R. HAVEN WILEY AND DAVID S. LEE

Stercorarius pomarinus

Pomarine Jaeger

FRENCH:
Labbe pomarin
SPANISH:
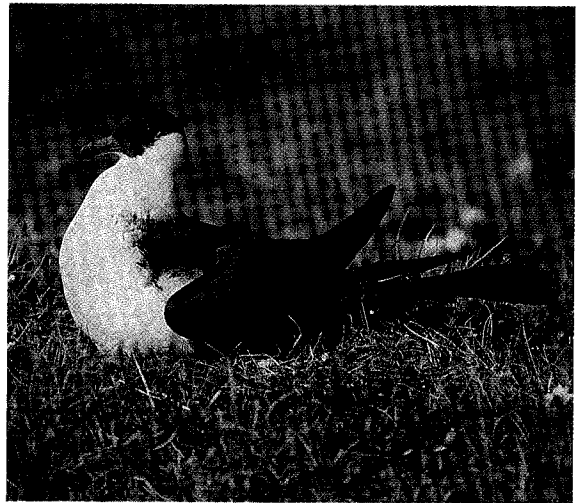*Estercorario pomarino,*
Salteador pomarino

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The Pomarine Jaeger, the largest of the three species of jaegers, is a powerful, heavily built predator. An adult in full plumage is a magnificent sight, with its twisted central rectrices often much more elongated than shown in illustrations. Like other jaegers, the Pomarine Jaeger nests in arctic tundra and spends the rest of its life at sea. The name "pomarine" is based on the scientific name, proposed in 1815 by C. J. Temminck, from Greek roots meaning "lid-nosed," a reference to the saddle-like sheath covering the base of the upper bill in all species of jaegers (Lockwood 1984).

Pomarine Jaegers are perhaps unique among birds in their dependence on a single species of prey for successful reproduction. Suitable conditions for nesting usually occur in low-lying wet tundra near arctic coasts where there are periodic irruptions of brown lemmings (*Lemmus trimucronatus*) or, in northern Russia, the very similar *L. sibiricus*. Successful reproduction occurs only in one of every three or four years in a typical lemming cycle, and only in areas where lemming populations reach high biomass. It is possible that most production of young occurs episodically at only a few places in the Arctic.

Because breeding is so variable at any one location, some investigators have speculated that this species is nomadic, breeding opportunistically wherever lemmings occur in sufficient numbers in a particular summer. In many summers, however, there are apparently no such opportunities over large areas of the Arctic and most Pomarine Jaegers leave the Arctic almost immediately.

The Birds of North America

Life Histories for the 21st Century
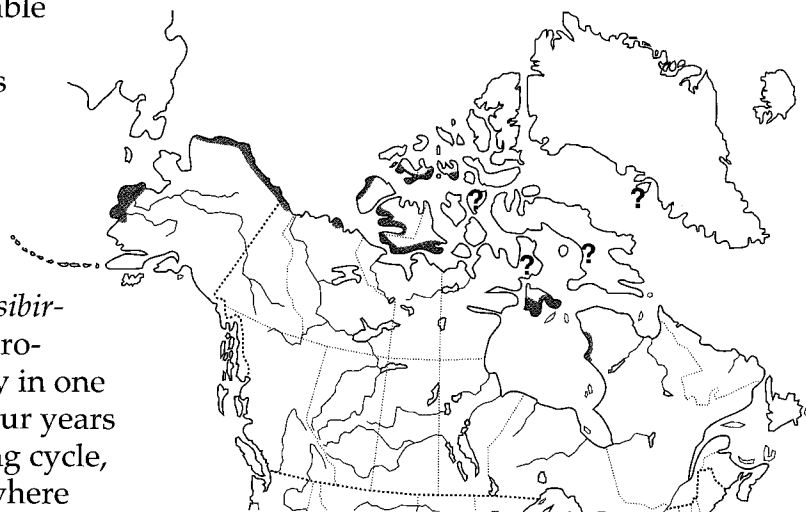
■ Breeding

Figure 1.
Breeding distribution of the Pomarine Jaeger in North America. This species winters at sea from California and Florida south. It also breeds in northern Russia and winters in tropical and subtropical waters throughout the world. See text for details.

Order CHARADRIIFORMES   Family LARIDAE

When not breeding, individuals spend their lives at sea, often far from land, in tropical and subtropical oceans. There they forage primarily by scavenging and by predation on small seabirds. They also practice kleptoparasitism, stealing food from other birds, but less often than do Parasitic Jaegers (*Stercorarius parasiticus*). The Pomarine's methods of parasitism are less elegant than those of the smaller jaegers; they often rely on surprise and brute force to tackle shearwaters and gulls feeding on the water rather than on acrobatics in flight.

The distinctive twisted rectrices of breeding Pomarine Jaegers are often lost soon after birds leave the Arctic. Many birds seen near North American coasts in autumn and winter are adults in Basic plumage, which closely resemble immatures. Identification of the three species of jaegers in these plumages presents a continuing challenge, as a result of general similarities among species and great variation within each species. Like the Parasitic Jaeger, Pomarine adults as well as immatures have dark and light morphs, although in the Pomarine Jaeger dark morphs are always scarce (<15% of birds in all populations).

The highly specialized reproductive ecology of the Pomarine Jaeger makes it one of the least studied birds of the Arctic, and its exceptionally localized and episodic reproduction make it one of the most potentially vulnerable to human disturbance. Intensive studies of breeding biology have been restricted to northern Alaska and a total of no more than 8 seasons (Pitelka et al. 1955a, Maher 1970, 1974, Andersson 1973a, 1973b).

DISTINGUISHING CHARACTERISTICS

Largest of the three jaegers but substantially smaller than large skuas (*Catharacta* spp.): males about 650 g on average, females about 750 g. There is great variation in size as a result of individual variation and sexual dimorphism (females average about 10–15% larger in mass). Otherwise sexes do not differ in appearance.

Adults in Definitive Alternate plumage have distinctive profiles: the two central rectrices, which extend well beyond the rest of the tail, are broad, blunt feathers with a half twist, so they are conspicuous in side view. This plumage has two morphs with few intermediates. Light morph has dark brown upperparts (except head), blackish cap, white underparts and collar, with yellowish wash on the sides of the neck, usually a bold brown band across the breast, and brown flanks and undertail-coverts. Infrequent dark morph is similar except underparts, sides of neck, and collar entirely dark brown. Both morphs and all plumages have whitish shafts of

3–8 outermost primaries and a whitish patch on the underside of the primaries.

Soon after they leave the Arctic in mid- or late summer, most adults lose their characteristic central rectrices. In this Definitive Basic plumage, adults are barred with brown or whitish to varying degrees above and below, especially on uppertail- and undertail-coverts. Rectrices project only slightly beyond the rest of the tail and lack twists. Except for plain underwing-coverts, these adults resemble immatures.

In Juvenal plumage, worn during the first southward migration, young are heavily barred with brown or whitish, especially on uppertail- and undertail-coverts and underwing-coverts. Pale bars on the upperparts often have a cinnamon (orangish brown) hue. Central rectrices hardly project beyond the rest. Later immature plumages are highly variable, and changes in appearance with age are poorly documented. Light morphs are brown above barred with whitish, whitish below barred, streaked, or spotted with brown. Dark morphs are often almost entirely dark brown, including their underwing-coverts, and can closely resemble adults in dark morph.

Because jaegers have such variable immature plumages, a large literature has focused on identification of species in the field (summarized by Olsen and Chrsitensen 1984, Olsen and Jonsson 1989, Olsen and Larsson 1997). Many proposed differences between species remain uncertain without a full study of variation within each species, and proposed changes with age require verification by study of marked birds of known age. The following discussion is based on examination of specimens in American Museum of Natural History (AMNH), U.S. National Museum (USNM), North Carolina State Museum of Natural Science (NCSM), and Museum of Vertebrate Zoology (MVZ), including excellent series of migrant Pomarine Jaegers from the east and west coasts of North America (NCSM and MVZ) and the best collection of specimens from the American Arctic (MVZ).

Pomarine Jaegers in all plumages can often be distinguished from other jaegers by heavier build (especially a "barrel-chested" appearance), broader wings (especially at the base), and relatively larger head and bill. Larger than other jaegers, about the size of a Ring-billed Gull (*Larus delawarensis*), and consequently with slower wing beats than other jaegers. Barely overlaps Parasitic Jaeger in mass and does not overlap in wing length, so differences in size (and associated differences in flight) alone make this species the most distinctive of the three jaegers.

Adults in Definitive Alternate plumage are easily recognized by their elongated, twisted central rectrices. Light morphs resemble Parasitic Jaeger in

coloration, but with more barring on flanks and breast, more extensive dark brown on undertail-coverts, yellowish pink bill with a dark tip (only breeding individuals), and no white spot above the base of the bill. The blackish cap sometimes extends farther ventrally than in any Parasitic Jaeger (only in a few individuals). Dark morph, less frequent in this species than in Parasitic Jaeger, closely matches that species in coloration (except that some dark Parasitics have a pale spot at the base of the bill).

Adults in Definitive Basic plumage and immatures in all plumages present a challenge for identification. Despite differences in size and profile, often difficult to separate from Parasitic Jaeger in the field. Most immatures and some adults have a double whitish flash on the underside of the wing (produced by extensive whitish bases of greater primary-coverts in addition to primaries), but some immature Parasitic Jaegers have a double flash as well. Other helpful characters include proportionately heavier bill (distinction between species less clear in immatures than in adults), absence of extensive orangish hues (but some Pomarine like some Parasitic jaegers have cinnamon tips on dorsal feathers), more outer primaries with white shafts (extensive overlap with Parasitic Jaeger), and lack of fine streaks on head and nape (also absent in some Parasitic Jaegers). In adult Basic or immature plumages, the central rectrices have rounded or acute tips like those of many Parasitic Jaegers.

Without the elongated central rectrices of Definitive Alternate plumage, dark Pomarine Jaegers can resemble the dark morph of South Polar Skua (*Catharacta maccormicki*). The latter, however, averages almost twice the mass (but the smallest South Polar Skuas are only 15% heavier than the largest Pomarine Jaegers; Furness 1987) and has a more prominent white patch on the upper surface of the primaries.

DISTRIBUTION

Breeding nearly circumpolar (Fig. 1) in areas with extensive low-lying tundra and cyclic populations of lemmings (especially *Lemmus trimucronatus* and *L. sibiricus*). Does not breed as far north as Long-tailed Jaeger nor as far south as either Long-tailed or Parasitic jaeger. Absent from e. Greenland, where *Lemmus* do not occur, and n. Europe west of the White Sea. When not breeding, highly pelagic; winters mostly in productive regions of tropical and subtropical oceans.

THE AMERICAS
Breeding range. Erratic breeding, coinciding with peaks in lemming populations, makes it difficult to determine breeding status in many places; reports often provide information for only one year's observations, which more often than not miss a peak for lemmings. Birds also wander widely in the Arctic during summer, so presence in an area does not necessarily indicate breeding.

In Alaska, often present during summer from Yukon delta northward along coast and on St. Lawrence I. Breeds along arctic coast and in Yukon delta (Brandt 1943, Gabrielson and Lincoln 1959), sporadically at any one site but sometimes in large numbers, especially near Barrow and in outer Yukon delta. Of 129 sets of eggs in North American collections (see Acknowledgments, below), 89 come from Barrow (other localities in Alaska include Bettell [Bethel], Hooper Bay, Ingiak [Igiak] Bay, Cape Lisburne, Wainwright, Alaktak, Cape Simpson, Chipp River, and Cape Halkett, all in coastal tundra). One nest reported along Colville River near 158°W, 200 km from coast, possibly in error (Reed 1956).

In w. Canadian Arctic, sporadically abundant during summer. Numerous on w. Banks I. in 1953 (Manning et al. 1956); numerous on Victoria I. in 1955 (Fraser 1957); numerous but patchy on s. Victoria I. in 1960, a year with plentiful lemmings (2 sets of eggs collected; Parmelee et al. 1967); numerous on w. Victoria I. in 1980 (Johnson and Herter 1989), scarce in 1983 (Lok and Vink 1986); abundant on s. Melville I. in 1909 (Manning et al. 1956), a nest and a pair with young in 1973 (Maltby 1978); numerous on Bathurst I. in 1969 and 1971, years with many lemmings, but absent in 1970, 1972, 1973 (Taylor 1974, Mayfield 1983). North American collections include a total of 9 sets of eggs from the w. Canadian Arctic coast: Herschel I., Baillie I., Cape Bathurst, and Franklin Bay (all 1905 or earlier). No nesting record from Mackenzie River Delta (Porsild 1943).

In e. Canadian Arctic, occasionally numerous but only 3 nests reported: on Southampton I., 1 fledged young in 1929, numerous in 1930, a year with plentiful lemmings, a nest and 4 other pairs in 1932, absent in 1936, 1937 (Sutton 1932, Bray and Manning 1943, Parker and Ross 1973); in nw. Quebec, a nest at Inoucdjouac (Port Harrison), another at Povungnituk, both 1930 (Todd 1963). Numerous on Boothia Peninsula in 1953, and on King William I. and Adelaide Peninsula in 1956, but no nests found (Fraser 1957); numerous, but no nests, on w. Baffin I. (Bray and Manning 1943). No breeding reported in long-term studies on n. Devon I. and Cornwallis I. (Geale 1971, Hussell and Holroyd 1974). Breeding indicated without details on Devon I., Prince of Wales I., and Somerset I. (Godfrey 1986). A set of eggs from Cape Chidley, n. Labrador, formerly in Carnegie Museum of Natural History (Todd 1963), possibly an identification error (R. Panzar pers. comm.).

Winter range. Known wintering areas are concentrated in localized zones with high biological productivity in tropical and subtropical seas. Many winter in the Caribbean (Wynne-Edwards 1935, Raffaele et al. 1998), perhaps especially off northern coast of South America and just east of s. Lesser Antilles (Cramp and Simmons 1983). Regular in winter in small numbers off Florida (Stevenson and Anderson 1994) and probably s. Texas.

Also winters from California to Peru (Bent 1921, Murphy 1936, Cramp 1985), although no reports of large numbers in this area; occasional as far north as central California in winter, the only jaeger regularly present then (Briggs et al. 1987, Stallcup 1990).

OUTSIDE THE AMERICAS

Breeding range. Sporadic breeding in w. Greenland on Disko I. and perhaps elsewhere (Salomonsen 1950). Absent as a breeder from n. and e. Greenland, Spitsbergen, and n. Europe east to the Kola Peninsula and White Sea. In n. Russia, nests irregularly from east of White Sea to Chukchi Peninsula, including Novaya Zemlya, New Siberian Is., and Wrangel I. On Taymyr Peninsula, nests on tundra from arctic coast southward to about 70°N (Rogacheva 1992). Numerous birds nest in years with abundant lemmings on north slope of Chukchi Peninsula and Wrangell I. (Portenko 1989).

Winter range. Near coast of nw. Africa, occurs commonly Nov to Mar at 8–25°N (Wynne-Edwards 1935, Bannerman 1963, Lambert 1971, Brown 1979); absent west of Cape Verde Is. (Brown 1979, Hazevoet 1995). Also common near fishing fleets in coastal waters of sw. Africa south to 25°S; most numerous north of 23°S, scarce elsewhere in s. Africa (Lambert 1971, Ryan 1986).

Regular in winter in Persian Gulf, Gulf of Oman, and Gulf of Aden (Bailey 1966, Cramp and Simmons 1983). Not observed in w. Indian Ocean away from land Jan–Jun (Gill 1967). Common in tropical Pacific during winter (Spear and Ainley 1993, Higgins and Davies 1996, R. Veit pers. comm.). Most numerous jaeger wintering off se. Australia (Brooks 1939, Wood 1989).

HISTORICAL CHANGES

No changes reported.

FOSSIL HISTORY

No fossil specimens. For information on fossil Stercorariidae in North America, see Olson 1985.

SYSTEMATICS

GEOGRAPHIC VARIATION; SUBSPECIES

No subspecies. No clear geographic variation in proportions of morphs, although Nearctic populations tend to have somewhat fewer dark birds (Southern 1944, Manning et al. 1956). Pomarine Jaeger breeds within a narrower latitudinal range than does Parasitic Jaeger, for which there are clear latitudinal trends in proportions of morphs. In n. Alaska, proportion of dark morphs is about 5% (Maher 1970); on Banks I., at most 1–5% (Manning et al. 1956); on Victoria I., about 10–15% (Parmelee et al. 1967). On St. Lawrence I., only about 1% of birds, including migrants, are dark (Fay and Cade 1959). Few data from Palearctic populations: on Franz Josef Land, 10% dark morphs (Collett and Nansen 1899, cited by Southern 1944; no other quantitative information from Russia.); in w. Greenland, about 10–15% dark morphs in Disko Bay (Salomonsen 1950). During boreal winter, proportion of dark morphs reported as high as 15–20% (Wood 1989) off se. Australia and 20% off nw. Africa (Brown 1979), but these values might include some immatures, some light morphs of which probably appear dark in the field.

RELATED SPECIES

The family Stercorariidae has traditionally included two genera, *Stercorarius* with the three jaegers and *Catharacta* with the large skuas. Recent evidence, however, suggests that Pomarine Jaeger is more closely related to the large skuas than to the two smaller jaegers. This evidence includes distinctive behavioral similarities between Pomarine Jaeger and large skuas (Pitelka et al. 1955b, Andersson 1973a, 1999a) including acoustic structure of the Long Call and Quavering Call (see Sounds, below), displays that accompany Long Calls (Slow Wingbeat Display, V-gliding, and Wing-raising Display, see Behavior: agonistic behavior, below), and absence of a distraction display in response to predators. The close relationship between Pomarine Jaeger and large skuas also appears in skeletal proportions (Schnell 1970 [Figs. 20 and 21], Andersson 1993a), ectoparasites, and both mitochondrial and nuclear DNA (Cohen et al. 1997). According to this evidence, if the family Stercorariidae retains two genera, *Catharacta* should include the Pomarine Jaeger with the large skuas. However, because jaegers and large skuas are closely related, it seems reasonable to unite them all in a single genus *Stercorarius*.

More controversial is a suggestion that Pomarine Jaeger and Great Skua (*C. skua*) are more closely related to each other than either is to the large skuas of the southern hemisphere (Cohen et al. 1997). On the other hand, similarities between these two species in mitochondrial DNA and ectoparasites might result from recent hybridization or from a mismatch between mitochondrial and species branching patterns during rapid speciation (Braun and Brumfield 1998, Andersson 1999a, 1999b).

Similarity of plumages in the three jaegers is probably a shared primitive state. The streaked Definitive Alternate plumage of the large skuas is, in this view, a recently derived state, possibly a result of neoteny (retention of immature traits in adulthood; Braun and Brumfield 1998, Andersson 1999a). Neotenic Definitive Alternate plumage might have reduced territorial aggression when the large skuas evolved colonial breeding and thus much closer proximity of neighboring pairs. The jaegers, on the other hand, might have retained more conspicuous Definitive Alternate plumage in order to defend large nesting territories. Some of the behavioral similarities uniting Pomarine Jaeger and large skuas could result from their large size. In effect, these species have evolved elaborate terrestrial displays instead of the acrobatic aerial displays of the smaller species. In addition, only the smaller species regularly use distraction displays as well as direct attack to divert predators from their nests.

The last word on skua and jaeger relationships has not been written. Based on current literature, the relationships of Northern Hemisphere birds are puzzling, but it is clear that Pomarine Jaegers are not so closely affiliated with the other two jaegers as previously believed.

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

Complete long-distance migrant between nesting areas in the Arctic and wintering areas in tropical and subtropical oceans (see Distribution, above). Away from the Arctic migrates mostly at sea.

TIMING AND ROUTES OF MIGRATION

Near-breeding areas. Migration is often conspicuous along arctic coasts. Bering Sea and Davis Strait serve as gateways to and from North American nesting areas. Migrants appear near St. Lawrence I. in mid-May every year (Fay and Cade 1959) and at this time become numerous in and north of Bering Strait (Jacques 1930, Gabrielson and Lincoln 1959, Kenyon and Brooks 1960, Portenko 1989). Along north coast of Chukchi Peninsula migrants fly northwestward 31 May–8 Jun (Portenko 1989); along north coast of Alaska they fly eastward. Most birds stay near the coast once north of Bering Strait, but they also occur far at sea more often than other jaegers do, where they follow ships to feed on discarded garbage (Portenko 1989).

Near Barrow, AK, in years with high lemming populations, arrives late May (earliest observation 19 May) following leads in ice near shore. Up to 90 birds congregate in roosts on frozen tundra in evening. By early Jun flocks continue eastward

from Barrow; roosting flocks continue to gather until mid-Jun. In years with low lemming populations and no nesting by jaegers, earliest birds do not appear until 4–8 Jun, no large roosts form, eastward migration is sparse, and all birds have disappeared by mid-Jun (Maher 1974). Low numbers migrating past Barrow in poor lemming years suggest that jaegers anticipate changes in lemming numbers. Large numbers passed Canning River delta in 1980, a year with dense nesting on Victoria I. (Johnson and Herter 1989). Migrants also occur in small numbers inland at least as far as the foothills along the Colville River (Kessel and Cade 1958) and sporadically in small numbers in passes of the Brooks Range (Irving 1960, Dean et al. 1976).

In n. Yukon, migrates eastward along coast 29 May–12 Jun (earliest 28 May), with highest rates 7–11 Jun (32–33 birds/h; observations in 1975; Salter et al. 1980). At Cape Dalhousie, Mackenzie District, NWT, >6,000 flew eastward between 29 May and 16 Jun 1972 (Johnson and Herter 1989). Early migrants on Banks and Victoria Is. fly northeastward, an indication that they have arrived from the west along the coast of the mainland (Manning et al. 1956, Parmelee et al. 1967). In contrast to these movements along the mainland coast, few migrants at this time occur offshore over leads in ice (Woodby and Divoky 1982).

Westward migration along the arctic coast begins in some years even before eastward movement ends. In n. Yukon in 1975, heavy westward migration began almost as soon as eastward migration subsided; birds first headed westward on 11 Jun and reached rates of 28 birds/h on 18–19 Jun (Salter et al. 1980). In a year with almost no nesting in n. Alaska (1959), similar westward movement began at Cape Sabine in nw. Alaska on 12 Jun; large numbers passed in last week of Jun and first week of Jul, and only occasional birds thereafter. Some migrants hunted on the tundra in good weather and roosted near the coast at night, but most continued westward near the coast (Childs 1969, Maher 1974). The scale of these early departures suggests that in some years few birds nest over very wide areas of the Arctic.

Southbound migrants are numerous in Aug far from shore in the Beaufort Sea north of Alaska and Yukon Territory (Frame 1973); often numerous around St. Lawrence I. in Aug (Fay and Cade 1959). At least 100 joined a huge flock of feeding Sooty Shearwaters (*Puffinus griseus*) and Black-legged Kittiwakes (*Rissa tridactyla*) off Kodiak I. in early Aug (Hoffman et al. 1981); noted in Aleutians from 21 May–19 Aug (Gabrielson and Lincoln 1959). Southbound migrants also numerous in Davis Strait west of Greenland in late Aug (Salomonsen 1950).

South of breeding range. Most numerous migrant jaeger in waters near eastern and western coasts of

Canada and U.S., although less often seen from shore than Parasitic Jaeger.

In Pacific Ocean, off se. Alaska, most numerous 13 Jul–3 Oct; few records in spring (Gabrielson and Lincoln 1959). Off w. Canada, the most numerous migrant jaeger. In spring, most are beyond the continental shelf; earliest observation 11 May; in fall, most are over the continental shelf or the shelf break, particularly in areas frequented by Sabine's Gull (*Xema sabini*); numbers are highest in the last half of Aug and decrease quickly in Sep; latest observation 31 Oct (Vermeer et al. 1987, Morgan et al. 1991).

Off Washington and California, the most numerous jaeger in autumn. Off Washington occurs from mid-Jul to mid-Oct, observed on 97% of trips offshore in Aug and Sep; also present in May (Wahl 1975). Off California numerous from mid-Aug into Nov; highest numbers in late Sep and Oct, when 30,000–70,000 estimated in California waters (Briggs et al. 1987). Off Monterey, central California, migrants pass between mid-Jul and mid-Nov and from mid-Apr through May; prefer the zone 3–80 km from shore near concentrations of shearwaters (Stallcup 1990). Occupies most of Southern California Bight by mid-Sep, reaching maximal numbers in Oct; most numerous over outer continental shelf, near underwater ridge between Santa Rosa I. and Cortés Bank, about 150 km southwest of Los Angeles (Briggs et al. 1987). In Oct, 1.5–3.6 birds/h reported over continental shelf off s. California; less numerous (<1 bird/h) beyond the shelf (Jehl 1973).

Regular in small numbers off Japan, Feb–Jun; northward movements noted at sea between 23 Apr and 30 May, especially in late Apr (Austin and Kuroda 1953). In nw. Pacific, last migrants observed 7 Jun; scattered birds reappear in late Jun and early Jul (Kuroda 1955).

Arrives off se. Australia in Nov (exceptionally Sep–Oct), most numerous Jan–Mar (7–12 observed/h), becoming scarce in late Apr and May; absent in Jun–Aug. From mid-Apr to early May groups of as many as 20 birds gather over the edge of the continental shelf 25–60 km offshore, just before the species disappears from se. Australia (Barton 1982, Wood 1989).

In Atlantic, the most numerous jaeger off e. Canada and U.S., although less often seen from shore than Parasitic Jaeger. Congregates on fishing banks between Greenland and Baffin I. in Aug and Sep; most numerous off e. Canada in Sep; most leave the Arctic by early Oct and become rare in waters off e. Canada after Oct (Wynne-Edwards 1935, Brown et al. 1975, Brown 1986). Over the continental shelf off ne. U.S., most numerous during late Apr and May and especially in Oct, when regular in small numbers over Georges Bank and in

sw. Gulf of Maine; extreme dates in fall, late Aug–Dec. In May most migrants are adults in Definitive Alternate plumage; in autumn most are adults in Basic plumage or immatures (Powers 1983). Scarce but regular in ne. Gulf of Maine, 6 Jun–21 Nov; none observed in spring (Finch et al. 1978).

Far offshore in North Atlantic, migrants are most numerous in eastern half (east of 35°W); most are observed in Oct, later than main movements of Long-tailed and Parasitic jaegers; latest in Dec (Baker 1947, Rankin and Duffey 1948). At 50°N in the Atlantic, northbound migrants pass between 24 Apr and 25 May (Wynne-Edwards 1935). Already concentrated at high latitudes (>68°N) by mid-May (Rankin and Duffey 1948).

On the continental shelf off New Jersey, Delaware, and Maryland, occurs in small numbers (usually <1/h) 25 Apr–29 May and 8 Aug–6 Dec, in all zones of the shelf, although less frequent than Parasitic Jaeger over shallow water near shore; largest numbers (>1/h) in Nov and early Dec (Rowlett 1980).

Off North Carolina, fall migration reaches a peak from second half of Oct through Nov (mean counts 8–12/d, maximal counts >35/d, $n = 15$ d of observation, latest specimen 20 Dec); spring migration occurs mostly from second half of Apr through May, usually in smaller numbers than in fall (mean count 5 birds/d in late Apr, <2 birds/d in May, $n = 32$ d of observation, earliest specimen 17 Apr; Lee 1995). Recorded on 100% of days of observation in May ($n = 10$ d), 20% in Jul ($n = 18$ d), 68% in Aug ($n = 20$ d), 80% in Sep ($n = 10$ d; N. Brinkley, B. Patteson pers. comm.).

Off eastern coast of Florida, most southward migration occurs late Oct–early Dec, with some counts of >1,000/d; northward migrants mostly Apr–May, in smaller numbers than in fall (Stevenson and Anderson 1994).

Near Bermuda, most numerous migrant jaeger, late Feb to mid-Jun, with greatest numbers 5–16 May, sometimes exceeding 10/h; smaller numbers in autumn, late Sep to late Dec (Amos 1991).

Regular spring migrant in English Channel, mostly 28 Apr–16 May, with some later in May and past headlands in w. Ireland and Scotland (Davenport 1975, 1981). Already numerous in wintering area off Cape Verde, nw. Africa, by mid-Nov; large numbers of individuals found flying northward along this coast on 7–8 May (Bierman and Voous 1950). Regular migrant in Red Sea and at Eilat, Israel, where small numbers occur mostly in Apr and May (Meininger and Sørensen 1986, Goodman and Storer 1987). Regular in Sep off Pakistan (van den Berg et al. 1991).

No clear evidence that Pomarine Jaegers regularly migrate overland to and from arctic North

America. On the Great Lakes, this jaeger is identified infrequently, about 15 individuals/yr in total, between early Aug and early Jan; immatures not recorded definitely before late Sep (Brock 1997, Sherony and Brock 1997). On Lake Michigan most observations occur between early Oct and early Nov (Brock 1997). Few records exist for interior of North America (Taylor 1993). Infrequent reports in n. Gulf of Mexico (about half as often as Parasitic Jaeger), throughout most of the year (except Feb and Jul; Williams 1965, Duncan and Havard 1980), probably include birds wandering from wintering population in s. Caribbean Sea. In Eurasia, Pomarine Jaeger is also much less often reported from interior than is Parasitic Jaeger. In n. Russia, occasionally occurs in early Jun along rivers well south of breeding range (Rogacheva 1992); also scattered records on large rivers and lakes throughout central Asia (Dement'ev and Gladkov 1969).

MIGRATORY BEHAVIOR

Migrants travel singly or in small groups, often only 2–3 (Parmelee et al. 1967, Portenko 1989). Most migrants passing the British Isles are in flocks that average 4–5 birds; about 35% of birds are alone; some flocks include >50 birds (Davenport 1981). Flocks of as many as 75 occur on fishing banks west of Greenland in Aug and Sep (Brown et al. 1975). Migrants accompany flocks of shearwaters in Pacific Ocean (Austin and Kuroda 1953). Early migrants near Japan are still in molt in Apr and have little fat, but by May have acquired Alternate plumage (see Appearance: molts and plumages, below) and become fatter (Austin and Kuroda 1953).

Coastal observers usually report most birds during onshore winds (southerly winds in s. England and Ireland, westerly winds in w. Ireland and Scotland; Davenport 1981), an indication that most birds migrate far from shore but drift in cross winds. Flocks travel at speeds of 35–55 km/h between headlands in s. England, an indication that migrants might average 200–500 km/d; most movement occurs during morning and during the last 3 h of daylight (Davenport 1975, 1981).

Migrants fly into headwinds up to about 35 km/h, but settle on the water in higher winds or when visibility is low (Davenport 1981). In mid-ocean, migrants can continue to fly in storms with winds of 80–90 knots; make slow headway but use wave troughs for shelter and occasionally rise to 30–50 m above the waves where they deftly maintain control (Rankin and Duffey 1948). In fine weather they often fly 10 m or more above the water; near the water, they follow straight paths with steady flapping and rarely arc or bank (Wynne-Edwards 1935, Stallcup 1990, Amos 1991).

CONTROL AND PHYSIOLOGY
No information.

HABITAT

BREEDING RANGE

Largely confined to low-lying wet coastal tundra, usually marshy areas with numerous small lakes and cyclic peaks in abundance of brown lemmings (Schaaning 1916, Pitelka et al. 1955a, 1955b, Maher 1970, Andersson 1973a, Rogacheva 1992). Reliance on low-lying, wet tundra contrasts with use of dry, barren tundra by Long-tailed Jaeger, the other jaeger relying primarily on rodents for successful reproduction (Maher 1974).

In n. Alaska, habitat includes marshes, wet polygonal tundra, well-drained but mesic tundra, and marshy swales between low ridges (Maher 1974). Suitable habitat extends along the coast in a narrow strip about 8 km wide, except in the area around Barrow, AK, where it extends 40 km south to the Inaru River. This area supports only low vegetation, not >15 cm high at end of summer; over half the area is covered with shallow water, mostly in the form of sedge (Cyperaceae) marshes; slightly higher areas on low ridges and the borders of tundra polygons have sparse tussock-heath tundra with low sedges and grasses mixed with prostrate willows (*Salix* spp.), heaths (Ericaceae), mosses, and lichens. Peaty soil thaws only to a depth of about 15 cm; tundra is free of snow from sometime in Jun to early Sep (Maher 1974).

On Victoria I., Canada, restricted to wet tundra usually near the coast (sometimes to 15 km inland; Parmelee et al. 1967). On Bathurst I., also usually nests in marshy meadows, although collared lemmings (*Dichrostonyx groenlandica*), their principal prey here, are most abundant in dry tundra (Taylor 1974). In n. Russia, also prefers wet tundra: wet coastal meadows, sedge bogs, and wet tundra with low mounds and ridges (Uspenskii 1984).

On Disko I., w. Greenland, nesting reported on cliffs (Kumlien 1879, quoted by Bent 1921) but this report is doubtful (Salomonsen 1950).

MARINE RANGE

Usually not in coastal waters. Off N. Carolina most often along edge of continental shelf and western edge of Gulf Stream, where migrating shearwaters and terns concentrate (Lee 1995).

Off w. Canada in spring, most migrants are beyond the continental shelf. In fall, most are over the continental shelf or the shelf break (Morgan et al. 1991), particularly in areas frequented by Sabine's Gull (Vermeer et al. 1987).

Off Washington State, 93% observed >10 km from shore. Off n. California in Sep when numbers of migrants reach a peak, most are seaward of continental shelf; in Oct, as overall numbers decrease, center of density shifts to continental shelf; few birds occur in central axis of California Current 200–500 km offshore (Briggs et al. 1987). Off Monterey, central California, migrants prefer the zone 3–80 km from shore near concentrations of shearwaters (Stallcup 1990). Off s. California in Oct, most numerous over the outer continental shelf (Briggs et al. 1987).

Off nw. Africa, highest numbers are in upwelling zone along margin of continental shelf near Cape Verde (10–20°N; Wynne-Edwards 1935, Bannerman 1963, Brown 1979), where counts in Feb–Mar average 15 birds/h (Brown 1979); less common beyond the continental shelf (<0.6 bird/h) and absent west of Cape Verde Is. (Brown 1979, Hazevoet 1995).

Off se. Australia, most numerous over continental shelf with water depths <200 m within 40 km of shore (counts average about 8/h); beyond 50 km from shore, about half as abundant (Wood 1989).

FOOD HABITS

FEEDING

Main foods taken. Breeders rely primarily on moderate to high densities of brown lemmings (Pitelka et al. 1955a, Parmelee et al. 1967, Maher 1970). Small numbers breed in localized areas with high densities of other microtine rodents (tundra vole [*Microtus oeconomus*], n. Alaska, Maher 1970; collared lemming, Bathurst I., Taylor 1974). High populations of brown lemmings occur in n. Alaska every 3–4 yr, with intermediate densities occasionally in a year preceding a high; densities of lemmings vary at least 400-fold among years (<1 to >160 lemmings/ha; Maher 1970). Near Barrow, AK, in a 12 yr period, 5 yr had intermediate or high densities of lemmings (Maher 1970). Sets of eggs in North American collections suggest a 2–4 yr interval between peaks of nesting (Fig. 2).

In years with moderate or dense lemming populations, these rodents are numerous in early summer following reproduction during winter. Lemmings resume vigorous reproduction following snow melt in early Jun, but predation progressively depletes their numbers until young begin to appear in mid-Jul. Consequently, prey available for jaegers usually decreases during Jun but then increases (although not to the levels in early Jun) about the time that jaegers' eggs are hatching (Pitelka et al. 1955a).

Although Pomarine Jaegers do not prey much on other birds, they appear to have a major impact on their populations. Shorebirds and passerines become scarce near Barrow in years with high densities of lemmings, probably because the numerous jaegers and lemmings disrupt successful nesting (Maher 1974).

Away from land Pomarines feed on fish along the ice margin (Smith 1973), follow ships for scraps, and steal Arctic cod (Gadidae) from Black-legged Kittiwakes (Portenko 1989). Migrants on St. Lawrence I. feed initially on debris along the shore, including carrion; shift to voles (*Microtus* spp.) as the tundra thaws (Fay and Cade 1959).

Migrants far from shore in North Atlantic rarely observed feeding (Wynne-Edwards 1935, Rankin and Duffey 1948). Northbound migrants past the British Isles also not observed feeding (Davenport 1975). During winter individuals often congregate around fishing vessels or other ships, mostly to forage for refuse but also to steal from other species (Brown 1979, Barton 1982, Cramp and Simmons 1983, Wood 1989).

Microhabitat for foraging. Apparently no special restrictions when foraging: tundra within nesting territories while breeding; otherwise, open ocean, often near concentrations of other feeding seabirds.

Food capture and consumption. Breeders search for lemmings from perches, on the wing, and on foot. Hunting methods change as vulnerability of lemmings changes during summer. Following snow melt, lemmings have little cover because the ground remains frozen and vegetation is minimal. At this time, a Pomarine often uses any small rise to scan for prey, which it can spot at distances of >150 m; then flies in pursuit, sometimes chasing the lemming on the ground, and strikes and grabs it with its bill; often returns to its perch to tear the lemming to pieces. When prey are less plentiful, a hunting Pomarine bird flies over the tundra watching the ground from 5–8 m up (3–10 m; Andersson 1973a), often hovers for 1–3 s, then swoops to grab a lemming (Pitelka et al. 1955a, Maher 1970, Andersson 1973a). In comparison to hunting Long-tailed Jaegers, Pomarines fly closer to the ground (3–10 m in contrast to 15–50 m) and hover less (about 1% of flying time in contrast to about 10%; Andersson 1973a). Only the bill is used to capture and handle prey, never the feet. Often lemmings, even adults, are swallowed whole within 1–2 min. When harassed by another jaeger, an individual can swallow a small or medium-sized lemming whole in flight.

After the surface thaws, lemmings take shelter and raise young in nests in shallow burrows under vegetation or in moist turf. Pomarine Jaegers in pursuit of a lemming dig vigorously into these burrows, using the bill to pull away vegetation and toss it aside (Andersson 1973a). When adult lem-
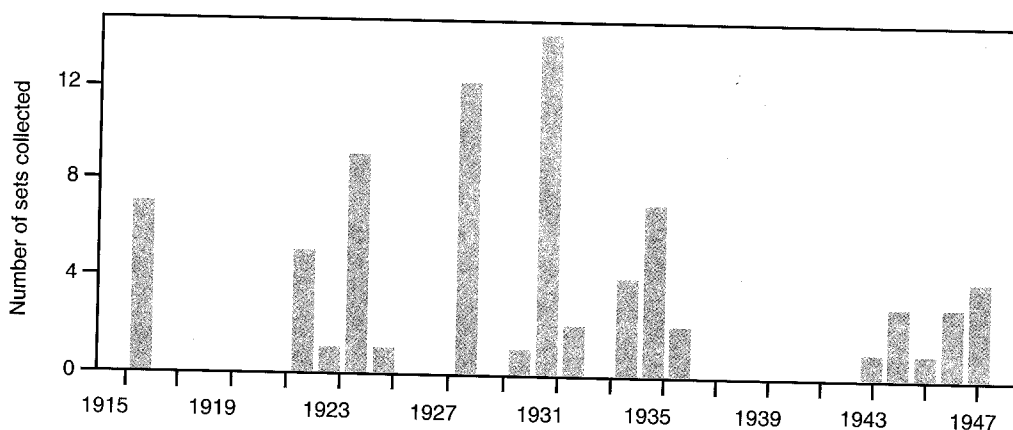
Figure 2. Distribution of sets of eggs collected near Barrow, Alaska, over 35 years. Although collectors' efforts were not evenly distributed, and some years probably had no visits by collectors, peaks are apparent every 2–4 years (n = 89 sets of eggs from Barrow in North American collections; see Acknowledgments).

mings become scarce, often later in the season, these jaegers hunt by walking over the tundra and digging into lemming burrows, presumably searching for nests with females and young. Sometimes groups of as many as 20 hunt in this way simultaneously in a small area. When lemmings are scarce, individual jaegers sometimes spend as much as a hour at a time digging. Pomarine Jaegers are the only avian predators that dig for lemmings (Pitelka et al. 1955a, Maher 1970, Andersson 1973a, 1973b).

Preys on birds infrequently. Several jaegers observed pursuing Red Phalaropes (*Phalaropus fulicaria*) migrating in large flocks along the coast near Barrow, AK; at least 6 phalaropes seized and thrown by the wing but not killed (Pitleka et al. 1955a, Bent 1921); migrating phalaropes sometimes seized in flight and killed (Tuttle 1911, Gabrielson and Lincoln 1959). Occasionally may take eggs of other birds (Lapland Longspur [*Calcarius lapponicus*] and Short-eared Owl [*Asio flammeus*]; Pitelka et al. 1955a). Nonbreeders occasionally follow people to find birds' nests (Parmelee et al. 1967). Breeders not observed chasing gulls or terns for food, but immatures chase Glaucous Gulls (*Larus hyperboreus*) and force them to disgorge food (Pitelka et al. 1955a).

To capture Arctic cod at sea, Pomarine Jaegers alight on the water (Portenko 1989); also swim in shallow water to catch fish at the surface (Salomonsen 1950). Off se. Australia, these birds feed on scraps from ships by seizing items from the surface in flight or by alighting and dipping the bill into the water (Wood 1989). Fearless in competing with large petrels and albatrosses for food discarded from fishing boats. Although usually taking food from the surface, they also dive either from flight or from the water and can swim under water (Barton

1982, but not observed by Wood 1989). Usually forages for itself instead of robbing other species (Higgins and Davies 1996). Off nw. Africa, likewise feeds mostly by scavenging near fishing boats (Brown 1979).

Attacks on other birds at sea sometimes involve attempts to steal food (see next section) but also include attempts at predation. An immature bird during a 2 wk period in Sep–Oct off the coast of the Netherlands daily killed and ate ≥1 Black-headed Gulls (*Larus ridibundus*) by grabbing them in flight, falling to the water, and drowning them (Meininger 1977).

Kleptoparasitism. Infrequently reported in Arctic. Breeders occasionally harass gulls (Taylor 1974); birds breeding near a Black-legged Kittiwake colony probably obtain fish from them (Maher 1974, Portenko 1989). In Disko Bay, w. Greenland, many obtain their food by attacking nesting Black-legged Kittiwakes and less frequently larger gulls (Kumlien 1879, quoted in Bent 1921), but most of these birds are presumably not breeding (Salomonsen 1950).

Migrants in mid-ocean rarely chase other species, only occasionally Black-legged Kittiwake (Wynne-Edwards 1935), but near shore and over the continental shelf attacks occur frequently. Migrants near Bering Strait regularly pursue Black-legged Kittiwakes and Horned Puffins (*Fratercula corniculata;* Jacques 1930). Off s. Alaska, join large flocks of Sooty Shearwaters and Black-legged Kittiwakes feeding on congregations of spawning capelin (*Mallotis villosus*) that persist for several days, attacking birds surfacing with fish in their bills (Hoffman et al. 1981). Off New England, targets include large shearwaters (mostly *Puffinus gravis*), which are pounced upon from above while feeding in flocks on the water (Bent 1921); off N. Carolina,

Audubon's Shearwater (*Puffinus lherminieri*), Black-capped Petrel (*Pterodroma hasitata*), and Sooty Tern (*Sterna fuscata*) are occasionally pursued in flight (T. Hass pers. comm.). Shearwaters are also frequent targets off the California coast (Stallcup 1990).

Kleptoparasitism occurs regularly in wintering areas. Like Parasitic Jaeger, pursues terns near beaches in sw. Africa (Ryan 1986). Off se. Australia rarely engages in aerial pursuit; instead usually attacks gulls or shearwaters feeding on the water near fishing boats, forcing them to relinquish their food (Barton 1982, Wood 1989). Even though Pomarines crash aggressively into their targets, large shearwaters often successfully defend their food by fighting back (Flesh-footed Shearwater [*Puffinus carneipes*]) or by sheer numbers (Wedge-tailed Shearwater [*P. pacificus*]; Barton 1982). When pursuit attempted, Pomarine Jaeger noticeably less agile than Parasitic Jaeger (Wood 1989). Off Central America, Pomarines force Audubon's Shearwaters to disgorge food; the latter seek to escape by plunging into the sea (Jehl 1974). Along the coast of Peru during the boreal winter, Pomarines parasitize Peruvian Boobies (*Sula variegata*) and Franklin's Gulls (*Larus pipixcan*; Duffy 1980). Despite these reports, kleptoparasitism is usually not the primary source of food for this jaeger during migration and in winter off Australia and Africa.

In e. tropical Pacific, however, kleptoparasitism constitutes 95% of all observed feeding attempts. Success is higher in attacks on larger species (especially Juan Fernandez Petrel [*Pterodroma externa*] and Wedge-tailed Shearwater, 61%) than on smaller gulls and terns (especially Sooty Tern, 17%), just the opposite of the situation for smaller jaegers. Pomarine Jaegers rely on speed, surprise, and physical contact for success, rather than on aerial agility; targets are sometimes bitten, shaken by the head, thrown from the air to the water, or held under water. Kermadec Petrel (*Pterodroma neglecta*) and to a lesser extent Herald Petrel (*P. arminjoniana*) resemble Pomarine Jaegers and South Polar Skuas in pattern and shape and thereby presumably avoid attacks and increase their own success in attacking other large petrels (Spear and Ainley 1993).

DIET

Major food items. Breeders rely almost exclusively on brown lemmings (occasionally collared lemmings or voles) and continued abundance of these rodents is necessary for successful reproduction (Pitelka et al. 1955a, Maher 1970, 1974). Nonbreeders during summer take a great variety of food, including rodents, birds, eggs, insects, marine invertebrates, and carrion (Maher 1970, 1974, Taylor 1974). Kleptoparasitism occurs rarely during summer in the Arctic (see above).

Breeders take a few birds, mostly chicks of shorebirds, plus a few ducklings and passerines (Maher 1970, 1974); when lemmings become scarce in Aug, some breeders forage along the coast for fish and Red Phalaropes (Maher 1974). Occasionally attack nesting Snow Geese (*Anser caerulescens*) or Brant (*Branta bernicla*) to obtain their eggs (Portenko 1989).

Nonbreeders in the Arctic also take the following: birds, mostly Red Phalaropes but even species as large as ptarmigan (*Lagopus* spp.); carrion, probably from vicinity of villages; marine invertebrates, including cephalopods and polychaete worms, probably obtained along the tide line (Maher 1970, 1974); occasionally spiders and insects or their larvae (Manning et al. 1956, Parmelee et al. 1967); garbage near villages (Manning et al. 1956); and fish from along ice edge (Smith 1973, Portenko 1989).

Quantitative analysis. In n. Alaska (Maher 1970), 98–100% of pellets from breeders contained brown lemmings (except a small population feeding on tundra voles). In years with high densities of lemmings, only 2–9% of pellets contained other items. In a year preceding a high, a few breeders included more birds and eggs in their diets (12% and 9% of pellets, respectively); insects occurred only incidentally in 3–6% of pellets. After mid-Jul young lemmings begin to appear above ground and in jaegers' diet; by early Aug young constitute 30–50% of all lemmings taken. Male lemmings predominate only slightly (54% in each of 2 yr), and the proportion of males declines slightly during summer; unlike some other avian predators, these jaegers do not take males disproportionately.

Nonbreeding birds in n. Alaska also rely primarily on lemmings (41% of 56 stomachs) but their diet also includes birds (25%), eggs (20%), carrion (14%), insects (predominated in 3% of stomachs), fish (12%), and marine invertebrates (3%; Maher 1970).

Migrants off coast of N. Carolina (n = 24 stomachs) contained unidentified fish (17 stomachs), squid (Onychotenthidae; 7), sargassum crab (*Planes* sp.; 2), brown alga (*Sargassum* sp.; 1), unidentified small eggs (1), feathers (1), an 8 × 14 mm piece of plastic (1); one stomach was empty (specimens, North Carolina State Museum of Natural Sciences [NCSM]).

FOOD SELECTION AND STORAGE

No reports of food storage.

NUTRITION AND ENERGETICS

To grow from hatching to fledging (24 d old), chicks consume about 9.3 kg or about 200 lemmings (50 g on average); thereafter about 200–220 g or 5.5 lemmings/d (Maher 1970). Based on 3 all-day
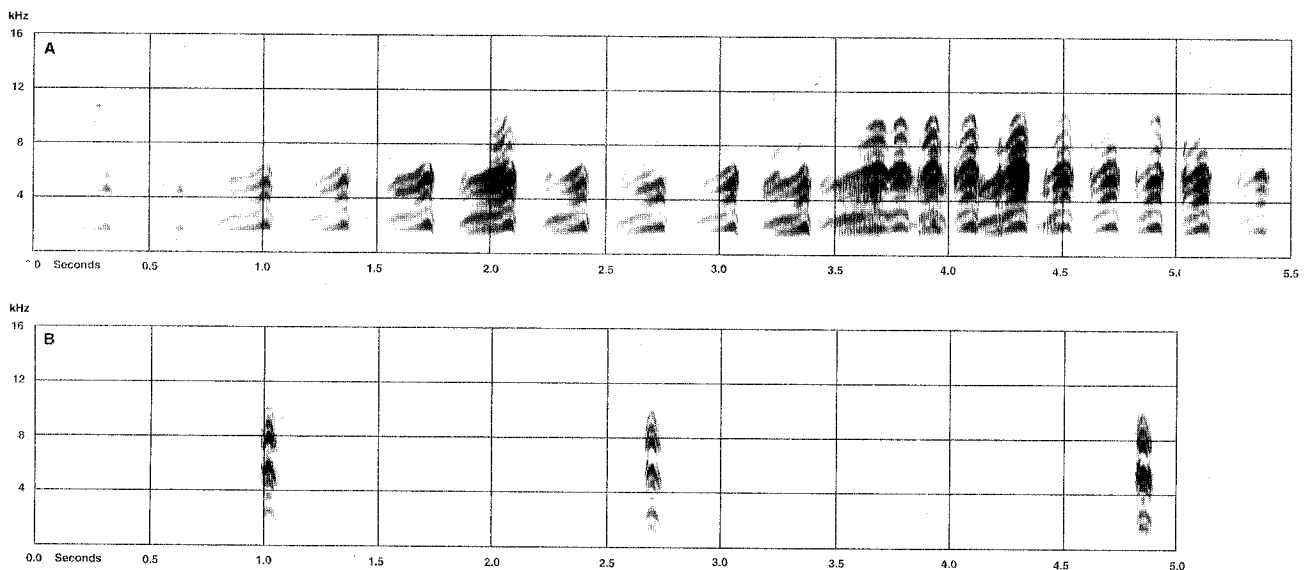
Figure 3. Vocalizations of the Pomarine Jaeger. A. Portion of a Long Call. B. Short calls. From R. T. Peterson's Western Bird Guide (NB 50, Track 5, recorded on Melville I., Northwest Territories, on 13 May 1977). Prepared by the staff of the Borror Laboratory of Bioacoustics, The Ohio State University, using a Kay Elemetrics DSP 5500 Sona-Graph (with an effective frequency resolution of 600 Hz and a 100 pt. transform size).

observations, adults consume about 7 lemmings/d or about 250 g (Maher 1970). During a summer, an adult consumes about 340 lemmings and each young about 170 (Maher 1970).

Near Barrow, AK, Pomarine Jaegers are the primary predator of lemmings (Pitelka et al. 1955a). Although Snowy Owls (*Nyctea scandiaca*) average over twice the mass and have clutches that average over 3 times as large as Pomarine Jaegers, the jaegers' population is at least 8–40 times denser than the owls' (Pitelka 1955a), so jaegers consume 10 times as many lemmings/ha (Maher 1970). During a summer these jaegers consume about 75 lemmings/ha, 63% of the total for all predators, with potentially important consequences for dynamics of lemming populations (Maher 1970).

On Bathurst I., where breeding Long-tailed Jaegers are over 3 times as numerous as Pomarines in years with high densities of collared lemmings, the greater mass of prey consumed by Pomarines makes them the predominant predator on these lemmings (Taylor 1974). Because collared lemmings are much smaller than brown lemmings (roughly 50 vs. 150 g on average), jaegers must eat many more each day to satisfy their energy requirements. As a result, Pomarine Jaegers apparently cannot breed successfully in areas where only collared lemmings are available (Taylor 1974).

METABOLISM AND TEMPERATURE REGULATION

Little information. Mean core body temperature of migrants off N. Carolina, 40.4°C (range 41.8–42.2°C, n = 14; Platania et al. 1986).

DRINKING, PELLET CASTING, AND DEFECATION

Little information. Birds feeding on lemmings cast pellets (frequency and sizes not reported; see Diet, above).

SOUNDS

VOCALIZATIONS

Development. No information.

Vocal repertoire. No quantitative study of variation based on sonograms. Long Call consists of simple notes with numerous harmonics repeated at a rate of 2–3/s for 1–5 s; lacks prolonged notes such as those in similar calls of smaller jaegers (Fig. 3A; Andersson 1973a). This call is a harsh, gull-like "yowk, yowk, yowk," which varies in pitch and tempo. When uttered by an excited bird, it grades into a "series of high-pitched sharp screams" (Pitelka et al. 1955b).

Two calls serve as alarm signals: Short Call (about 0.1 s with numerous harmonics, Fig. 3B) and Quavering Call (about 1.0 s with harmonics and varying frequency). Other jaegers have no calls similar to the latter (Andersson 1973a).

Both the Long Call and the Quavering Call resemble calls of the Great Skua, but more information about variation in these and other calls is needed for all species of this family.

Feeding birds at sea utter sharp "which-yew, which-yew" followed by repeated "week, week, week" (Barton 1982).

NONVOCAL SOUNDS
    No information.

BEHAVIOR

LOCOMOTION
    Flight. Larger in size than smaller jaegers and consequently less agile in flight. Parasitic Jaeger can easily outmaneuver Pomarine Jaeger in flight and drive the larger species away (see Food habits: feeding, above). Nevertheless, like other jaegers, Pomarine is capable of astonishing maneuvers; can execute a backward somersault in order to pounce on feeding shearwaters (Bent 1921). Maximal speed in flight similar to that of Long-tailed Jaeger and slower than Parasitic Jaeger (DSL pers. obs.)
    Swimming and diving. Observers disagree on whether or not Pomarine Jaeger can dive from flight or the surface and swim under water (see Food habits: feeding, above). Swims on surface.

SELF MAINTENANCE
    At sea often gathers in groups of as many as 15 (sometimes >100; R. Veit pers. comm.) after feeding and rests on the surface, often in flocks with other seabirds. During high winds, faces into waves and ducks as they hit. In calm conditions, bathes in the usual way, by dipping head and flapping wings to throw water over the back; then ruffles plumage and preens (Barton 1982).

AGONISTIC BEHAVIOR
    Intruders into a territory usually evoke Long Call in Oblique Posture with Wing-raising Display by the resident bird (Fig. 4). In Oblique Posture, foreparts are raised to a variable degree, breast feathers fluffed, and bill pointed toward the intruder. Wing-raising Display varies from barely lifting the wings to extending them fully almost straight upward; often the wings are raised above horizontal and partly extended so the tips point backward. The neck is either bent forward so the bill points downward or pulled backward so the bill points upward. Upright Posture with bill held below horizontal alternates with Long Call in Oblique Posture. Birds often quickly take flight to pursue intruders (Andersson 1973a).
    Once in flight, territorial resident flies directly toward the intruder in Slow Wing-beat Display with Long Calls. In this display, wing-beats are slower, higher, and stiffer than normal. This display can intensify into V-Gliding (wings held upward at an angle of about 100°, for 3–5 s), often accompanied by Long Call. A bird displaying thus sometimes glides to land in Oblique Posture with Wing-raising Display. Slow Wing-beat Display and V-Gliding

often alternate with chasing an intruder (Pitelka et al. 1955b, Andersson 1973a, Maher 1974).
    Wing-raising Display is absent in the two smaller jaegers, but conspicuous in the larger skuas. The species that display their wings while on the ground all have conspicuous white patches in the primaries, much larger than those of the smaller jaegers. In addition, Oblique Posture, in which Long Calls are uttered, is more variable in both Pomarine Jaeger and skuas than it is in the 2 smaller jaegers. Upright Posture, in contrast, is very similar in all jaegers and skuas, as well as many gulls (Andersson 1973a).
    Slow Wing-beat Display and V-Gliding are also similar to displays of Great Skua. In the gliding displays of other jaegers, in contrast, the wings are held either nearly horizontal (Parasitic Jaeger) or bowed well below horizontal (Long-tailed Jaeger; Andersson 1973a).
   Raising the tail, especially the central rectrices, during courtship is characteristic of Stercorariidae (Andersson 1973a).

SPACING
    Intraspecific territoriality. Defends large all-purpose territories from which all conspecifics are excluded. Nests usually located near center of defended area. Breeders normally confine foraging to their territories (Pitelka et al. 1955a, Andersson 1973a, Maher 1974), but in sparse breeding populations sometimes leave to forage at local concentrations of lemmings (Maher 1974). Spacing of neighboring nests ranges from a median of 330 m (range 210–580) in 3 yr of dense nesting to a median of 700 m (range 300–1850) in a year with intermediate densities (Pitelka et al. 1955a, Maher 1974). Territories reach maximal densities of 9–10/km², regardless of densities of lemmings in peaks, so compression of territories is apparently limited (Pitelka et al. 1955a, Maher 1974). Particularly in years with plentiful lemmings, this species nests at much higher densities than Long-tailed Jaeger, the other jaeger specializing on lemmings, which rarely exceeds densities of 1/km² (Wiley and Lee 1998).
    Rates of territorial defense in 2 years with high nesting densities reached 5.0–5.7/h in Jun; if lemmings remained numerous in Aug rates of defense remained high also (mean 4.7/h). In a dense population, 47–62% of interactions occurred with neighbors, 37–42% with transient conspecifics, and 1–11% with other species. Territorial adults display toward intruding young of the year but usually do not chase them.
    If a bird approaches its boundary in flight, the neighbor usually retaliates by approaching and calling. Except when territories are packed at maximal densities, a boundary zone 30–60 m wide
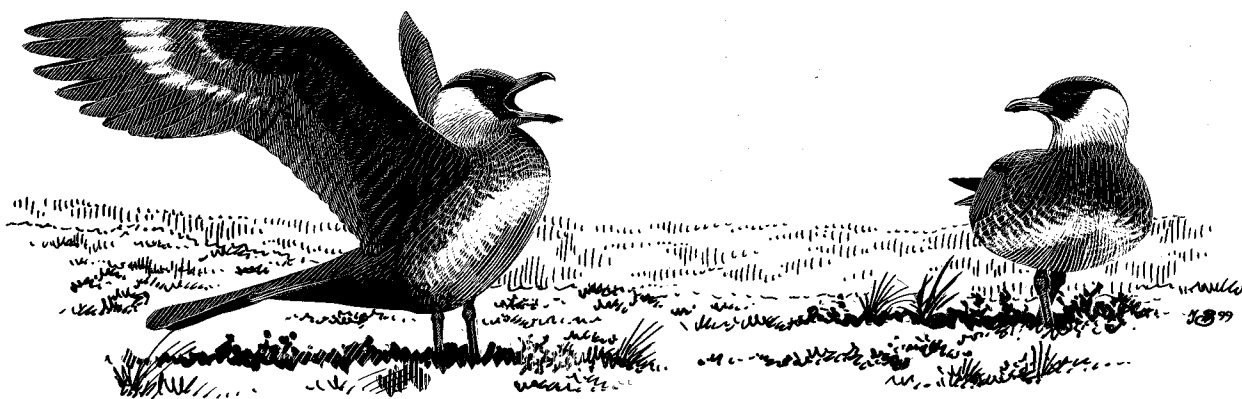
Figure 4. Oblique Display with Long Call of Pomarine Jaeger, showing the Wing-raising Display characteristic of this species. Drawing by N. John Schmitt.

separates territories, in which neither neighbor has an advantage. After a chase near a boundary, a bird often banks steeply to return to its territory (Maher 1974).

Prolonged contests between territorial neighbors can involve repeated swooping and calling by all 4 birds. In the most intense encounters, territorial neighbors sometimes clash in the air and drop to the ground fighting. Once territories are established, however, residents are usually silent; territorial advertisement consists simply of the presence of an alert resident perched on a slight rise or foraging in flight (Pitelka et al. 1955a).

Establishment of territories occurs quickly when conditions are right. In years with dense lemmings, birds leave roosting flocks, become localized on the tundra, and begin to defend territories as soon as snow cover and inclement weather permit. Often most territories established within a week of intense activity. Even in years of plentiful lemmings, some birds establish territories but abandon them before laying eggs (Maher 1974). On Bathurst I., near the northern limit of the species' range, in years with high densities of collared lemmings, pairs establish territories soon after arrival but some quickly depart without nesting (Taylor 1974).

Near Barrow, AK, in years with minimal numbers of lemmings, few birds appear, and no territories are established (Maher 1974). Unlike Long-tailed Jaeger, this species seems not to establish territories early every season and then abandon them when food is inadequate; instead when lemmings are sparse few birds appear and no territories are established.

Nonbreeding birds migrating westward in late Jun quickly became territorial for a few days in a localized area with high densities of tundra voles: 7 territories defended by single birds, 3 by pairs (Maher 1974).

In Aug pairs gradually extend their foraging ranges beyond their territories at a time when young are 2–3 wk old. Some adults continue to defend territories until late Aug when lemmings are sufficiently numerous, even after their flying young have begun to make excursions outside the territory (Pitelka et al. 1955b, Maher 1974). When lemmings become scarce, however, birds often leave their territories to forage along shore (Maher 1974).

Interspecific territoriality. Interspecific territoriality is difficult to separate from reactions to potential predators of eggs or young, because many of the latter species are also potential competitors for lemmings. Breeders exclude both Parasitic and Long-tailed jaegers from their territories, as well as Glaucous Gulls (Pitelka et al. 1955a, Maher 1974). In addition, many other intruding predators are attacked (Snowy Owl, Short-eared Owl, Gyrfalcon [*Falco rusticolus*], Arctic fox [*Alopex lagopus*]) but also apparently innocuous targets (Arctic Loon [*Gavia arctica*], Brant, and Sandhill Crane [*Grus canadensis*]; Pitelka et al. 1955a, 1955b, Maher 1974).

Reactions to Parasitic Jaegers are nearly the same as those to conspecifics (almost all intruders evoke both display and attack). Long-tailed Jaegers, in contrast, are usually ignored (Andersson 1973a). Parasitic Jaegers are more likely to prey on eggs or young, while Long-tailed Jaegers might compete with Pomarine Jaegers for lemmings (but usually take the smaller collared lemming).

SEXUAL BEHAVIOR

Mating system and sex ratio. Socially monogamous. No information on extra-pair copulations. No indications that morphs mate nonrandomly (Southern 1944).

Pair bond. Some pairs appear to have formed (or re-formed) bonds before establishing territories, but some single birds (perhaps breeding for the

first time or replacing mates that have failed to return) establish territories and then attract mates (Pitelka et al. 1955b). By analogy with other jaegers, these single territorial birds are probably males.

A single territorial bird responds to an approaching potential mate with Wing-raising Display, much like the response to other intruders. As a prospective mate comes closer, the resident responds by raising its head to a position behind vertical (with bill either raised or lowered), erecting its breast feathers, raising its tail slightly and then elevating the two central rectrices above the rest. Long Calls accompany this display. Occasionally two birds perform this display facing each other or alternately. Similar displays occur throughout Jun between established pairs. Preceding copulation, the male sometimes performs elements of this display, including raising the central rectrices (Pitelka et al. 1955b).

During pair formation, the female often approaches the male in Hunched Posture, with body horizontal and neck withdrawn, much like the similar posture of many gulls, except that the tail is elevated—especially the elongated central rectrices, which are thus prominently displayed. In this situation, females also adopt Erect Posture with bill elevated above horizontal (Andersson 1973a).

Competition for mates can become overt. Sometimes 2 birds display before a third, followed by one of the displaying birds chasing the other. Also one bird displaying before another is sometimes chased away by a third, which returns to display before the partner (Pitelka et al. 1955b).

During incubation relief, the arriving bird often utters either a shortened or a full Long Call; its mate adopts Oblique Posture, sometimes with Wing-raising Display (Andersson 1973a). During incubation relief, as well as during nest building, one bird sometimes tosses grass blades sideways or over its shoulder (Maher 1974).

Remating rarely occurs after a mate disappears; one male obtained a mate in early Jul, which began laying 9 d after his first mate disappeared (Maher 1974).

SOCIAL AND INTERSPECIFIC BEHAVIOR

No indications of loose coloniality, unlike some populations of Parasitic Jaeger (Pitelka et al. 1955a). During nonbreeding season, often in groups (see Behavior: self-maintenance, above).

PREDATION

Kinds of predators. No predators reported for adults; eggs and young are taken by Arctic fox, Glaucous Gull, and perhaps Snowy Owl and other Arctic predators (see Demography and populations: causes of mortality, below).

Responses to potential predators. Other species of jaegers, which are potential predators on eggs and young, often evoke responses like those directed at intruding conspecifics, including Long Call with Oblique Posture and Wing-raising Display (see Agonistic behavior, above, and Spacing, above). Other potential predators usually evoke direct chases and attacks. Snowy Owls and Short-eared Owls evade these attacks by fleeing from the territory or ascending 50–80 m in the air (Andersson 1973a).

When an intruder persists in remaining in the territory, it evokes repeated swoops by both members of the pair in turn. After each dive, the jaegers soar upward. Particularly during attacks on humans, Snowy Owls, or other large birds on the ground, the jaegers often use their feet to strike the intruder (Pitelka et al. 1955b, Maher 1974). Arctic fox elicit especially intense attacks, with mated birds alternating in dives to within 20–30 cm of the fox's head. The fox often cringes in response and usually leaves the territory (Andersson 1973a).

Both members of a pair participate in defense against intruders, by calling from the ground, raising their wings, or flying to join the mate. Incubating birds call to alert the mate or raise their wings without rising from the eggs (Pitelka et al. 1955b, Maher 1974). In one pair the male performed 60% of attacks on intruders (Andersson 1973a).

Interactions with Snowy Owls are particularly frequent, because Pomarine Jaegers and Snowy Owls cannot exclude each other from their territories and both often nest in areas with dense populations of lemmings. In n. Alaska, Snowy Owls in flight are attacked by pairs of jaegers, often swooping in turn; owls perched on the ground evoke diving attacks. The owls sometimes ignore these attacks but often dodge them or flip over to present their talons to the jaegers (Pitelka et al. 1955a). In one case a pair of Pomarine Jaegers killed a Snowy Owl near its nest after repeated attacks (Bailey 1948), and it is possible that territorial jaegers interfere significantly with foraging by Snowy Owls (Pitelka et al. 1955a). In contrast, Snowy Owls never harass Pomarine Jaegers (Pitelka et al. 1955a).

BREEDING

PHENOLOGY

Arrival in breeding areas. Arrival depends on lemming densities. In years with many lemmings near Barrow, AK, earliest observations 19–23 May (Pitelka et al. 1955a, Maher 1974). Many birds establish territories within a week of intense activity, between last week of May and third week of Jun, depending on snow melt and harsh weather,

although some birds do not establish territories until early Jul (Pitelka et al. 1955a, Maher 1974). In years with few lemmings and no nesting, few birds are observed in early Jun (Maher 1974). In Yukon River Delta, arrives somewhat earlier (15 May in a year with many nests; Brandt 1943).

In nw. Canada, on Banks I., earliest arrivals noted on 30 May (Manning et al. 1956). On Victoria I., in a year with plentiful lemmings, arrived by 31 May, earlier than other jaegers; first territorial pair noted on 4 Jun, many present by 7 Jun (Parmelee et al. 1967). On Bathurst I., arrives in first half of Jun in years with many lemmings; numbers of territories increase quickly to reach a peak somewhat later (20–30 Jun) than at Barrow (Taylor 1974).

On Wrangell I. birds arrive by 1 Jun; pairs appear on territories by 7–12 Jun (Portenko 1989).

Egg-laying. Figure 5. Near Barrow, in years with numerous lemmings, egg-laying begins 5–25 Jun, earlier in years with earlier snow melt and less adverse weather. Copulations first occur about 3–6 d before egg-laying begins. Laying is roughly synchronized, with half of all eggs usually laid within 1 wk (5–10 Jun to 21–29 Jun in different years) and remainder in following 10–16 d. Last eggs laid in final week of Jun or first week of Jul (two replacement clutches). In w. Alaska, fresh clutches found 9–22 Jun (Brandt 1943); in Eurasian Arctic, 13 Jun–5 Jul (Pleske 1928, Portenko 1989). On Victoria I., first clutch found on 13 Jun, latest with nearly fresh eggs on 10 Jul (Parmelee et al. 1967). On Southampton I., fresh clutch found 19 Jun (Sutton 1932). At higher latitudes, in Novaya Zemlya, first eggs laid 26 Jun–5 Jul (Schaaning 1907) or 19 Jun–18 Jul (Dement'ev and Gladkov 1969).

Hatching. In n. Alaska, first young hatch between 1 and 17 Jul, most hatch 2–6 Jul to 17–20 Jul in different years (Pitelka et al. 1955a, 1955b, Gabrielson and Lincoln 1959, Maher 1974). In w. Alaska, hatching in one year occurred between 24 Jun and 10 Jul (Brandt 1943).

Fledging. First flying young appear on 3–25 Aug in different years; in most years chicks begin to fly in early to mid-Aug (Pitelka et al. 1955a, Gabrielson and Lincoln 1959, Maher 1974).

Departure from breeding areas. Successful breeders apparently leave as soon as their young reach independence, while young of the year remain in small groups along the coast (Maher 1974). Birds with failed nests begin to gather along the coast in late Jul to mid-Aug; by end of Aug all birds have ceased territorial defense and small groups of adults and young frequent the coast (Pitelka et al. 1955a, Parmelee et al. 1967). When lemming populations decline drastically during the summer, birds abandon territories as early as late Jul; most have left by 20 Aug (Pitelka et al. 1955a, Maher 1974).

Molt — Immatures / Adults
Breeding — Young / Eggs
Migration
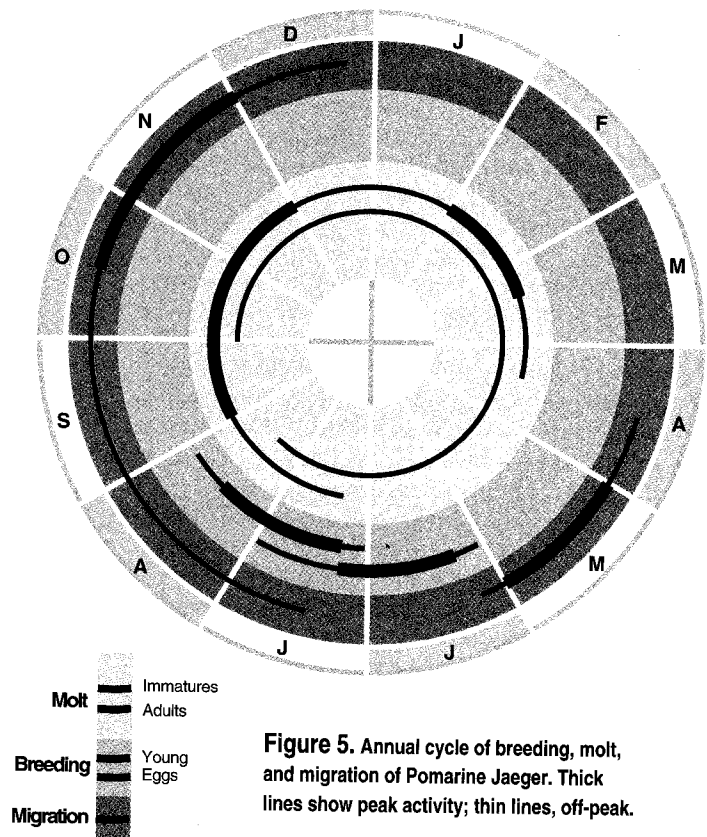
Figure 5. Annual cycle of breeding, molt, and migration of Pomarine Jaeger. Thick lines show peak activity; thin lines, off-peak.

Following a rapid decline in numbers of brown lemmings in ne. Alaska, almost all birds departed without nesting before the end of Jun (Andersson 1973a). Latest date at Barrow, 20 Sep (Pitelka et al. 1955a).

In years with little nesting in n. Alaska, birds begin to leave by the middle of Jun and most have departed by early Jul (Maher 1974; see Migration: timing and routes of migration, above). On Victoria I., in a year with few lemmings, individuals were seldom seen after 5 Jun (Parmelee et al. 1967). Likewise on Bathurst I., when lemmings are only moderately dense, individuals depart quickly after arrival; when lemmings are scarce, few Pomarine Jaegers seen (Taylor 1974). Apparently most birds capable of breeding return to the Arctic each summer but leave quickly if low densities of lemmings preclude nesting.

NEST SITE

Usually a slight rise in the ground, for instance, the rim of a low-center tundra polygon (Pitelka et al. 1955b, Maher 1974). On dry knolls in wet moss-sedge tundra (Portenko 1989).

NEST

Construction. Nest is a slight depression formed by trampling with breast and feet; both sexes

participate (Maher 1974). Sometimes includes some plant material from the immediate vicinity in the bottom or around the edge; no material carried to the nest (Pitelka et al. 1955b, Parmelee et al. 1967, Maher 1974).

Microclimate. No information.

GONAD CYCLES

Males arrive in the Arctic with fully developed gonads, both in years with frequent nesting and in years without nesting (means 1,170 mm³ and 1,020 mm³, $n = 17$ and 7, respectively; not significantly different). When breeding occurs, testes remain large (mean 1130 mm³, $n = 16$) through egg-laying in late Jun; otherwise testis size decreases to 600 mm³ by late Jun ($n=9$); testes of all males decrease rapidly thereafter (Maher 1974).

Females arrive in Arctic with largest follicles 5–7 mm in diameter. When breeding occurs, largest follicles reach 5–25 mm in diameter by middle of Jun; otherwise, the largest follicles slowly decrease through summer. Some breeding females develop >2 enlarged follicles. Follicles are >20 mm in diameter when ovulated; follicles resorbed within 2 wk following ovulation (Maher 1974).

Circumstantial evidence suggests that gonad development after arrival depends primarily on availability of lemmings for food (Maher 1974).

EGGS

Shape. Ovate or pointed ovate (Gabrielson and Lincoln 1959).

Size. Victoria I.: Mean 62.25 mm (range 59.2–64.9) × 45.02 mm (range 43.5–46.3, $n = 2$ clutches; Parmelee et al. 1967). Franklin Bay, Mackenzie District, NWT: 62.05 mm × 40.98 mm ($n = 1$, Florida Museum of Natural History [UF]). Point Barrow, AK: mean 60.83 mm (range 59.19–62.01) × 44.28 mm (range 43.05–45.50, $n = 7$; UF). Various locations: mean 62 mm (range 57.2–72.6) × 44 mm (range 40.0–48.0, $n = 49$; Bent 1921).

Color. Brownish olive to dark olive-buff, with sparse dark brown spots and occasional grayish blotches (Bent 1921, Gabrielson and Lincoln 1959). One female produced white eggs with brown spots, without the usual olive brown color (Maher 1974).

Surface texture. Smooth, slightly glossy (Gabrielson and Lincoln 1959).

Eggshell thickness. No information.

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

Egg-laying. Can occur throughout the day. Interval between eggs usually 2 d, averages 1.7 d ($n = 10$; Maher 1974). Rarely renests, but occasionally lays second clutch if first is destroyed during incubation (interval 2 d when first egg destroyed before clutch completed, 6 d when clutch destroyed later in incubation; Maher 1974).

INCUBATION

Onset of incubation in relation to laying. Begins when first egg is laid (Parmelee et al. 1967, Maher 1974).

Incubation patches. Two distinct oval brood patches, side by side, each about 4 × 6 cm in both sexes (Pitelka et al. 1955b, Maher 1974); begin to develop just before first egg is laid (Maher 1974).

Incubation behavior. Shared by both parents about equally (Pitelka et al. 1955b, Maher 1974); in one pair studied intensively, however, female incubated most of the time (18.5 h compared to 5 h by male; Andersson 1973a). Male of this pair hunted more; female sometimes flew to join him after a kill, or the male regurgitated a lemming near the nest for the female (Andersson 1973a).

Incubation period. Mean 23.6 d (range 23–25, $n = 14$) between laying and pipping of the first egg in a clutch; mean 25.9 d (range 25–27, $n = 11$) to hatching (Maher 1974).

HATCHING

No information.

YOUNG BIRDS

Conditions at hatching. Down well developed.

Growth and development. Young able to leave the nest after 2 d; usually do so by 4 d. After a week can move fast and swim well; many are no longer near the nest. First fly at 31–32 d; fly well by 35–40 d (Pitelka et al. 1955a, Maher 1974). Instantaneous relative growth rate in first 10 d averages 18–19% ($n = 7$–15/d). In a year with abundant lemmings, growth leveled off at about 600 g by day 30; in another year, in which lemming populations fell during the summer and few chicks survived, growth leveled off at about 450 g by day 25. When nesting success is high, large chicks from nearby territories sometimes gather in groups of 4–6 and wander across territorial boundaries without being challenged (Maher 1974).

PARENTAL CARE

Brooding. No information available.

Feeding. Both parents feed young by tearing pieces from lemmings and presenting them to chicks (Pitelka et al. 1955a). Male and female apparently must work together to tear prey into pieces suitable for young chicks; young failed to eat whole lemmings delivered by a single male after losing its mate (Maher 1970). No information on rates of feeding chicks.

When one parent is shot by hunters, the other usually abandons the territory, but in 2 cases the survivor (1 male, 1 female) fed young to fledging (Maher 1974). In a year when lemming numbers fell precipitously in late summer and few young survived, some were abandoned by parents before they could fly (Maher 1974).

Nesting sanitation. No information.

COOPERATIVE BREEDING
    Not reported.

BROOD PARASITISM
    Not reported.

IMMATURE STAGES
    Independence from parents. Both parents attend flying young and feed them in the nesting territory for at least 2 wk, but adults at this stage often leave their territories and young for long periods (Maher 1974). About a week after beginning to fly, young temporarily leave parents' territories to forage along the coast, where they chase Glaucous Gulls and feed on disgorged food (Pitelka et al. 1955b). By 26–28 Aug, some young already independent but others still attended by an adult (Parmelee et al. 1967). Feeding of young observed as late as 7 Sep, although nearly all young feed themselves by this date (Pitelka et al. 1955a). Young usually remain with their parents after fledging until they reach independence (Sutton 1932); no indication that young remain with parents once migration begins.
    Nonbreeding immatures. Few immatures join the northward migration of adults in spring. Spring migrants past British Isles are >90% adults in Definitive Alternate plumage (Davenport 1975, 1981). During spring migration in central North Atlantic, no immatures observed (Wynne-Edwards 1935). Off N. Carolina, only 2 of 30 specimens from late Mar–early Jun are immatures (NCSM).
    Unclear how many immatures reach the Arctic during summer. Some immatures in the Arctic, with barred body and underwing-coverts, have projecting central rectrices, although shorter than usual for Definitive Alternate plumage (de Korte 1972; specimens from Alaska, MVZ, NCSM).
    Immatures range widely during the boreal summer. Occasional immatures appear Jun–Aug over the continental shelf off ne. U.S. (Powers 1983), during Jun–Aug off se. U.S. (Stevenson and Anderson 1994, Lee 1995), in Jun and Jul off the British Isles (Davenport 1975, 1981), in Jul off Mauritania, w. Africa (Wynne-Edwards 1935), in Jun–Jul in n. Indian Ocean and Red Sea (van den Berg et al. 1990). Immatures with variable amounts of barring visit Spitsbergen, where the species does not breed, during Jun–Sep (de Korte 1972), and immatures also visit the north slope of Alaska during summer (specimens, MVZ).

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY
    Intervals between breeding. Near Barrow, AK, large numbers nest in years with abundant or intermediate populations of lemmings, none in years with few lemmings (Pitelka et al. 1955a, Maher 1974). On Victoria I. in years with few lemmings, individuals arrive in substantial numbers but most depart quickly; few remain through Jun and Jul but do not breed (Parmelee et al. 1967). In Eurasian Arctic, similarly dramatic changes in nesting occur in accordance with density of lemmings (Schaaning 1907).
    Nomadism. Sporadic breeding by this species near Barrow, coinciding with dense populations of lemmings, has prompted a suggestion that this species is nomadic in the breeding season (Pitelka et al. 1955b, Maher 1974). Migrants, it is proposed, continue eastward along the arctic coast until they locate an area with enough lemmings to support breeding efforts. Observations of late migrants establishing territories in nw. Alaska on their return westward support the possibility of opportunistic breeding (Maher. 1974). Furthermore, in years when nesting does not occur at Barrow, almost all birds collected in late summer show signs of incubation patches, an indication that they attempted to breed elsewhere (Maher 1974). Nevertheless, in some years observations of large numbers of birds departing soon after arrival and few young along the coast in Aug suggest that lemming populations are insufficient for breeding over large portions of the Alaskan and Canadian Arctic. Birds not breeding at Barrow might not breed anywhere in those years.
    Little is known about synchronization of lemming cycles in different parts of the Arctic, but in some years low numbers of lemmings occur over wide areas; in 1970, for instance, throughout w. and n. Alaska and at least w. Canada (Andersson 1973a). Likewise, in some years Pomarine Jaegers fail to breed throughout wide areas of the Arctic (for instance, throughout n. Alaska in 1959; Childs 1969, Maher 1974). It is thus possible that most of the North American population normally nests only once or twice every 4 yr.
    Age at first breeding. No information from marked birds. In years with dense nesting populations at Barrow, breeders include some heavily barred birds with shorter and less twisted central rectrices than typical adults (Pitelka et al. 1955a, Maher 1970, 1974, see also Sutton 1932; see Appearance: molts and plumages, below). On Bathurst I., in contrast, all birds, even transients, have Definitive Alternate (adult) plumage, although a few, including breeders, have short central rectrices (Taylor 1974). These observations suggest that some birds breed before attainment of full Definitive Alternate plumage. It is unlikely that Pomarine Jaegers breed in their first summer (despite a suggestion by Pitelka et al. 1955a), by analogy with Parasitic Jaeger (modal age of first breeding = 4, see Wiley and Lee 1999). Most Pomarine Jaegers hatch in years of dense lemming populations and might thus have their first chance to breed in the next such year, usually 2–4 yr later.
    Clutch. Two eggs, although in some years of moderate to high nesting densities 4–12% of clutches have only one egg (Pitelka et al. 1955b, Maher 1974); near

Barrow in 2 yr of dense nesting, 4–5% had one egg (*n* = 125 and 113 nests; Maher 1974).

Nesting success. Breeding success depends on moderate to high populations of lemmings (Pitleka et al. 1955a, Maher 1970). Varies considerably even in years with high initial densities of lemmings (4–55% of eggs fledge, n. Alaska; Maher 1970). Densities of lemmings after mid-Jul determine survival of young to fledging; in years with low initial densities or poor reproduction of lemmings, predation by adult jaegers can drive lemming densities in late summer to low levels and result in widespread nesting failure (Maher 1970). Snowfall in Aug, in a year in which lemmings had already decreased drastically, caused nearly total mortality of young (Maher 1974). In years when lemmings are scarce, foraging flocks of nonbreeding Pomarine Jaegers disrupt nesting attempts of the few breeders.

Egg loss is low in dense populations: 25/154 eggs (9 full clutches, 7 single eggs lost) and 19/227 eggs (including 6 taken by humans) in 2 yr. About half of pairs that lose their clutches lay replacements. Early loss of chicks is also low; later losses are difficult to assess, because unpenned chicks quickly become difficult to find (Maher 1974).

Over 9 yr near Barrow, including 3 with high initial densities of lemmings, successful nesting by large numbers of pairs occurred only twice (Maher 1970). In these 2 yr, aerial reconnaissance suggested that nesting densities and success were similar over the entire area north of the Inaru R. 40 km south of Barrow (Maher 1974).

On Bathurst I., Canada, where only collared lemmings occur, successful nesting not observed in 2 yr including one with high densities of lemmings (Taylor 1974). In both years Arctic fox took all eggs laid, perhaps a consequence of the demands on adults for foraging.

Lifetime reproductive success. No information.

LIFE SPAN AND SURVIVORSHIP

No information, but survivorship of adults is probably high, by analogy with Parasitic Jaeger (see Wiley and Lee 1999).

DISEASE AND PARASITES

Four species of ectoparasitic feather lice (Mallophaga) reported: *Austromenopon fuscofasciatum*, *Haffneria grandis* (rarely), *Quadraceps normifer stellaepolaris*, and *Saemundssonia stresemanni*. The first 2 are shared with both Parasitic 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), but Pomarine Jaeger shares both of the latter two forms with Great Skua, an indication of close phylogenetic relationship (see Systematics, above). Also a feather mite, *Zachvatkinia stercorarii* Dubinin, reported (Ballard and Ring 1979).

CAUSES OF MORTALITY

Among breeders near Barrow, mortality other than human hunting (see Conservation and management: effects of human activity, below) occurs rarely. In one year 4 of >100 adults died from unknown causes, apparently not disease or humans; in another year no adult was known to have died, except by human hunting (Maher 1974).

Most mortality among chicks results from starvation when lemmings become scarce (Maher 1974). Chicks penned for observations often survived to fledging; in one year when lemmings became scarce in Aug, chicks killed and ate smaller siblings in 4 of 8 cases, and several were taken by predators, perhaps Glaucous Gulls; but both kinds of mortality are unlikely for unconfined chicks (Maher 1974).

On Bathurst I., eggs in all nests for 2 yr were taken by Arctic fox (*n* = 14 eggs; Taylor 1974).

RANGE

No information about nonbreeding home range, fidelity to breeding site, or natal dispersal.

POPULATION STATUS

Densities of breeding birds vary with the densities of lemmings. When lemmings are scarce, nearly all birds quickly leave areas where, in years with abundant lemmings, they nest in large numbers. Because ornithological expeditions to the Arctic more often than not miss the peaks of lemming abundance by chance, it is difficult to determine the status of Pomarine Jaeger. Only for the area near Barrow is there information on populations over an entire cycle of lemmings. Near Barrow, in 3 years with high densities of lemmings (100–200/ha in early Jun), this species reached 7.1–8.0 pairs/km^2 over areas of about 15 km^2, but as many as 10.1 pairs/km^2 in smaller areas of optimal habitat (Pitelka et al. 1955a, Maher 1970, 1974). With intermediate densities of lemmings (40–50/ha) Pomarine densities were 1.5/km^2; in 2 years with low but detectable lemming populations (2–10/ha) Pomarine numbers were only 0.05–0.08/km^2; when lemmings were barely detectable (<0.5/km^2), this jaeger did not breed (3/9 yr; Maher 1970, 1974). Elsewhere in Alaska, densities are low even in the best years: 0.1–4.0 pairs/km^2 (Maher 1974, Andersson 1973b).

Breeding densities appear similar in aerial reconnaissance over coastal Alaska from Barrow south at least to Inaru R., perhaps 2,000 km^2 (Maher 1974). If so, in years of dense nesting and high nest success, some 10,000–20,000 pairs might nest in this area and produce as many young. No other Nearctic area is known to support such high numbers of this species. Populations of Pomarine Jaegers appear to depend on infrequent pulses of successful reproduction in a few areas.

On Bathurst I., near the northern limit of this species' range (76°N), densities reach 0.2–0.3 territorial

pairs/km² in years with high densities of collared lemmings (only 0.15 pairs/km² actually nest); few birds establish territories in years with intermediate densities of lemmings, and none in years when lemmings are scarce (Taylor 1974).

POPULATION REGULATION

At high densities of lemmings, densities of Pomarine Jaegers hardly vary despite 2-fold variation in densities of lemmings, so territorial behavior apparently sets an upper limit to densities (Maher 1970). Minimal territory size in densely populated areas, 6–8 ha (Pitelka et al. 1955a). Although availability of lemmings strongly influences reproductive success (see Breeding, above), survival in wintering areas may regulate populations in the long term.

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Egg collection. Near Barrow, AK, Inuit occasionally take eggs (Maher 1974).

Shooting and trapping. Near Barrow, people shoot adults during years of dense nesting, but only occasionally. In 2 yr at least 10 and 12 adults were killed in dense populations of >200 (Maher 1974, see also Parmelee et al. 1967), but individuals in these populations were not marked so mortality rates from hunting cannot be calculated reliably. On the Grand Banks, off Newfoundland, especially before 1875, fishermen caught small numbers of jaegers for bait (presumably mostly this species), a by-catch of the much larger numbers of shearwaters taken (Collins 1884).

Contaminants. Mean mercury content of tissues from individuals collected off N. Carolina: muscle, 0.22 µg; liver, 0.95 µg; kidney, 0.62 µg; feathers, 2.98 µg (n = 19 specimens, NCSM). Few records of contamination with oil (Texas, May 1973, Audubon Field Notes; Florida, Nov 1959, Audubon Field Notes; Louisiana, Apr 1962, Lowery 1974, Louisiana State University Museum of Zoology [LSUMZ] 28731).

MANAGEMENT

No reports. Not a species of management concern.

APPEARANCE

MOLTS AND PLUMAGES

The following descriptions are based on examination of specimens in NCSM, MVZ, AMNH, and USNM. Sexes alike in all plumages except as noted below.

Hatchlings. Completely covered with down. Down entirely grayish brown except slightly paler on crown or around eye (specimens, MVZ; Bent 1921, Fjeldså

1977). Grayer, especially on face, and more uniform than Parasitic Jaeger (Fjeldså 1977).

Juvenal plumage. Complete by Aug. Light morph has upperparts heavily barred with tan or cinnamon (orangish brown), light bars on uppertail-coverts usually narrower than brown bars (sometimes wider), head and nape brown, breast and belly barred with cinnamon or tan, undertail-coverts like uppertail-coverts, underwing-coverts barred irregularly with whitish. Remiges and rectrices blackish brown. Shafts of 5–8 outermost primaries creamy white. Under-primary-coverts show white bases, which along with whitish bases of primaries create a double white flash underneath the wing. Dark morph is brown with whitish or tan scalloping above and below, often most prominent on belly; barring on uppertail- and undertail-coverts varies as in light morph; underwing-coverts like those of light morph but darker.

Later immature plumages. Immature plumages and molts are highly variable. In the absence of specimens of known ages to confirm hypotheses about plumage progressions, we present here a description of overall variation in immature plumages.

Prebasic and Prealternate molts are protracted and difficult to distinguish in immatures. As in all jaegers, immatures replace remiges once a year from the innermost outward, beginning as early as Oct and extending sometimes into Aug. New central rectrices are acquired as early as Sep; other rectrices are replaced from Nov–Aug, often in irregular sequence (specimens, NCSM). Some body molt in every month; presumably individuals have protracted molts and different individuals are not in synchrony. A proposal that immatures skip Prealternate molt in their second calendar year and thus their first Alternate plumage (Cramp and Simmons 1983) seems unlikely; instead molts are unusually variable in timing and duration.

Molt continues throughout summer. Immatures collected off N. Carolina in late Jun–Aug have 1–2 outermost primaries growing (4 of 11 specimens) as well as molting rectrices (4 of 11) and body plumage (all birds). Immatures in Aug–Oct usually have slightly worn remiges, but by Oct some birds have resumed molt (2 of 5 specimens with new primaries in Oct, 1 of 4 in Nov–Dec, NCSM); Oct–Dec specimens also have molting wing-coverts, rectrices, and body plumage. Immatures visiting Spitsbergen in Aug are molting body plumage (de Korte 1972).

Light morph is highly variable. Upperparts brown barred with whitish (about one-third with buff or pale cinnamon bars), white and brown bars on uppertail-coverts usually about equal in width, top of head blackish spotted with white, nape whitish with yellow wash, throat whitish often spotted or streaked with brown, breast barred with brown (often heavily), belly whitish usually barred or spotted with brown, white bars on undertail-coverts equal to or much narrower than brown, underwing-coverts barred and

spotted irregularly with whitish. Remiges and rectrices blackish brown. Shafts of outermost primaries creamy white, those of inner primaries progressively more tan. Most have outermost 5–8 primaries with completely whitish shafts (60% with 6–7 whitish shafts, range 3–8, n = 18; MVZ). Whitish bases of primaries and underprimary-coverts create a double white flash on the undersurface of the wing (occasionally only a single flash, MVZ, NCSM). Central pair of rectrices extends 1–3 cm beyond the rest of the tail, with either rounded (60%, n = 15, NCSM) or acute tips.

Dark morph is dark brown with varying amounts of whitish scalloping throughout. Underwing-coverts show much less whitish than in light morph, no more than narrow scalloping. Some dark immatures thus difficult to separate from adults in Definitive Basic plumage. Dark birds also usually show only a single white flash on the underside of the primaries, as a result of their darker underprimary-coverts.

Definitive Basic plumage. Definitive Prebasic molt complete. Molt begins after birds have left the breeding areas (Maher 1974, correcting brief mention to the contrary by Pitelka et al. 1955a). Unlike other jaegers, however, adults begin to molt soon after leaving the Arctic, during southward migration. By Sep most migrating adults on the coasts of California and N. Carolina have already acquired much of their Basic body plumage, have lost one or both of their elongated central rectrices, and have molted at least half of their remiges (MVZ, NCSM). One adult from N. Carolina in Jul, probably an early migrant following a poor year for breeding, already had 5 new primaries. These adults in Definitive Basic plumage often closely resemble birds in immature plumages, except for their plain brown underwing-coverts. Most dark morphs, in particular, become almost indistinguishable from immatures.

Some adults have completely new remiges by Oct–Dec, a few have completely new dorsal feathering by Nov–Dec. In contrast, few have any new lateral rectrices as early as Dec (specimens, NCSM). Contrary to Cramp and Simmons (1983) birds appear to grow their central rectrices twice each year, as in other jaegers. Upperwing- and underwing-coverts, scapulars, and remiges molt once a year (Stresemann and Stresemann 1966, Cramp and Simmons 1983).

As in all jaegers, plain underwing-coverts are present in all Definitive plumages; they remain unbarred during winter because they are replaced only once a year with the remiges. Age at which plain underwing-coverts are first acquired is unclear; occasional specimens with a mixture of plain and barred underwing-coverts suggest that this molt occurs in the winter before the first Definitive Alternate plumage (3 specimens, NCSM). Bursa of Fabricius present in 6 of 7 specimens with barred underwing-coverts, absent in 8 of 9 specimens with plain underwing-

coverts and in 1 specimen with mixed underwing-coverts (specimens, NCSM).

Light morph has head and back dark brown, each feather tipped with white, uppertail- and undertail-coverts prominently barred brown and white, and breast and flanks white barred with brown. Often the belly and throat are mostly white, but there is much variation in the extent of brown barring and spotting on the underparts. Remiges and rectrices blackish brown. The central pair of rectrices extends only 1–6 cm beyond the rest of the tail (65% extend 2–4 cm, n = 17, NCSM) with rounded or acute tips. About two-thirds of these adults have only a single white flash on the underside of the primaries, because they retain their adult primary-coverts (n = 45, NCSM, MVZ). Dark morph similar to dark morph in immature plumages (see above) but underwing-coverts always plain brown.

Definitive Alternate plumage. Adult Prealternate molt partial, includes body feathers and 2 central rectrices. Adults have attained nearly complete Alternate Plumage by the time they reach North American waters in Apr and May. Specimens from North Carolina have completely new dorsal plumage by Apr or May, new remiges and central rectrices by Apr. One on 26 Mar has outermost primary still growing; some still retain worn lateral rectrices in May. Some birds have white tips on feathers of the upper back, similar to those in Basic plumage, but these feathers are apparently renewed with other dorsal feathers by Apr or May (n = 24, NCSM). Migrants in the Pacific are still in final stages of molt in Apr but in full Definitive Alternate plumage by May (Austin and Kuroda 1953). By late Apr about 20% of those still in Australian waters are growing new central rectrices, and some have not finished wing, tail, and body molt (Barton 1982).

Breeding birds are notably variable in plumage (see Demography and populations: measures of breeding activity, above); specimens suggest that some are older immatures with partial Definitive Alternate plumage (MVZ). For instance, a female with a ruptured follicle (hence presumably a breeder) has Definitive Alternate plumage except for heavily barred uppertail- and undertail-coverts and streaked throat; underwing-coverts are a mixture of plain and spotted feathers (adult and immature, respectively); central rectrices project 5 cm (MVZ). This bird apparently failed to complete its first adult Prealternate molt; other specimens from the Arctic have similar plumage (Sutton 1932). It appears that older immatures molt to Definitive Alternate plumage later than do adults but can arrest this molt if they discover large numbers of lemmings and hence an opportunity to breed when they arrive in the Arctic.

Light morph has upperparts dark brown (often with white tips of feathers on the upper back), top of head including the malar area blackish (also rarely

the chin), underparts and collar around nape white with yellowish-buff wash on sides of head and neck, band across breast usually heavily barred with brown, lower belly and undertail-coverts dark brown, and flanks heavily barred with brown. Underparts vary considerably: flanks barred, spotted with brown, or solidly brown; breast varies from nearly entirely white with a few brown flecks to nearly entirely brown with a few white flecks. An occasional bird has its entire breast pure white, others have the center of the breast white. An occasional bird has an incomplete white collar, with brown streaks on the nape. Underwing-coverts entirely brown. Remiges and rectrices blackish brown. Outermost 5–6 primaries have creamy white shafts (83%, range 3–7, $n = 41$, MVZ); inner primaries have progressively more tan shafts. Underneath the whitish bases of the primaries usually create a single white flash (one third have a second white flash in the underprimary-coverts, $n = 18$, NCSM). Two central rectrices extend 7–11 cm beyond the rest of the tail; the broadly rounded or truncated tips are twisted about 90° so their width is visible from the side. They look like spoons in silhouette but are not concave like spoons.

Males average smaller in mass but have longer central rectrices on average than females. Males also average whiter on anterior underparts but darker on lower belly and undertail-coverts (Cramp and Simmons 1983).

BARE PARTS

Bill. In hatchlings, gray, darker distally (Fjeldså 1977). In immatures, gray with a dark tip, much like that of other jaegers; contrast between tip and base of bill varies, so claims that immature Pomarine Jaegers have more contrast than other species need confirmation (Olsen and Christensen 1984, Olsen and Larsson 1997). In adults, grayish black, slightly paler on lower mandible, especially at base (Sutton 1932). Some breeding adults have a conspicuous yellowish-pink bill with a dark tip.

Gape. Yellowish pink (Sutton 1932).

Iris. Dark brown.

Legs and feet. Black in adults, sometimes with spots of bluish gray in immatures, mostly gray in the first few months of life (Sutton 1932; specimens, MVZ); occasional immature specimens have legs all bluish gray (NCSM).

MEASUREMENTS

LINEAR

Banks I.: Flattened wing of adult males, 354.3 mm ± 8.3 SD (range 342–367); of adult females, 360.8 mm ± 5.4 SD (range 350–370). Exposed culmen, males, 35.35 mm ± 1.52 SD (range 32.3–37.3); females, 35.34 mm ± 1.34 SD (range 33.4–38.0). Tarsus: males,

53.91 mm ± 1.46 SD (range 51.5–57.4); females, 55.90 mm ± 1.31 SD (range 54.0–57.8, $n = 13$ adult males and 13 adult females; Manning et al. 1956).

MASS

Females about 10–15% heavier than males. Barrow, AK: males, 683 g ± 17.2 SD (range 521–852, $n = 27$); females, 829 g ± 22.5 SD (range 675–1,000, $n = 13$; Pitelka et al. 1955a). N. Alaska: males, 648 g ± 6.2 SD (range 542–797, $n = 73$); females, 740 g ± 11.7 SD (range 576–917, $n = 52$; Maher 1970). Victoria I.: male, 665 g; female, 775 g (Parmelee et al. 1967). Banks I.: males, 1,100 g and 625 g ($n = 2$; Manning et al. 1956).

Off N. Carolina: adult males, 636 g ± 80.9 SD (range 512–787, $n = 14$); immature males, 609 g ± 81.1 SD (range 520–850, $n = 11$); adult females, 675 g ± 92.2 SD (range 430–825, $n = 24$); immature females, 676 g ± 35.5 SD (range 616–707, $n = 7$; NCSM).

Wing loading for one specimen 1.32 g/cm² (mass/[area of single wing × 2]; NCSM).

PRIORITIES FOR FUTURE RESEARCH

Because this jaeger relies on sporadic populations of large lemmings for successful reproduction, it is probably the most vulnerable of the 3 species to human disturbance. Most of the young produced in the Arctic probably come from occasional enormous nesting colonies coinciding with outbreaks of brown lemmings, such as those studied near Barrow, AK, by Pitelka and Maher. Nesting on this scale is not known elsewhere in North America, and it is not clear how many places in the Arctic such nesting ever occurs. Most observers in the Arctic by chance miss years of successful reproduction by this species, so we have very incomplete information on when and where successful reproduction occurs. There are no studies of reproduction and plumages in marked birds of known ages, and we also know little of the distribution and biology of this species away from its breeding grounds.

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