, sometimes up-ends while swimming or wades in pools, alights to take invertebrates from fields or drift on a beach, or hawks for insects high in air (Wetmore 1926, Løppenthin 1943, Bell 1965, van Beusekom 1985). On occasion, chases migrating passerines at sea (Sage 1974; see Diet, below). Once observed catching 10-cm flying fish (Exocoetidae; T. Hass pers. comm.). On fishing grounds off sw. Africa, frequently kleptoparasitizes other birds, such as terns and small gulls (see below), but elsewhere in South Atlantic and off Australia, kleptoparasitism occurs infrequently, much less than by Parasitic and Pomarine jaegers (Ryan 1989, Wood 1989).

**Kleptoparasitism.** Exceptional during breeding season; unlike Parasitic Jaeger, breeding Long-tailed Jaeger usually ignores terns and small gulls (Løppenthin 1943). Birds of unknown breeding status in

summer occasionally pursue Arctic Terns, but successful in forcing terns to relinquish food only when  $\geq 2$  jaegers join pursuit (Drury 1960, de Korte and Wattel 1988). Once observed to force immature Glaucous Gull (*Larus hyperboreus*) to disgorge food (Drury 1960). Targets in n. Russia include Black-legged Kittiwake (*Rissa tridactyla*), Sabine's Gull (*Xema sabini*), and Arctic Tern (Dement'ev and Gladkov 1969). Kleptoparasitism is the most important source of food for birds breeding in Disko Bay, w. Greenland, where rodents are absent (Kampp 1982). Here groups of nonbreeding birds pursue Arctic Terns overland near their colonies (28% success,  $n = 47$  chases); territorial birds, in contrast, chase terns at sea (45% success,  $n = 20$  chases; Kampp 1982). Why this species, rather than Parasitic Jaeger, parasitizes terns in Disko Bay, is unclear.

Storm-driven migrants on coast of Argentina chased Snowy-crowned Terns (*Sterna trudeaui*) until the terns dropped fish, which the jaegers retrieved (Wetmore 1926). Immatures in nw. Pacific occasionally chase Red-legged Kittiwakes (*Rissa brevirostris*) and Slender-billed Shearwaters (*Puffinus tenuirostris*; Kuroda 1955). Off se. Australia, targets include Silver Gull (*Larus novaehollandiae*) and Great-winged Petrel (*Pterodroma macroptera*; Wood 1989, Higgins and Davies 1996); off sw. Africa, Arctic and Common (*Sterna hirundo*) terns, Sabine's Gull, prions (*Pachyptila* spp.), and even albatrosses (*Diomedea* spp.) and Cape Gannet (*Sula capensis*; Lambert 1980, Ryan 1989). Also chase each other until one regurgitates food (Kuroda 1955, Lambert 1980). In Bermuda, migrants regularly chase breeding White-tailed Tropicbirds (*Phaethon lepturus*) and Common Terns (D. Wingate pers. comm.).

Off N. Carolina, migrants often associate with mixed feeding flocks of seabirds (D. Lee pers. obs.), but chasing of other species is observed infrequently. Targets include Audubon's (*Puffinus lherminieri*) and Cory's (*P. diomedea*) shearwaters, Wilson's Storm-Petrel (*Oceanites oceanicus*; see also Brady 1994), Bridled Tern (*Sterna anaethetus*), and Common Tern. On one occasion, 2 Bridled Terns being harassed by a juvenile Long-tailed Jaeger turned to chase the jaeger (T. Hass pers. comm.).

#### DIET

**Major food items.** Nesting birds rely primarily on microtine rodents, when available, for both themselves and their young, but they take a great variety of other food when necessary. In ne. Greenland, diet includes collared lemming, fledgling passerines, berries, caterpillars, and adult and larval crane flies (Tipulidae); for populations nesting near coast, also fish and zooplankton (Manniche 1910, Løppenthin 1932, 1943, Salomonsen 1950, de Korte and Wattel 1988). On n. Ellesmere I., NWT, food includes collared lemming, Snow Bunting, shorebirds, insects, and in coastal areas, fish (Parmelee and MacDonald 1960, Maher

1970); on Bathurst I., NWT, collared lemming (Taylor 1974); in foothills of n. Alaska, a diversity of microtine rodents (collared lemming, brown lemming [*Lemmus trimucronatus*], root vole [*Microtus oeconomus*], and tundra redback vole [*Clethrionomys rutilus*]; Maher 1974). In n. Sweden, microtines again predominate (primarily gray-sided vole [*Clethrionomys rufocanus*] and Norway lemming), except when rodent populations are low (Andersson 1976a).

When lemmings are scarce, these jaegers subsist mainly on insects, immature birds, and fish (Manning et al. 1956, Parmelee and MacDonald 1960, Andersson 1976a). Smaller size than that of other jaegers permits more efficient exploitation of smaller items like insects (Maher 1974, de Korte and Wattel 1988). Insects consumed include a wide variety of flies (Diptera, mostly crane fly adults and eggs), beetles (Coleoptera), ants (Hymenoptera), earwigs (Dermaptera), mayflies (Ephemeroptera), and moths (Lepidoptera, mostly caterpillars; Witherby et al. 1944, Portenko 1992). Fish are the predominant prey on Wrangel I., Russia, in early Jun after ice thaws (Portenko 1992). Avian prey include chicks and juveniles of King Eider (*Somateria spectabilis*), Black-bellied Plover (*Pluvialis squatarola*), Red Knot (*Calidris canutus*), Sanderling (*Calidris alba*), Long-tailed Jaeger (Taylor 1974), Ruddy Turnstone (*Arenaria interpres*; Savile and Oliver 1964), and Lesser Yellowlegs (*Tringa flavipes*; Dekker 1974). Most passerine prey are juvenile Lapland Longspurs (*Calcarius lapponicus*; Maher 1974) and Snow Buntings (Taylor 1974, de Korte and Wattel 1988).

Nonbreeders in Arctic have very different diet from that of breeding birds, including large proportions of insects and carrion (Manniche 1910, Swartz 1966, Maher 1974). At sea away from breeding areas, diet little known, but includes fish, crustaceans, and polychaete worms (Witherby et al. 1944, Løvenskiold 1964).

**Quantitative analysis.** Diet differs markedly in years of high and low rodent populations, but no study of diet has included a complete cycle of rodent populations in one area. Breeding birds apparently take rodents preferentially, and other food only when rodents cannot be caught.

In comparison with Parasitic Jaeger, breeding Long-tailed Jaegers rely more on microtine rodents and include higher proportions of insects and lower proportions of adult birds in diet (Maher 1974). Reliance on rodents for breeding resembles that of Pomarine Jaeger, except that small microtines, not just large lemmings, suffice (Maher 1974).

In ne. Greenland during 3 breeding seasons with low to moderate populations of lemmings, consumed biomass included 72% terrestrial vertebrates (mostly collared lemmings and fledgling Snow Buntings), 10% berries, 10% marine animals (gadid fish [*Gadidae*] and amphipods), and 8% larval and adult arthropods (mostly caterpillars and larval and adult crane flies;  $n = 150$  stomachs; de Korte and Wattel 1988).

On n. Ellesmere I., NWT, 90% of pellets from breeding adults included collared lemming, 30% insects (mostly crane flies and caterpillars), and 18% birds (80% Snow Buntings, remainder mostly shorebirds; 83% of buntings and 93% of shorebirds are juveniles;  $n = 242$  pellets; Maher 1970). On Bathurst I., NWT, >99% of pellets from breeding adults included lemmings, 12–18% arthropods, 19% vegetation, <1% birds; 76–83% of pellets consisted entirely of lemming ( $n = 1,005$  pellets). Of pellets from chicks, 49% consisted entirely of lemming; 87% included lemming, 48% arthropods (perhaps indicating that chicks take some arthropods on their own), 15% birds ( $n = 47$  pellets). Arthropods were mostly midges, <10% larval moths (Geometridae). Two stomachs of nonbreeding adults contained only large adult midges (Taylor 1974).

In foothills of n. Alaska, vertebrate prey in pellets included microtine rodents (46%), passerines (44%, primarily Lapland Longspurs), shorebirds (6%, nearly all juveniles), ptarmigan (*Lagopus* spp.) adults and young (3%); pellets also contained insects (21%), berries (20%), and remains of eggs (2%,  $n = 524$  food items in >300 pellets). Of 24 remains of shorebirds, only 1 was adult; the primary passerine prey was Lapland Longspur. In an area with high numbers of root voles, root vole constituted 90% of prey in pellets ( $n = 431$  food items in >285 pellets) and 88–95% of prey delivered to young ( $n = 3$  nests with 53–151 pellets each; Maher 1974).

Most detailed comparison of breeders' diets in years with different abundances of rodents comes from n. Sweden (Andersson 1976a). In a year of high rodent populations, rodents appeared in 99% of 365 pellets (including gray-sided vole in 46%, Norway lemming in 20%, and unidentified rodents in 32%) juvenile birds appeared in 4%, insects in 4%, and berries in 4% of pellets ( $n = 365$  pellets). In a year of moderate rodent populations, rodents appeared in 63% of pellets, juvenile birds in 29%, insects in 36%, and berries in 42% ( $n = 72$  pellets). By mass, rodents constituted approximately 66% and juvenile birds 29% of vertebrate prey in the latter year; in the former year, rodents constituted >96% by mass of vertebrate prey.

Transients in ne. Greenland (mostly immatures) consumed about 60% marine organisms (by mass) and only 20% terrestrial vertebrates: 19 stomachs contained gadid fish, 2 only amphipods ( $n = 34$  stomachs; de Korte and Wattel 1988). Transients collected in n. Alaska had eaten insects (62% of stomachs examined), carrion (22%), microtines (22%), birds (10%), and rarely eggs, fish, and marine invertebrates ( $n = 40$  stomachs; Maher 1974).

Migrants off N. Carolina ( $n = 15$  stomachs) contained unidentified fish (10 stomachs); file fish (Balistidae) (1); insects, including beetles, butterflies and moths, leafhoppers (Homoptera), crickets (*Gryllus*), and unidentified (4); shell fragments of pelagic snails (*Janthina*; 4, first report of predation on this



genus; see Lalli and Gilmer 1989); squid beaks (1); Acadian Flycatcher (*Empidonax virescens*; 1); unidentified pelagic egg mass (1); pieces of *Sargassum* (3); unidentified organic matter (1); 2-mm piece of plastic (1)—in total 3–22 g of food. Some of these items indicate that *Sargassum* patches are important foraging sites in tropical and subtropical waters. Presence of migrant passerine indicates opportunistic feeding and perhaps a benefit of migrating earlier than other jaegers. Presence of insects suggests terrestrial foraging and perhaps direct flights from tundra to sea. U.S. Migrants also are attracted to chum and slicks produced by discharge from ships (Lee 1987, D. Lee pers. obs.).

#### NUTRITION AND ENERGETICS

Arrives on breeding grounds with large reserves of subcutaneous fat (Taylor 1974, de Korte 1985). In years of low lemming numbers, individuals do not lay eggs and nevertheless lose more mass than in years when more lemmings are available and eggs are laid (de Korte 1985). On Bathurst I., NWT, a pair consumes on average 3.5 lemmings/d (up to 7.8/d late in season when diet includes more young lemmings) or about 260 lemmings total between 15 Jun and 15 Aug ( $n = 2$  pairs). Including the small fraction of arthropods, total biomass consumed by a pair is 150–180 g/d, about 25% of a pair's total mass, equivalent to about 1.0 kg prey/10 km<sup>2</sup>/d. In years of high lemming densities, Long-tailed Jaeger took about 35–40% of total biomass of prey taken by all avian predators (mostly Long-tailed and Pomarine jaegers and Snowy Owl [*Nyctea scandiaca*]) and almost 100% in years of moderate lemming densities (Taylor 1974).

#### METABOLISM AND TEMPERATURE REGULATION

No information.

#### DRINKING, PELLET-CASTING, AND DEFECATION

Pellets with remains of prey accumulate around roosting areas (small mounds on tundra) and nests (Maher 1970, 1974, Anderson 1971, Taylor 1974).

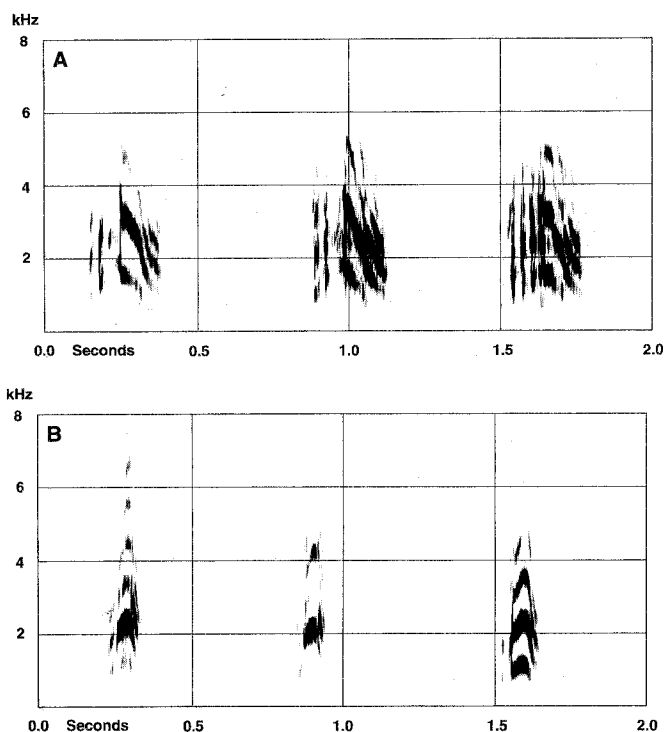
## SOUNDS

#### VOCALIZATIONS

*Development.* No information.

*Vocal repertoire.* Three basic vocalizations: *kreck*, *kliu*, and *kuep* (Andersson 1971).

*Kreck* and *kliu* (*kreeah*, *kreeah* and *kree*, *kree*; Witherby et al. 1944; see Fig. 2) differ from mewing calls of Parasitic Jaeger. In interactions with other species, these 2 calls highly specific for mammalian and avian intruders, respectively, regardless of intruder's location or activity. Gulls often have 2 alarm calls with some acoustic similarities to these 2 calls, but without



**Figure 2.** Vocalizations of the Long-tailed Jaeger. A. Calls resembling *kreck* of Andersson (1971). B. Calls resembling *kuep* (left and right) and *kliu* (center) of Andersson (1971). From R. T. Peterson's Western Bird Guide, recorded in Sweden, Northwest Territories, Yukon Territory, and Alaska. Prepared by the staff of the Borror Laboratory of Bioacoustics, The Ohio State University, using a Kay Elemetrics DSP 5500 Sona-Graph™ (with an effective frequency resolution of 600 Hz and a 100 pt. transform size).

the specificity for type of intruder (Andersson 1971, Kampp 1982).

Long Call, in interactions with conspecifics, is composed of *kreck* and modified *kliu* notes. *Kreck* notes at beginning and end and downward inflection of longer *kliu*-like notes in middle are characteristic of the species (Andersson 1971). Long Call described as shrill *kri*, *kri-kri-kri* followed by rattling mew *kr-r-r-r*, *kr-r-r-r* (Witherby et al. 1944) or *krrrrreeeeuuu* (Drury 1960). Contagious among neighboring birds (Drury 1960).

Young utter a variant of *kliu* to call their parents. This call changes to shrill, vibrant note when parent alights nearby (Andersson 1971).

*Kuep* (*weep* [Drury 1960, Kampp 1982]; *queek* or *yowk* [Witherby et al. 1944]) is given by female (occasionally male) when flying over an area where young hide in low vegetation in order to make contact with young, by female when flying to meet her mate bringing food, and by either sex sometimes in conjunction with Slow Wing-Beat Display during territorial encounters (see Behavior: agonistic behavior, below), especially near boundaries. Other jaegers and skuas apparently lack a similar call (Andersson 1971).

## NONVOCAL SOUNDS

No information.

**BEHAVIOR**

## LOCOMOTION

*Flight.* Of the 3 jaegers, Long-tailed is the most agile in flight (Andersson 1971). Frequently hovers like a kestrel (see Food habits: feeding, above). Few observers of this species hunting in the Arctic have failed to note its extreme grace and agility. Nevertheless, in direct flight, Parasitic Jaeger can outfly Long-tailed (D. Lee pers. obs.).

*Swimming and diving.* See Food habits: feeding, above.

## SELF-MAINTENANCE

After feeding on rodents, often visits nearby pond to bathe, by dipping beak in water and shaking it back and forth, sideways (Andersson 1971).

## AGONISTIC BEHAVIOR

Greater dependence on aerial displays, in comparison to other jaegers, is associated with this species' smaller size and larger territories (Andersson 1971).

Most territorial conflicts include Gliding with Long Call (see Sounds: vocalizations, above): Wings bowed downward below horizontal so that the white shafts in outer primaries become conspicuous. Beak is wide open during the call; trajectory of glide is slightly upward. This display is directed toward conspecific intruders approaching nest or parallel to intruders leaving or crossing territory at distance from nest. Attacks against intruders accompany about 50% of occurrences. Disputes near boundary sometimes involve both members of each pair, all performing Gliding with Long Call. This display given more often in central parts of the territory, Slow Wing-Beat Display (see below) more often near boundaries (Andersson 1971).

Territorial disputes, especially early in breeding season, also include flying in Slow Wing-Beat Display, with wings raised more and lowered less than in normal flight, at a rate slower than normal ( $2.1 \text{ beats/s} \pm 0.16 \text{ SD}$ , in contrast to  $3.4 \pm 0.13$ ), usually accompanied by *kuup* calls synchronized with (or slower than) wing-beats. Attacks accompany about 30% of occurrences of this display (Andersson 1971); this display also often elicits aggressive responses from rivals (Kampp 1982). Before taking flight in this display, perched birds sometimes raise wings and then beat them strongly 2-3 times (Drury 1960), perhaps to reveal white flashes in the wings.

Territorial disputes infrequently include flying in Rapid Wing-Beat Display (observed 10 times in 2 seasons): Somewhat shallower wing-beats than normal, at a rate much faster than normal ( $6.0$

$\text{beats/s} \pm 0.41$ ), and accompanied occasionally by short *kreck* or *kliu* calls (Andersson 1971).

Upright Display occurs frequently when confronting intruder on the ground near nest: Neck stretched upward and slightly forward, beak directed horizontally or slightly downward, and carpal joints lifted slightly (Andersson 1971). According to Drury (1960), nonterritorial individuals that perform this display wag head side to side, particularly when they land near another bird, but others have not observed this action (M. Andersson pers. comm.).

Oblique Posture accompanies Long Call: Breast lifted so that tail angles downward to the ground, neck-feathers erected to produce thicker appearance during call, and sometimes carpal joints raised. Gives this display in territorial disputes and in disputes over food; can lead to direct attack with beak (Andersson 1971). Often directed at conspecifics flying over a territorial bird on the ground (Kampp 1982). In this posture, white breast is conspicuous; males have whiter breasts on average than females (see Appearance: molts and plumages, below), as appropriate for their more active role in territorial defense (Andersson 1971).

Tail-Up Posture is similar to Hunched Posture (see Sexual behavior, below): Tail nearly vertical, and beak points downward; accompanied by repeated *kuup* or *weep* calls. Used by territorial birds toward swooping rivals, in an area where intrusions by immatures occurred frequently (Kampp 1982).

Upright Posture is similar to but less complex than comparable displays in gulls (Aggressive Upright; Tinbergen 1959), nearly identical to this display in Parasitic Jaeger, although beak usually held a little higher in Long-tailed. Variants of Upright (Intimidate or Anxiety Upright; Tinbergen 1959) and displays like Forward Posture, Oblique Posture, Choking, Facing Away, Head-Tossing, all of which occur in various gulls (Moynihan 1959, Tinbergen 1959), are not normally performed by territorial birds of this species (Andersson 1971). Nevertheless Tail-Up (Hunched) Posture suggests comparison with Choking (Kampp 1982); head-wagging reported in nonterritorial birds suggests Facing Away in some gulls (Drury 1960). Ground-pecking or grass-pulling is rare. Rarely raises wings with Long Call, unlike Great Skua (*Catharacta skua*; Andersson 1971), but in modified form wing-raising often precedes Slow Wing-Beat Display (Drury 1960). Gliding with Long Call resembles displays in other jaegers and skuas, except deep bowing of wings is characteristic of this species (Andersson 1971, Furness 1987). Slow Wing-Beat and Rapid Wing-Beat displays are absent in gulls, skuas, and other jaegers, but former resembles V-flying display of some terns (Andersson 1971).

## SPACING

*Intraspecific territoriality.* Breeding pairs defend large, all-purpose territories from which they exclude

most conspecifics (Andersson 1971, Taylor 1974). In ne. Greenland, distances between nests of neighboring pairs in a year with plentiful rodents averaged 990 m (range 640–1,440,  $n = 7$ ; de Korte 1977); in a year of intermediate rodent densities, 1,500 m (range 900–2,300,  $n = 5$ ; Hansen 1984). On n. Ellesmere I., NWT, in a year of high rodent densities, nests averaged 1,030 m apart (range 320–1,520,  $n = 12$ ; nests are not always near center of territory; Maher 1970). In foothills of n. Alaska, with moderate rodent densities, distances between nests averaged 410–510 m (range 220–790) in 3 yr ( $n = 7$ –12; Maher 1974). Often hunts over an area larger than territory, so hunting areas of neighboring pairs usually overlap. In n. Sweden, hunts as far as 2.7 km from nest, but usually within 600–700 m (Andersson 1971). In n. Alaska, pairs defend their entire territories briefly early in season; once nesting begins, pairs defend only core areas 400–600 m in diameter, but they hunt over wider areas, including peripheral areas of neighbors; territorial birds do not patrol boundaries (Maher 1974). In n. Sweden, 4 territories were 0.8–1.0 km<sup>2</sup> in size (Andersson 1971). Territorial interactions more frequent when pairs nest closer together (1.3 interactions/h when 300 m apart [60 h of observation at 2 nests] compared with 0.2 interactions/h when 1,300 m apart [12 h of observation at 1 nest]; Andersson 1971). Territory sizes in general lie near the value predicted by Schoener (1968) from a regression of territory size on body mass for avian predators (Maher 1974).

In ne. Greenland, nonbreeding birds and those with failed nests join flocks foraging near their territories. Separation from mate and flocking can begin within 1 d of nest failure, but more often begin several weeks later. In years with plentiful lemmings, birds with failed nests stay on their territories until mid-Aug; in other years, such birds often return to their territories for brief visits until mid-Aug (Pedersen 1930, Taylor 1974, de Korte 1984). In n. Alaska, where breeding areas are farther inland, nonbreeding birds and failed breeders often move to coast (Maher 1974). In years of low lemming density, some birds establish territories early in breeding season, but most remain in flocks of 10–15 roaming over tundra, coast, and leads in ice (Drury 1960).

Territorial advertisement includes flying slowly around territory with deep wing-beats (presumably Slow Wing-Beat Display [see above]; Drury 1960, Kampp 1982) and conspicuously perching on small mounds (Sutton 1932, Drury 1960, Kampp 1982). Interactions between rivals often include slow flying parallel to each other. Chases begin and end abruptly, often followed by further parallel flying (Drury 1960). Territorial chases are extremely acrobatic, often with  $\geq 2$  birds in powerful flight rising to  $>100$  m and then diving steeply with abrupt turns, so fast that the rush of air is audible 50 m away (Andersson 1971). Actual fighting is rare (in only 1 of 150 contests did birds

grapple with beaks in midair; Andersson 1971). Territorial displays most frequent in midmorning and midafternoon, 09:00–11:00 and 14:00–17:00 (Drury 1960). Territorial defense thus suggests assessment by rivals, with occasional escalation, as in many other animals.

Territorial defenders often approach conspecific intruders on the ground by walking, running, or flying between performances of Upright Posture or Oblique Posture with Long Call (see Agonistic behavior, above); intruders usually walk or fly away. If an intruder stays in one place, defending bird usually remains about 1 m away and displays at intervals until intruder leaves (Andersson 1971, Kampp 1982).

Conspecific intruders landing within 100 m of a nest are invariably approached and chased; intruders flying within 200 m of nest are usually chased (88% of 75 cases). Male reacts earlier and pursues longer than female when both are present (Andersson 1971).

**Interspecific territoriality.** Where different species of jaeger nest in same area, each pair defends its territory against all other jaegers, regardless of species. In n. Alaska, distances between 2 Long-tailed Jaeger nests do not differ statistically from distances between Long-tailed and either Parasitic or Pomarine jaeger (Maher 1974). Single Long-tailed Jaegers can also defend captured prey against a pair of Parasitic Jaegers by means of direct blows in flight (Childs 1969).

#### SEXUAL BEHAVIOR

**Mating system and sex ratio.** Social monogamy reported by all observers. No reports of extra-pair copulations; no study of paternity and extra-pair fertilizations.

**Pair bond.** Usually rejoins previous year's mate. One marked pair joined together again the following year; another was together 3 yr later (de Korte 1984). Two marked pairs remained together on same territories the following year; another had separated 3 yr later (Andersson 1981). Male usually smaller than female in a pair (Pitelka et al. 1955, Manning 1964, Andersson 1971, Maher 1974). Birds apparently arrive singly or in small flocks and rejoin surviving mates on breeding territories (de Korte 1984, Hansen 1984). Otherwise, no information about pair formation or interactions early in season.

Copulations last about 10 s; female crouches on ground, withdraws her neck; male mounts from side, supports himself with his wing-tips on the ground and by grasping neck-feathers of mate (Childs 1969, Andersson 1971).

Before copulation or when begging for food, female performs Hunched Posture: Holds head and body horizontal and withdraws neck, as in similar posture of gulls. Female often lowers breast and sometimes raises her long tail almost to vertical. Never extends neck forward as Parasitic Jaeger sometimes does;

otherwise this display like that in other jaegers and skuas (Andersson 1971).

As male approaches incubating female with food, she often flies to a nearby mound, uttering soft *kuep* calls; she then approaches male on the ground in Hunched Posture; he regurgitates food, which she eats or the 2 share (Andersson 1971). Otherwise no special behavior occurs when members of pair meet after separation, unlike large skuas, which have elaborate greeting displays, but like Parasitic Jaeger (Andersson 1971).

#### SOCIAL AND INTERSPECIFIC BEHAVIOR

**Degree of sociality.** Pairs more or less evenly dispersed in suitable habitat when breeding, without indications of clustering (Manniche 1910, Andersson 1971); in n. Sweden, distances between nests have variance/mean ratio of 0.47 (Andersson 1976a).

Nonbreeding birds in the Arctic roost on sea ice or gravel bars along coast in groups sometimes exceeding 60 (Parmelee and MacDonald 1960). At sea during nonbreeding season, as many as 100 birds congregate around fishing vessels. Flocks resting on water attract recruits until as many as 80 birds assemble, although more often 10–15 (Lambert 1980, Veit 1985).

**Nonpredatory interspecific interactions.** Vigilance in evicting and harassing other predators probably indirectly reduces predation within jaeger territories on species such as ptarmigan, marmot (*Marmotus*), and ground squirrel (*Spermophilus*; Price 1973), all larger than species preferred as prey by jaegers. Bristle-thighed Curlews (*Numenius tahitiensis*) and King Eiders sometimes nest in association with these jaegers, apparently to reduce predation on their nests (McCaffery and Peltola 1986, Blomqvist and Elander 1988).

Nesting Arctic Terns ignore these jaegers, which apparently do not take terns' chicks (Kampp 1982). Ruddy Turnstones and other shorebirds, however, harass them vehemently (Manniche 1910, Bent 1921, Pedersen 1926). In ne. Greenland, occasionally pursued by Parasitic Jaeger (Løppenthin 1943).

#### PREDATION

**Kinds of predators.** Predators on immature birds include, at least occasionally, Peregrine Falcon (*Falco peregrinus*) and Gyrfalcon (*F. rusticolus*; Childs 1969, Kessel and Cade 1958, Parmelee and MacDonald 1960). One adult plunging underwater while feeding was seized by a ringed seal (*Phoca hispida*) but escaped apparently unharmed (Drury 1960); another escaped after attack in midair by an immature Great Black-backed Gull (*Larus marinus*; Bent 1921).

**Response to predators.** Nesting birds defend their territories against predatory birds and mammals. Attack mammals by swooping from above with repeated *kreck-kreck* calls (*kreck* uttered twice, followed by pause of several seconds). Red foxes (*Vulpes vulpes*) elicit attack as much as 500 m from nest, humans

200 m, reindeer (*Rangifer tarandus*) 50 m. In intense attacks on foxes or humans near nest, male and female swoop with rapid wing-beats from 15–20 m above target to within 0.5–1 m. Nesting birds attacking arctic foxes (*Alopex lagopus*) in a frenzy sometimes repeat their dives so fast that they turn upside down in air (Maher 1974). Arctic Terns sometimes join jaegers, or jaegers join terns, in attacking a fox; each species responds to the other's calls (Andersson 1971). Individuals vary in attacking humans—some coming within 20 cm, although rarely making contact, others remaining 100 m away; attacks less intense after young hatch (Hanson et al. 1956, Andersson 1971, Maher 1974, de Korte 1986). Other mammals harassed near nests include gray wolf (*Canis lupus*), brown bear (*Ursus arctos*), and wolverine (*Gulo gulo*; Price 1973).

Birds attacked near nests include Willow Ptarmigan (*Lagopus lagopus*) and American Golden-Plover (*Pluvialis dominicus*, within 10 m of nest), various gulls (*Larus*, within 100 m), Short-eared Owl and Common Raven (*Corvus corax*, within 200 m), Rough-legged Hawk, Gyrfalcon, Golden Eagle (*Aquila chrysaetos*) and White-tailed Eagle (*Haliaeetus albicilla*, within 300 m), and Peregrine Falcon (Drury 1960, Childs 1969, Andersson 1971, Price 1973). Attacks avian intruders, either flying or alighted, by swooping and uttering *kliu* calls (Andersson 1971).

When approached on nest, sometimes performs Distraction Display: Runs from nest while fluffing plumage, spreads wings, and utters squeaking sounds. Not observed at all nests, less frequent than in Parasitic Jaeger, sometimes after mobbing of humans or dogs has failed (Sutton 1932, Andersson 1971, Maher 1974, Meltofte 1975, Portenko 1992). Also occasionally performs false brooding to decoy humans away from a nest (Bent 1921).

## BREEDING

#### PHENOLOGY

Smaller size than other jaegers permits shorter breeding cycle, an important adaptation for high-arctic breeding range of this species (see Fig. 3).

**Arrival in breeding areas.** First individuals arrive in last week of May or first week of Jun and begin to establish territories within a few days. In ne. Greenland, arrives along edge of sea ice about a week before flying inland; sometimes visits territories briefly several days before defense begins. Territories established within a few days of the date of 50% snow cover, often earlier in inland areas than in coastal areas where snow cover persists longer (de Korte 1984). In years with plentiful lemmings, some territories established while snow cover still 80% (Meltofte et al. 1981).

**Egg-laying.** Figure 2. Birds arrive on breeding grounds with fully enlarged gonads and maximal fat

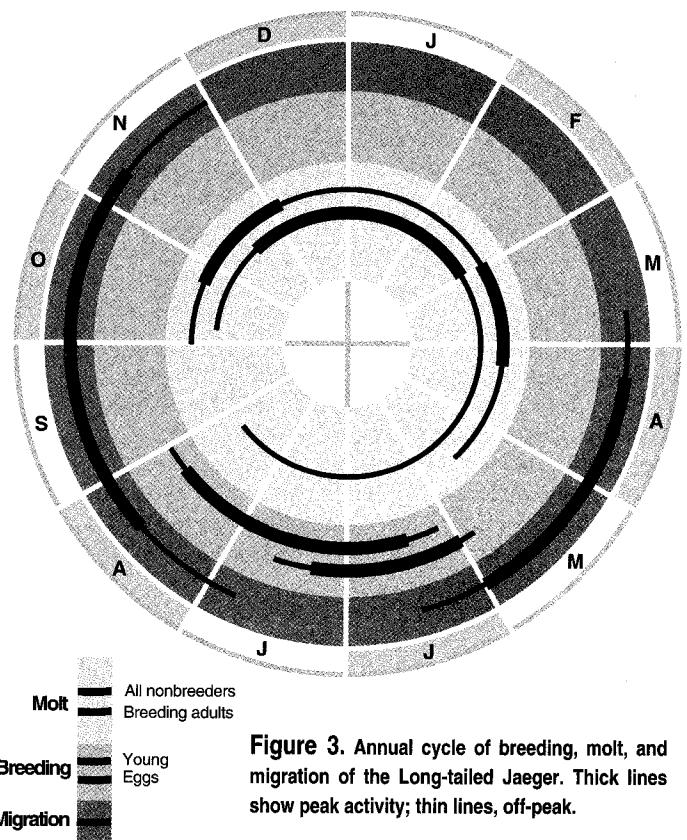
stores; laying can begin a week after a pair's arrival (Taylor 1974, de Korte 1985, Portenko 1992). In ne. Greenland, laying extends from first week of Jun to second week of Jul (median 11 Jun,  $n = 36$ ); 52% completed in second week of Jun (de Korte 1985). Some eggs hatch as late as 21 Jul (Hall and Wadingham 1966). In n. Alaska, eggs are laid 1–19 Jun ( $n = 16$ ) and hatch 26 Jun–14 Jul (most 26 Jun–3 Jul,  $n = 14$ ; Maher 1974). In Canada, eggs are laid usually in latter half of Jun (Parmelee and MacDonald 1960, Parmelee et al. 1967). On n. Ellesmere I., NWT, eggs are laid 10–27 Jun ( $n = 14$ ), with no pronounced peak (Maher 1970). On Bathurst I., NWT, laying begins in last week of Jun or first week of Jul; onset of laying apparently influenced by disappearance of snow (Taylor 1974). Pairs that have lost their eggs to predators sometimes remain on their territories for as long as 3 wk before departing in late Jul or early Aug (Maher 1970, de Korte 1984).

**Fledging.** Young begin flying in ne. Greenland usually about mid-Aug (de Korte 1984), but sometimes as early as 20–31 Jul (Pedersen 1930, Hall and Wadingham 1966, Hansen 1984); on n. Ellesmere and Victoria Is., NWT, in early Aug (Parmelee et al. 1967, Maher 1970); on Southampton I., as early as 18 Jul (Parker and Ross 1973); in n. Alaska, at end of Jul or early Aug (Childs 1969). Time from laying of first egg to fledging of young is about 50 d in years of high rodent densities; a few days longer when rodent densities are lower (Andersson 1976a).

**Departure from breeding areas.** Scandinavian breeders begin to leave in early Aug; few remain by end of month (Andersson 1976a). In ne. Greenland, most birds depart in last week of Aug or first week of Sep, but late juveniles can remain until first week of Oct (Manniche 1910, Pedersen 1926, de Korte 1984). In n. Alaska and on Ellesmere I., NWT, few birds remain by end of Aug (Parmelee and MacDonald 1960, Maher 1974). In years with low rodent densities, nonbreeding adults depart by late Jul or early Aug (Løppenthin 1943, Maher 1970). Molt does not begin until after birds leave breeding area (see Appearance: molts and plumages, below).

#### NEST SITE

In ne. Greenland, 22 of 24 nests were on gentle slopes or low elevations; 21 were placed among shrubs or moss, 3 on bare clay, always in locations covered by snow until early Jun (de Korte 1985), often on small mounds on tundra (Pedersen 1930). In n. Alaska, nest sites were often on low ridges or slopes, in general on sites more elevated and drier than those used by Parasitic Jaeger in same area; unlike Parasitic Jaeger, Long-tailed Jaeger had no tendency to prefer proximity to rivers or lakes (Maher 1974). Of 25 nests in n. Sweden, 10 were on mounds of peat, the others on gravel; all were on small rises with low vegetation and clear views of surroundings (Andersson 1971).



**Figure 3.** Annual cycle of breeding, molt, and migration of the Long-tailed Jaeger. Thick lines show peak activity; thin lines, off-peak.

#### NEST

Eggs laid on the ground in shallow depression with no nest material (Andersson 1971). On 1 occasion before egg-laying, individual of unidentified sex was observed making slow turns with belly pressed to ground, perhaps shaping a depression for eggs (Andersson 1971). An experiment with artificial nests showed that absence of nest material reduces risk of predation (Andersson 1976b). Absence of nest material also presumably related to use of feet in incubation (see Incubation, below).

#### GONAD CYCLES

Largest ovarian follicle usually 6 mm in diameter (maximum 9) in late May and early Jun at time of arrival in breeding areas (Maher 1974, de Korte 1985, Portenko 1992). Testis size maximal at time of arrival and clutch initiation ( $500\text{--}600\text{ mm}^3$ ); volume decreases steadily thereafter, faster in years when breeding does not occur (Maher 1974, de Korte 1985, Portenko 1992).

#### EGGS

**Shape.** Oval to subelliptical.

**Size.** On Southampton and Baillie Is., NWT, Canada:  $52.33\text{--}57.26 \times 37.84\text{--}42.48$  mm (mean  $54.18 \pm 1.98$  SD  $\times 38.96 \pm 1.68$  SD,  $n = 9$ ; Western Foundation of Vertebrate Zoology [WVZ]). In various North American locations:  $51.00\text{--}60.18 \times 35.36\text{--}42.48$  mm

(mean  $53.94 \pm 2.62$  SD  $\times 36.30 \pm 7.82$  SD,  $n = 15$ ; Florida State Museum). In ne. Greenland:  $50.0\text{--}58.8 \times 37.9\text{--}40.4$  mm ( $n = 13$ ), one  $44.0 \times 36.2$  mm (Manniche 1910, Hansen 1984).

**Mass.** Two eggs from ne. Greenland were 37.7 and 42.6 g, respectively, when laid; these eggs lost 0.24–0.30 g/d during incubation. Mass averaged 39.2 g ( $n = 32$ ) in a year of intermediate lemming density, 42–44 g in years with high lemming density; second eggs in clutches and eggs laid later in season tended to have lower mass, but neither trend was significant (de Korte 1985).

**Color.** Greenish to olive brown, rarely pale blue, with a few dark brown spots or scrolls, chiefly on large end (Witherby et al. 1944).

**Surface texture.** Smooth and slightly glossed (Cramp and Simmons 1983).

**Eggshell thickness.** Shells of 2 eggs were both 0.46 mm thick (Greenland, 1867 [WFVZ]; Northwest Territories, 1901 [Florida State Museum]).

**Clutch size.** Maximum of 2 eggs. See Demography and populations: measures of breeding activity, below.

**Egg-laying.** Interval usually 2 d (9 of 11 clutches); 1 d in 2 of 11 clutches (de Korte 1985). Replacement eggs, always just 1, produced as early as 8 d after first clutch lost (Maher 1970, Taylor 1974, Hansen 1984).

#### INCUBATION

**Onset of incubation in relation to laying.** Incubation usually begins soon after first egg is laid.

**Incubation patches.** Two, each averaging  $55 \times 32$  mm, in both sexes (Andersson 1976b, de Korte 1985). Final development coincides with start of incubation; refeathering begins in incubating birds 16–18 d after completion of clutch (de Korte 1985). Incubating birds hold each egg between one foot and corresponding incubation patch, an arrangement that limits effective incubation to just 2 eggs (Andersson 1976b).

**Incubation period.** On n. Ellesmere I., NWT, incubation averaged 24.2 d (range 23–25,  $n = 5$  eggs; Maher 1970); in ne. Greenland, about 23 d (Manniche 1910, Hansen 1984); in Alaska (Maher 1974), on Victoria I. (Parmelee et al. 1967), and in n. Sweden (Andersson 1976a), 24–25 d ( $n = 1$  nest in each case).

**Parental behavior.** Both sexes incubate, but female more than male: 59 versus 37% of total time, respectively ( $n = 1$  pair, observation for 1 d, ne. Greenland; de Korte 1985); about 76 versus 16%, respectively ( $n = 2$  pairs), but about 55 versus 42% during renesting (Bathurst I.; Taylor 1974); 75 versus 25%, respectively ( $n = 3$  nests, w. Greenland; Kampp 1982). Turns eggs every 75 min on average (Kampp 1982).

#### HATCHING

Hatching interval for 2 eggs in same clutch 0–3 d, often 2 (Taylor 1974, Andersson 1976a); <24 h in 1 case (Hansen 1984).

#### YOUNG BIRDS

**Condition at hatching.** Down well developed.

**Growth and development.** Hatchlings remain in nest 1–2 d (minimum 18.5 h; Parmelee and MacDonald 1960), then wander away to hide, usually among dwarf birch (*Betula*) and willow (*Salix*). Siblings often stay within 20–100 m of each other. Young can move 300 m from nest in 2 wk, 300–500 m or more from nest before fledging (Pedersen 1930, Andersson 1971, 1976a).

In n. Alaska, mass 29.0 g (range 24.4–31.5,  $n = 3$ ) 1 d after hatching; maximum mass (280–315 g) reached by about 15–16 d (Maher 1974). In ne. Greenland, newly hatched chicks (<24 h old) averaged 26.5 g (25.0–29.5,  $n = 7$ ) one year and 29.9 (27.0–35.0 g,  $n = 4$ ) another year; chicks reached 232 g (84% of adult mass,  $n = 2$ ) by day 24 (de Korte 1986). In n. Alaska, growth rates nearly exponential for first 8 d after hatching (mean 21%/d, range 20–23,  $n = 4$ ; Maher 1974); rates similar on n. Ellesmere I., NWT (mean 23%/d, range 19–26,  $n = 4$ ; Maher 1970) and in ne. Greenland (mean 19%/d,  $n = 4$ ; de Korte 1986). Because incubation begins with first egg, young in same nest differ in mass by as much as 20–50% (Andersson 1976a, de Korte 1986).

Lower growth rates and starvation of some young in years of intermediate rodent densities (Andersson 1976a, de Korte 1986). After 2 young hatch, often 1 eventually loses weight and dies (Maher 1970); when mortality of chicks is high, first chick to hatch usually survives longer ( $n = 5$  nests; Taylor 1974). Overt aggression between chicks not reported.

#### PARENTAL CARE

**Brooding.** Parents brood young for at least 1 d after hatching, often for first week (Andersson 1971, de Korte and Wattel 1988).

**Feeding.** One parent remains near nest while the other forages; young left alone only 3% of time. For first week after hatching, female mostly broods young and male brings food; by fourth week, both parents bring food, although male still predominates (de Korte 1986, de Korte and Wattel 1988). Male regurgitates in front of female, who then gives food to young; when young are older, male regurgitates in front of young and female eats whatever they leave, but she often regurgitates some of this food later for the young (de Korte and Wattel 1988). When male brings a lemming, he and his mate first share it, then female gives morsels to young. Large young often cooperate with female to tear large items to pieces, much as mates cooperate (Andersson 1971). Small young must have rodents torn apart for them; in 1 case when a female was killed, her young could not eat voles brought by the male (Maher 1974).

Young run, with wings spread, toward parent that is carrying food and peck upward at parent's beak. When begging for food, young adopt Hunched

Posture (see Behavior: sexual behavior, above; Andersson 1971).

One young confined for observation in ne. Greenland received caterpillars at first, then other arthropods; parts of lemmings, juvenile Snow Buntings, and berries beginning in second week; fish beginning in fourth week. Between 9 and 25 d of age, received 11 lemmings and 7 juvenile Snow Buntings (de Korte and Wattel 1988).

**Nest sanitation.** Eggshells removed from nest by parents within minutes after egg hatches (Andersson 1971).

#### COOPERATIVE BREEDING

Not reported.

#### BROOD PARASITISM

Not reported.

#### FLEDGLING STAGE

In n. Alaska, chicks first fly at about 25 d of age and can fly well 30–33 d after hatching (Childs 1969, Maher 1974). In n. Sweden, young make short flights at 22–24 d of age and fly well by 24–28 d (Andersson 1976a). One chick left its natal area and moved to coast by 34 d (Parmelee and MacDonald 1960).

#### IMMATURE STAGE

**Independence from parents.** Adults continue to feed young after they move to nearby coast, at least to age 42 d (Parmelee and MacDonald 1960). Adults continue to accompany young until late Aug (Parmelee et al. 1967), but association with parents apparently terminates when birds depart on migration. No records of parents feeding young outside breeding range. No indication that young associate with adults during migration off N. Carolina.

**Nonbreeding immatures.** Numerous in Arctic in years following high nesting success, an indication that many 1-year-olds return to breeding range (Manniche 1910, Pedersen 1942, Andersson 1976a, Meltofte et al. 1981); most of these birds stay at sea near breeding areas (Manniche 1910, Pedersen 1942). Visits to breeding habitat presumably more likely by older immatures and in years of dense rodent populations (de Korte 1985). These patterns need confirmation with marked birds of known age.

In ne. Greenland, immatures appear along ice edge in middle of Jun and on tundra in last week of Jun (de Korte 1985). They sporadically defend areas vacated by failed breeders, but they rely less on terrestrial food, particularly vertebrates, than territorial birds do (Manniche 1910, de Korte and Wattel 1988), and they often join flocks of nonbreeding adults both along coast and inland (de Korte 1984).

Immatures south of Arctic in late Jun and early Jul have presumably visited breeding areas only briefly, if at all (nw. Pacific [Kuroda 1955]; California [Stallcup

1990]; N. Carolina [specimens, NCSM]; tropical North Atlantic and North Pacific [specimens, USNM]; Peru [Murphy 1936]; Argentina [Brown et al. 1975a]; s. Africa [Urban et al. 1986]). Yet nearly all move north of equator: None off Chile in May–Jun (Jehl 1973a), off se. Australia in Jun–Aug (Higgins and Davies 1996), or off sw. Africa in Aug (Lambert 1980).

## DEMOGRAPHY AND POPULATIONS

### MEASURES OF BREEDING ACTIVITY

**Age at first breeding.** No information from marked birds. In ne. Greenland, some birds apparently breed for first time at age 3 yr. Although these new breeders arrive at same time as older birds, some are the last to nest and perhaps only half eventually breed (de Korte 1985). Adult plumage presumably acquired at age 3 yr (see Appearance: molts and plumages, below). Age at first breeding presumably depends on densities of lemmings in summers following hatching; perhaps most birds first breed in a year with high lemming densities (usually 3–5 yr after hatching).

**Intervals between breeding.** Throughout Arctic, most adults return to their breeding territories at beginning of each season, since numbers of birds early in season are similar regardless of rodent densities (Manniche 1910, Bird and Bird 1940, Andersson 1981). When rodent populations are low, these birds do not breed, and within a few weeks they gather into flocks before departure between late Jun and early Aug (Manniche 1910, Pedersen 1930, Løppenthin 1932, Bird and Bird 1940, Manning et al. 1956, Parmelee et al. 1967, Maher 1974, Meltofte 1975, Andersson 1976a, de Korte and Wattel 1988). In years of intermediate rodent populations, some but not all pairs breed. In years with high rodent populations, all pairs breed and no flocks are observed (Hall and Waddingham 1966, Andersson 1976a). Unlike Pomarine Jaeger, Long-tailed remains numerous in areas with intermediate densities of lemmings (Taylor 1974). No indication that populations are nomadic (Andersson 1981), although in n. Alaska some opportunistic birds stop in migration to take territories wherever high rodent populations are encountered (Maher 1974).

**Clutch.** Maximum 2 eggs. Experimental addition of extra eggs to 2-egg clutches resulted in failure of incubation, evidently a consequence of the use of feet for incubation (see Breeding: incubation, above). Removal of eggs during laying period revealed that some birds can produce at least 4 eggs in years of high rodent densities (Andersson 1976b), so at least in these conditions availability of food seems not to limit egg production. Replacement clutches sometimes laid 8–15 d after predation of first clutch (Maher 1970, Taylor 1974, Hansen 1984).

Egg production depends on availability of microtine rodents. Many studies report no nesting or smaller



clutches in years when rodent densities are low (Manniche 1910, Løppenthin 1943, Parmelee et al. 1967, Maher 1970, 1974, Andersson 1976a, de Korte 1985, de Korte and Wattel 1988). In years of high or moderate lemming numbers, all or nearly all pairs produce eggs. As a result, in ne. Greenland >90% of pairs lay eggs about 2 yr out of every 4–5 yr (de Korte and Wattel 1988). Dense lemming populations and prolific jaeger reproduction often coincide across locations as much as 800 km apart in ne. Greenland, although in some years locations no more than 200 km apart differ markedly (de Korte and Wattel 1988).

In years with high rodent densities, nearly all pairs lay 2 eggs (Andersson 1971, Maher 1974, Taylor 1974, de Korte 1985). In years with intermediate lemming numbers, some pairs lay only 1 egg, so clutches average 1.1–1.7 eggs; and in years with low rodent populations, sometimes 2 yr in succession, no eggs are laid (Williamson et al. 1966, Andersson 1976a, de Korte 1985). In foothills of n. Alaska, where rodent populations do not cycle markedly, clutches average 1.8 eggs ( $n = 28$ ; Maher 1974). In ne. Greenland, pairs on territories bordering coast, with access to sea for supplemental food, have larger clutches than those with territories farther inland in a year of intermediate lemming densities: Mean clutch sizes 1.7 ( $n = 10$ ) and 1.0 ( $n = 13$ ), respectively (de Korte 1985).

Loss of fat reserves between arrival and initiation of laying affects clutch size in ne. Greenland (if <12 g lost, always 2 eggs laid; if 33–49 g lost, always 1 egg laid; if >49 g lost, no eggs laid); females laying 2 eggs lost no more mass overall (mean 31%,  $n = 9$ ) than those laying 1 egg (mean 33%,  $n = 12$ ; de Korte 1985). Breeding birds averaged about 9% greater mass in years with high, in comparison to intermediate, densities of rodents and laid correspondingly larger clutches of larger eggs (Andersson 1976a).

**Annual and lifetime reproductive success.** In ne. Greenland, nearly all pairs have 1 fledgling in years with dense populations of lemmings (Manniche 1910); in a year with intermediate lemming density, 43% of initial clutches hatched (29% of eggs,  $n = 7$  clutches), no replacement eggs hatched, and no young fledged (Hansen 1984). On n. Ellesmere I., NWT, in a year with high population of nesting jaegers, 25% of nests fledged 1 young each (12% of eggs laid,  $n = 8$  nests), 14% in years with low populations (11% of eggs,  $n = 7$  nests; Maher 1970). On Bathurst I., NWT, 10–17% of eggs produced young ( $n = 6$ –20 eggs in 3 successive years); loss of eggs to predators (0–70%) correlated with densities of arctic fox; also most chicks were lost to predators before fledging (67–83%; Taylor 1974). In n. Alaska, in an area of high vole populations, 58% of eggs produced fledged young, roughly 1.1 young fledged/nesting pair ( $n = 10$  nests); in an area with lower rodent densities, 0.2 young/nesting pair ( $n = 5$  nests; Maher 1974). Near Cape Thompson, nw. Alaska, in 2 yr with intermediate and low rodent densities,

75% and 25% of nests were successful, 0.9 and 0.5 young fledged/nesting pair ( $n = 8$  nests each year; Williamson et al. 1966). In n. Sweden, in a year of intermediate rodent density, 0.5–0.7 young fledged/pair in the population, including those that did not attempt to breed ( $n = 12$  pairs). In a year of high rodent density, when all pairs in population bred, 1.4 young fledged/pair ( $n = 11$  pairs). Most production of young thus occurs in years of high rodent density, so perhaps 75% of all young are produced 1 year in every 4 (Andersson 1976a). Abandonment of clutches results from food scarcity in years of intermediate rodent densities (de Korte 1985).

No information on lifetime reproductive success.

#### LIFE SPAN AND SURVIVORSHIP

Of 10 breeding adults banded in n. Sweden, 9 known to have survived to following year; of 26 banded adults, 19 observed in a subsequent year (some surviving birds were probably missed; Andersson 1976a, 1981). Of 4 birds marked on Ellesmere I. and 7 on Bathurst I., NWT, all returned the following year (Maher 1970, Taylor 1974). Longest reported longevity is an adult with estimated age of at least 8 yr 1 mo (Clapp et al. 1982); however, birds that were banded as nesting adults and returned for 6 seasons in Sweden and Canada (Andersson 1971, 1976a, Maher 1970) were presumably at least 9 yr old. No information on survival during immature stages.

#### DISEASE AND PARASITES

Only 4 species of ectoparasitic feather lice (Mallophaga) reported: *Austromenopon fuscofasciatum*, *Haffneria grandis*, *Quadriceps normifer normifer*, and *Saemundssonina inexpectata*. The first 2 are shared with both Parasitic and Pomarine jaegers. Each of the 3 jaegers has a different subspecies of *Q. normifer* and a different species of *Saemundssonina* (Cohen et al. 1997; see also Melville 1985).

#### CAUSES OF MORTALITY

In ne. Greenland, predation by arctic fox responsible for 60–100% mortality of young before fledging in different years. In years with long-lasting snow, foxes easily find nests in restricted snow-free areas. Predation also high in years following maximal lemming abundance, when reproduction of foxes is high, and in years of minimal lemming abundance because lemmings do not provide alternative prey for foxes. Jaegers reproduce successfully only in years with low predation by arctic fox (de Korte 1986, de Korte and Wattel 1988). On n. Ellesmere I., NWT, predators (mostly arctic fox) responsible for 62% of losses during incubation ( $n = 8$  nests; Maher 1970). In a remarkable case of survival, a chick managed to dodge the hooves of an estimated 100,000 caribou (*Rangifer tarandus*) that passed through its territory (Childs 1969).



## RANGE

*Initial dispersal from natal site.* No information.

*Fidelity to breeding site.* Of 7 territorial birds marked on Bathurst I., NWT, 6 occupied same or immediately adjacent territory a year later, and the other was 3.5 km away (Taylor 1974). A banded female on n. Ellesmere I., NWT, nested in same territory for at least 6 seasons, and her mate nested there for at least 4 (Maher 1970). Of 9 adults returning the year after banding in n. Sweden, 7 nested within their previous territories; the other 2 nested 1.5 and 3 km away, respectively. One bird nested in same territory over period of 6 yr (Andersson 1976a, 1981). Ten marked birds remained faithful to their breeding sites despite intervening years of low lemming populations when no jaegers nested; 1 marked bird moved >6 km after a year with no nesting (Andersson 1981). No information on fidelity to winter range.

*Home range.* No information on size, except for territorial nesting pairs (see Behavior: spacing, above).

## POPULATION STATUS

Most abundant and widespread jaeger in Arctic. No detailed estimates of total numbers or trends, but European Bird Census Council provides estimates (with wide range of possible error) of 5,000 pairs in Scandinavia and 30,000 in European Russia, in an area of tundra <20% of that in North America (Hagemeyer and Blair 1997). Furness (1987, Table 11) suggests a total population in low hundreds of thousands of pairs. Throughout nesting range, densities of breeding pairs vary from year to year by factors of 15–25. In ne. Greenland around Scoresby Sound (71°N), densities of territorial pairs range from 0.2 to 0.9/km<sup>2</sup> in different years and sites (de Korte 1977, 1984, Hansen 1984). Farther north in Germania Land (77°N), densities reach 1.5–1.7 pairs/km<sup>2</sup> (Maniche 1910). In Canada, densities of breeding pairs are 0.1–0.2/km<sup>2</sup> on Victoria I. (69°N) when lemmings are abundant (Parmelee et al. 1967), 0.5/km<sup>2</sup> on Bathurst I. (76°N) in years with intermediate or high densities of lemmings (Taylor 1974), and 0.8/km<sup>2</sup> on Ellesmere I. (82°N) in good years (Maher 1970). On Bathurst I., these densities are at least twice as high as for any other avian predator (Taylor 1974). In Alaska, densities of breeding pairs vary: 0.26–0.51/km<sup>2</sup> in foothills along Kaolak River and 0.07–0.90/km<sup>2</sup> near coast at Cape Sabine (Maher 1974); 0.5/km<sup>2</sup> in 2 yr with intermediate and low rodent densities near Cape Thompson (Williamson et al. 1966). In n. Sweden, in years of low rodent populations, densities fall to <0.02 pair/km<sup>2</sup> (no birds detected breeding) in comparison to densities of 0.54–0.63 pair/km<sup>2</sup> in years of high rodent populations when densities reach 0.8 pair/km<sup>2</sup> in optimal habitat (Andersson 1976a, 1981). In wintering range, densities reach 0.05 bird/km<sup>2</sup> in waters off South Africa (Ryan 1989).

## POPULATION REGULATION

Because jaegers spend their lives at sea, except for breeding, and have high survival, fluctuations in densities of lemmings have no clear influence on total numbers. Unlike other avian predators in Arctic, this species does not experience high mortality and irruptive emigration in years with scarce prey. Because survival after fledging depends on conditions at sea, nothing is known about long-term regulation of populations. See also Causes of mortality, above.

**CONSERVATION AND MANAGEMENT**

## EFFECTS OF HUMAN ACTIVITY

*Shooting and trapping.* Occasionally shot by Greenlander hunters for dog food (de Korte and Wattel 1988). One of 26 marked birds shot by hunter in Scandinavia (Andersson 1981); 1 of 20 marked birds shot 2 yr later by hunter in Greenland (de Korte 1984).

*Fishing nets and contaminants/toxics.* Not recorded. Probably subject to contamination by pollutants in oceans.

*Disturbance at nest and roost sites.* Not recorded.

## MANAGEMENT

Not attempted in natural populations. Maintenance in captivity is difficult (Irving 1960, Mowat 1993).

**APPEARANCE**

## MOLTS AND PLUMAGES

Molts and plumages of this species remain uncertain. No study of immature plumages, after Juvenal plumage, has been based on individuals of known age. Most molting occurs at sea in nonbreeding season, so no extensive series of relevant specimens exists. Age at first breeding is also not certain (see Demography and populations: measures of breeding activity, above). Immature plumages (Alternate and Basic I, II, and possibly III) and molts vary considerably, so definite information on progression with age requires samples of birds for which ages are known from independent evidence. Unlike some gulls (Larinae), in which individuals acquire adult plumages progressively in a succession of molts, Long-tailed Jaegers normally molt into adult plumage in a single step. The accounts of plumage progression in Cramp and Simmons 1983, Olsen and Christensen 1984, Olsen and Jonsson 1989, and Olsen and Larsson 1997 are thus best considered to be hypotheses that require confirmation.

Color morphs in this species are another source of confusion. As described below, a distinct dark morph occurs in Juvenal and other immature plumages, much as in Parasitic and Pomarine jaegers. Despite a few

reports, however, there is no convincing evidence for dark morphs among adults. There is no specimen of a dark morph in Definitive Alternate plumage (Murphy 1936, Løppenthin 1943, Salomonsen 1950, Løvenskiold 1964). Occasional reports of sightings (Wynne-Edwards 1935, Veit 1985) lack details to exclude misidentification of species or age. Dark morph of Juvenal and other immature plumages usually has little or no barring on underwing-coverts (Olsen and Jonsson 1989, Olsen and Larsson 1997, specimens from USNM and AMNH) and thus can look like an adult in Definitive Basic plumage. Color of legs of dark immatures is also uncertain, so specimens of dark birds in Basic plumage with dark legs (Vooren and Chiaradia 1989) might also be immatures. Furthermore, dark immatures acquiring Definitive Alternate plumage occasionally retain immature underparts into summer and thus can suggest dark adults (specimens in AMNH: Jun, North-west Territories; Jul, Greenland; and Aug, Labrador). Some birds in Definitive Alternate plumage have gray (not dark brown) extending from undertail-coverts to neck (see Systematics: geographic variation; subspecies, above), but throat is always white.

**Hatchlings.** Down nearly uniform brown; paler than on Parasitic and Pomarine jaegers (Fjeldså 1977). Two morphs reported: paler and darker; both can appear in same clutch (Manniche 1910, Pedersen 1930). Legs and feet bluish at hatching, hindtoe pinkish; by third week, distal parts of webs begin to turn blackish; by mid-Aug, on average 70% of foot is black, but legs remain bluish (de Korte 1985).

**Juvenal plumage.** Prejuvenal molt completed in second half of Aug. Light morph typically dark brown above, whitish below, with somewhat paler head and plain gray brown breast. Head finely streaked (sometimes spotted or plain) gray brown; rarely a slightly paler collar on hindneck. Breast plain gray brown (sometimes tipped or barred with white); belly white usually barred with brown; undertail-coverts barred brown and white (brown bars usually, but not always, wider than white); underwing-coverts dark brown, spotted with white. Back, upperwing-coverts, and uppertail-coverts dark brown, with narrow white (sometimes buff) tips, producing scaled appearance that varies in prominence (uppertail-coverts sometimes barred prominently with white). Remiges and rectrices blackish brown, not contrasting significantly with rest of upperparts. Shafts of 2 outermost primaries mostly creamy white (7% with 1 shaft; 10% with 3 shafts;  $n = 66$ ); shafts of adjacent primaries often tan, paler than vanes. Two central rectrices slightly elongated (10–20 mm), with rounded tips. Dark morph differs primarily in dark brown head and underparts (sometimes thin white tips on feathers of head and belly). Although both morphs vary, true intermediates are infrequent (Manniche 1910). Dark morphs much less common than light morphs (4 of 24 specimens in Juvenal plumage; NCSM, AMNH, and USNM).

**Later immature plumages.** Complete Prebasic I molt occurs during first winter at sea; apparently highly variable in timing. Juvenal contour feathering usually shows no sign of molt before Oct, by which time narrow buff or white tips of dorsal feathers have been reduced by wear (specimen, USNM). Primary molt begins with innermost, first of which are replaced as early as 7 Nov (NCSM). Rounded central rectrices of Juvenal plumage lost by Nov and usually replaced by pointed rectrices (de Korte 1985, Olsen and Jonsson 1989, specimens from AMNH and USNM).

In all molts, regardless of age, primaries are replaced sequentially from innermost outward, secondaries from outermost inward, rectrices from center outward. Central rectrices and contour feathers are replaced twice a year in adults (see below), and this schedule probably applies to immatures but lacks confirmation. Variability of immature plumages and molts and uncertainties about ages of specimens make it difficult to determine the sequence of plumages and timing of molts that precede Definitive Alternate plumage. Most promising attempt at distinguishing age classes of immatures—on basis of molt of remiges and rectrices during arctic summer, barring of underwing-coverts, and coloration of feet and legs—did not assess variation in these characters in birds of known age (de Korte 1985).

Some immatures do not finish molting until Aug (Stresemann and Stresemann 1966, de Korte 1985). Three of 12 immatures collected off N. Carolina in Jun–Aug were still molting rectrices or remiges; head and body molt can also extend into Aug. Two immatures in Sep showed no signs of molt (NCSM). An immature from Peru in Jun was growing its outermost primary (AMNH). Specimens from Canada and Alaska in Jun–Aug showed similar variation in molt. By Nov, some immatures in wintering areas have begun to molt, again with much variation in timing.

Without independent criteria for identifying age classes, we present here a single description of immature plumages and variation. All immatures have central rectrices with pointed tips (occasionally rounded) that project slightly beyond remainder of tail.

Light morphs of immature plumages are similar to Definitive Basic plumage: Mostly brown above and white below, with variable amounts of barring, especially on breast, flanks, and uppertail- and undertail-coverts. Head brown to gray brown, usually paler than back, streaked to varying degree, with paler collar varying from absent to well marked. Throat usually streaked or spotted gray brown (sometimes plain white or gray brown); breast usually plain gray brown (sometimes feathers tipped with white or plain white); belly white or barred with brown (sometimes plain gray brown); undertail-coverts barred brown and white (brown bars less than or equal to white in width). Back and upperwing-coverts dark brown, with white (sometimes buff) tips; uppertail-coverts

barred with white (highly variable; white bars less than or greater than brown bars in width). Remiges and rectrices blackish brown, not contrasting significantly with remainder of upperparts. Outer 1–3 remiges have cream white shafts. Central rectrices pointed (occasionally rounded), usually extending 10–30 mm beyond others (during arctic summer, many have longer extensions, to 130 mm). Underwing-coverts brown, spotted with white.

Dark morphs occur in all immature plumages (de Korte 1985); always a minority of birds. Differ from other birds in that head and underparts brown, often somewhat paler than remainder of upperparts, with variable white tips to feathers. Several specimens show transition from dark morph of final immature plumage to normal Definitive Alternate plumage (see below).

**Definitive Basic plumage.** Complete Definitive Prebasic molt begins at sea in Southern Hemisphere. By Oct and Nov, most birds have begun molt of contour feathers and have lost their long central rectrices (specimens: 12 from AMNH, 2 from USNM). Some Nov birds have already completed molt of dorsal feathers, and most have new central rectrices, usually with tapering tips projecting 2–4 cm (some have longer slender tips). Some birds begin molting primaries in Nov (2 out of 5 specimens; AMNH); replacement of remiges continues slowly over 5–6 mo (Stresemann and Stresemann 1966). Off sw. Africa, adults in Definitive Alternate plumage observed as late as Dec, although many had presumably begun molting before then (Lambert 1980). Adults in Definitive Basic plumage at this time had 2–4 fully grown new primaries (Lambert 1980). Late migrants apparently postpone molt (1 female from New Mexico had full Definitive Alternate plumage in Nov; USNM).

Like immature plumages, Definitive Basic is dark brown above, not gray; and whitish below, with varying degrees of brown barring. Head and throat gray brown to brown—streaked, spotted, or plain; paler collar usually moderately well developed (sometimes absent or prominent); breast barred or streaked brown or plain white; belly white (rarely barred with brown); undertail-coverts barred with brown (brown bars much less or equal to white bars in width). Upperparts dark brown, with variable white tips and bars on feathers; uppertail-coverts barred with white (white bars less than or equal to brown in width). Remiges and rectrices blackish brown, not contrasting significantly with dorsal contour feathering. White shafts of outer primaries as in other plumages. Two central rectrices have pointed tips (often abruptly tapered), usually extending 20–40 mm beyond others (rarely to 60 mm). Underprimary-coverts, like remiges, apparently molt only once each year, and thus remain plain gray brown, unlike those of immatures.

**Definitive Alternate plumage.** Definitive Prealternate molt partial; includes contour feathering

and 2 central rectrices. Most authors agree that this plumage is complete by age 3 yr (requires confirmation with marked birds of known age; Cramp and Simmons 1983, de Korte 1985, Olsen and Jonsson 1989). Most young jaegers have their first opportunities to breed at about age 3–5 yr (see Demography and populations: measures of breeding activity, above). We might thus expect Definitive Alternate I plumage to develop just before bird reaches age 3 yr. This plumage, an abrupt change in coloration from preceding immature plumages, is the first with plain gray upperparts and unspotted underwing-coverts.

Plain, unspotted underwing-coverts are probably first acquired during the winter preceding first acquisition of Definitive Alternate plumage (de Korte 1985, Olsen and Jonsson 1989). Nevertheless, some specimens with predominantly Definitive Alternate plumage still have spotted underprimary-coverts (specimens from AMNH and USNM).

According to many authors, final immature Alternate plumage is like Definitive Alternate, but with some persistent barring (Witherby et al. 1944, Walter 1962, Dement'ev and Gladkov 1969, Cramp and Simmons 1983, Olsen and Jonsson 1989). This condition, however, is not a distinct plumage, but a result of incomplete Prealternate I molt. Such Jun–Aug specimens (9 from USNM, 7 from AMNH) show mixtures of Definitive Alternate plumage with worn brown feathering on back and upperwing-coverts and barred feathers on uppertail- or undertail-coverts and underparts. Probably most are immatures that have failed to complete their molt to Definitive Alternate plumage (14 of 16 such specimens have spotted underwing-coverts; AMNH, USNM). These specimens vary from immature plumage, except for a few gray feathers on back, to Definitive Alternate plumage, including elongated central rectrices, except for brown or barred feathers on tail-coverts and underparts. Such specimens indicate that Definitive Alternate feathering appears first on back and head, last on tail-coverts and underparts. Although its first acquisition is incomplete in some birds, Definitive Alternate plumage is distinctly different from earlier plumages.

Prealternate molt of contour feathering occurs primarily in Mar or Apr (Stresemann and Stresemann 1966, Olsen and Jonsson 1989). Some adults have completed molt of primaries but still lack Alternate contour plumage and central rectrices in Mar (Veit 1985). Occasionally central rectrices have still not reached full length by May (specimen, NCSM). Thus in nonbreeding range, after southward and before northward migrations, birds apparently molt almost continuously: first body plumage, then wing- and tail-feathers, then body plumage again.

Older adults, like those first acquiring Definitive Alternate plumage, occasionally fail to complete Prealternate molt and retain brown or barred feathers

on back and tail-coverts. This incomplete molt not necessarily an indication of age (de Korte 1985). That some adults fail to complete Prealternate molt is shown by Nov specimen from Argentina (USNM) that had 3 generations of feathers on its back: very worn brown feathers from preceding winter, worn gray feathers from summer, and new brown feathers with white tips.

Head and neck white, with distinct dark brown cap extending to gape and below eye; sides of neck yellowish; back and upperwing- and uppertail-coverts medium brownish gray. Throat, breast, and anterior belly white; posterior belly and undertail-coverts brownish gray; extent of gray on underparts varies individually and geographically (see Systematics: geographic variation; subspecies, above), but throat always white; underwing-coverts gray brown, without markings. Remiges and rectrices blackish brown, contrasting with gray back and upperwing-coverts. Two central rectrices greatly elongated and flexible. Usually outermost 2 primaries have creamy white shafts for most of their length (4% with 1 white shaft, 16% with 3, 2% with 4;  $n = 97$ ).

No dark morph. Breeding birds vary in intensity of yellow on sides of neck and in extent of gray on abdomen (Manniche 1910). Males have whiter breasts on average than females, with wide overlap (Parmelee and MacDonald 1960, Manning 1964). Newly established breeders in Scandinavia have slightly shorter central rectrices than returning breeders (mean difference 10%, rarely 50%; Andersson 1976a), but de Korte (1985) found no such difference with age in Greenland. No other reported changes with age.

#### BARE PARTS

**Bill and gape.** Bill black; dark horn brown at base. On immatures, proximal half light gray blue, distal half brown black. Gape pinkish.

**Iris.** Dark brown. No orbital ring.

**Legs and feet.** Tarsus gray blue, toes and webs black; black on distal parts of webs and toes increases from 70 to 100% from fledglings to adults; some adults have black on distal part of tarsus (Manniche 1910, de Korte 1985). On immatures in migration off N. Carolina, about 75% of toes and webs black (NCSM).

## MEASUREMENTS

#### LINEAR

Females average about 5% larger in linear measurements than males (Manniche 1910). No evidence for geographic variation (Manning 1964). Cramp and Simmons (1983) and Furness (1987) summarize standard measurements from specimens throughout species' range (see Appendix for data from Greenland).

**Wing area.** For 3 specimens: 3,685, 3,335, and 3,271 cm<sup>2</sup>, respectively (1 spread wing each; NCSM).

**Wing-loading.** For 3 specimens: 6.61, 5.14, and 4.85 g/cm<sup>2</sup>, respectively (mass/[2 x area of single wing]; NCSM).

#### MASS

Females usually average 10–12% heavier than males; slightly less dimorphic than other jaegers. Mean mass (g ± SD) in ne. Greenland: female, 307.2 ± 39.2 (range 262–444,  $n = 48$ ); male, 269.6 ± 21.6 (range 218–320,  $n = 38$ ; de Korte 1985). In Canada: Adelaide Peninsula—female 338.6 ( $n = 8$ ), male 296.8 ( $n = 10$ ); Prince of Wales I.—female 385.0 ( $n = 6$ ), male 317.5 ( $n = 8$ ); birds from latter locality had more fat on average than those from former (Manning 1964). In n. Alaska: female, 312.8 ± 7.4 (range 258–358,  $n = 18$ ); male, 280.1 ± 6.1 (range 236–343,  $n = 26$ ; Maher 1974). For additional information, see Cramp and Simmons 1983 and Furness 1987.

## PRIORITIES FOR FUTURE RESEARCH

Long-term study of marked individuals would clarify stages of immature plumages, establish the age at first breeding, and reveal individual and age-related differences in breeding. Padded fox traps placed on the ground near bait are highly effective in trapping individuals for banding (Parmelee and MacDonald 1960). Wintering areas and migration routes remain poorly documented, particularly in the Pacific. Study is also needed of possible contamination by oceanic pollution. This species' conspicuousness in the Arctic should make it a convenient subject for monitoring the health of arctic ecosystems.

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**Appendix.** Linear measurements (mm) of adult Long-tailed Jaeger from Greenland. Data shown as mean  $\pm$  SD (range, *n*). From Cramp and Simmons 1983, except as noted.

Culmen length	
Male	28.5 $\pm$ 1.34 (26–31, 75)
Female	28.4 $\pm$ 1.32 (26–31, 53)
Wing length	
Male	30.6 $\pm$ 6.5 (29.2–31.8, 36)
Female	30.9 $\pm$ 8.1 (29.4–32.3, 38)
Tail length	
Male	112 $\pm$ 5.2 (104–121, 73)
Female	111 $\pm$ 4.0 (104–121, 55)
Projection of central rectrices <sup>1</sup>	
Male	173 $\pm$ 27.0 (125–231, 21)
Female	170 $\pm$ 17.2 (127–208, 27)
Tarsus length	
Male	42.6 $\pm$ 1.82 (34–46, 75)
Female	42.5 $\pm$ 1.60 (34–45, 54)
Middle-toe length	
Male	35.1 $\pm$ 1.90 (32–38, 75)
Female	36.0 $\pm$ 1.79 (39–45, 54)

<sup>1</sup>From de Korte 1985.

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