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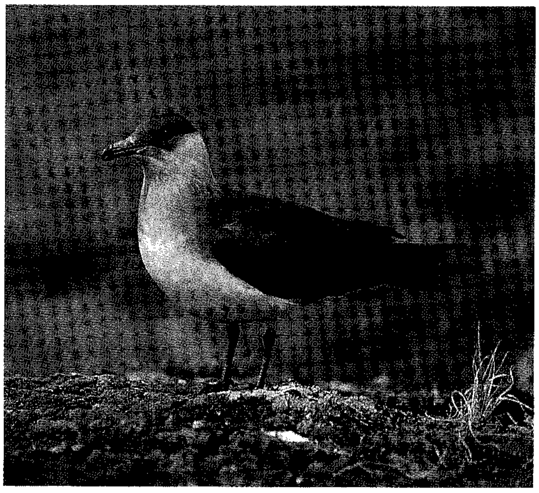
Stercorarius parasiticus

Parasitic Jaeger

FRENCH:
Labbe parasite
SPANISH:
Salteador parásito
RUSSIAN:
Korotkokhvosty Pomornik



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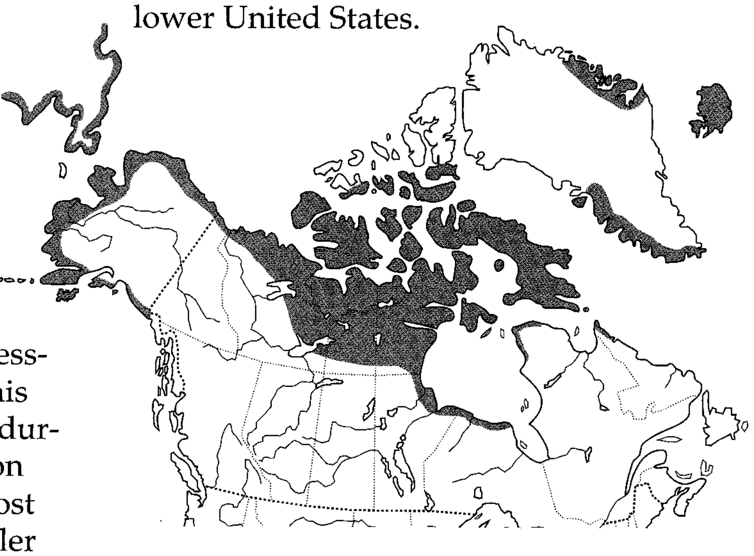
Parasitic Jaegers are well named for their habit of forcing other seabirds to disgorge their food, which the jaegers deftly swoop down to retrieve. Their acrobatics and aggressiveness in pursuing their targets have evoked both admiration and defilement by human observers. In the northeastern Atlantic, and possibly also in the Aleutian Islands, Parasitic Jaegers obtain most of their food by stealing from colonial seabirds. Nevertheless, in most of their circumpolar breeding range, "kleptoparasitism" is not the main way of life for Parasitic Jaegers. Throughout the tundra regions of the Arctic, they defend large territories within which they hunt for birds, mammals, and eggs. They are the most important predator of small birds in the Arctic and among the two or three most important predators of birds' eggs. Because they are so effective at such diverse forms of predation and parasitism, they do not require dense populations of lemmings (*Lemmus, Dichrostonyx*) for successful reproduction. In this respect, their ecology during the breeding season differs from that of most other arctic predators, including the smaller Long-tailed Jaeger (*Stercorarius longicaudus*) and the larger Pomarine Jaeger (*S. pomarinus*).

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

During migration and winter in the southern hemisphere, Parasitic Jaegers depend primarily on food obtained by kleptoparasitism. Some parasitize colonial seabirds feeding their young in the southern hemisphere and thus take advantage of nesting seabirds year round. On their way southward in autumn, they often accompany migrating terns (*Sterna*) and thus remain near shore more often than do other jaegers. Consequently, of the three species of jaegers, they are the ones most often seen in southern Canada and the lower United States.



▨ Breeding

Figure 1.
Distribution of the Parasitic Jaeger in North America. This species also breeds in Europe and Asia and winters primarily in oceans of the southern hemisphere. See text for details.

Order CHARADRIIFORMES Family LARIDAE

Field identification of jaegers is difficult, especially when they are not in their characteristic breeding plumages. The difficulty arises in part because Parasitic Jaegers overlap the other two species in size. In addition, all three species have complex variation in their plumages. Because molts occur primarily at sea in the southern hemisphere, winter specimens of Parasitic Jaeger are not well represented in museums.

In all plumages, Parasitic Jaegers have two contrasting morphs, dark and light, as well as intermediates. In breeding populations in the north Atlantic and the north Pacific, the frequencies of these morphs vary with latitude. Studies of banded birds for more than 30 years on Fair Isle, northern Scotland, have yielded detailed information on demography and sexual selection of the morphs in this population (O'Donald 1983). In addition, many studies in the northeast Atlantic have evaluated the efficiency of the two morphs in kleptoparasitism (Furness 1987). As a consequence of this work, Parasitic Jaegers are among the best studied of all seabirds. Nevertheless, away from the kleptoparasitic populations in the northeast Atlantic, they remain little known. It is the scarcest and least studied of the three jaegers in the Arctic, and almost nothing is known of its life during winter in the southern hemisphere.

DISTINGUISHING CHARACTERISTICS

Intermediate in size between smaller Long-tailed and larger Pomarine jaegers: males about 380–420 g, females about 460–510 g. The smallest and largest individuals, however, overlap the other two species of jaegers in mass. Females about 15–20% larger than males.

Adults in Definitive Alternate plumage occur in two morphs, with some intermediates. Light morphs have brown upperparts with a blackish cap and white collar, white underparts, yellowish sides of the neck, and often a partial or complete brown band across the breast. Dark morphs are similar except white areas on head and underparts replaced with brown. Intermediates resemble dark morphs but show some white on belly and have paler collars with some yellowish brown on the sides of the neck. All morphs have whitish shafts of the outermost 4–6 (occasionally 3–8) primaries, a whitish patch on the underside of the wing at the base of the primaries, plain brownish underwing-coverts, and pointed central rectrices extending 6–10 cm beyond the rest of the tail.

In Basic plumage, adults lose their long rectrices and acquire barred uppertail- and undertail-coverts. Light morphs have a variable amount of barring below, like immatures, but retain plain underwing-coverts, unlike the barred underwing-coverts of immatures. Adults normally wear Basic plumage only in the winter range.

In Juvenal plumage, there is much variation between dark and light extremes. All have brown upperparts with variable amounts of barring, including barred uppertail- and undertail-coverts and underwing-coverts. Underparts vary from mostly white with brown bars on flanks and undertail-coverts to mostly dark with whitish bars on undertail-coverts. Central rectrices, either pointed or rounded, extend only slightly beyond others. About half of all birds have pronounced orangish brown or cinnamon (instead of whitish or buff) barring on back and wash on neck and head. Later immature plumages are poorly known, but resemble Juvenal and adult Basic plumages. Because it takes several years to acquire Definitive Alternate plumage, barred immature plumages occur throughout the year.

Adults in Definitive Alternate plumage are readily identified by their elongated central rectrices, which are pointed, unlike those of Pomarine Jaeger, but not so long and flexible as those of most Long-tailed Jaegers. Size, approximately that of a Laughing Gull (*Larus atricilla*), overlaps with that of both Pomarine and Long-tailed jaegers. Lacks the deep-chested, broad-winged build of most Pomarine Jaegers. Most have 4–6 primaries with white shafts, more than Long-tailed Jaegers. Light morphs also differ from adult Pomarine Jaeger in Definitive Alternate plumage by sharper contrast between brown and white areas below and from adult Long-tailed Jaeger in Definitive Alternate plumage by a lack of contrast between brown upperwing-coverts and blackish remiges, a white spot at base of forehead, and often a complete or partial band across the breast (absent in some birds). Parasitic Jaeger also has a proportionately shorter tail (not including the central rectrices) and broader wings than Long-tailed Jaeger, although these differences are slight. The average differences in size and proportions result in differences in flight, but overlap occurs between species in these features.

Immature Parasitic Jaegers are much more difficult to identify (Olsen and Christensen 1984, Olsen and Jonsson 1989, Olsen and Larsson 1997) as a result of substantial individual variation in plumage and overlap in size with both Pomarine and especially Long-tailed jaegers. Differences in size and proportions between adult jaegers apply also to immatures, although the differences are not so pronounced and greater overlap occurs. About half of immature Parasitic Jaegers differ from all Long-tailed and most Pomarine jaegers in having conspicuous cinnamon or orangish brown, rather than tan or whitish, barring above and below and tinting on head and neck.

Immature Parasitic often differs from immature Pomarine Jaeger in lacking a double white flash near the base of the primaries on the underside of the wing (some show a double flash like most Pomarine Jaegers) and in having more pointed central rectrices (with much variation in both species). Some immature Parasitic Jaegers can resemble adult Pomarine Jaeger in Definitive Alternate plumage as a result of heavy barring on the breast and flanks.

Differs from immature Long-tailed Jaeger in having more primaries with whitish shafts (only a few have 3 whitish shafts, most have 4–6, see Appearance: molts and plumages). Although the number of whitish shafts is one of the best demarcations between these two species in immature and Basic plumages, care is necessary in its application. In both species, all primaries have shafts paler than vanes; in many individuals the transition from whitish shafts of outer primaries to tan shafts of inner primaries is gradual; and the outermost primary, and to a lesser extent the next, have wider shafts than others. Consequently, the outer one or two shafts are likely to be more conspicuous than others on any jaeger, and the demarcation between predominantly white and predominantly tan shafts is not always clear.

Other differences between these two species in immature plumages are more problematic. Contrary to statements in many field guides, immature Long-tailed Jaegers and adults in Definitive Basic plumage have dark brown upperparts, which do not contrast with remiges; in this respect they are unlike adults in Definitive Alternate plumage but similar to all Parasitic Jaegers. Juvenile Long-tailed Jaegers usually have rounded central rectrices, but later immature plumages have pointed rectrices similar in length and shape to those of most immature Parasitic Jaegers; about a quarter of Parasitics have rounded central rectrices in Juvenal plumage. Many immature Long-tailed Jaegers have plain gray-brown breast bands and pale collars, but some immature Parasitic Jaegers are very similar. There are also average differences in the size and proportions of the beak (Long-tailed Jaegers often have smaller bills with proportionately shorter unguis and gonys), but at least a third of immature Parasitic Jaegers overlap Long-tailed in these measurements. Long-tailed Jaeger also has a relatively longer tail, even without the projecting feathers. A combination of the above features, along with measurements, allows identification of all or nearly all specimens; careful observation in the field, even without measurements, should allow identification of many, but probably not all, immature jaegers.

DISTRIBUTION

Holarctic breeder (Fig. 1), extending farther south than either Pomarine or Long-tailed jaeger and not so far north as Long-tailed. Usually the least numerous of the three jaegers in the arctic. Most numerous in ne. Atlantic (perhaps also n. Pacific) in the vicinity of subarctic seabird colonies. Most birds spend the boreal winter at sea in the tropics or southern hemisphere, particularly in productive areas near coasts of Australia, South Africa, and South America.

THE AMERICAS

Breeding range. In Alaska, breeds along the entire arctic and west coasts, the Alaska Peninsula, and throughout the Aleutians. Breeding records are scarcer on the south coast but has nested on Kodiak I. and presence throughout the summer indicates possible breeding as far east as Glacier Bay (Gabrielson and Lincoln 1959, Johnson and Herter 1989). Breeds inland throughout Yukon-Kuskokwin delta and the arctic coastal plain as far south as the foothills of the Brooks Range, where breeding occurs at elevations of 150 m (Maher 1974) but not at higher elevations (Sage 1974). Analogy with n. Atlantic suggests that the densest populations might occur in the Aleutians near subarctic seabird colonies in areas without nesting Pomarine or Long-tailed jaegers; this species is indeed numerous in the Aleutian Is. (Murie 1959) but no reports of nesting on Pribilof Is. (Preble 1923).

In n. Canada, widely spaced but conspicuous throughout tundra regions of the mainland and southern arctic islands: widely scattered within 20–50 km of coast in n. Yukon (Salter et al. 1980); common in Mackenzie River delta (Porsild 1943, Martell et al. 1984); scattered pairs in Anderson River delta (Ryder 1971, Martin and Barry 1978); scarce in Perry River delta (Hanson et al. 1956); widely dispersed on Victoria and Jenny Lind Is. (Parmelee et al. 1967, Smith 1973); widespread on Southampton I. (Sutton 1932); scarce on Baffin I. (Soper 1928); common on west coast of Hudson Bay (Preble 1902). Also widespread in tundra south of the arctic coast: common around larger lakes in tundra north of Great Slave Lake (Seton 1908); but scarce near Thelon River east of Great Slave Lake (Clarke 1940). Breeds along coasts of Hudson Bay south at least to Cape Henrietta Maria, Ontario (Manning 1952).

Winter range. Poorly understood; because of difficulties in identifying small jaegers in Basic and immature plumages, some confusion is possible in reports of wintering jaegers.

Widely distributed off both coasts of South America (Wetmore 1926, Murphy 1936, Johnson and Goodall 1965, Cooke and Mills 1972, Brown et al. 1975, Escalante 1985). Observed repeatedly in Sargasso Sea in winter (Jespersen 1930); occasional reports from Gulf of Mexico, e. Florida, and throughout Caribbean Sea in winter (Stevenson 1959, Williams 1965, Duncan and Havard 1980, Raffaele et al. 1998).

OUTSIDE THE AMERICAS

Breeding range. In w. Greenland, breeds north to Disko I. (61–70°N) and near Thule (77.5°N); in e. Greenland, sparsely along the central coast (Manniche 1910, Nicholson 1930, Salomonsen 1950). In n. Europe, breeds in Iceland, Faeroe Is. and other n. Atlantic islands, n. Baltic Sea, coast of Norway, and in n. Scotland, especially on Orkney and Shetland Is.

Densest populations occur in Iceland and Scotland, areas without lemmings where neither Pomarine nor Long-tailed jaeger breeds.

Widely scattered along the Russian arctic coast and islands. Common on Kola Peninsula and Pechora Bay, nw. Russia, less numerous eastward along the arctic coast, common again on Kamchatka and Commander Is. From Taymyr Peninsula eastward in the Arctic, much less numerous than Long-tailed Jaeger (Dement'ev and Gladkov 1969, Kjellén 1997). On Taymyr Peninsula, breeds in small numbers throughout tundra regions, from 66–68°N to the arctic coast (Rogacheva 1992). Also breeds on Spitzbergen and Franz Josef Is. in Barents Sea (Dement'ev and Gladkov 1969) but scarce on eastern arctic islands, including New Siberian Is. and Wrangel I. (Dement'ev and Gladkov 1969, Portenko 1989, Kjellén 1997).

Winter range. Common near coasts of s. Africa from late Oct to early May, most numerous Jan to early Mar, when as many as 200 congregate behind trawlers over the continental shelf off Namibia (Lambert 1971, Ryan 1986, Ryan 1989). Along the desert coast of n. Namibia groups often roost on land (Ryan 1986). Absent from tropical and n. Atlantic in Jan (Lambert 1971). Occurs off s. Arabian Peninsula in winter, especially Gulf of Aden and Gulf of Oman (Bailey 1966); common in Persian Gulf (Løppenthin 1951). Not observed in w. Indian Ocean away from land Jan–Jun (Gill 1967). Common, although not so numerous as Pomarine Jaeger, off se. Australia, including Bass St. (Brooks 1939, Wood 1989).

HISTORICAL CHANGES

See Conservation and management: effects of human activity, below.

FOSSIL HISTORY

The scant information on fossil Stercorariidae is summarized by Olson (1985). Humerus close to that of Parasitic Jaeger reported from N. Carolina (Miocene or lower Pliocene). A number of jaegers and skuas have inhabited the n. Atlantic from Miocene onward.

SYSTEMATICS

GEOGRAPHIC VARIATION

No geographic variation in measurements, but pronounced geographic variation in proportions of dark and light morphs.

Plumage polymorphism. In general, dark morphs more common in southern populations; high proportions of dark birds (>75%) occur in Aleutian Is., n. Scotland, and Baltic Sea; low proportions of dark morphs (<25%) occur along the Siberian coast and islands, the arctic islands of Canada and n. Atlantic, and in Hudson Bay. No overall correlation with climatic parameters or with dependence on kleptoparasitism during nesting (Southern 1943). Nevertheless, at least in the ne. Atlantic, higher proportions of dark morphs occur in southern populations that rely more on kleptoparasitism.

In Aleutian and Commander Is., almost all birds are dark morph (Gabrielson and Lincoln 1959, Murie 1959); in ne. Alaska, 65% dark (*n* = 57; Andersson 1973). No geographic variation in proportions of morphs reported in Canada; overall 12% dark morph (*n* = 49 specimens in National Museum; Manning et al. 1956). In n. Canada, however, dark birds common in the interior (roughly 80%, Great Slave Lake; Preble 1908); along the mainland coast west of Hudson Bay, dark morphs less common but still constitute about half of all birds; the situation is similar in n. Labrador. On the arctic islands, Southampton I., and coasts of Hudson Bay, dark birds are almost absent (<5%, usually <1%; Bent 1921, Sutton 1932, Southern 1943, Manning et al. 1956).

In n. Atlantic colonies, dark morphs are more common farther south. Highest proportions occur in Baltic Sea and s. Norway (>95%) and in n. Scotland, Faroe Is., and Iceland (55–90%). In n. Norway morphs are about equally common (45–60% dark). In w. Greenland proportions of dark morphs constant along the entire coast 61–78°N (6%; Salomonson 1950). On Spitzbergen and ne. Greenland dark birds are almost or entirely absent (<1%; Southern 1943, Salomonsen 1950, Berry and Davis 1970, O'Donald 1983). On Kola Peninsula, nw. Russia, dark morphs predominate somewhat (50–65%); in marked contrast, light birds predominate (>95%) along the rest of the Russian arctic coast (Southern 1943, Dement'ev and Gladkov 1969, Portenko 1989, Kjellén 1997).

Proportions of morphs can vary markedly in limited areas. In Iceland, more dark morphs occur on the south coast than on the north (82–90%, 61–81%, respectively; Southern 1943, Berry and Davis 1970, Bengtson and Owen 1973, O'Donald 1983); proportion of dark morphs increased throughout Iceland between Southern's (1939–1943) and Bengston and Owen's (1970–1971) studies (O'Donald 1983). In n. Scotland (59–61°N), proportions of morphs vary among colonies without any predictable relation to latitude (Orkney Is., 58.7–59.4°N, 62% dark morphs; Fair I., 59.5°N, 79%; Shetland Is., 60–61°N, 72–74%); no changes over time (1934–1979; O'Donald 1983).

Fewer estimates for wintering populations: off se. Australia, about 50% dark birds (Wood 1989) or about 66% dark (Barton 1982)

Maintenance of polymorphism. This species has served as the subject of the most extensive studies of plumage polymorphism in any bird. At issue are both the maintenance of the genetic polymorphism in any one population and also clinal variation among populations. The principal hypotheses include (1) sexual selection and assortative mating, (2) differences in timing of breeding, (3) differences in thermoregulation, (4) aggressive camouflage by dark morphs, and (5) apostatic selection for the rarer morph (Furness 1987). In support of the first two hypotheses, O'Donald (1983) argued that the cline results from a gradient of selection (alleles for light morphs favored in the north, those for dark morphs in the south) combined with gene flow between areas. On Fair I., n. Scotland, where dark birds have an overall advantage as a result of earlier breeding and advantages in obtaining mates (see Behavior: sexual behavior, and Demography and populations: measures of breeding activity, below), polymorphism is stabilized by immigration of light birds from farther north.

In contrast, the last two hypotheses predict that the different morphs differ in success at kleptoparasitism, either because dark birds are less often detected by targets of attack or because the rare morph is less readily identified as a threat (Arnason 1978). Studies of five colonies in Scotland, Norway, and Iceland failed to reveal any differences between morphs in methods of attack or in success rate, regardless of which morph was rarer (Furness and Furness 1980, Götmark et al. 1981, O'Donald 1983, Caldow and Furness 1991). Likewise during migration, morphs appear not to differ in success rate in kleptoparasitism (Paterson 1986). Nevertheless, in Scotland, during a period of food shortage as a result of a drastic decline in availability of sandeels (*Ammodytes marinus*) for breeding seabirds, light morphs declined in relative abundance while their success rate increased (Caldow and Furness 1991). This result suggests that apostatic selection, as a result of frequency-dependent success in kleptoparasitism, might explain the persistence of this polymorphism.

SUBSPECIES

None described.

RELATED SPECIES

Most closely related to Long-tailed Jaeger, on the basis of morphological and molecular evidence (Schnell 1970, Cohen et al. 1997). Possibly isolated from other jaegers during periods of maximal glacial advance, either south of continental glaciers (Maher 1974) or in refugia north of the continental glaciers (de Korte and Wattel 1988).

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

Complete, long distance migrant between breeding range in Arctic and Subarctic and wintering range in tropical and southern temperate oceans. Often migrates near coasts but also far at sea and probably over land.

TIMING AND ROUTES OF MIGRATION

Near breeding areas. Unlike other jaegers, large movements rarely noted on arctic coasts: no movements evident at Barrow (Maher 1974); scarce migrant on north coast of Chukchi Peninsula (Portenko 1989). See also Breeding: phenology, below.

Instead migration to and from the North American Arctic probably occurs over land from the Atlantic and Pacific coasts. Evidence for overland migration is strongest in autumn. On Great Lakes, regularly observed in autumn: about 10–20 jaegers observed annually at promontories along the south coast or at the south end of each lake; as many as 42/yr on the south coast of Lake Ontario, 43/yr at the south end of Lake Michigan; 70–90% of birds identified to species are Parasitic Jaegers; 70% of these are immatures; most migrants observed between mid-Sep and mid-Oct; earliest dates in mid-Aug, latest in late Dec (Brock 1997, Sherony and Brock 1997). Most occur on days with strong northerly winds following passage of a cold front (Brock 1997, Sherony and Brock 1997). In lower St. Lawrence River, regular in late Aug and Sep (Belisle and Giroux 1995). In w. Lake Superior and Manitoba, occurs in small numbers almost annually, both adults and immatures, with most observations in Aug–Oct and late May–early Jun (Janssen 1987, Taylor 1993). Elsewhere in central North America and in Chesapeake Bay, occurs occasionally during Jul–Nov, mostly Sep, Oct (Wirenga 1976).

This evidence suggests that many migrants southbound from the Arctic shortcut over land from Hudson Bay to the Atlantic; a few, particularly immatures, stop briefly on the eastern Great Lakes (Sherony and Brock 1997); others seem to head for the Gulf of Mexico or possibly the west coast of Mexico, a few of which stop on the western Great Lakes.

Scarcity of spring records for se. Alaska suggests that northbound migrants either stay well offshore (Gabrielson and Lincoln 1959) or fly over land. On Great Lakes, very scarce and irregular in spring migration (Sherony and Brock 1997), perhaps an indication that adults pass quickly to the arctic, while immatures stay at sea.

Atlantic Ocean. Although most frequent near shore, migrants also occur far offshore, including in midocean. Spring migrants are scattered across the width of the North Atlantic in the middle two weeks of May (Wynne-Edwards 1935, Brooks 1939, Rankin and Duffey 1948). Autumn migrants first appear in late Aug, are most numerous in Sep, and are last recorded in Nov; after Sep all migrants are immature birds (Wynne-Edwards 1935, Rankin and Duffey 1948). Main southward movement thus occurs after that of Long-tailed Jaegers in Aug and before that of Pomarine Jaegers in Oct (Rankin and Duffey 1948, Brown 1986).

Leaves arctic waters by end of Oct; regular off w. Greenland and Baffin I. in Aug and Sep; most numerous off se. Canada in Sep (Brown et al. 1975, Brown 1986). Over the continental shelf off ne. U.S., uncommon and scattered during Sep–Oct (Powers 1983). Spring migrants return to waters off ne. U.S. and e. Canada in May (Powers 1983, Brown 1986).

In ne. Gulf of Maine, regular in small numbers in late May and early Jun and between late Jun and late Sep; few reports after Sep; more often observed than Pomarine Jaeger (Finch et al. 1978). On the continental shelf off New Jersey, Delaware, and Maryland, occurs in small numbers (usually <1/h) 23 Apr–16 May and 11 Aug–6 Dec, in all zones of the shelf, although perhaps most frequent over shallow water near shore (Rowlett 1980).

Off N. Carolina, least common of the jaegers offshore, but most common near shore. Spring migration occurs mostly from second half of Apr through May, in smaller numbers than in fall (mean count 0.4 birds/d in late May, n = 11 days of observation, otherwise scattered records, earliest specimen 29 Apr); fall migration occurs from the second half of Aug through Nov (mean counts 0.3–0.5/d in most 15-d periods during this time, except 1.3/d in first half of Oct, maximal count 7/d, n = 73 d of observation, latest specimens, 25 Nov, 5 Dec; Lee and Booth 1979, Lee 1995). Off N. Carolina, recorded on 30% of days of observation in May (n = 10 d), 6% in Jul (n = 18 d), 25% in Aug (n = 20 d), 30% in Sep (n = 10 d; N. Brinkley pers. comm., B. Patteson pers. comm.). Off eastern coast of Florida, northward migrants occur in small numbers mostly Apr–May; southward migrants occur mostly Sep–early Dec, less numerous than Pomarine Jaeger (few counts of >5/d; Stevenson and Anderson 1994).

Near Bermuda, occurs from late Mar to early Jun, with several/hour usually observed during early and mid-May; less numerous in autumn, between mid-Oct and late Dec (Amos 1991).

Regularly occurs in small numbers in n. Gulf of Mexico, where it outnumbers other jaegers. Some remain throughout winter; fewest records in Jul–Aug (Williams 1965, Duncan and Havard 1980). Jaegers (presumably mostly this species) are numerous here in Apr and Nov (0.7 and 1.2 observed/hour from ship; Williams 1965). Although these records have suggested overland migration to and from the arctic, the dates seem inappropriate. Direct flights to the arctic would take a few days, but birds do not arrive in the arctic until late May and depart by Sep.

In e. Atlantic, Parasitic Jaeger is a regular spring migrant in English Channel, mostly 28 Apr–16 May, when 10–30 observed/day; some large movements as early as 8 Apr (Davenport 1981). Northward movements also occur in early May past w. Ireland and Scotland (Davenport 1981). Regular migrant through the Baltic Sea in spring, with most birds passing in the second half of May (about 150 observed/yr; Hildén 1971). Migrants are clearly headed for the Russian arctic, because over 90% are light morph, whereas 95% of birds breeding in Baltic are dark (Hildén 1971). In Finland, regular migrant overland, between middle of May (average 17–18 May) and early Jun (Kapanen 1977). Scarce migrant in autumn in Baltic Sea (Hildén 1971, Cramp and Simmons 1983). In s. Spain, occurs regularly Sep–Dec, most numerous in Oct, but a few present in all months (Paterson 1986).

Recoveries of birds banded in Scotland suggest that adults have more restricted migration routes than immatures. Distant recoveries of adults are confined to the coasts of w. Europe and w. Africa; none has come from w. Atlantic or Mediterranean Sea. Immatures, however, have been recovered from both sides of South Atlantic and North Atlantic and from Mediterranean Sea (O'Donald 1983, Cramp and Simmons 1983). Birds banded as nestlings in Baltic Sea have been recovered in their first year in Egypt (Mediterranean coast), Ghana, and Brazil (Hildén 1971).

Pacific Ocean and elsewhere. Off w. Canada, occurs in small numbers in May and from mid-Jul through late Oct; highest numbers occur in last half of Aug and in late Sep (Vermeer et al. 1987, Morgan et al. 1991). Off Washington, occurs Apr–Jun (including 80% of offshore trips in May) and Aug–

Nov (74% of trips in Aug–Sep), but not so numerous as Pomarine Jaeger (Wahl 1975). Off California, occurs Aug–Nov and Mar–Apr; overall numbers are no more than one-tenth those of other jaegers (Briggs et al. 1987). Off Monterey Bay, central California, migrants occur from early Jul to early Oct (most in Aug) and in Apr (Stallcup 1990). Rarely reported in Japan, including offshore (Austin and Kuroda 1953). Arrives off se. Australia in Sep–Oct, becomes numerous by Nov–Dec, disappears abruptly in Apr or May (Barton 1982, Wood 1989).

In central Asia and se. Europe, regular in small numbers on large rivers and lakes; on Dnieper River, Ukraine, occurs mostly in Sep (occasionally Aug–early Nov) and in Apr or May (Dement'ev and Gladkov 1969). Occurs occasionally along rivers in taiga during spring migration (24 Apr–6 Jun); birds in the summer (29 Jun–25 Jul) are possibly returning migrants or wandering nonbreeders (Rogacheva 1992). Regular in Red Sea (Meininger and Sørensen 1986) and at Eilat, Israel, mostly Mar–May (Goodman and Storer 1987).

MIGRATORY BEHAVIOR

Migrants usually travel singly or in small groups (Sherony and Brock 1997, Hildén 1971, Davenport 1981), but occasionally gather into flocks of 12–65 (Davenport 1981). Migrants often stay close to shore and chase terns and gulls for food (Davenport 1975). Just before departure from se. Australia in late Apr, small groups (up to 6–7 birds) form 25–60 km offshore over the continental slope (Barton 1982).

In a headwind migrants fly close to the surface of the water, flapping steadily, sometimes rising to bank above the crests of waves (Sherony and Brock 1997); otherwise they often take a straight course 8–10 m above the water. Migrants in mid-Atlantic often accompany migrating Arctic Terns (*Sterna paradisaea*); these terns rarely feed in midocean and the jaegers only occasionally chase them (Wynne-Edwards 1935).

CONTROL AND PHYSIOLOGY

No information.

HABITAT

BREEDING RANGE

Breeds in a wider range of arctic habitats than the other two jaegers.

In n. Alaska, occupies both low-lying marshy tundra and drier tussock-heath tundra, near the coast and inland to foothills and passes of the Brooks Range (Maher 1970, 1974). Nests usually placed in low-lying marshy tundra, with sedge meadows, low-center polygons, and sphagnum or frost mounds, often near a lake, river, or coast (Brandt 1943, Parmelee et al. 1967, Maher 1974, Taylor 1974, Portenko 1989). Differs from Long-tailed Jaeger in its preference for nesting near a body of water (Maher 1974). In coastal tundra of n. Yukon, found at 17 of 60 lakes surveyed (Salter et al. 1980). In late summer visits riparian vegetation, dominated by shrubby willows, which provide habitat for juvenile passerines hunted by these jaegers (Maher 1974).

In ne. Greenland, breeds near mouths of fjords and along the outer coast, usually near lakes, unlike Long-tailed Jaeger, which usually breeds farther inland (Pedersen 1926, Bannerman 1963). In Iceland, by contrast, breeds throughout much of the island to elevations of 700 m, often in marshy depressions, but also on uplands with low shrubs, lava flows, sandy or gravelly flats in fjords, and on outwash plains of glaciers (Bannerman 1963). In Faroe Is., breeds in swampy areas with small lakes (Perdeck 1963). In n. Scandinavia, pairs with large territories prefer lower, wet areas rather than the higher, dry areas favored by Long-tailed Jaegers (Andersson and Götmark 1980). In n. Russia, nests throughout the tundra, from shrub tundra to polar deserts, but is most numerous in tundra with patches of low birches and willows (Rogacheva 1992). In n. Scotland, where other jaegers do not occur, occupies upland stony tundra and patches of bare ground, moss, and grasses (O'Donald 1983); prefers areas with shorter vegetation than does Great Skua (*Catharacta skua;* Ewins et al. 1988).

MARINE RANGE

More often observed in migration near shore and in estuaries than other jaegers. Most common jaeger observed from land in e. U.S.; often frequents inlets between barrier islands were terns congregate. Off N. Carolina, less numerous than other jaegers more than a few kilometers from shore (Lee 1995). Off w. Canada, mostly at or beyond the edge of the continental shelf (Vermeer et al. 1987, Morgan 1991). Off Washington State, 20% of observations are <10 km from shore (compared to only 7% of the more numerous Pomarine Jaegers; Wahl 1975). Off California, occasionally as far as 75 km offshore, although most are found within 15 km of shore (Briggs et al. 1987). Off Monterey Bay, central California, most occur within 3 km of shore or in estuaries, often with terns or small gulls (Stallcup 1990). Nevertheless, migrants occur in midocean as well (see Migration: timing and routes of migration, above). Off se. Australia, unlike other jaegers, occurs mostly within 10 km of land (about 4 observed/h from ship); it is scarce beyond 20 km and absent beyond 50 km (Barton 1982, Wood 1989).

FOOD HABITS

FEEDING

Main foods taken. Breeding populations differ in their primary sources of food: some depend mostly on hunting for birds, eggs, and rodents; others depend on kleptoparasitism of colonial seabirds. Unlike other jaegers, this species has a minor role as a predator on lemmings (Maher 1974, Taylor 1974). In some areas of the Arctic, on the other hand, it is the most important predator of passerines and small shorebirds and, along with Glaucous Gull (*Larus hyperboreus*) and arctic fox (*Alopex lagopus*), also of birds' eggs.

Breeders take fledgling and adult passerines, shorebirds, ducks, and terns (Preble 1908, Seton 1908, Summerhayes and Elton 1923, Pleske 1928, Sutton 1932, Clarke 1940, Venables and Venables 1955, Parmelee et al. 1967, Hussell 1972, Salter et al. 1980), birds' eggs of many species (Summerhayes and Elton 1928, Bailey 1948, Løvenskiold 1964, Campbell 1990), insects (Preble 1908, Løvenskiold 1964, Taylor 1974), fish (Preble 1908, Pedersen 1926, Løvenskiold 1964, Dement'ev and Gladkov 1969), berries (Turner 1886), offal along shores and carrion (de Korte 1972). In n. Alaska breeders concentrate on birds and sometimes rodents for food (Maher 1974, Taylor 1974, Pedersen 1926). In the interior of Canada, often feeds on carrion and ground squirrels (genus *Spermophilus*, Seton 1908). Nonbreeders in n. Alaska take a more diverse diet than do breeders (Maher 1974).

Near colonies of nesting seabirds, especially in ne. Atlantic (possibly also in n. Pacific), kleptoparasitism provides the primary source of food (Pedersen 1926, Løvenskiold 1964). Wintering birds also obtain most of their food by kleptoparasitism. See separate section, below.

Microhabitat for foraging. In n. Alaska, most food obtained on upland tundra, but pairs also hunt for juvenile passerines in willows along rivers (Maher 1974).

Food capture and consumption. This jaeger is among the few predatory birds in which breeding pairs often cooperate in hunting, although demands of defending the nest and chick constrain the time available for cooperative hunting. During incubation, birds hunt alone when not on the nest. When the first chick hatches, the parent remaining near the nest often begs from the other, which regurgitates food. Pairs sometimes cooperate to pull prey apart and then both partake. In n. Yukon, the parent remaining near the nest sometimes leaves to join its partner in hunting (Martin and Barry 1978). In n. Alaska, in contrast, pairs feeding chicks usually hunt together and leave chicks unguarded (Maher 1974). In n. Scandinavia, pairs with large territories leave chicks unattended only 4% of time and are not reported to hunt together; those in colonies almost never leave chicks unguarded (<1% of time; Andersson and Götmark 1980). See Breeding: parental care, below.

When hunting alone over tundra, usually flies slowly 1–3 m above ground, sometimes hovering briefly (1–2 s, much shorter than Long-tailed Jaegers), scrutinizing the ground for prey (Sutton 1932, Andersson and Götmark 1980). Also uses low rises in the ground for cover in order to approach flocks of shorebirds in the arctic and take them by surprise (Sutton 1932). Flocks of small shorebirds flush immediately when approached by one of these jaegers, but the jaeger usually ignores them unless a pair can separate a target from the flock (Sutton 1932).

When hunting passerines or shorebirds, pairs often work together. After one initiates pursuit in the air, the other joins; one partner often chases the prey near the ground while the other remains about 6–10 m above to intercept upward dodges; the two pursuers often change roles. If the prey alights in grass, one lands to stalk the prey on the ground, while the other hovers overhead to resume aerial pursuit if necessary (Clarke 1940, Martin and Barry 1978, Pruett-Jones 1980). Sometimes a pair forces a longspur higher and higher in the air, until one can grab it (Sutton 1932). By alternating attacks, a pair can even kill a 680 g Willow Ptarmigan (*Lagopus lagopus*; Eisenhauer and Paniyak 1977). Once a kill is made, the pair shares in plucking the prey and in holding it while the partner pulls off pieces (Sutton 1932, Pruett-Jones 1980).

Pairs also cooperate in stealing eggs; alternating attacks can allow a pair to rob all 3 eggs in a nest vigorously defended by a Glaucous Gull (Gabrielson and Lincoln 1959). Goose eggs are particularly vulnerable before incubation begins; during incubation, geese are sometimes harassed by these jaegers, sometimes in groups, trying to drive them from their nests, usually unsuccessfully (Angstadt 1961, Martin and Barry 1978). These jaegers quickly take advantage of any disturbance in a goose colony—by eagle, airplane, fox, bear, or human—to prey on eggs left exposed by frightened geese (MacInnes and Misra 1972, Mickelson 1975, Martin and Barry 1978, Strang 1980).

Loon eggs are also regularly taken by these jaegers in some areas. In Iceland, where about 50% of Red-throated Loon (*Gavia stellata*) eggs are lost to Parasitic Jaegers, jaegers apparently learn where to search for loons' nests. Experimental tests with artificial nests showed that jaegers search for eggs preferentially along the edges of lakes and in locations where taxidermic mounts of loons have been placed (Enquist 1983). Also takes eggs of cliff-nesting seabirds, including murres (genus *Uria*) and Black-legged Kittiwakes (*Rissa tridactyla*, Spitzbergen and Bear I.; Summerhayes and Elton 1928).

Few birds are able to drive away marauding Parasitic Jaegers; exceptions include a single Whimbrel (*Numenius phaeopus*) on one occasion. In addition, mobbing by colonial Arctic Terns effectively prevents predation on their eggs by Parasitic Jaegers (Summerhayes and Elton 1928, Sutton 1932, Bannerman 1963).

Jaegers not mated sometimes hunt together when prey is flushed; there is then no cooperation in the pursuit or in feeding (Sutton 1932, Pruett-Jones 1980); it is nevertheless possible that several jaegers hunting together would have higher success in flushing potential prey than do single birds. Nonbreeders often join flocks of all three jaegers foraging over the tundra near Barrow in Jul (Maher 1974).

Also walks through grass apparently catching insects (Martin and Barry 1978). Catches small fish from tidal pools and lakes or from dense schools at sea by dipping into the water while swimming or plunging from flight, although unable to get far under water (Bent 1921, Sutton 1932, Løvenskiold 1964). When hunting tundra voles (*Microtus oeconomus*), uses outstretched wings to herd prey, while hopping and lunging at them (Childs 1969).

On migration and in winter, feeds by swooping and plucking scraps from the surface behind boats, by predation on crustaceans (*Gammarus* spp.) taken on foot on tidal flats or on small birds chased in flight, but mostly relies on kleptoparasitism of other seabirds for food (Watson et al. 1971, Barton 1982, Spear and Ainley 1993, Belisle and Giroux 1995; see kleptoparasitism, below). Less likely to approach boats or to follow wakes than the other two jaegers (DSL).

In the lower St. Lawrence River, migrants also regularly prey on small sandpipers, occasionally on Red Knot (*Calidris canutus*), Ruddy Turnstone (*Arenaria interpres*), and Black-bellied Plover (*Pluvialis squatarola*). Sandpipers hiding in vegetation or flying alone are more vulnerable than birds in flocks (40%, 25%, and 15% successful hunts, respectively). Prey are caught by grasping or striking them with beak or wing or by forcing them into the water or ground. A pair of jaegers hunting together has no greater success than single jaegers (17% success overall), although they share the kills. After a successful hunt, jaegers are vulnerable to kleptoparasitism by larger gulls, usually Herring Gulls (*Larus argentatus*); single jaegers have 75% of their prey stolen, but pairs lose only 42% of their kills (Belisle and Giroux 1995).

Kleptoparasitism. All nonbreeders and most breeders in the ne. Atlantic obtain most of their food by stealing it from other seabirds. Together with frigatebirds (Fregatidae), they are the most specialized kleptoparasites among birds.

Breeders in arctic North America, however, do not regularly steal food from other species, although occasional targets include Glaucous Gulls, Arctic and Red-throated loons, Arctic Terns, and Sabine's Gulls (*Xema sabini*; Eisenhauer and Paniyak 1977, Martin and Barry 1978, Ryder 1957). Juvenals make their first attempts at kleptoparasitism almost as soon as they can fly, at which time Glaucous Gulls sometimes reverse the tables to steal food from Parasitic Jaegers (Martin and Barry 1978). Parasitic Jaeger has never been studied near large seabird colonies in the Aleutians, where they might rely on kleptoparasitism, as do populations in the ne. Atlantic.

In ne. Atlantic, breeders often congregate in loose colonies near large concentrations of nesting seabirds and specialize in kleptoparasitism. In ne. Greenland, targets are usually Arctic Terns and Thick-billed Murres (*Uria lomvia*), occasionally Glaucous Gulls (Pedersen 1926); in Spitzbergen, Black-legged Kittiwakes and less often Black Guillemots (*Cephus grylle*) and Dovekies (*Alle alle*; Løvenskiold 1964, de Korte 1972); in Baltic Sea, Caspian Terns (*Sterna caspia*; Forssgren 1981). In nw. Russia, targets include Black-legged Kittiwakes, murres, Puffins, and Black Guillemots; apparently each colony of Parasitic Jaegers concentrates on one of these targets even when others are available (no statistical comparisons provided; Belopol'skii 1961).

In n. Scandinavia, jaegers parasitizing Black-legged Kittiwakes fly 1–5 m above the sea to intercept birds returning to their nests with full crops. Those parasitizing Common Murres (*Uria aalge*) fly much higher, 20–25 m above water, and stoop on their targets from above. Because murres carry fish in their beaks, suitable targets are easier to detect from above (Andersson and Götmark 1980).

In n. Scotland, parasitizes primarily Arctic Terns and less frequently Black-legged Kittiwakes and Atlantic Puffins (*Fratercula arctica*); in contrast, the sympatric Great Skua parasitizes mostly Common Murre, Razorbill (*Alca torda*), Altantic Puffin, and Northern Gannet (*Sula bassanus*; Furness 1978). Success rates of chases at four sites varied from 13–28%, without any consistent differences between target species (Furness and Furness 1980).

In s. Iceland and n. Scotland, some colonies obtain food mostly by parasitizing Atlantic Puffins; hatching of jaegers coincides with that of puffins. Jaegers patrol cliffs with nesting puffins and approach incoming puffins. Successful chases last 12.3 s ± 1.6 SD ($n = 18$); an individual jaeger obtains food on average every 6.3 min of hunting. Puffins try to escape either by reaching their burrows or by dropping to the sea and diving. About one third of all chases include >1 jaeger; group chases have higher overall success in forcing puffins to drop fish (79% and 63% success, respectively), but success rate/individual decreases with additional participants. When puffins drop fish on or near shore, gulls and Common Ravens (*Corvus corax*) compete with jaegers for the fish (Grant 1971, Andersson 1976, Arnason and Grant 1978).

Migrants routinely harass other species to force them to relinquish their food. In Alaska, targets are usually Arctic Terns, Sabine's Gulls, and Black-legged Kittiwakes, but even large gulls are attacked (Gabrielson and Lincoln 1959, Davenport 1975). Off s. Alaska, 1–2 Parasitic Jaegers join most large flocks of Sooty Shearwaters (*Puffinus griseus*) and Black-legged Kittiwakes feeding on persistent spawning congregations of capelin (*Mallotis villosus*). Ephemeral flocks of these species feeding on other fish rarely attract a jaeger (Hoffman et al. 1981). Elsewhere rarely attacks shearwaters (Wynne-Edwards 1935).

In the lower St. Lawrence River, migrants parasitize Arctic Terns, Black-legged Kittiwakes, and Ring-billed Gulls (*Larus delawarensis*). Arctic Terns are preferred as targets, and success rates are higher with terns (46%) than with kittiwakes or gulls (20%). Success rates with terns increase with the number of jaegers participating; in contrast, success rates with gulls decrease (Belisle and Giroux 1995).

In e. Scotland, migrants chase terns feeding on herring (*Clupea harengus*) in estuaries; attacks consist of rapid approach (estimated to reach 80 km/h) just above the water behind the fleeing tern, a swoop upward at the tern, and a brief tortuous pursuit. Success rates depend on the species of tern: 32%, 17%, and 6% for Arctic Tern, Sandwich Tern (*Sterna sandvicensis*), and Common Tern (*S. hirundo*), respectively. Jaegers show corresponding preferences in selecting targets. Success rates increase when >1 jaeger joins (20% of chases); success/individual pursuer is greatest with 2 pursuers, especially for Arctic Terns (overall success rate increases to 100%, individual success to 50%); nevertheless these migrant jaegers do not hunt together but opportunistically join chases begun by others (Taylor 1979). In s. Spain, migrants attack Black-headed Gulls (*Larus ridibundus*) and Sandwich Terns, but also Mediterranean Gulls (*L. melanocephalus*) and Herring Gulls (Paterson 1986).

During fall and spring in e. tropical Pacific, kleptoparasitism accounts for 86% of all feeding attempts by "small jaegers" (Parasitic and Long-tailed jaegers reported to have similar behavior); targets include storm-petrels (Hydrobatidae), especially Leach's Storm-Petrel (*Oceanodroma leucorrhoa*), terns and small gulls (Laridae), especially Sooty Tern (*Sterna fuscata*; Spear and Ainley 1993).

Wintering birds in s. Africa frequent sites, such as an offshore sewerage outfall, where breeding and migrant gulls and terns forage regularly, about one jaeger/100–200 potential targets. Targets (Silver Gull [*Larus novaehollandiae*], Sabine's Gull, Common Tern) reflect the numbers in the area (Furness 1983). About 25% of chases are successful, regardless of species. Although some chases are joined by a second jaeger (30%) or by a Kelp Gull (17%), these chases were no more successful than single chases (Furness 1983, Ryan 1986).

In coastal waters of se. Australia, >90% of foraging consists of chasing breeding Silver Gulls feeding behind fishing boats. Other targets include Crested Terns (*Sterna bergii*), White-fronted Terns (*S. striata*), Australasian Gannets (*Sula serrator*), and Fluttering Shearwaters (*Puffinus gavia*; Wood 1989).

The migrations of Parasitic Jaegers are thus closely coordinated with opportunities for kleptoparasitism. During autumn and spring, they follow migrating terns and gulls (Furness 1983). During the boreal winter, they parasitize breeding gulls in the southern hemisphere, much as they parasitize breeding Black-legged Kittiwakes in the northern hemisphere during the boreal summer.

DIET

Major food items. Throughout n. Alaska and Canada, breeders rely mostly on passerine birds and secondarily on rodents, in marked contrast with both other jaegers in this region (Sutton 1932, Clarke 1940, Parmalee et al. 1967, Maher 1974, Taylor 1974, Martin and Barry 1978). In n. Russia, breeders take mostly lemmings when these are abundant, but mostly small birds when lemmings are scarce (Belopol'skii 1961, Dement'ev and Gladkov 1969), a pattern that might apply in the Nearctic as well. Breeders that rely on parasitizing colonial seabirds have a diet that reflects that of their principal targets, primarily fish and planktonic crustaceans (Belepolsk'ii 1961, de Korte 1972).

Adult passerines taken as well as young; nonpasserine prey are usually chicks or fledglings, except for phalaropes (*Phalaropus* spp.) and the smallest sandpipers (*Calidris* spp.). Passerine prey is mostly Lapland Longspur (*Calcarius lapponicus*) but also includes American Pipit (*Anthus americanus*), Yellow Wagtail (*Motacilla flavus*), Horned Lark (*Eremophila alpestris*), Northern Wheatear (*Oenanthe oenanthe*), Savannah Sparrow (*Passerculus sandwichensis*), Hoary Redpoll (*Acanthis hornemanni*), and Snow Bunting (*Plectrophenax nivalis*). Nonpasserine prey includes plovers (*Pluvialis*), sandpipers, dowitchers (*Limnodromus*), phalaropes, Willow Ptarmigan, Common Eider (*Somateria mollissima*), and other ducks (Summerhayes and Elton 1923, Congreve 1930, Sutton 1932, de Korte 1972, Maher 1974). Along the Yukon coast in Aug, associates with flocks of Red Phalaropes (*Phalaropus fulicarius*), which are frequently hunted (Salter et al. 1980). On Spitzbergen in Aug, preys heavily on fledging Dovekies (Løvenskiold 1964).

In n. Alaska, mammalian prey includes both brown lemming (*Lemmus trimucronatus*) and collared lemming (*Dichrostonyx groenlandicus*), tundra vole, arctic shrew (*Sorex arcticus*), ermine (*Mustela rixosa;* Maher 1974), and arctic ground squirrel (*Spermophilus arcticus;* Nelson 1887, Gabrielson and Lincoln 1959). The diet of breeders also includes birds' eggs, insects, berries, and seeds (Maher 1974). Near Barrow, AK, breeders evidently rely on fish and carrion, as well as birds and lemmings (Pitelka et al. 1955, Maher 1974). On Victoria and Jenny Lind Is., feeds on lemmings, especially when easily found, small birds, insects and spiders, and eggs of Rock Ptarmigan (*Lagopus mutus*); attempts to take eggs of Snow Goose (*Anser caerulescens*) and Red-throated Loon (Parmelee et al. 1967). On Bathurst I. feeds mostly on collared lemmings, young Sanderlings (*Calidris alba*) and Red Phalaropes, eggs of King Eider (*Somateria spectabilis*), carrion, and insects (Taylor 1974). In the Anderson River delta, breeders take many passerines, but also shorebirds, carrion, and eggs of many species (Martin and Barry 1978).

Proportion of birds' eggs in the diet is difficult to assess because these jaegers often eat eggs without ingesting the shells. Perhaps takes any eggs available. In s. Alaska, takes eggs of Canada Goose (*Branta canadensis;* Campbell 1990); in the Anderson River delta, eggs of loons, Tundra Swan (*Cygnus columbianus*), three species of geese, several ducks, Whimbrel, Glaucous Gull, Willow Ptarmigan, and Lapland Longspur (Martin and Barry 1978); on Spitzbergen, eggs of geese, eiders, loons, and cliff-nesting seabirds (Summerhayes and Elton 1923, Løvenskiold 1964); in nw. Russia, eggs of eiders and Herring Gull (Dement'ev and Gladkov 1969).

When readily available near the nest, breeders also eat substantial quantities of berries (*Vaccinium, Rubus,* and *Empetrum* spp.; Murie 1959, Martin and Barry 1978) and on occasion insects (Martin and Barry 1978).

Near large seabird colonies in Aleutian Is., diet frequently includes Fork-tailed Storm-Petrels (*Oceanodroma furcata*) and several species of auklets and murres (Alcidae), presumably obtained as carrion from kills by large gulls (Murie 1959).

Nonbreeders in n. Alaska are opportunistic in foraging and take birds, rodents, birds' eggs, fish, insects, crabs and other crustaceans, and carrion (Maher 1974, Portenko 1989). Birds include passerines, phalaropes, and small sandpipers; eggs include those of Red Phalarope (Maher 1974). Insects rarely constitute a substantial proportion of prey (Maher 1974). Stomachs of migrants on St. Lawrence I. contained bits of unidentified marine invertebrates and berries (Fay and Cade 1959).

Quantitative analysis. In foothills of the Brooks Range, birds constituted 82% (75–88% in 3 yr) and rodents 16% of items in breeders' pellets during 3 yr. Passerines alone amounted to 45–75% of items (mean 65%); shorebirds 7–20% of items and varied inversely with passerines. Microtine rodents accounted for 11–21% of items and also varied inversely with passerines. Berries (*Vaccinium, Rubus*) and seeds also constituted important sources of food in Aug. Around lakes in the Brooks Range, the diet includes an even higher proportion of birds (87% passerines, 6% shorebirds; Maher 1974). In the Anderson River delta, 85% of 173 pellets contained remains of birds (81% passerines, all others shorebirds), rodents only in 25%, fragments of eggshells in 16% (Martin and Barry 1978).

Even in an area with a dense population of tundra voles, breeders relied mostly on birds (75%, nearly all passerines) but voles constituted nearly all of the remainder of the diet (25%, nw. Alaska; Maher 1974). At Barrow, items in pellets from one nest included fewer birds (28%) than mammals (mostly brown lemming, 72%); these birds probably ate substantial amounts of fish and carrion also (Maher 1974).

Of passerines identified in pellets in Alaska, most are Lapland Longspur (62%), one of the most abundant passerines available in this jaeger's habitat. Secretive species, like Savannah Sparrow, and flocking species, like Hoary Redpoll, seem less frequent in this jaeger's diet than their abundance would suggest. Of shorebirds, the most common prey were Pectoral Sandpiper (*Calidris melanotos*), Baird's Sandpiper (*C. bairdii*), and Semipalmated Sandpiper (*C. pusilla;* 28%, 28%, and 18%, respectively); juveniles constituted 68% of all shorebirds eaten. All of the large shorebirds (Pectoral Sandpiper and larger), as well as all ducks and ptarmigan, were juveniles; in contrast the small shorebirds were either all adults (both phalaropes) or evenly divided between adults and juvenals. Thus unlike Long-tailed Jaeger, this species regularly preys on adults of the smaller species of shorebirds (Maher 1974).

In n. Scandinavia, pairs defending large territories in years with low or moderate densities of rodents fed mostly on birds and berries (50 and 34% of pellets, respectively, *n* = 32) with rodents, insects, fish, and birds' eggs also represented (10–25% of pellets); fish were probably obtained by occasional kleptoparasitism; pairs nesting in colonies relied more on kleptoparasitism (Andersson and Götmark 1980).

On Kola Peninsula, nw. Russia, adults ate fish (in 40% of 602 stomachs, berries (25%), birds' eggs

(17%), and insects (13%), with voles, birds, and marine invertebrates making up the remainder; males and females had similar diets; nestlings ate fish (56% of 24 stomachs) and insects (33%; Belopol'skii 1961). Food regurgitated to nestlings on Kola Peninsula ($n = 24$ food masses) included insects (23), fish (11), grass (14), and egg shells (2; Dement'ev and Gladkov 1969). In s. Yamal Peninsula, in contrast, diet depended strongly on availability of rodents: when voles were abundant, they constituted 85% of items in 372 stomachs; when voles were scarce, birds (51% of items in 69 stomachs), voles (32%), and berries (10%) constituted most of the items; birds' eggs, fish, and insects were infrequent in stomachs (Belopol'skii 1961).

Almost no quantitative information is available for diets of nonbreeders. In n. Alaska 32 stomachs from nonbreeders contained birds (28%), eggs (28%), microtine rodents (22%), insects (30%), fish (22%), and marine invertebrates, seeds, and carrion (<10% each; Maher 1974). Also no quantitative studies of diet away from breeding areas, but since kleptoparasitism is the primary source of food, diet must reflect that of the seabirds that constitute their targets.

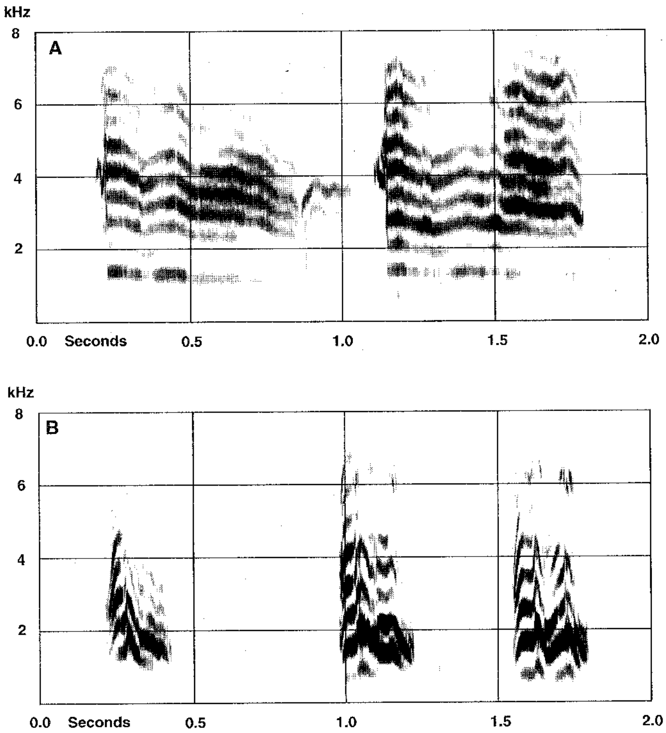


Figure 2. A. Long Call (in part) of the Parasitic Jaeger. B. Short Calls of the Parasitic Jaeger. From Peterson's Western Bird Songs. Prepared by the staff of the Borror Laboratory of Bioacoustics, The Ohio State University.

FOOD STORAGE

No reports of food storage.

NUTRITION AND ENERGETICS

Durations and success rates for kleptoparasitism of Atlantic Puffins suggest that a Parasitic Jaeger needs to chase 37 puffins for a total of 7.3 mins to obtain the 15 fish needed to satisfy its daily energy requirements (Arnason and Grant 1978, O'Donald 1983). Incubating females retain 4–5% additional mass, apparently as a reserve of energy, which is quickly lost once eggs hatch (Phillips and Furness 1997; see Measurements: mass, below).

METABOLISM AND TEMPERATURE REGULATION

Core temperature, 40.4°C (41.8–42.2, $n = 2$, Platania et al. 1986). Usually has moderate to heavy stores of subcutaneous fat during summer (de Korte 1972).

DRINKING, PELLET CASTING, AND DEFECATION

No information available.

SOUNDS

VOCALIZATIONS

Development. No information available.

Vocal repertoire. No quantitative study of variation in calls; many calls with different verbal descriptions (Cramp and Simmons 1983) might represent intergrading variants of a few basic vocalizations. Long Call consists of 1–12 (usually 3–4) bisyllabic notes at a rate of about 1.3 notes/s (Perdeck 1963, Cramp and Simmons 1983, Furness 1987, Fig. 2A); differs from similar call of Long-tailed Jaeger in predominantly rising rather than falling pitch (Andersson 1971); uttered from ground or in flight, in response to passing conspecifics; also uttered at the end of Pursuit Flight when rivals separate to return to their territories (O'Donald 1983). Short Call consists of staccato notes in irregular sequence; often precedes Long Calls; also occurs during aerial pursuits, during swoops at opponents, and in response to an attacker (Perdeck 1963, Fig. 2B). Yelp Call, variable piercing sound like a small dog, sometimes repeated, produced by birds under attack and in response to predators (Perdeck 1963). Only one form of alarm call, unlike Long-tailed Jaeger, which has different calls for aerial and terrestrial predators (Andersson 1971). Also a harsh scream in uncertain circumstances (Perdeck 1963).

Calls also include male's Copulation Call; female's Purring Call during copulation; Squeaking Call, a hissing sound with a squeak at the start, during nest-building; Begging Call during courtship feeding; and a Nest Call, a nasal doubled note (Perdeck 1963, O'Donald 1983). Squeaking and Begging calls are only slightly different, unlike in Great Skua, and occur in overlapping situations (Perdeck 1963). See Behavior: sexual behavior, below.

Figure 3. Parasitic Jaeger in Intimidated Upright Posture (left) and Aggressive Upright Posture (right). Drawing by N. John Schmitt.

Calls during Distraction Display resemble mewing of kitten (Williamson 1949, Portenko 1989) and Begging Call by young and by females during courtship feeding.

Birds feeding on offal at sea utter high-pitched *weet, weet* when near conspecifics, but this species much less vocal than Pomarine Jaeger in similar situations. Silent when pursuing other species (Barton 1982).

NONVOCAL SOUNDS

None reported.

BEHAVIOR

LOCOMOTION

Flight. Migrants usually fly directly either near the surface or as high as 5–10 m above the surface. More agile than Pomarine Jaeger in kleptoparasitic chases (Wood 1989, Spear and Ainley 1993).

Swimming and diving. Swims readily; no reports of diving.

SELF-MAINTENANCE

No information available.

AGONISTIC BEHAVIOR

From Perdeck (1963) except as noted. Territorial birds on the ground react to a conspecific intruder on the ground by adopting an Aggressive Upright posture, with neck extended vertically and beak horizontal (occasionally angled downward), a posture similar to the one an alert bird adopts when approached by a predator. Often this display alone discourages further intrusion; otherwise, the displaying bird approaches or performs Long Calls and sometimes pecks the intruder with its beak. The threatened bird adopts an Intimidated Upright posture, with extended neck somewhat behind vertical and beak angled upward, usually followed by escape. A territorial bird performs Long Calls with neck extended either obliquely or vertically, depending on whether an intruder is approaching in the air or on the ground, with beak either obliquely upward or horizontal, and with side to side movements of the head to fix the opponent with each eye alternately. Unlike similar posture in many gulls, carpal joints are not raised, perhaps because wings are not used in fighting. Unlike Long-tailed Jaeger, beak not usually angled downward in Upright postures (Andersson 1971). Aggressive encounters occasionally include pecking at the ground or intensive preening.

Often an intruder on the ground is attacked from the air. The attacker performs swoops from above, which can occur at high speed and involve striking the opponent with feet. When the attacked bird is on the ground, it crouches, faces its swooping rival, and often jumps upward toward the rival; the two birds strike each other with their feet, the lower bird performing a somersault just above ground in order to confront its rival with its feet. A swooping bird utters Short Calls during descent, Long Calls as it soars away. After repeated swoops, a bird sometimes tries to land and then is attacked by its rival. During fights on the ground, two birds face each other, jump upward with flapping wings, and strike each other with their feet. More often an attacked bird flees, and long pursuits can follow.

Pursuits involve high speed and steep dives, with each bird attempting Swoops at the other from above and the lower bird rolling over in the air to meet its opponent with its feet. Attacking birds often utter Short Calls; attacked birds seeking escape utter Yelp Calls. After swoops or pursuits, birds often utter Long Calls while soaring with wings horizontal (unlike downward bowing of wings by Long-tailed Jaegers; Andersson 1971). Shortly after first arrival on breeding areas, several birds sometimes join in aerial pursuits and displays (Perry 1948).

In comparison to Great Skua, aerial displays and vocalizations are more elaborate and ground displays less elaborate (no Oblique, Bend, or Wing-raising displays).

SPACING

Intraspecific territoriality. Territory sizes depend on a population's primary source of food: larger for predation, smaller for kleptoparasitism. Where breeders mostly hunt for food, in n. Alaska, nests are spaced 1.1–4.1 km apart (Maher 1974); in Anderson

River delta, 0.9–7.3 km apart (Martin and Barry 1978); on Bathurst I. at least 2.3 km apart (Taylor 1974). Because all three jaegers defend territories against each other, in areas where Parasitic Jaegers are the least numerous, pairs rarely have conspecific neighbors. Pairs consistently defend only a core area around the nest (Maher 1974, Martin and Barry 1978). In n. Alaska, intruding conspecifics beyond a core area 400–600 m in diameter are challenged opportunistically; boundaries are not regularly patrolled (Maher 1974). In Anderson River delta, pairs not observed to challenge conspecifics beyond a core area 200–300 m in diameter; instead pairs often joined other jaegers to hunt there (Martin and Barry 1978). Some hunting occurs in the core area but mostly in outer portions of the territory or beyond (Maher 1974) as far as 3 km (Parmelee et al. 1967, Martin and Barry 1978) or 5 km from nest (Taylor 1974). Territorial defense continues until late Aug or early Sep (Maher 1974). In n. Scandinavia, pairs with large territories foraged over areas averaging 0.95 km^2 (Andersson and Götmark 1980).

Migrants on occasion defend territories in small coastal bays within which other jaegers, large gulls, and raptors are attacked. In the lower St. Lawrence River, 42% of attacks by territorial birds were directed at other Parasitic Jaegers (Belisle and Giroux 1995, see also Barton 1982).

Interspecific territoriality. Wherever this species nests near other jaegers, it defends exclusive territories (Maher 1974, Taylor 1974). When Parasitic Jaegers nest among Long-tailed Jaegers, nests are evenly spaced, regardless of species (Maher 1974). In foothills of n. Alaska, mean distance to other (usually Long-tailed) jaeger nests is 1,200 m ($n = 26$), on coast at Cape Sabine 730 m ($n = 8$; Maher 1974). In n. Scotland, territories are defended vigorously against Great Skuas, even after young have fledged. Great Skuas establish territories earlier than Parasitic Jaegers; jaegers, although much more agile in flight, cannot displace established skuas (O'Donald 1983).

Coloniality. In areas where Parasitic Jaegers obtain most of their food by kleptoparasitism, territories are much smaller (see above) and often clustered into loose colonies. On islands in North Atlantic, colonies often include several hundred closely spaced pairs. No such colony reported in arctic North America or in arctic Russia.

Distances between nests in Faroe Is., 30–140 m (60%, 30–60 m). On Fair I., n. Scotland, minimal distance between nests 30 m. If each pair's territory is defined as the area closer to its nest than to any other nests, these areas average about 11,000 m^2 (0.011 km^2, $n = 113$) and do not differ with males' ages or plumage morphs (O'Donald 1983, *contra* Davis and O'Donald 1976) but do correlate with hatching date ($r = -0.23$, $n = 100$). Indirect evidence suggests that this effect might result in part from earlier pairing by males with larger territories (O'Donald 1983), but confirmation of this hypothesis is needed.

In n. Norway colonial breeders feed mostly by kleptoparasitism at nearby seabird colonies, solitary breeders hunt within large territories around their nests (Andersson and Götmark 1980). Colonies consist of concentrations of nests (16–21 / km^2, with closest nests 60–75 m apart), surrounded by areas where pairs defend much larger territories (0.4–0.6 pairs / km^2). Concentrations of nests permit group defense of nests and presumably reduce predation on eggs and chicks by a variety of birds and mammals. No evidence that colonies serve as "information centers" to optimize foraging (Andersson and Götmark 1980). See Demography and populations: causes of mortality, below.

SEXUAL BEHAVIOR

Pair formation and copulation. Pair formation involves female searching for single territorial male. Male assumes Aggressive Upright posture as female approaches on the ground; she often flies away but soon returns or adopts Intimidated Upright posture. Sometimes male begins displays associated with selection of nest site (see below), and both birds utter Squeaking Calls. During the reunion of a pair for the first time in a season, female throws her head upward with her bill open, male bows with raised tail and calls loudly (Perry 1948).

Copulation is often preceded by the male feeding his mate: mates approach each other with neck lowered but not withdrawn; male regurgitates after female pecks upwards or sideways at his open bill; both birds utter Squeaking Calls (female sometimes makes Begging Call). In well established pairs, regurgitation and copulation are less often associated, and copulation involves few preliminaries. Preceding copulation, male utters Copulation Calls, and female assumes Hunched posture, with body horizontal, head withdrawn, and carpal joints lifted slightly. During 3–5 cloacal contacts after mounting, male rests wingtips on ground and female sometimes utters Begging Call (Perdeck 1963, O'Donald 1983). Feeding of female by male can continue at least 9 d after first egg is laid (Perry 1948).

Unlike in gulls, choking call does not occur in Parasitic Jaeger, although the posture during Squeaking Call is similar except for the lack of up-and-down head movements, perhaps associated with the absence of carrying nest material (Tinbergen 1959). Head-tossing of gulls also absent, although female's movements while pecking upward at male's beak are similar. Ritualized Facing-away, characteristic of pair formation in gulls, also absent. Intimated Upright, a posture also present in gulls, is used in pair formation instead of Facing-away (Perdeck 1963). During copulation, male gulls flap their wings for balance, instead of bracing themselves with their wing-tips on the ground (Perdeck 1963, Andersson 1971). Repertoire of displays thus lacks some elements present in most gulls.

Mating system and sex ratio. Mating between morphs is random in n. Norway (Götmark et al. 1981). In Iceland disassortative mating (more unlike matings) is statistically significant but might be explained by sex differences in proportions of morphs (Bengtson and Owen 1973).

On Fair I., Scotland, the proportion of dark morph birds has remained constant for 15 yr; proportions of the morphs are the same in young fledged, in recoveries of banded birds away from the island, and in males that return to breed. In contrast, among returning females, dark morphs are about 7% less frequent. Among breeding pairs the proportion of dark morphs is about 9% higher among males than females, and in about 60% of all breeding pairs the male is darker than the female (Berry and Davis 1970). How these differences in proportions of morphs arise in breeding pairs is not well understood. Possibly light morphs are more aggressive in general, behavior that in males might interfere with pair formation (Berry and Davis 1970).

Pair bond. In n. Alaska, pairs often form quickly after arrival; copulation sometimes occurs the day of arrival (Maher 1974). A report that pairs return together needs confirmation (Sutton 1932). On Fair I., n. Scotland, individuals return to their territories separately. Experienced pairs usually return to same territory each year, but 50% of newly established pairs fail to remate the following year. This difference is explained in part by higher failure to return after first nesting season (20% versus 10% for more experienced birds; Williamson 1965). When pairs separate, although both members survive, the male usually remains on a territory overlapping or adjacent to the previous year's (91%, $n = 33$), the female usually moves more than one territory away (60%, $n = 43$). Males tend to return earlier and claim their former territories; when his mate fails to return, a male eventually takes a new mate but sometimes acquires a neighboring female as his mate if he can drive away her former mate. When a male fails to return, the female sometimes defends the former territory and takes a new mate. New pairs are less likely to persist the following year (55%, $n = 245$) than are old pairs (together for >1 preceding year, 65%, $n = 386$); this difference presumably reflects a higher divorce rate among new pairs, as mortality presumably affects new and old pairs equally (O'Donald 1983).

On Fair I., n. Scotland, some females prefer to mate with dark or intermediate males, a conclusion based on earlier hatching dates of newly formed pairs with dark males (O'Donald 1983; see Breeding: phenology, below). However, there is no evidence of assortative mating among the different morphs in this population ($n = 392$; O'Donald 1983, *contra* Davis and O'Donald 1976). Evidence for assortative mating in colonies throughout n. Scotland is based on complex statistical models (O'Donald 1983).

Pair bonds usually not evident away from nesting territories. Only one report indicates an occasional exception: one year a mated pair (as judged by courtship behavior) defended a territory and hunted together for almost 2 wk in late Aug in the lower St. Lawrence River (Belisel and Giroux 1995). Rarely 3 birds jointly defend the same territory (mating relationships unknown; Elmberg 1992).

Reversed sexual dimorphism. Like other avian predators, females are larger than males; the degree of reversed sexual dimorphism is somewhat greater (15–20%) than in other jaegers (10–15%). The association between proportion of avian prey in the diet and the degree of reversed sexual dimorphism in jaegers fits the pattern in other genera of avian raptors (for instance, *Accipiter* spp. and *Falco* spp.; Mueller 1990). Careful study found no evidence that breeding success in Parasitic Jaegers varies with either male or female mass, nor with degree of female dominance in pairs. Large females, however, have advantages in pairing with older males, and birds mate assortatively by size (pairs similar in size). It remains unclear whether these patterns affect reproductive success, but they challenge hypotheses relating reversed sexual dimorphism to specialized roles for the sexes during breeding (Catry et al. 1999).

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. During nonbreeding season, usually single or with a few others (Wood 1989).

Nonpredatory interspecific interactions. Common Gulls (*Larus canus*) occasionally nest within colonies of these jaegers in n. Norway, presumably to obtain protection from mammalian and other avian predators on eggs and young (Götmark and Andersson 1980).

PREDATION

Kinds of predators. No known predators on adults.

Responses to potential predators. See Breeding: parental care.

BREEDING

PHENOLOGY

Arrival in breeding areas. Figure 4. Arrives singly or in small flocks in foothills and mountain passes in n. Alaska between 21 May and 1 Jun (Irving 1960, Maher 1974), in interior Northwest Territories 30 May (Clarke 1940), in Colville River delta 25 May (Johnson and Herter 1989), on coast of Yukon Territory 22 May (Salter et al. 1980); in Mackenzie River delta 29 May ($n = 2$ years, Johnson and Herter 1989), in Anderson River delta 25 May–1 Jun (Martin and Barry 1978), not until 4–10 Jun in Barrow (Maher 1974), 2–6 Jun on Banks I. (Manning et al. 1956), 4–8 Jun on Victoria I. (Parmelee et al. 1967), 10–13 Jun on Bathurst I. (Taylor 1974), 11–14 Jun at Karrak Lake inland in Anderson River region ($n = 3$ years, Ryder 1971), 10–11 Jun on Southampton I. (Sutton 1932, Parker and Ross 1973). Arrival is thus earliest in Brooks Range and on coasts of ne. Alaska and Yukon Territory, a suggestion that many birds arrive in this area by overland routes.

Unlike Pomarine and Long-tailed jaeger, obvious movements along the coasts of Alaska and Yukon Terr. not reported (Maher 1974, Salter et al. 1980). Farther east, at Cape Dalhousie, Mackenzie District, NWT, large numbers migrate eastward in first 2 wk of Jun (Johnson and Heter 1989). On n. slope of Chukchi Peninsula, migrates along shore to northwest 31 May–15 Jun (Portenko 1989), an indication that some birds migrate through Bering Strait. In sw. Alaska, on territories from 14 May onward (Petersen et al. 1991). In Greenland, arrives between late May and mid-Jun, depending on latitude (Salomonsen 1950); in ne. Greenland, in 1 yr all birds arrived between 10 Jun and 15 Jun (Pedersen 1926). On Fair I., n. Scotland, first birds on territories 16–20 Apr, one third of adults have returned by end of Apr; nonbreeding birds arrive in late Jun (O'Donald 1983).

Egg-laying. Figure 4. 29 May–10 Jun in foothills of n. Alaska ($n = 11$), 14–19 Jun in one year near Barrow ($n = 4$); first eggs laid within 10 d of first arrival; copulation occurs as early as the day of arrival. Prelaying period shorter and first egg dates earlier than for Pomarine Jaeger (Maher 1974). At Point Storkersen, n. Alaska, laying begins 10–16 Jun ($n = 3$ yr, R. D. Bergman, cited in Johnson and Herter 1989). In Yukon River delta, eggs laid slightly earlier, earliest 29 May, many 5–6 Jun (Brandt 1943). In Commander Is., eggs likewise mostly laid in late May–early Jun (Dement'ev and Gladkov 1969). In Anderson River delta, first eggs laid 3–9 Jun in one year, as soon as 7 d after arrival (Martin and Barry 1978). On Victoria and Jenny Lind Is., eggs laid 20–30 Jun ($n = 6$; Parmelee et al. 1967). On Southampton I., 21 Jun (Sutton 1932). On Fair I., n. Scotland, first eggs laid 16–19 May (O'Donald 1983). On Spitzbergen at 76–80°N, the first eggs are laid in mid-Jun but the majority of clutches are initiated 1–10 Jul ($n = 29$ clutches, Løvenskiold 1964). In nw. Russia, first eggs are laid 27 May–7 Jun (average 2 Jun, $n = 8$ yr); almost 50% of eggs are laid 5–15 Jun ($n = 36$ eggs in 2 yr; Belopol'skii 1961).

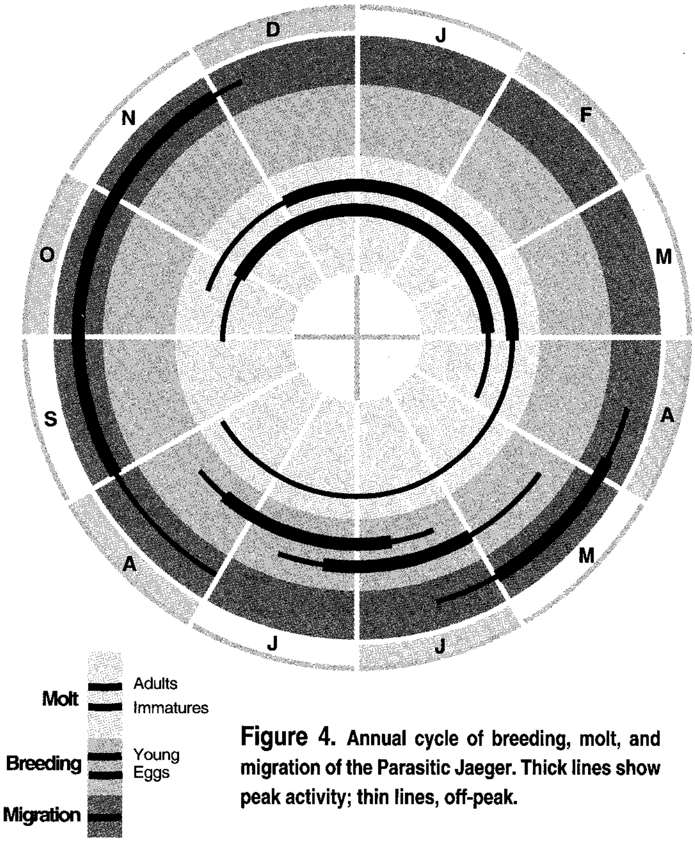


Figure 4. Annual cycle of breeding, molt, and migration of the Parasitic Jaeger. Thick lines show peak activity; thin lines, off-peak.

Renesting is rare; one pair produced a second clutch 9 d after losing its first (Perry 1948).

Hatching. From 25 Jun to 7 Jul in inland areas of n. Alaska, 25–17 Jul at Barrow (Maher 1974), 30 Jun–6 Jul in Anderson River delta (Martin and Barry 1978). On Fair I., n. Scotland, first eggs hatch 11–13 Jun; distribution of hatching dates is strongly skewed with a tail extending to 22 Jul (O'Donald 1983). In Greenland, earliest nestling found 17 Jun (Salomonsen 1950).

On Fair I., n. Scotland, studies over >30 yr indicate that hatching dates depend on previous breeding experience and on plumage of males. Among newly established pairs, those with dark males have earlier hatching dates than those with intermediate or light males (28.3, 29.8, and 33.4 d after 1 Jun, respectively, $n = 328$ males over >20 yr); pairs in their second or later years have much earlier hatching dates, with no differences among morphs (21.0, 22.6, 21.0 d after 1 Jun, respectively, $n = 462$ males). By subtracting the figures for experienced pairs from those for new pairs, it appears that light male takes almost twice as long to find a new mate as does dark male (O'Donald 1983). Female's morph has no consistent influence on hatching date. Previous breeding experience by both the male and the female affects hatching date about equally (mean hatching dates for pairs with one experienced partner, 31.7 and 31.2 d, respectively; Davis 1976). These differences in breeding chronology affect reproductive success (see Demography and populations: measures of breeding activity, below).

Fledging. Young in Alaska fly by last week in Jul or first week in Aug (Maher 1974, Petersen et al. 1991), in Anderson River delta 29 Jul–4 Aug ($n = 2$; Martin and Barry 1978). On Victoria I. in one year flying young first noted on 13 Aug; some young still attended by adults 26 Aug (Parmelee et al. 1967). On Fair I., n. Scotland, fledging occurs 11 Jul–14 Aug (O'Donald 1983). In nw. Russia, first young fledge on 21 Jul–8 Aug (average, 27 Jul, $n =$ 4 yr; Belopol'skii 1961).

Departure from breeding areas. Breeders still defend territories until late Aug or early Sep (Maher 1974), but some territories vacated as early as 3 Aug (Petersen et al. 1991). On Victoria I. last birds noted 29 Aug–1 Sep (Parmelee et al. 1967). Migrants move westward on coast of Yukon in Aug and Sep, latest on 28 Sep (Salter et al. 1980, Johnson and Herter 1989). Few observed in Aug in Beaufort Sea north of Alaska and Yukon (Frame 1973). Departs Barrow in Sep; most have left by middle of month (Bailey 1948). Departs Bering Sea usually by Sep 13–16, Pribilof Is. by 18 Oct, se. Alaska by 7 Oct (Gabrielson and Lincoln 1959). On Fair I., n. Scotland, nonbreeding birds leave in Jul; breeders and fledged young begin to leave in Aug; last birds depart by mid-Sep (Perry 1948, O'Donald 1983). In Greenland, departure begins in mid-Aug, last birds in late Sep and early Oct (Salomonsen 1950).

NEST SITE

Selection process. Usually male initiates choice of a nest site by walking or flying toward a suitable site and uttering the Nest Call. At the site, both birds produce Squeaking. Male usually has neck withdrawn and beak pointing downward; female lowers her neck and pecks at male's beak (sometimes male pecks at female's beak). Meanwhile nesting-building movements occur mostly by the female (Scraping, Sideways Building; Perdeck 1963).

Site characteristics. In wet areas of tundra, nests are usually on slight rises, such as the edges of low-center polygons or frost mounds (Maher 1974). On Southampton I., nests are often in flat grassy meadows or on low ridges away from any cover (Sutton 1932). In areas with sparse vegetation, fertilization from the birds' feces around nest sites and habitual perches creates "skua hummocks," slight rises (10–90 cm high, 3–8 m in diameter) covered with a turf of grass, the first places free of snow (Summerhayes and Elton 1923, Summerhayes and Elton 1928, Løvenskiold 1964).

In arctic river deltas, pairs often nest near colonies of Snow Geese and Brant (*Branta bernicla*), McConnell River, NWT (Angstadt 1961) and Anderson River (Martin and Barry 1978). In North Atlantic loose colonies form in places convenient for robbing seabirds returning to their nesting colonies (Løvenskiold 1964).

NEST

A slight depression in the ground or in moss and lichens formed by pressure with breast and feet (Gabrielson and Lincoln 1959, Maher 1974); sometimes lined with a little dry grass or lichens (Sutton 1932). On Fair I., n. Scotland, a slight scrape with a few twigs or dry grasses; in some cases, eggs laid directly on stones or bare ground; in wetter areas, a deeper depression is made and more nest material accumulated (O'Donald 1983).

GONAD CYCLES

Males arrive with testes at maximal sizes (about 650 mm^3); females can have follicles over 6 mm in diameter (Belopol'skii 1961, Maher 1974). Both testes and ovaries mature rapidly in the second half of May (Belopol'skii 1961).

EGGS

Shape. Ovate.

Size. Average 57 mm (range 51–61) × 41 mm (range 38–43, $n = 50$; Bent 1921).

Color. Dull greenish, grayish, or brownish olive, with spots, blotches, and lines of brown in various shades and tints, either evenly distributed or clustered near the large end (Gabrielson and Lincoln 1959).

Surface texture. Smooth.

Eggshell thickness. No information available.

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

Egg-laying. Little information. One nesting pair produced a second clutch 9 d after losing its first (Perry 1948).

INCUBATION

Onset of incubation in relation to laying. Begins immediately after the first egg is laid (O'Donald 1983).

Incubation patches. Two oval patches in both sexes.

Incubation behavior. Shared by both sexes approximately equally (Maher 1974, Martin and Barry 1978). Incubation periods 15–110 min, the shorter periods usually the result of disturbance by an intruding jaeger, gull, or eagle (one nest; Martin and Barry 1978). Nest relief usually involves the sitting bird leaving as its partner glides toward the nest (Martin and Barry 1978).

Incubation period. In n. Alaska, one egg pipped in 23 d, hatched in 26.5; hatching interval between two eggs in one clutch, 2.5 d (Maher 1974). On Fair, I., n. Scotland, median and modal incubation period 26 d (43% 26 d, 37% 25 d, 11% 27 d, range 24–29 d, *n* = 214; O'Donald 1983). Mean incubation periods of first and second eggs virtually identical (25.7 and 25.6 d, *n* = 123 and 91, respectively); returning and new pairs do not differ; morphs do not differ (O'Donald 1983). In another study on Shetland Is., n. Scotland, 25–26 d (*n* = 16; Perry 1948).

HATCHING

No information.

YOUNG BIRDS

Condition at hatching. Down well developed. No reports of mass.

Growth and development. Young move away from the nest within 1–2 d after hatching (Martin and Barry 1978). In n. Alaska, young had relative growth rates of 15–20% in the first 10 d after hatching (*n* = 2; Maher 1974) and fledge at 400–450 g (Maher 1974, Martin and Barry 1978). Young first flew in 27–30 d and 26–29 d (*n* = 2; Maher 1974). In Shetland Is., n. Scotland, fledging occurred in 27–33 d (*n* = 22 young, mean 29–30 d), and juveniles departed 21–33 d (mean 28 d) after fledging (Perry 1948). First flights only a few meters; within 2–3 d they can fly well; within 2 wk they seem as agile in flight as adults. Fledging period 26–38 d (median and mean = 31 d ± 2.2 SD, mode = 30 d, *n* = 214); about 1 d shorter during a summer with unusually warm and dry weather; no difference between returning and new pairs, nor between first and second chicks to hatch, nor between morphs (O'Donald 1983).

PARENTAL CARE

Distraction Display and nest defense. Nest defense grades into interspecific territorial defense in this species, so that virtually any large bird, mammal, or other moving object evokes aggression, including Tundra Swan, Brant (*Branta bernicla*), Common Raven, barren-ground caribou (*Rangifer tarandus*), domestic dogs and sheep, and humans (Williamson 1949, Maher 1974, Taylor 1974, Martin and Barry 1978). In particular, routinely attacks other predators: Rough-legged Hawk (*Buteo lagopus*), Golden Eagle (*Aquila chrysaetos*), White-tailed Eagle (*Haliaeetus albicilla*), Gyrfalcon (*Falco rusticolus*), Peregrine Falcon (*F. peregrinus*), Glaucous and Herring gulls, Great Black-backed Gulls (*Larus marinus*), Snowy Owl (*Nyctea scandiaca*), Carrion Crows (*Corvus corone*), Common Ravens, and arctic fox (Nicholson 1930, Bannerman 1963, Maher 1974, Taylor 1974, Götmark and Andersson 1980).

In response to an approaching human, Distraction Display begins at a distance of 75–100 m, changes to direct attack at a distance of 20–30 m from the nest (Martin and Barry 1978). Attacks on human intruders vary greatly among individual jaegers but involve diving at high speed from behind or one side and occasionally striking the intruder with wings or feet (Williamson 1949, Maher 1974, O'Donald 1983). Repeated visits by humans to a nest result in reduced aggression (Maher 1974). In Faeroes, jaegers nesting in colonies make attacks on humans more often than do those with widely dispersed nests, although the latter often attack other intruders (Williamson 1949).

Both sexes perform Distraction Display (feign injury) near nests and young at the beginning of incubation; display becomes more intense and regular just before and after hatching (Williamson 1949, Martin and Barry 1978, O'Donald 1983). Upright or crouched, sometimes on their sides, birds flop their wings asymmetrically and spasmodically; also lurch or scurry away with dragging or partly spread wings; often regurgitate food while feigning injury; sometimes perform on nearby ponds as well as on land; often utter a whimpering call but sometimes remain silent (Sutton 1932, Williamson 1949, Salomonsen 1950, Hanson et al. 1956, Parmelee et al. 1967, Martin and Barry 1978). Often performs 25–50 m from a human (Williamson 1959). Pairs often perform close together, alternate between attacks in flight and injury feigning (Williamson 1949, O'Donald 1983). Birds also occasionally interrupt injury feigning with false brooding, in which a bird suddenly sits still, as if incubating or brooding (Williamson 1949).

Brooding and attendance. Unlike Long-tailed Jaeger, parents often leave chicks unguarded while they hunt together (Perry 1948, Maher 1974). In n. Alaska, both parents absent about 50% of time (<5% in Long-tailed Jaeger; Maher 1974); in Anderson River delta, chicks left alone only 8% of time (Martin and Barry 1978). One parent (probably the female, by analogy with Long-tailed Jaeger) stays near the chicks much more often than the other (for one pair 92% and 38% of time, respectively; Martin and Barry 1978).

In n. Scandinavia, among pairs defending large territories, both parents remained near chicks 48% of time and both were away simultaneously 4%; pairs in colonies almost never left chicks unattended (<1% of time) and both parents were present 60% of time, presumably because the risk of egg predation by conspecific neighbors was higher in colonies (Andersson and Götmark 1980).

On Fair I., n. Scotland, if one parent dies, the remaining one usually rears chicks successfully (O'Donald 1983).

Feeding. No information.

Nest sanitation. No information.

COOPERATIVE BREEDING

Not reported.

BROOD PARASITISM

Not reported.

FLEDGLING STAGE

Young remain on territories with parents for 2–3 wk after fledging, as late as first week of Sep (Maher 1974), usually until departure from the breeding grounds (Sutton 1932).

IMMATURE STAGE

Independence from parents. Few indications that young remain with parents once migration begins: isolated report of adult feeding 2 young during migration in England (Felton 1969, cited in Cramp and Simmons 1983). Immatures among migrants in s. Spain have lower success rates (12%) in attacks on gulls and terns than do adults (25%; Paterson 1986).

Nonbreeding immatures. Nonbreeding immatures return to Fair I., n. Scotland, in Jun and Jul, where they gather in "clubs" along shore (O'Donald 1983). Some birds evidently fail to return to breeding areas in their first summer (nestling banded in Finland recovered the following Jun in Brazil; Hildén 1971). Nonbreeding immatures occur throughout summer in Baltic Sea, including many light morph birds from arctic populations (Hildén 1971); few observed in Jun–Jul on the arctic coast of Russia (Kjellén 1997). Some remain in s. African waters during the arctic summer (Ryan 1986), but apparently not off se. Australia (Barton 1982, Wood 1989). Occasional immatures reported on coasts of Chile and Peru in Jun (Murphy 1936, Jehl 1973).

Recoveries of birds banded in ne. Atlantic (mostly in Scotland) indicate movements during the first few years of life. Birds in their second year of life wander widely: recoveries in Jun in Togo and Brazil; in Aug in Newfoundland, in Sep off Long Island, New York, as well as on wintering grounds off sw. Africa and at a few inland localities in Europe and Africa. Birds in their third year of life usually visit the Arctic during summer: 4 recoveries off Greenland in Jul–Aug, none in these months from farther south (Cramp and Simmons 1983). Hundreds of immatures chased Black-legged Kittiwakes in the mouth of the Bay of Fundy on 29 Sep, an indication of the opportunistic distribution of immatures of this species (Brooks 1939).

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Intervals between breeding. Normally breeds every year (O'Donald 1983).

Age at first breeding. On Fair I., n. Scotland, long-term banding has shown that birds first breed at age 3-7 yr (mode = 4 yr, n = 111). Light morphs first breed significantly earlier than either intermediate or dark morphs: by age 4, 75% of light morphs have bred, 53% of intermediate and dark morphs (O'Donald 1983). In nw. Russia, Belopol'skii (1961) reported 3 cases of banded 1-yr-olds breeding, an unlikely possibility.

Clutch. Usually 2 eggs. In n. Alaska, 14% of clutches contained one egg (n = 21; Maher 1974); on Fair I., n. Scotland, 13% of clutches had one egg (n = 836). Most one-egg clutches are produced by new pairs; new pairs are more likely than returning pairs to lay only one egg (16.5%, 6.2% respectively), so one-egg clutches are more frequent late in the breeding season (O'Donald 1983). Clutches with 3 eggs occasionally reported (Fair I., Scotland, 0.4% of all clutches; Williamson 1965, O'Donald 1983); some females regularly produce 3-egg clutches, but these eggs do not hatch (O'Donald 1983).

Nesting success. In n. Alaska, 50% of eggs resulted in fledged young (n = 8 eggs, 4 nests); in 2 nests only one of 2 chicks survived; in 2 other nests only one egg hatched, the other damaged in unknown way (Maher 1974). In Anderson River delta, youngest of two chicks always disappeared within a few days of hatching (n = 4); 14% of eggs fledged (n = 14; Martin and Barry 1978). In s. Iceland a colony obtaining food mostly by kleptoparasitism had 89% hatching success but fledged only 0.27 young/pair (1 yr); high mortality of young resulted from failure of nearby colony of Arctic Terns (Arnason and Grant 1978).

Nesting success of marked birds studied for 15 yr on Fair I., n. Scotland (O'Donald and Davis 1975, 1976, Davis 1976, O'Donald 1983). Pairs that have nested together previously fledge more chicks than those with one or both partners inexperienced (both experienced, average 1.51 ± 0.034 SE, n = 167; only male experienced, 0.97 ± 0.109 SE, n = 31; only female experienced, 0.93 ± 0.095 SE, n = 40; neither partners experienced, 0.65 ± 0.066 SE, n = 60; Davis 1976). Mean fledging success increases progressively with the sum of partners' previous experience, but the largest effect comes with one year of experience (Davis 1976). Plumage morph also affects number of chicks fledged, but only for inexperienced males: among these males, light morphs have less success than intermediate or dark morphs: average 0.37 ± 0.106 SE (n = 16), 0.84 ± 0.077 SE (n = 55), and 0.83 ± 0.104 SE (n = 29), respectively (Davis 1976;

slightly different figures in other references above). This effect is ascribed to later pairing dates and hence laying dates for inexperienced light-morph males (Davis 1976). Effects of previous experience on breeding success are confounded by effects of age. For both males and females, both age and experience appear to affect fledging success, but sample sizes for combinations of age and experience are low, and partial correlations are not significant (Davis 1976). Breeding success is clearly related to date of hatching, and both age and previous experience, either separately or together, are related to date of hatching.

Among nestlings banded on Fair I., Scotland, there are no differences between morphs in rates of fledging or recovery away from the island (Berry and Davis 1970). Proportion of eggs raised to fledging has varied from 39–75% among years (55–75% in later years with larger populations; Berry and Davis 1970).

Lifetime reproductive success. No information.

LIFE SPAN AND SURVIVORSHIP

On Fair I., n. Scotland, mortality in first year of life is estimated to be about 28% (see O'Donald 1983 for numerous assumptions). Adult mortality was 11%/yr for 3 yr when observers were present in the colony for the entire breeding season (*n* = 660) but more than doubled (25%/yr, *n* = 707) when observers were there less often and shooting by residents of the island increased. Also 20%/yr during an earlier period when observers were present irregularly (*n* = 697). No differences in mortality between morphs in any of these periods (O'Donald 1983). Oldest banded bird >18 yr (Cramp and Simmons 1983).

DISEASE AND PARASITES

Four species of ectoparasitic feather lice (Mallophaga) reported: *Austromenopon fuscofasciatum* Piaget, *Haffneria grandis* Piaget (rarely), *Quadraceps normifer normifer* Grube, and *Saemundssonia cephalus* Denny. The first 2 are shared with both Pomarine and Long-tailed jaegers. Each of the 3 jaegers has a different subspecies of *Q. normifer* and a different species of *Saemundssonia* (Cohen et al. 1997).

The fly *Ornithomyia lagopodis* Sharp, the feather mite *Zachvatkinia stercorarii* Dubinin, and the flea *Ceratophyllus garei* Rothschild also reported (Rothschild 1952, Ballard and Ring 1979).

CAUSES OF MORTALITY

Penned chicks killed by arctic fox and probably Glaucous Gull (Maher 1974). Arctic foxes take eggs and chicks (Bathurst I.; Taylor 1974). On Fair I., in n. Scotland, most mortality of young chicks results from storms soon after hatching (O'Donald 1983).

In n. Scotland, Great Skua preys on both adults and chicks. On Foula I., Shetland Is., skuas took an estimated 31% of fledgling jaegers, 4% of adults (Furness 1977; these estimates might be too high, see O'Donald 1983). Most fledglings taken just after they have begun to fly (O'Donald 1983).

See also Conservation and management: effects of human activity, below.

RANGE

Natal dispersal. On Fair I., n. Scotland, where nearly all chicks were banded from 1973–1979, 57% of new breeders in 1979 were unbanded (*n* = 60); because some chicks raised on Fair I. probably were not banded, true rate of immigration from other localities is probably about 45–55%; all immigrants banded elsewhere (*n* = 6) have come from Shetland Is. within 160 km (O'Donald 1983).

Fidelity to breeding site. In foothills of n. Alaska and on Bathurst I., similarities of morphs suggest that pairs return to the same site each year (Maher 1974, Taylor 1974). Nests often located within 100 m in successive years (Maher 1974, Taylor 1974). On Spitzbergen a banded bird occupied the same territory for three consecutive years (de Korte 1972).

Fidelity to wintering site. In se. Australia, consistent presence of particular combinations of light- and dark-morph birds in coastal bays suggest that birds occupied well-defined home ranges and might even return to the same areas in subsequent years (Barton 1982).

POPULATION STATUS

Numbers. No estimates of total numbers available for any area in Nearctic. In n. Scotland, only area with systematic censuses, 1,090 pairs reported, but this estimate probably too low (Cramp et al. 1974). Of 33 sites, 5 had populations of >100 pairs (O'Donald 1983). 8,000 birds estimated in Iceland (Bengtson and Owen 1973); 225 pairs counted in n. Finland (Hildén 1971).

In foothills of Brooks Range, density about 0.1 pair/km^2 in one area and apparently no higher in several other coastal and inland sites (Maher 1974); in coastal ne. Alaska, 0.9 pair/km^2 (Andersson 1973); at Point Storkersen, n. Alaska, 0.9 birds/km^2 (3 yr; R. D. Bergman in Johnson and Herter 1989). On Jenny Lind I., in a year with few lemmings, pairs nested 5–6 km apart (Parmelee et al. 1967); on Bathurst I., near the northern limit for the species (76°N), 0.03 nesting pairs/km^2 regardless of lemming densities; also there are constant low numbers of nonterritorial birds present (Taylor 1974). In Anderson River delta, overall density is 0.04 nesting pairs/km², but nests are concentrated near colonies of nesting geese (Martin and Barry 1978). Nonterritorial birds vary in number from year to year around the Anderson River goose colonies, from 10–60 birds (Martin and Barry 1978).

In sw. Greenland, 0.3 pairs/km² (Nicholson 1930). In n. Scandinavia, this species breeds in years with moderate and low rodent densities, unlike Long-tailed Jaegers. In optimal habitat near ponds and wet bogs, densities reach 1–2 pairs/km²; on dry heathland with sparse vegetation, densities are only 0.1 pairs/km² (Andersson and Götmark 1980). Colonies reach much greater densities (see Behavior: spacing) but occur only in the vicinity of large concentrations of nesting seabirds (Andersson and Götmark 1980).

Less dependent on lemmings for reproduction than are Pomarine and Long-tailed jaegers (*contra* Southern 1944). Pomarine Jaeger might exclude or reduce the numbers of this species from areas with dense *Lemmus* populations (reviewed by Pitelka et al. 1955, also Parmelee et al. 1967). Great Skua excludes this species from nesting areas in n. Scotland as a result of arriving earlier and then persistence in the face of attacks by Parasitic Jaegers (Furness 1977, O'Donald 1983).

Trends. In Shetland Is., some populations have been displaced since 1950 by increasing numbers of Great Skuas (O'Donald 1983, Ewins et al. 1988; see Behavior: Spacing, above). Nevertheless, the total number of Parasitic Jaegers in n. Scotland increased at a rate of about 1%/yr between 1969 and 1986 (Ewins et al. 1988). On Fair I. increased at a rate of 14%/yr from 1950–1960, at a rate of 4%/yr from 1960–1975 (O'Donald 1983). On Foula I., despite the presence of Great Skua, increased rapidly during the 1970s as the colony of Arctic Terns increased (Furness 1977).

During the 1980s, in contrast, numbers on Foula I. declined steadily, as populations of sandeels (genus *Ammodytes*) plummeted and Arctic Terns and Altantic Puffins raised few or no young. Breeding success fell from at least 0.63 to 0.09 chicks/pair and numbers of territories dropped by 58% (although clutch size and hatching success did not change); as sandeels recovered in the early 1990s, these trends reversed (Caldow and Furness 1991, Furness 1993, Phillips et al. 1996). Evidently chick growth and survival, but not clutch size, are determined by feeding conditions near the nesting area. Normal adult mortality (10%/yr; see Life span and survivorship, above) combined with low recruitment could explain the decrease in numbers.

POPULATION REGULATION

See preceding section.

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Taming. On Shetland Is., occasional tamed individuals have been fed regularly by inhabitants (Venables and Venables 1955). Unlike Pomarine Jaeger, chicks penned for observation rarely survive (Maher 1974).

Disturbance at nest and roost sites. In the Baltic Sea, breeding populations decreased during the 1900s as a result of human disturbance. Destruction of nests by people with an aversion to the jaegers' predatory habits were the main causes of decline; more educated views of predators have permitted some recovery (Hildén 1971).

Shooting and trapping. During the 1800s, almost eliminated from Scotland as a result of shooting by gamekeepers convinced that predation by jaegers affected the numbers of gamebirds. By the early 1900s only small populations remained. Breeders recolonized Fair I. in the early 1920s and had increased to 70 pairs by 1960 (Holloway 1993). Since then shooting by residents of Fair I. has claimed at least 10% of the adult population in years when outside observers have not been present for the entire breeding season. Shooting is prompted by annoyance with attacking jaegers and by attempts to reduce harassment of grazing sheep. Harrying jaegers can sometimes confine sheep to the interstices of jaeger territories (O'Donald 1983).

Native Greenlanders shoot this species but not in large numbers; recoveries of banded birds suggest that about 7% are shot (Salomonsen 1950). Native American hunter on Victoria I. shot a nesting bird; Inuit do not eat this species but apparently shoot them in annoyance with birds defending their nests (Parmelee et al. 1967).

Fishing nets and contaminants. No reports of contamination by pollutants, including oil, in North America. In Scotland, concentrations of methylmercury reach 2.52 mg/g ± 2.23 SD in feathers of adults ($n = 28$) and 0.46 mg/g ± 0.22 SD in feathers of chicks ($n = 30$), an indication that birds accumulate mercury with age. Down of chicks has almost the same concentration of mercury (2.00 mg/g ± 0.91 SD, $n = 36$) as feathers of breeding females (Stewart et al. 1997). No information on effects of mercury on reproduction.

MANAGEMENT

Most nesting birds are readily caught for banding with walk-in funnel traps placed over nests so as to face downwind; clap nets are also effective but more time-consuming (O'Donald 1983).

Accurate censuses of nesting colonies require repeated visits during the period after all pairs have laid and before chicks begin to fledge. Counts of "apparently occupied territories" (those with nesting, defensive, or localized pairs) provide an estimate within 4% of the actual number of nesting pairs (Ewins et al. 1988, Lloyd et al. 1991).

APPEARANCE

In mated pairs, no difference in size noted between sexes (Perdeck 1963) and sexes indistinguishable by plumage (O'Donald 1983). For 2–3 weeks after egg-laying, females can be recognized in the hand by enlarged cloaca (O'Donald 1983).

MOLTS AND PLUMAGES

Hatchlings. Completely covered with down. Brownish with considerable variation among individuals, paler on abdomen and around eye (Fjeldså 1977).

Juvenal plumage. Complete by Aug. Variation among individuals becomes pronounced by about 21 d of age as Juvenal plumage develops on back, wings and belly; unlike in adults, variation is continuous between dark and light extremes (O'Donald 1983). For genetic analysis, light morphs recognized by entirely white feathers in center of belly, intermediates by feathers with white bases and dark tips, darks by entirely dark feathers. Morphs in Juvenal plumage do not always correspond to morphs in Definitive Alternate: of 38 birds classified as chicks and recovered as adults, 11 had changed morph (O'Donald 1983).

Both morphs have back and upperwing-coverts dark brown barred with buff or cinnamon; upper- and undertail-coverts prominently barred, and underwing-coverts spotted and irregularly marked with whitish, tan, or cinnamon. Light morph has abdomen white barred and streaked with brown, breast usually brown or grayish brown barred or streaked with buff or cinnamon (almost plain in some individuals), throat usually streaked with brown. Dark morph has dark brown underparts barred with buff or cinnamon (throat and breast sometimes streaked or nearly plain). Intermediates vary continuously between characteristics of light and dark morphs (O'Donald 1983).

About half of Juvenals, regardless of morph, have tips of feathers cinnamon (orangish brown) rather than buff (53%, $n = 15$, U.S. National Museum [USNM]), a feature not found in Long-tailed or in most Pomarine jaegers in Juvenal or later immature plumages. The intensity of orange varies continuously from very pronounced to completely absent, with most individuals more or less evenly distributed between the extremes.

Remiges and rectrices blackish brown. Most birds have 4–5 outer primaries with shafts predominantly creamy white (13% and 15% with 3 and 6 white shafts, respectively, $n = 40$, USNM, American Museum of Natural History [AMNH]; also see Olsen and Larsson 1997; as in all jaegers, other primaries have tan shafts). Unlike Long-tailed Jaeger, most Juvenals have whitish or buff tips on outer several primaries, but these tips are sometimes lost by wear as early as Sep. Whitish bases of primaries create a whitish patch on the lower surface of the wing; in some individuals, whitish bases of underprimary-coverts produce a small second patch. Two central rectrices usually have pointed tips (27% rounded, 20% intermediate, $n = 15$, USNM) and project 0–30 cm beyond the rest of the tail.

Later immature plumages. First and all subsequent Prebasic molts, like those of Long-tailed Jaeger, normally begin in winter quarters, after migration southward. This molt is complete and proceeds simultaneously in wing, tail, and body plumage. Rectrices molt from center of the tail outward, remiges from the center of the wing outward (primaries) and inward (secondaries). Some immatures from the southern hemisphere (Argentina, Chile, Australia, New Zealand, $n = 4$, USNM, AMNH) have not yet started to molt their primaries by Nov-Jan, but others have started by Nov–Dec ($n = 3$). Two of three Nov specimens show molt of dorsal body feathering, as do four Dec and Jan specimens.

Prealternate molt begins before migration northward. Unlike adults, immatures normally continue their Prealternate molt through the northward migration and often into the summer. Immatures collected off California, Massachusetts, New York, and N. Carolina in Jun–Sep often retain worn Basic feathers on the back (USNM, North Carolina State Museum [NCSM], Museum of Vertebrate Zoology [MVZ]) and some have growing or recently new primaries, secondaries, and rectrices. An occasional immature in late summer has three generations of feathers on its back, an indication that both Prebasic and Prealternate molts are sometimes not completed (Sep, Massachusetts, USNM).

In view of the great variability in immature plumages and the absence of information about plumages in birds of known age, we present here a general description of these plumages. Proposals to distinguish age-classes (Cramp and Simmons 1983, Olsen and Jonsson 1989, Olsen and Larsson 1997) seem best treated as working hypotheses.

Upperparts dark brown barred with whitish, tan, or cinnamon. Head brownish, nape sometimes paler, both often finely streaked. Upper- and undertail-coverts prominently barred (dark and pale bars usually about equal in width), and underwing-coverts barred or spotted with whitish. Unlike Juvenals, most older immatures lack strong cinnamon coloration (52% lack orange entirely, only 16% have strong orange coloration, $n = 25$, USNM, NCSM). Remiges and rectrices blackish brown. Most have 5-6 outer primaries with predominantly creamy white shafts (21% and 17% have 3–4 and 7–8 white shafts respectively, n = 29, USNM, AMNH; also see Olsen and Larrson 1997), more on average than either Juvenals or adults. Whitish bases of underprimary-coverts often create a second white patch in addition to the whitish bases of the primaries underneath (15% have a prominent second patch, 50% have a small one, and 35% have none, n = 20, MVZ). Central rectrices are usually pointed (6% rounded, n = 25, USNM, NCSM) and project 0.5–6 cm beyond the rest of the tail (median = 42 mm, n = 23, USNM).

Underparts highly variable, from mostly white to mostly brown. Light birds have white abdomen barred with brown to variable extent, breast barred with brown or plain grayish brown, throat usually streaked but sometimes plain grayish brown. Dark birds have brown underparts with white scalloping, sometimes plain or streaked breast and throat.

Definitive Basic plumage. Definitive Prebasic molt complete. Adults in Basic plumage resemble immatures, with variable amounts of barring above and below, but differ in having plain brown underwing-coverts. Wing-coverts are replaced once a year during molt of remiges; as a result, plain underwing-coverts are usually diagnostic for adult birds in all Definitive plumages (an occasional immature has plain underwing-coverts: specimen molting from immature Alternate to Basic, California, Oct, AMNH). Almost all adults from the southern hemisphere have molting primaries from Nov to Mar (80%, n = 20, AMNH; Stresemann and Stresemann 1966). New central rectrices are usually acquired by Nov (less often by Oct or not until Jan).

Upperparts dark brown with variable whitish barring. Upper- and undertail-coverts variable: dark bars vary from much narrower to much wider than white bars. Head brownish; paler collar on nape extremely variable from absent to conspicuous. Intensity of cinnamon coloration also varies from absent to conspicuous. Remiges and rectrices blackish. Usually the shafts of the outermost 4–5 primaries are predominantly whitish (25% have 3 or 6 whitish shafts, n = 20, AMNH). Whitish bases of primaries create a single white flash below. Unlike in immature plumages, about as many birds have rounded tips of central rectrices as have pointed tips, with some intermediates (n = 18, AMNH).

Light birds are mostly whitish below; abdomen barred to variable extent (absent to prominent); breast barred or spotted with brown or plain brown; throat plain white or spotted (sometimes streaked) with brown. Dark birds are brown below barred to a variable extent with whitish. Intermediates occur between light and dark birds. Sexes similar.

Definitive Alternate plumage. Definitive Prealternate molt incomplete, includes body plumage and central rectrices. By the time birds leave se. Australia about half have regrown their elongated central rectrices (Barton 1982). Four Mar specimens from Chile have the inner 2 primaries growing, an indication that some primaries might be replaced during Prealternate molt (AMNH). By Mar about half have acquired new dorsal body feathering and have plain brown backs and uppertail-coverts (n = 7, AMNH).

Light and dark morphs differ distinctly; although both forms have some variation, there are few true intermediates. Light morphs have dark brown upperparts. Top of head blackish, extending to just below eye, with a small white spot at the base of the upper mandible. Underparts and wide collar around nape white with yellowish sides of the neck. Undertail-coverts and underwing-coverts plain brown. Most have a dark brown band across the breast and brown flanks, but every gradation occurs between those with wide dark bands across the breast, brown flanks and spots on the abdomen to those with completely white breasts, flanks, and bellies (O'Donald and Davis 1959, Bengtson and Owen 1973). Remiges and rectrices blackish. Usually the shafts of the outermost 4–6 primaries are predominantly whitish (5% have 3 or 7 whitish shafts, n = 41, AMNH). Whitish bases of primaries produce a single white flash below. Stiff pointed central pair of rectrices projects 6–10 cm beyond the rest of the tail.

Dark morphs are entirely brown, with slightly darker cap, remiges and rectrices; some have a small white spot at the base of the upper mandible. There is much variation, however, from birds with almost white collars and often paler or white-flecked bellies to entirely dark birds with no pale feathers on neck or belly. Paler variants of dark morph are called "intermediate"; some have yellowish necks and yellowish gray underparts; others have whitish throats and necks (Hildén 1971, Bengtson and Owen 1973, Götmark et al. 1981, O'Donald 1983). For genetic analysis, intermediates are recognized by white bases of feathers on the abdomen (not visible except in hand). Individually marked adults vary only slightly in plumage from year to year (O'Donald 1983).

Morphs apparently influenced by two alleles at one locus; light morphs are homozygous for the light allele, darker variants of the dark morph are homozygous for the dark allele. Paler variants of the dark morph are mostly heterozygous (O'Donald and Davis 1959, O'Donald 1983). On Fair I., n. Scotland, matings involving intermediate morphs produce a mixture of morphs among chicks, but not in proportions that fit Mendelian expectations for two alleles at one locus. When offsprings' adult morphs are analyzed, however, proportions then do fit these expectations. Intermediates represent 60% of the adult population, theoretically impossible for two alleles at one locus, so some intermediates must actually be homozygous for dark alleles (O'Donald 1983). This analysis, however, did not take into consideration the possibility of extra-pair fertilizations, which might substantially affect the conclusions.

BARE PARTS

Bill. Hatchlings, gray to bluish pink, darker distally (Fjeldså 1977). During first summer, dull gray; adults, almost black (Sutton 1932).

Gape. During first summer, pink; adults, yellowish (Sutton 1932).

Iris. Blackish brown.

Legs and feet. Hatchlings, light blue with distal parts of webs blackish (Fjeldså 197). Juvenals, tarsi bluish gray, duskier behind, toes and webs blackish (Sutton 1932, Parmelee et al. 1967). Some immatures retain bluish legs (specimens, NCSM). In adults, tarsi bluish gray to blackish, sometimes in blotches, toes and webs black (Sutton 1932). On Spitzbergen, specimens show progressively more black on legs with age: in Juvenal plumage, all have bluish-gray legs with patches of black; in later immature plumages, 20% have legs entirely black; nonbreeding adults, 70%; breeding adults, 100% (*n* = 4–6 for each age; de Korte 1972).

MEASUREMENTS

LINEAR

On Banks I., males had flattened wing 325.8 mm ± 6.2 SD (range 314–341, *n* = 23), females 333.9 mm ± 8.6 SD (range 321–352, *n* = 17); exposed culmen, males 28.30 mm ± 0.76 SD (range 26.8–29.5, *n* = 22), females 27.78 mm ± 0.77 SD (range 27.0–29.6, *n* = 16); tarsus, males 45.48 mm ± 1.29 SD (range 42.7–48.0, *n* = 23), females 46.03 mm ± 1.40 SD (range 43.23–39.0, *n* = 17; Manning et al. 1956).

On Victoria and Jenny Lind Is., males had flattened wings 329.8 mm (range 324–336, *n* = 6), females 339.8 mm (range 335–349, *n* = 2); tail, males 202.7 mm (range 192–211), females 201.3 mm (range 196–205); exposed culmen, males 29.83 mm (range 28.0–32.5), females 31.5 mm (range 30.0–33.5); tarsus, males 45.6 mm (range 44.5–47.0, *n* = 5), females 46.9 mm (range 46.0–48.0; Parmelee et al. 1967).

Wing area. 1,115 cm^2 ± 57 SD; wing span, 1,038 mm ± 30 SD; aspect ratio, 9.7 ± 0.2 SD (*n* = 6; Spear and Ainley 1997).

Wing-loading. 32 Nm^{-2} ± 6 SD (*n* = 6; Spear and Ainley 1997).

MASS

Females about 15–20% heavier than males. Barrow, AK: males 424 g ± 14.4 SD (range 354–513, *n* = 11), females 499 g ± 18.5 SD (range 412–540, *n* = 6; Pitelka et al. 1955). N. Alaska, males 421 g ± 11.6 SD (range 301–540, *n* = 20), females 508.5 g ± 24.4 SD (range 346–644, *n* = 11). On Victoria and Jenny Lind Is., males weigh 445.7 g (range 429–475, *n* = 6), females 515.0 g (range 455–580, *n* = 2). Banks I., one female, 519 g (Manning et al. 1956). Immature females off N. Carolina average 471.5 g (range 439-516, *n* = 3; NCSM).

In large samples from nw. Russia, males average 429.2 g (range 306–585, *n* = 108), females 461.9 g (315–636, *n* = 125; Dement'ev and Gladkov 1969); males, 413.2 g (306–523, *n* = 219), females 477.5 g (306–604, *n* = 189; Belopol'skii 1961). Both sexes lose mass during the course of the summer (average masses in May, Jun, Jul, and Aug for males, 434, 411, 400, and 403 g; for females, 510, 486, 453, and 441 g; *n* > 10 in each case, except for Aug samples; Belopol'skii 1961). On Foula I., n. Scotland, females lose 4–5% of their mass soon after eggs hatch (mass during incubation, 470.2 g ± 28.3 SD, *n* = 57; during first half of raising chicks, 444.1 g ± 30.5 SD, *n* = 11; during second half of raising chicks, 450.9 g ± 37.1 SD, *n* = 29); males in contrast lose little mass at this time (respectively, 404.9 g ± 25.1 SD, *n* = 45; 402.5 g ± 17.5 SD, *n* = 8; 401.9 g ± 25.6 SD, *n* = 21; Phillips and Furness 1997).

PRIORITIES FOR FUTURE RESEARCH

The Parasitic Jaeger is one of the most intensively studied of all seabirds. Yet it illustrates the maxim of scientific research that the more we know, the more questions arise. For instance, evolutionary mechanisms maintaining plumage polymorphism in this species remain elusive. Part of the problem is that virtually nothing is known about the biology of the two morphs in populations away from the ne. Atlantic. Its biology in the Arctic is particularly poorly documented, despite its role as the primary predator on small birds and birds' eggs. Almost nothing, other than reports of kleptoparasitism, is known about this species away from its breeding areas.

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