COOPER ORNITHOLOGICAL SOCIETY

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ECOLOGY OF POMARINE, PARASITIC, AND LONG-TAILED JAEGERS IN NORTHERN ALASKA

by
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Introduction

Collectively, the three species of jaegers are the most abundant, widespread, and hence most significant avian predators in northern Alaska. They are the pomarine jaeger (*Stercorarius pomarinus*), the parasitic jaeger (*S. parasiticus*), and the long-tailed jaeger (*S. longicaudus*). The three differ in size, but all are ground-nesters on flat or rolling tundra, and they overlap in distribution, habitat, and other features of their ecologies. The parasitic jaeger nests in northern Alaska from the Brooks Range north to the Arctic Ocean. The pomarine jaeger nests only in coastal areas. The long-tailed jaeger nests regularly from the Brooks Range north to the southern part of the coastal plain. The long-tailed and pomarine jaegers are usually allopatric; the parasitic jaeger is sympatric with both species, and occasionally, all three are sympatric.

This study of the ecology of these three jaegers deals primarily with the density of their breeding populations, their fluctuations in time and space, and their food habits. All three species are considered as actual or potential competitors, and study of the degree of niche overlap among them has been an important objective of this work.

An additional concern has been how these three closely related predators have adapted to tundra ecosystems. The arctic environment imposes severe constraints on any species adapting to it. Most important of these to the jaegers are temporal and spatial fluctuations of food supply, the brief period in which the climate is suitable for breeding, and the paucity of suitable prey types for the three species to exploit without competing.

The project began in 1956 as a study of the ecology of the pomarine jaeger and continued through five successive seasons. Dense populations of pomarine jaegers associated with lemming highs were studied at Barrow in 1956 and 1960. Because pomarine jaegers did not remain to breed near Barrow in non-lemming years, in 1957 and 1958, the parasitic and long-tailed jaegers were studied at locations away from Barrow where these species bred. A mixed population of the three species was studied at Cape Sabine in 1959. Observations on parasitic and long-tailed jaeger populations are lacking for the early part of each season, because I spent the beginning of each season at Barrow assessing the pomarine jaeger population there.

Much of the information concerned with the role of the pomarine jaeger as a predator of the brown lemming (*Lemmus trimucronatus*) and its influence on the lemming cycle in northern Alaska has already been published (Maher, 1970a). Only such information necessary to compare the ecology of the pomarine jaeger with that of the other two jaeger species is presented here.

Acknowledgments

Financial support for the field portion of this project was by the Arctic Institute of North America under contract with the Office of Naval Research. The Naval Arctic Research Laboratory at Barrow, Alaska provided logistic support. I received a predoctoral fellowship from the National Institutes of Health in the academic year 1959-60. The assistance of these agencies is gratefully acknowledged. I am grateful to Frank A. Pitelka for advice in the course of this study.

I also wish to thank Ira L. Wiggins, Director of the Naval Arctic Research Laboratory in 1956 and Max C. Brewer, his successor, for their generous support of my field activities.

Many investigators and staff members at the Naval Arctic Research Laboratory generously provided information and time to this project. Their contributions, considered as a whole, have been large, and it is certain that this work would not be as comprehensive without them. I regret that I cannot express my appreciation individually. Lack of records and space force me to list only the names of those who, among others, made significant contributions. In this regard I am happy to acknowledge the help of J. Brown, T. J. Cade, H. E. Childs, Jr., E. Clebsch, J. Dow, J. Hobbie, R. T. Holmes, J. Koranda, M. P. Marsh, F. A. Pitelka, J. Reynolds, D. Schalk, P. Sovalik, and T. Sovalik.

Jay Dow helped map the pomarine jaeger nests in 1956; Richard T. Holmes and Jack Reynolds helped with the same chore in 1960; Ralph Langenheim recorded for me all of the parasitic and long-tailed jaegers he observed along the Kaolak River in 1956; Richard T. Holmes, Michael P. Marsh, Jack Reynolds and Tom Sovalik assisted in several 24-hour watches of pomarine jaegers in 1956 and 1960.

I gratefully acknowledge the facilities and support provided by the Museum of Vertebrate Zoology and the Department of Zoology of the University of California, Berkeley.

Itinerary

The study was conducted at thirteen localities in northern Alaska (Figure 1). The time spent in northern Alaska each year was as follows: 1956, 99 days, from 28 May to 4 September; 1957, 104 days, from 27 May to 8 September; 1958, 92 days, from 2 June to 2 September; 1959, 119 days, from 14 May to 10 September; and in 1960, 96 days, from 24 May to 28 August. The dates spent in the field at each locality are in Table 1. Reconnaissance trips made each season are listed in Table 2. Such trips were normally made in light aircraft flown between 200 and 500 feet above the ground. Travel between study localities was also usually done in light aircraft.

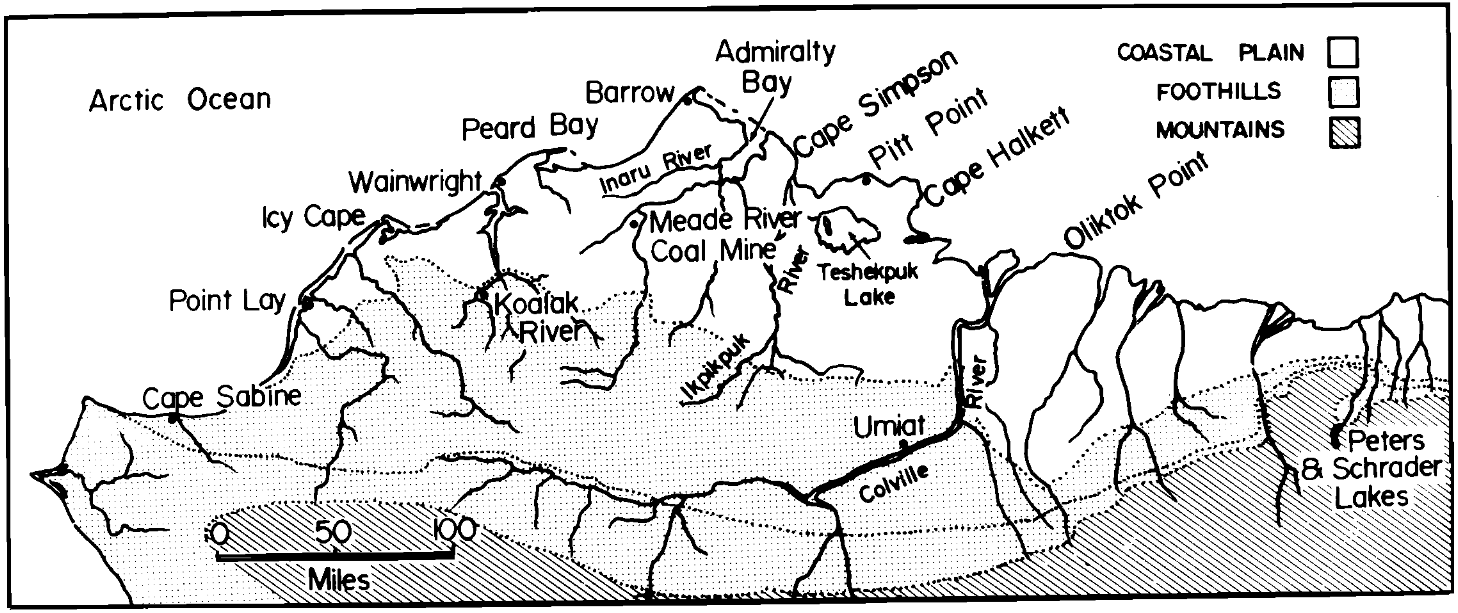

Figure 1. Map of northern Alaska with place names mentioned in text.

TABLE 1

Dates spent at different study areas in northern Alaska

Locality	*Year*	*Inclusive dates*
Barrow	1956	28 May–2 September
	1957	27–30 May, 1–4 June, 6–8 June, 18–26 June, 2–5 July, 14–17 August, 22 August–5 September
	1958	3–6 June, 10 June, 13–17 June, 19–20 June, 27–28 June, 7–8 July, 15–21 August, 24 August–1 September
	1959	14–20 May, 29 May–12 June, 27–28 June, 1–2 July, 11–16 August, 27–30 August, 5–10 September
	1960	24 May–26 June, 30 June–3 July, 5–25 July, 26 July–28 August
Cape Sabine	1959	20–29 May, 12–27 June, 2 July–11 August
	1960	4–5 July
Cape Thompson	1960	25–26 July
Ikpikpuk River	1957	28 June–7 July
Kaolak River	1957	8 July–10 August
	1958	21–27 June, 9 July–15 August
	1959	28 June–1 July, 30 August–5 September
	1960	26–30 June
Kuk River	1957	10–14 August
Lakes Peters and Schrader	1959	16–27 August
Meade River Coal Mine	1957	8–18 June
Nigisaktuvuk River	1957	30 May–1 June
Pitt Point	1957	26 June–2 July, 19–22 August
Sagavanirktok River	1957	21–24 August
Umiat	1956	2–4 September
	1957	5–8 September
	1958	2–3 June, 1–2 September
Wainwright	1957	5–8 June
	1958	11–13 June

In addition to the intensive work of 1956-1960, I made observations at Barrow in 1954 and 1955 while employed by the United States Geological Survey. In the summer of 1953 I was on the North Slope as an employee of Dr. Chester A. Arnold, University of Michigan, and witnessed the lemming decline in the early part of that summer and the jaeger populations exploiting it.

TABLE 2

Reconnaissance flights, northern Alaska 1956 to 1960

Year	*Date*	*Origin*	*Destination*
1956	22 August	Barrow	Teshekpuk Lake and return
	2–3 September	Umiat	Barter Island and return
1957	4 June	Barrow	Wainwright and return
	17 August	Barrow	Teshekpuk Lake, Pitt Point and return
1958	9 June	Barrow	Barter Island and return
	11 June	Barrow	Cape Sabine, Wainwright
	18 June	Barrow	Teshekpuk Lake and return
1959	29 May	Cape Sabine	Noatak River, Kotzebue, Barrow
	4 June	Barrow	Pitt Point, Umiat and return
1960	14 June	Barrow	Cape Simpson, Pitt Point, Cape Halkett, Oliktok Point and return
	16 August	Barrow	Ipewik River and return

General methods

Breeding jaegers are easily watched and censused because they are both conspicuous and aggressive and because tundra vegetation offers negligible interference with observation. At Barrow the study area was systematically traversed using a tracked vehicle, a weasel, for transportation. Territorial pairs were plotted on an outline map traced from aerial photographs, and nests were marked with inconspicuous numbered stakes. Considerable accuracy was eventually obtained in maps of nest distribution by continually re-checking the location of nests in relation to neighboring nests and landmarks. In 1956 and 1960 the nests on part of the area were mapped with an alidade and plane-table. In study areas away from Barrow, censusing was done on foot, and nest localities were marked on aerial photographs. This method is accurate in foothills where there are many identifiable topographic features. Censuses were made regularly in the season to document population changes.

Nests were enclosed for feeding and growth studies with a fence one foot high and nine or ten feet in diameter. When nests were fenced during incubation the adults quickly accepted the enclosures, and the chicks were fed normally. Chicks fenced after hatching usually died because the adults did not feed them properly. Enclosed nests were visited at regular intervals, the chicks were weighed with a beam balance, and regurgitated pellets and other food remains were collected. As jaeger chicks cannot jump, they were not able to escape from the enclosures until they flew.

Regurgitated food pellets were softened in water and picked apart. Jaws, skulls, humeri, femurs, and pelves of small mammals, and the humeri and any identifiable remains of birds were saved. Much of the material collected from nest enclosures, especially from the parasitic jaeger nests, was trampled or torn apart, and individual pellets were not recognizable. When the material was of this nature the quantitative occurrence of such items as insect remains, seeds, fruit, or egg-shell fragments was estimated. When most food remains were in pellets, items were recorded as per cent of occurrence in the total number of pellets.

In the seasons of 1957 and 1958, transient jaegers along the ocean near Barrow and Wainwright were sampled with the help of Eskimos. The specimens were kept frozen at the Naval Arctic Research Laboratory, and processed at the end of the field season for data on reproductive condition and weight.

Systematic observations were made on territorial behavior and frequency of feeding of nesting birds. Notes were also kept on other aspects of the breeding biology and behavior of all three species. Further details on methods will be given where they are appropriate.

Environmental Description

The following information on topography, climate, and vegetation in northern Alaska provides background for the consideration of spatial and temporal aspects of breeding distribution of jaegers.

Topography

Alaska north of the Brooks Range is a triangular area, approximately 600 miles wide from east to west and 200 miles from north to south. It is widest near its center, south of Point Barrow, and narrows towards both ends. Geologists have divided this region into three physiographic provinces: the Brooks Range province, the foothill province, and the coastal plain province (Payne *et al.* 1951) (Figure 1).

The Brooks Range is a rugged, glaciated mountain system, which runs west-east from Cape Lisburne to the mouth of the Mackenzie River. The mountains are highest in the east where they reach over 9,000 feet. Westward from there the elevation of the peaks gradually drops to an average of 4,000 feet at the western end of the range. Two of the principal passes in the central and western Brooks Range, Howard Pass and Anaktuvuk Pass, are important migration routes for many species of birds moving to the North Slope (Irving, 1960).

The foothill province is the hilly section lying between the mountains and the coastal plain. It occupies almost half of the Arctic Slope and is about equal in area to the coastal plain. This province is narrow towards the eastern end where the mountains are near the coast. In its central and western portions it is more than 100 miles wide.

The southern part of the foothills resembles the mountains in having very rough topography consisting of "irregular, isolated hills and ridges . . . which rise above low lying . . . areas of little relief" (Payne *et al.*, 1951). One of the localities dealt with in this report, Peters and Schrader Lakes, is at the boundary of the southern foothills and the mountain province. The norther part of the foothills is of much more regular topography and occupies a greater area than the southern part, particularly on its western half. It consists of persistent ridges, mesas, and hills that are approximately accordant in altitude. Two study areas, the Kaolak River area (Maher, 1959) and Cape Sabine (Childs, 1969), are in this section.

The coastal plain is a region of low relief, extensive marshy areas, meandering streams, and numerous lakes and ponds. The low relief and the underlying permafrost have impeded the development of mature drainage. Spetzman (1959) estimates that 20 per cent of the plain consists of lakes. Black and Barsdale (1949) have estimated that over 50 per cent of the plain is covered by standing water. Almost all authors who have traversed the region comment dolorously on its monotonous appearance. Principal study areas on the coastal plain are at Barrow, Meade River Coal Mine, Pitt Point, and Wainwright.

Climate

The climate of the Arctic Slope is severe. Winters usually last nine to ten months and are cold, while summers are short and comparatively warm. There is some variation in climate over the area caused by differences in altitude, the influence of the Arctic Ocean, and the effect of currents entering the Arctic Ocean through Bering Straits. The movements of the ice pack also strongly affect the summer climate of coastal areas.

All data discussed in this section are from summaries published by the Weather Bureau, U. S. Department of Commerce. Long-term summaries of climatic data are available only from Barrow. The only weather data from inland are from Umiat, 160 miles southeast of Barrow.

The annual average temperature for Barrow and Umiat is almost equal, 10.0°F for Umiat and 10.1°F for Barrow, although there is a noticeable difference in the amplitude of annual variation (Figure 2). February is the coldest month of the year. At Barrow the mean temperature for that month is −18.1°F, at Umiat it is −23.9°F. July is the warmest month at both stations. At Barrow the mean for this month is 40°F, and for Umiat 53.1°F. The mean minimum and mean maximum for July at Barrow are 33.5 and 46.2°F; for Umiat they are 42.9 and 63.3°F, respectively. The maximum temperature recorded at Barrow is 78°F, and at Umiat 85°F. The mean temperature is above freezing from late May to mid-September at Umiat and from early June to early September at Barrow. Frost occurs in all months. The tundra is free of snow for the latter part of June, July, August, and early September. Melt-off is essentially complete by mid- to late June at Barrow. The major rivers break up in late May or early June.

Thus, while the mean temperatures are almost identical at these two stations, the annual extremes are significantly different. This has an important influence on the growing season, which is approximately two weeks to one month longer at Umiat than at Barrow. Considering the shortness of the growing season, these temperature differences suggest significant differences in primary productivity between coastal and foothill areas.

Mean annual precipitation is 4.1 inches at Barrow and 5.8 inches at Umiat. The amount of snowfall at the two stations is approximately equal with no apparent difference in monthly distribution (Figure 2). Total precipitation is greatest in June, July, August, and September. Snow may fall in any month, and occasional summer snow storms strongly affect the success of breeding bird populations.

Daylight is continuous during the summer. At Umiat the sun is above the horizon continuously for 66 days from 19 May to 24 June; at Barrow, for 87 days from 9 May through 4 August. The sun is below the horizon for corresponding periods in the winter months.

There is great variation in climate among years. The average July temperature at Barrow since 1921 has varied nearly ten degrees from 34.6° to 45.3°F. These variations among years are important in considering the well known fluctuations of Arctic bird populations in their breeding occurrence at any one place, as they must in part reflect fluctuations of more or less similar magnitude in primary productivity and in insect and other invertebrate populations, as well as the time of melt-off of snow cover.

In the spring northern Alaska warms up from the south and west, and snow melt-off proceeds northward from the mountains and eastward from Cape Lisburne to Barrow. The difference in melt-off between Cape Sabine and Point Barrow in the same season can be as much as three weeks. Differences of such magnitude influence populations of migratory birds, particularly with regard to arrival time, pattern of spring movements, and the onset of breeding.

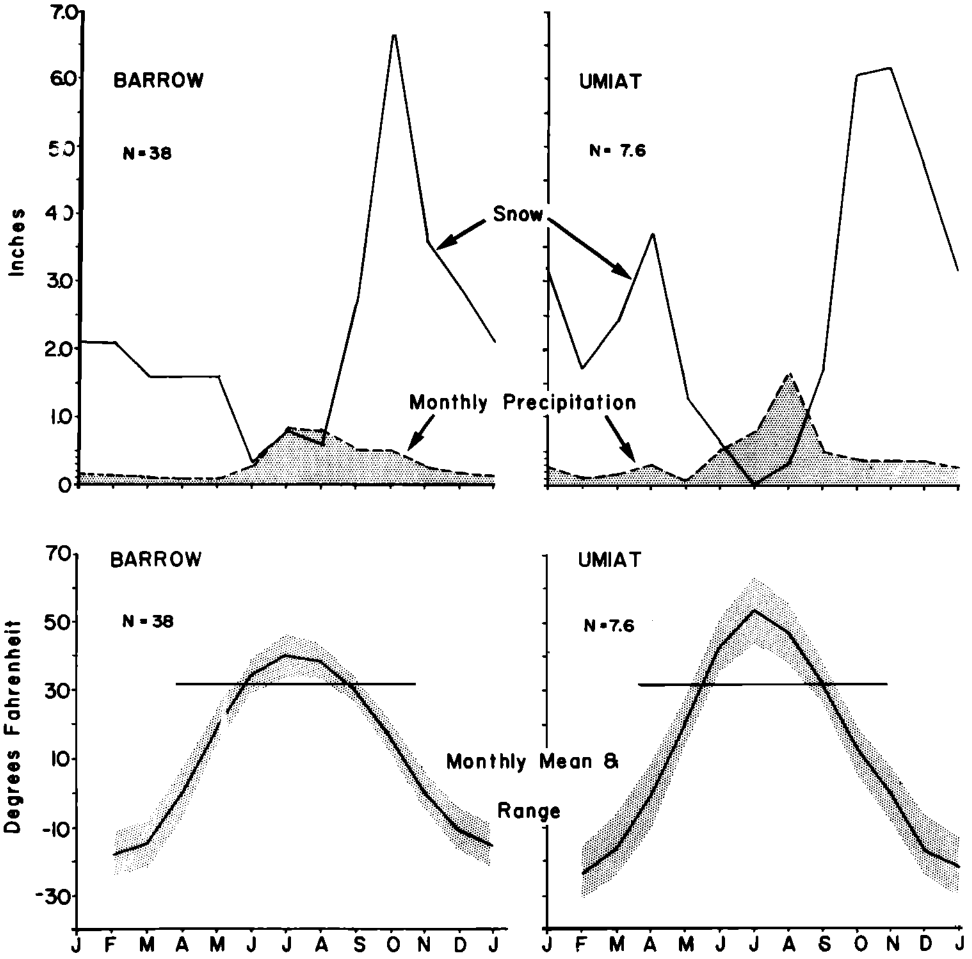

Figure 2. Climatic data from Barrow and Umiat from U.S. Weather Bureau records.

Vegetation

The vegetation of the Arctic Slope, as of the tundra generally, appears monotonous because of its prostrate habit and the few life-forms of the plants which are present. Hanson (1953), Spetzman (1959) and Britton (1957) have summarized the vegetation of Arctic Alaska. This brief account is based on their descriptions, as well as my own field observations.

The three major plant formations in northern Alaska are found in all three of the physiographic provinces, though their relative extent in each province differs depending upon the presence of suitable habitat.

Tussock-heath Tundra: — This formation includes all communities dominated by *Eriophorum vaginatum* and its associated heath plants. *Eriophorum vaginatum* is a tussock-forming sedge that produces the characteristic "basket-ball" structure of the formation. The tussocks vary considerably in size and number in different areas, but commonly attain heights of 10 to 14 inches and somewhat lesser diameters. Channels between tussocks are usually only a few inches wide and are occupied by mosses, lichens and vascular species. Common heath plants associated with *E. vaginatum* are *Ledum palustre* subsp. *decumbens, Vaccinium vitis-idaea, Cassiope tetragona, Arctostaphylos alpina,* and *Rubus chamaemorus.*

Tussock-heath is probably the most widespread formation in northern Alaska. It occurs on the low slopes of mountain valleys and is especially widespread and almost unbroken in the lower foothills. In some areas, as along the Kaolak River, it is dominated by low scrub willows (*Salix pulchra*), and the heath elements are greatly reduced (Maher, 1959).

Tussock-heath tundra also extends onto the coastal plain in suitable areas, although the proximity of the Arctic Ocean reduces the occurrence of heath forms and inhibits the formation of tussocks in an area a few miles wide along the entire north Alaskan coast. The development of *Eriophorum vaginatum* tussocks is increasingly inhibited northward as well as altitudinally. Thus, at the Inaru River, 20 to 25 miles south of Barrow, the tussocks are only 4 to 5 inches in height compared to 10 to 14 inches or more in the foothills. Though *Eriophorum vaginatum* itself occurs in the vicinity of Barrow, it occurs locally and forms only small tussocks.

Carex marsh: — *Carex* marsh occurs in level, poorly drained lowlands, on the edges of lakes, on floodplains, and at the bends of rivers. Approximately one-half of the coastal plain and one-quarter of the foothills are covered by this community (Spetzman, 1959). It is scarce in the mountains.

This community is a wet meadow dominated largely by *Carex* species, especially *Carex aquatilus.* It usually occurs on a saturated peat substrate, often with one to three inches of standing water, and is frequently dissected into "low-center" polygons. Several low shrubs such as *Betula glandulosa* and *Salix* spp. occur.

Riparian shrub: — Stands of tree-like shrubs occur along the edges of the rivers and streams as well as the sides of draws, on alluvial fans, and on the more protected slopes of the river valleys. Willows (*Salix alaxensis, S. richardsonii,* and *S. arbusculoides*) are the dominant forms. Balsam poplar, *Populus balsamnifera,* occurs along some of the rivers in the central and eastern Brooks Range, and alder, *Alnus crispa,* is found in some areas of the foothills.

The trees may be 10 to 15 feet tall in the mountains and foothills, but are shorter northward onto the coastal plain. At the Meade River Coal Mine, they are three to four feet tall, and along the Inaru River near Barrow, one and one-half to two feet tall.

These three formations, tussock-heath, carex marsh, and riparian shrub, make up most of the north Alaskan tundra. Tussock-heath tundra is important nesting habitat of the long-tailed jaeger, carex marsh is the preferred habitat of the pomarine jaeger, while the parasitic jaeger nests in both communities. Riparian shrub is an important nesting habitat of several species of passerine birds (Maher, 1959), and is an area of mid-summer concentration of premigratory juvenile and adult passerines exploited by parasitic jaegers. Talus and cliff communities and dry meadow communities, which cover a small area of the foothills and mountains are not utilized by jaegers.

The vegetation of a triangular area of coastal plain extending north from the Inaru River to the coast and east and west of Barrow approximately 60 or 70 miles is quantitatively distinct from that of the remainder of the coastal plain. The diminution in size and occurrence of the tussocks of *Eriophorum vaginatum* and associated heath plants towards the coast has already been mentioned. The vegetation of this northern part of the coastal plain in both mesic and marshy areas is essentially a simple mat of sedges and grasses with a minor element of prostrate willow shrubs present. It is within this part of northern Alaska that the brown lemming population undergoes its strongest cyclic fluctuations and that the pomarine jaeger occurs in its densest breeding populations.

In some zoogeographic studies, notably that of Kessel and Cade (1958), the avifauna of the North Slope has been analyzed on the basis of the distribution of the species in the three physiographic provinces outlined above. The bases for defining the three provinces are geological and physiographic, and the differences between them are not necessarily reflected in the boundaries of habitats and plant communities. For example, the distinctions between the foothills and the coastal plain appear to reflect mostly the difference in the development of drainage in the two regions. Ecologically this affects the relative extent of the marshy and mesic plant communities in the two provinces but not the nature of the communities themselves. The most significant division which occurs on the North Slope, and the one which results in the greatest ecological consequences to the organization of local ecosystems, is that between the relatively simple tundra vegetation of the northern triangle of the coastal plain just described and the remainder of the North Slope.

Seasonal changes in the avifauna

Most species of birds known to nest in northern Alaska are migrants. Only five (6 per cent) of the 90 species of birds breeding on the North Slope are permanent residents (Kessel and Cade, 1958). Migrants begin to return to the North Slope in April and early May, but most species arrive in the second half of May. In Anaktuvuk Pass peak migration is probably in late May and early June (Irving, 1960).

Migration onto the North Slope is predominantly from the south and west. There is no known migration from the east (Irving, 1960), although Smith's Longspur (*Calcarius pictus*) may come in from the east or southeast (T. Cade, personal communication). Arrival of migrants at Cape Sabine (Childs, 1959) is about as early as at Anaktuvuk Pass, as would be expected from the timing of spring melt-off in the two areas. Migration pathways in northern Alaska are then northward and eastward.

Arrival at Barrow averages 10 days to two weeks later than at Anaktuvuk Pass. Although several species of waterfowl that migrate along the leads in the ocean ice arrive at Barrow in late April, most tundra nesting species do not reach Barrow until the first week in June. Breeding begins as soon as the birds arrive.

Late May and June constitute the period when eggs are present. Passerines are usually out of the nest by the latter half of June at the Kaolak River and then spend two weeks or more secluded in the vegetation. In mid-July young passerine fledglings are ubiquitous as they begin moving about. In a few days they congregate into mixed species flocks while they undergo their postjuvenile molt. The adults also molt at this time and seclude themselves in the vegetation.

Their presence in late July or early August is indicated only when a bird is flushed.

Young shorebirds are present from late June with peak numbers of newly hatched young probably in the first half of July. In the foothills they are usually flying by the last of July; at Barrow the nesting cycles are one or two weeks later. Eggs of larger species (loons, ducks, and geese) hatch by mid- or late July.

Departure from the breeding grounds is gradual. At inland localities, numbers of passerine birds decline slowly; the adults disappear first and then the young. Presumably they are departing on fall migration, although large-scale movements are usually not seen. A few groups of shorebirds may be seen in early August, but these are probably local concentrations of family groups banded together in preparation for departure.

At coastal localities such as Barrow there are large concentrations of shorebirds beginning in July, when female phalaropes occur in dense premigratory flocks. In August large numbers of shorebirds feed along the ocean shore, in marshes, and on the shores of lakes, sloughs, and streams.

These late summer concentrations suggest that the fall migration of shorebirds is primarily a coastal one. Departing birds from the interior localities simply move to the coast and travel along the coast toward the west, sometimes in large concentrations. The Colville River valley and other large river valleys on the North Slope are apparently only of minor importance as flyways for shorebirds in the fall migration but may be the main route for passerines. As yet no systematic observations are available from these areas for the fall season.

From the point of view of available food supply, July is the optimum period for a bird predator in the north. In mid-July especially, passerine chicks emerge from the cover where they spend the first two to three weeks after leaving the nest. They are abundant and vulnerable to a predator, as they still fly weakly and have not yet begun flocking in the willow and alder thickets. Shorebird chicks are hatched but unable to fly and are also vulnerable to predators. Shorebirds and passerines are the two avian groups most significant as prey for jaegers, although some ptarmigan chicks and ducklings are also taken.

Microtine rodent populations

There are five species of microtine rodents in northern Alaska: The brown lemming (*Lemmus trimucronatus*), the collared lemming (*Dicrostonyx groenlandicus*), the red-backed vole (*Clethrionomys rutilis*) the tundra vole (*Microtus oeconomus*), and the singing vole (*Microtus miurus*). All five occur in the foothills and southern part of the coastal plain, but only two species, the brown and collared lemmings, are widespread and regularly present in the northern part of the coastal plain. Near Barrow, the collared lemming is uncommon and locally distributed, so that the brown lemming is essentially the only small herbivorous mammal in that area.

In the northern part of the coastal plain, where the brown lemming is essentially the only small herbivore, its population undergoes cyclic fluctuations of great amplitude with a periodicity of three to four years. Population fluctuations of the brown lemming on the North Slope are known in some detail since 1949 (Rausch, 1950; Thompson, 1955; Pitelka, 1957 and Pitelka *et al.*, 1955a and 1955b). There have been four major highs: 1949, 1953, 1956, 1960, the last being the most recent considered in this account. A general, moderate population occurred in 1952, and low populations occurred in 1950, 1951, 1954, 1957, 1958 and 1959. In 1957 there were two local lemming highs at Pitt Point and Wainwright.

A more detailed discussion of the history of the brown lemming populations in northern Alaska during the course of this study has already been published (Maher, 1970a), and the reader is referred there for further information.

Several species of microtines occur together in the foothills and mountains. While their population levels do fluctuate, they seem to do so independently, and as yet no regular periodicity in the fluctuations has been shown to occur (Pitelka, MS). A localized peak population of *Microtus oeconomus* occurred at Cape Sabine in 1959 where foothill tundra is adjacent to the coast (Childs, 1969).

General Characteristics of Jaegers

The jaegers are related to gulls, but they are morphologically distinct and are usually grouped in a separate family, the Stercorariidae, which also includes the skuas of the genus *Catharacta.* Jaegers are dark brown to black on the upper parts and typically have light under-parts. The median rectrices of all three species are elongate in the adult plumage. They have no known signal function in social behavior but may be important in species recognition. The jaegers are circumpolar species with arctic and subarctic breeding ranges; all winter on the oceans into south temperate and tropical regions. Much of their food in winter is obtained by chasing other birds and forcing them to regurgitate. In summer they are important predators in arctic communities, where they very rarely resort to "parasitism." The nest is situated on the open tundra, two eggs are usually produced, and both sexes incubate the eggs and care for the young.

The pomarine jaeger is the largest of the three species in the genus *Stercorarius* and appears to be the least abundant of them. It has the most restricted breeding range. Adult females collected in northern Alaska average 739.7 ± 11.7 grams in weight (range, 576 to 917 grams, N = 52). The average weight of north Alaskan males is 648.0 ± 6.25 grams (range, 542 to 797, N = 73), 87 per cent as much as the females.

The breeding range of the species is essentially circumpolar in the arctic although it is not known to breed in eastern Greenland or northern Europe; and in the remainder of its range, it is restricted to low lying coastal areas. Its range does not extend northward beyond approximately Latitude 75° N., or as far south as either of the other jaegers. Breeding in North America occurs in western and northern Alaska, Mackenzie, the southern Canadian Archipelago (Banks, Melville, Somerset, and Baffin Islands), Southampton Island, northern Quebec and central, western Greenland. In the Old World, breeding records are available from Spitzbergen, Bear Island, Novaya Zemlya, northern Russia, and Siberia including the New Siberian Islands, Wrangel Island, and Herald Island. The report of it breeding regularly on the Commander Islands (Johansen, 1961) is an unusual southerly extension of its range.

The species occurs in two color phases, one light or "normal," the other melanistic. Melanistic birds make up approximate five per cent of the breeding population in northern Alaska. Southern (1944) has analyzed the variation in proportion of the two color phases over the entire breeding range. No races have been described.

The parasitic jaeger is smaller than the pomarine jaeger. Adult females from northern Alaska weigh 508.5 ± 24.4 grams on the average (range, 346 to 644 grams, N = 11). Males are 82 per cent as large with an average weight of 421.2 ± 11.56 grams (range 301 to 540 grams, N = 20).

The breeding range of this species is holarctic, extending almost to the northern limit of land and south into subarctic and temperate maritime regions. In North America it breeds from the Aleutian Islands, Kodiak Island, and the Alaska Peninsula, in western and northern Alaska, across the Canadian Archipelago (Banks, Baffin, southern Melville and southern Ellesmere islands), Southampton Island, to the east coast of Greenland, and across the northern edge of the Canadian mainland to southern Mackenzie, northern Ontario, Quebec, and Labrador. Its breeding range extends farther south on the North American mainland than either of the other two jaegers and farther north than that of the pomarine jaeger. Its North American range is approximately coextensive with that of its main avian prey, the lapland longspur *Calcarius lapponicus* (*See*, Godfrey, 1966). In the Old World it breeds on Iceland, Jan Mayen, Spitzbergen, Bear Island, to northern Scotland, northern Scandinavia, and across northern Russia and Siberia in coastal regions (Dement'ev *et al.*, 1951).

The parasitic jaeger also occurs in light and melanistic color phases (see Southern, 1943). Many intermediate individuals exist, resulting in great variation in color in the adults. Dark forms appear to predominate in northern Alaskan populations. No races have been described.

The long-tailed jaeger is the smallest member of the genus. The average adult female from northern Alaska weighs 312.8 ± 7.4 grams (range, 258 to 358 grams, $N = 18$). Males average 280.1 ± 6.1 grams in weight (range, 236 to 343 grams, $N = 26$), or 89 per cent as much as the female average.

The breeding range of this species is also circumpolar and is similar to that of the parasitic jaeger, but it extends further north, to the northern limit of land at approximately 80° N Latitude, and lacks the maritime populations of the latter species in western Alaska and the northern Atlantic islands.

It breeds in the New World from western and northern interior Alaska to Mackenzie, in the Canadian Archipelago (Banks, Melville, and Ellesmere islands), to northern Greenland, and south to Southampton Island and northern Quebec. In the Old World it breeds in Iceland, Jan Mayen, Spitzbergen, Bear Island, Novaya Zemlya, northern Scandinavia, and across northern Russian and Siberia to Kamchatka (Dement'ev *et al.*, 1951).

The long-tailed jaeger lacks a melanistic color phase. Two races have been described by Loppenthin (1943), the nominate race *Stercorarius longicaudus longicaudus* from northern Eurasia east to eastern Siberia, and *S. l. pallescens* from eastern Siberia, Alaska, Canada, and Greenland. These races were not recognized by the American Ornithologist's Union (1957) but in a recent revision Manning (1964) strongly supports the distinction.

Population Biology of the Pomarine Jaeger

Breeding range in northern Alaska

The pomarine jaeger breeds on the part of the coastal plain on which the brown lemming population cycles regularly, as well as on a narrow strip of coastal tundra along the entire arctic Alaskan coast. Occasional microtine rodent highs occur in this coastal strip; for example, that of *Microtus oeconomus* at Cape Sabine in 1959, and an eastward coastal extension of the 1960 brown lemming high. Reed's (1956) report of nesting pomarine jaegers in the interior foothills is probably erroneous.

Location and areal extent of nestings

Rausch (1950) has published some information on the 1949 nesting at Barrow, and Pitelka *et al.* (1955a, b) studied the jaeger populations there in 1952 and 1953. Data obtained on the pomarine jaeger population in several locations in northern Alaska in the years 1956 through 1960 are presented here.

The abundant nesting of pomarine jaegers in northern Alaska in 1956 was co-extensive with the lemming high of that year. Lemming numbers were high in a triangular area bounded on the south by a line from Peard Bay to the delta of the Ikpikpuk River with Barrow at its apex. An area with a moderately dense lemming population bordered this region narrowly on the south and west but extended eastward approximately to Pitt Point (Pitelka, 1957). Intensive study of the jaeger population was conducted in the vicinity of Barrow.

No pomarine jaegers nested in the Barrow area in 1957. The two local lemming highs that occurred at Wainwright and Pitt Point were exploited by pomarine jaegers. The Pitt Point high attracted a moderately dense jaeger population, but the Wainwright high did not, although a few pairs of pomarine jaegers bred there. The difference in the degree to which pomarine jaegers exploited these two highs may have been a result of the very local extent of the high at Wainwright.

There was no known breeding of the pomarine jaeger in northern Alaska in 1958, as determined by reconnaissance flights along the coast east of Barrow to Barter Island on 9 June, and by a flight westward from Barrow to Cape Sabine on 11 June. However, some late summer adults collected along the coast showed evidence of having bred (see section on gonad cycle); hence a few pairs probably attempted to breed in this season, as they probably do scatteredly in every season.

Three pairs of pomarine jaegers nested on 15 ± sq. mi. near Barrow in 1959, the third season since the previous extensive population high of *Lemmus* on the north Alaskan coast. It is possible that a population of comparably low density bred elsewhere near Barrow in response to a slight upswing of lemming numbers, but none was observed. In the same season a local high of *Microtus oeconomus* occurred at Cape Sabine, 260 miles west of Barrow, and a small population of pomarine jaegers nested there in association with parasitic and long-tailed jaegers.

An extensive nesting of pomarine jaegers occurred in 1960 in response to the lemming high of that year, the fourth since 1949. The high lemming population probably extended over an area of coastal plain approximately comparable in extent to that of 1956, but it differed slightly in geographic outline (See Maher, 1970a).

Thus, in the decade from 1949 to 1960 the pomarine jaeger bred near Barrow in northern Alaska only five times in significant numbers. Breeding at moderate to high density occurred in 1949, 1952, 1953, 1956, and 1960. In addition, some pomarine jaegers bred in 1955 and 1959. The fact that the jaeger population reproduced on a significant scale in less than one half of these twelve seasons, and on areas representing mere fractions of the coastal plain, poses several questions concerning the adaptations of this species for survival with such an infrequent breeding schedule.

Schedule of breeding events

Arrival and breeding density at Barrow: — A few pomarine jaegers reached Barrow in 1956 on 19 May by following lanes of open ocean water parallel to the coast (P. Sovalik, personal communication). They were first seen on the tundra near Barrow on 26 May (J. Koranda, personal communication), when a flock of approximately 15 was roosting on a large snow-covered marsh, called "Central Marsh" (Figure 3).

The population increased for several days. Flocks roosted on broad, level and low areas of the tundra with Central Marsh as a focus of concentration. On 28 May, 26 jaegers were seen there; on 29 May, 60; and on 30 May, a total of 90 were present.

The jaeger flocks began to disperse during the day on 31 May but tended to congregate to roost in the evening. Although a located pair was observed on 2 June, the general dispersal of the flocks did not take place until 4 June. On that day the first territorial defense was observed, and along with it, the first courtship activities. On 5 June territorial defense and pairing behavior were widespread in the population.

The delay observed in the breakdown of the flocks may have been owing to inclement weather. From 26 May, the day on which the jaegers arrived, through 4 June, the wind blew steadily from the southeast at 25 to 30 miles an hour, and temperatures were well below freezing. The beginning of territorial defense and pairing behavior coincided with the cessation of wind on 4 June. The temperature rose to near thawing on 5 June, when breeding activities became general in the population.

The spring population increased until all available habitat was occupied, including some that was obviously marginal. Arriving jaegers appeared to come in waves, so that marked increases in numbers were noted on 6 and 7 June.

Beginning on 5 June, groups of jaegers were observed flying eastward from the Barrow area, though loose flocks of jaegers, either newly arrived or surplus individuals that could not locate territories, were present until egg-laying began. One of these flocks roosted in the northeast corner of Central Marsh. It contained 19 birds on 8 June, 37 on 9 June, and 49 on 12 June. On 15 June a noticeable drop took place in the jaeger population generally, and the next day the flock in Central Marsh was gone. The corner of the marsh it had occupied was under water on 16 June, and its final departure may have been induced by the partial flooding of the marsh by melt water.

An attempted copulation was seen on 8 June; the first completed copulation was observed on 11 June. Egg-laying began in the resident population on 14 June. By 16 June the population was essentially stable in numbers, although occasional transient birds were present all season.

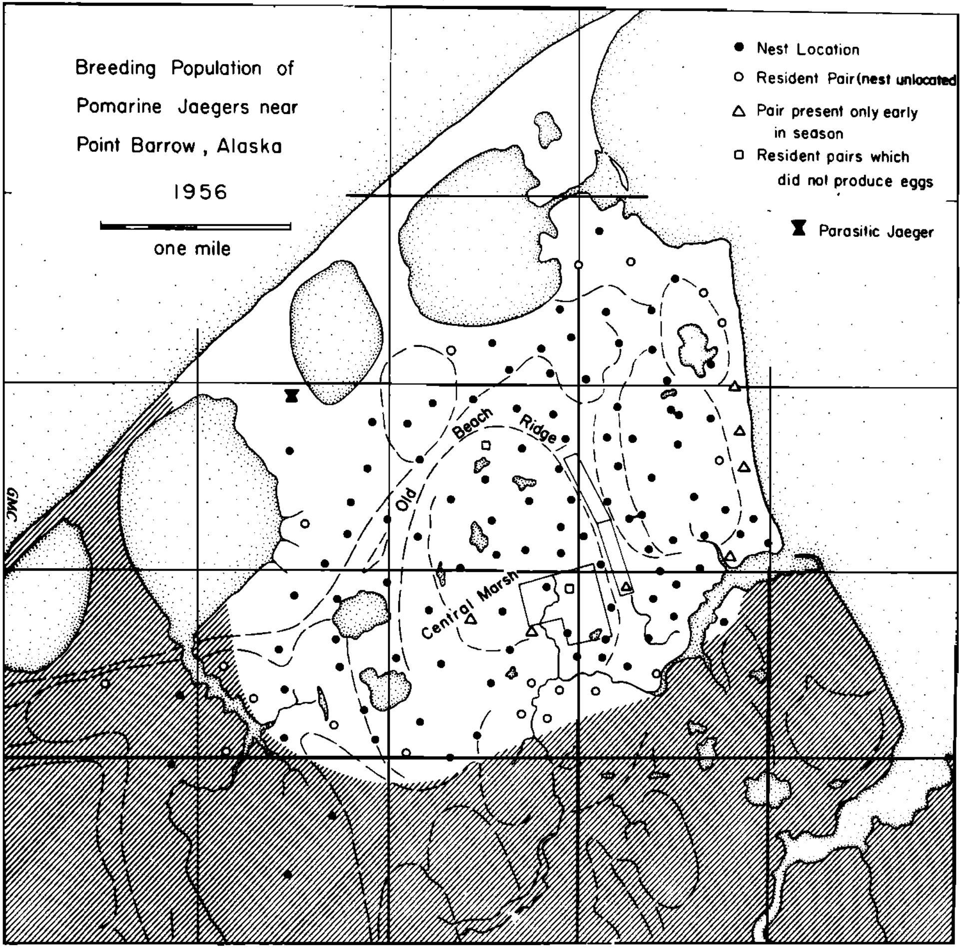

Figure 3. Map of the breeding population of pomarine jaegers on the main study area near Barrow in 1956. The pairs of nest symbols connected by solid lines indicate two pairs which renested. Elongated rectangle on the old beach ridge is Pitelka's plot 1, six-sided figure in Central Marsh is his plot 3 (see text).

A study area of about six square miles in the vicinity of the Naval Arctic Research Laboratory was censused periodically during the season (Figure 3). The initial census made in mid-June at the peak of egg-laying gave a total of 114 pairs, or a density of 19 pairs per square mile. Maximum densities on two, separate square miles were 22 and 23 pairs. The number for the total area includes several pairs that departed without producing eggs, but since it includes all pairs known to have established territories it is considered to be the initial breeding population.

It is difficult to estimate the proportion of excess birds that were present in the population before its numbers stabilized. Certainly it was high. On 12 June, 121 jaegers were counted on a survey of Central Marsh from its southeast corner. The survey included the part of the marsh in which a flock of 49 jaegers was present on 15 June, and the area had an eventual breeding population of between 50 and 60 birds. These observations suggest that only about half of the population in the marsh in early June eventually established territories. However, marshes are preferred roosting areas for non-territorial jaegers, so that the proportion of surplus birds in the total population in mid-June was probably near 25 per cent.

The pomarine jaeger did not breed at Barrow in 1957 or 1958. In 1957, one jaeger was seen at Barrow Village on 28 May, and a second one on 2 June. On 4 June three jaegers were seen over Central Marsh. A few individuals occurred sporadically from then through the middle of June. None established territories, and no courtship was seen. On 4 June, 16 jaegers, probably all pomarine jaegers, were seen along the coast between Barrow and Wainwright. None appeared to be settled.

As in 1957 the first jaeger seen on the tundra near Barrow in 1958 was recorded on 4 June. In the evening of 5 June, a broad-front migration of pomarine jaegers reached Barrow. Few of these birds remained, and only occasional individuals were seen or reported from then until 14 June. On that date a population of jaegers estimated at 7 to 10 per square mile was present. Most seemed to be flying about at random, although several pairs appeared to be attached to specific areas, but no courtship activity or territorial defense was noted. By 16 June the population had dropped to an estimated two to four transient birds per square mile. On 17 June there were one to two birds per square mile, none territorial, and no breeding ensued.

Pomarine jaegers were first seen on the tundra at Barrow on 8 June in 1959, although they had been along the ocean as early as 24 May. Some birds were locally settled by 12 June, and settled birds were observed through mid-June. The population density was then estimated by Pitelka (personal communication) to be one pair per two to six square miles. By 20 June most of the jaegers had left, although three pairs remained and bred. These were the only pairs on approximately 15 square miles, a breeding density of 0.2 pairs per square mile. The three pairs were about one mile apart.

It was expected that in non-lemming years, particularly 1957, the jaegers would arrive in numbers as they had in 1956, establish territories, and perform some courtship activities before dispersing. A similar response was described by Manniche (1910) for a long-tailed jaeger population in northeast Greenland in a spring following a lemming high. There was no such occurrence at Barrow in either 1957 or 1958, and this fact suggests that the pomarine jaeger is completely nomadic and forms no permanent territorial attachment. The tendency for jaegers to become locally settled in 1959 and the breeding of a few pairs were evidently responses to a slight upswing in lemming numbers.

Pomarine jaegers arrived at Barrow on 24 May in 1960, when four birds were seen. The following day jaegers were abundant, already dispersed, and incipient courtship behavior had begun. Density was estimated to be 15-20 individuals per square mile. Territorial defense was general in the population on 26 May, and on 27 May attempted copulation was noted. Completed copulations were first seen on 31 May. Egg-laying began on 5 June.

By 28 May jaeger density had risen to 20-25 birds per square mile, and excess birds were first observed then. On 31 May a flock of 30 roosted in Central Marsh. Flocks of 59 and 56 were on the study area on 8 June, a flock of 16, on 9 June, and one of approximately 50 birds, on 10 June. The flocks were gone on 11 June, as the population had apparently declined to breeding level. There were fewer surplus birds on the study area in 1960 than in 1956. They were estimated to be less than 25 per cent of the breeding population.

The breeding population censused on 23 June, 1960 was 118 pairs on an area of 5.75 square miles. The mean density was 20.5 pairs per square mile, with a range of 17 to 26 pairs per square mile. Thus, in both of the dense breeding years of 1956 and 1960 the pomarine jaeger populations built up rapidly to aggregations well above the final breeding density; the surplus jaegers remained in the area until breeding began and then quickly departed. The rapid dispersal of arriving flocks and the early onset of breeding in 1960 contrast strongly with the observations of 1956. In 1960 the weather was calm and warm, and melt-off occurred rapidly compared with the cold weather and delayed thaw of 1956. Presumably the difference in weather conditions allowed the birds to become established early in 1960.

Other populations: — Pomarine jaegers bred at Wainwright in three of the five years from 1956 to 1960 in densities ranging from approximately 1.5 pairs per square mile (1956) to 2 pairs per square mile (1957 and 1960). The densities in 1956 and 1960 were very much less than the high densities at Barrow in those years, while in 1957 a few pairs bred at Wainwright when none bred at Barrow. A few settled pairs were near Wainwright in June 1958 but did not breed.

Year to year changes in breeding density of pomarine jaegers at Pitt Point from 1956 to 1960 differed from both Barrow and Wainwright. None bred in 1956, 1958, or 1959. Breeding occurred in 1957 in response to a local lemming high, and in 1960, in response to the general lemming high of that year.

In 1957 pomarine jaegers arrived at Pitt Point between 19 May and 22 May. Data on the spring build-up are scanty. On 12 June, jaegers were reported to be numerous and usually in pairs. On 15 June the numbers had noticeably decreased "in the past week or so," although stray birds were still present in groups along the shore. The population apparently followed a trend similar to that of the Barrow population in 1956 and 1960, i.e., a rapid build-up to an early peak in numbers, followed by a decline as unreproductive birds departed.

I visited Pitt Point from 26 June to 2 July and censused six square miles of tundra. Fifty-nine pairs of pomarine jaegers were breeding (Figure 4). The estimation of initial breeding density is complicated by the fact that local personnel had collected 16 jaegers at my request in mid-June. In addition, 15 to 20 were shot before 12 June "to keep them from molesting ducks," and two clutches of eggs were collected.

It is difficult to judge the effect of this collecting on breeding density. I have assumed that it was slight. Most birds were taken from a small area near the camp. Some were transients, judging by the size of the gonads of some males in the sample obtained for me. Established pairs displaced before mid-June would probably be replaced by surplus individuals in the area. The 59 pairs censused and the two nests that were destroyed give a total of 61 pairs known to have nested on six square miles, or a mean density of 10 pairs per square mile. Maximum density on one mile was 15 pairs. Initial breeding density for the area was probably 10 to 12 pairs per square mile.

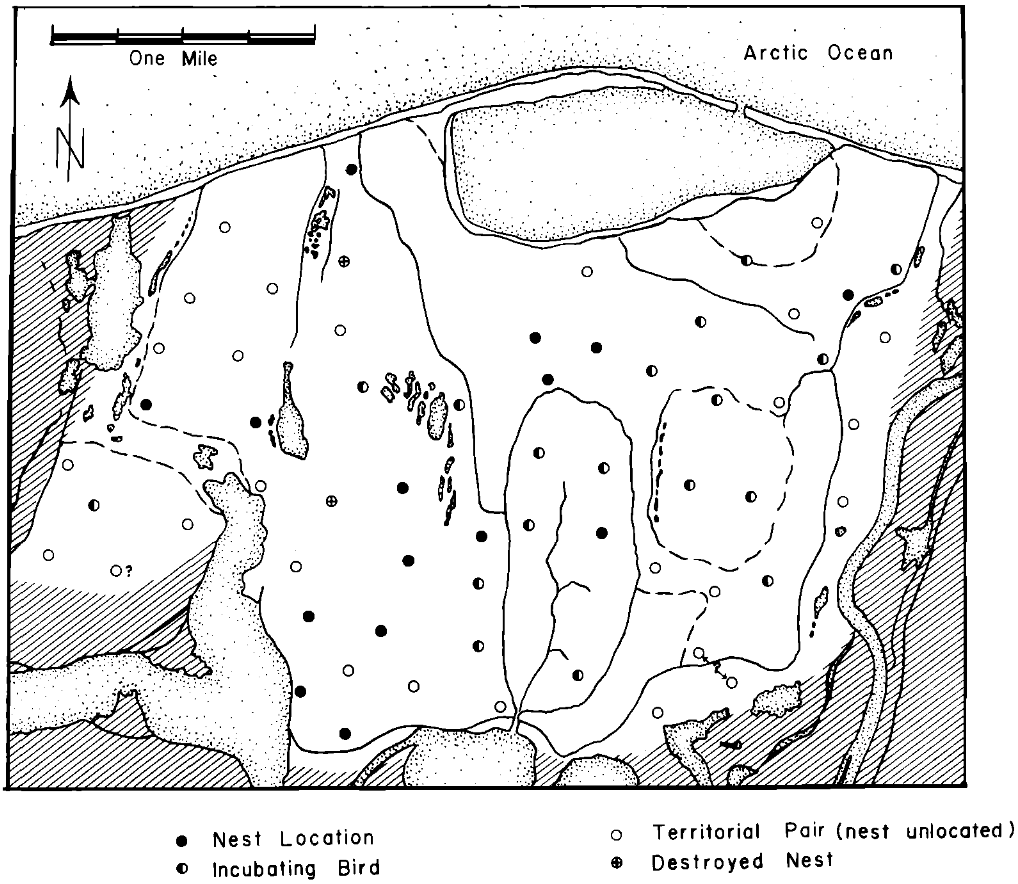

Figure 4. Map of the breeding population of pomarine jaegers at Pitt Point in 1957.

In 1960 pomarine jaegers were already established on 14 June, and an estimated four to five pairs were nesting per square mile. On a visit from 15 to 20 July, J. C. Reynolds located six pairs on approximately 1.75 square miles. It is not known to what extent personnel at the government installation in the area interferred with the breeding population. One pair was shot, and probably others were killed also. The original estimate is considered close to the initial breeding density.

No pomarine jaegers bred at Cape Sabine in 1957, 1958 or 1960. Nothing is known of the population prior to 1957. In 1959 a small population bred in response to the local *Microtus oeconomus* high. They arrived at Cape Sabine on 22 May. Flocks were seen then and on the morning of 23 May. By evening the flocks had broken down, the birds were generally distributed, and territorial announcements were witnessed. The density was estimated at 10 to 12 individuals per square mile. The population appeared to decline slightly on 25 May to a density of three to five pairs per square mile. Density remained stable until observations ended on 28 May. When observations were resumed on 12 June four pairs were present on approximately eleven square miles, a maximum density of 0.36 pairs per square mile (Figure 5).

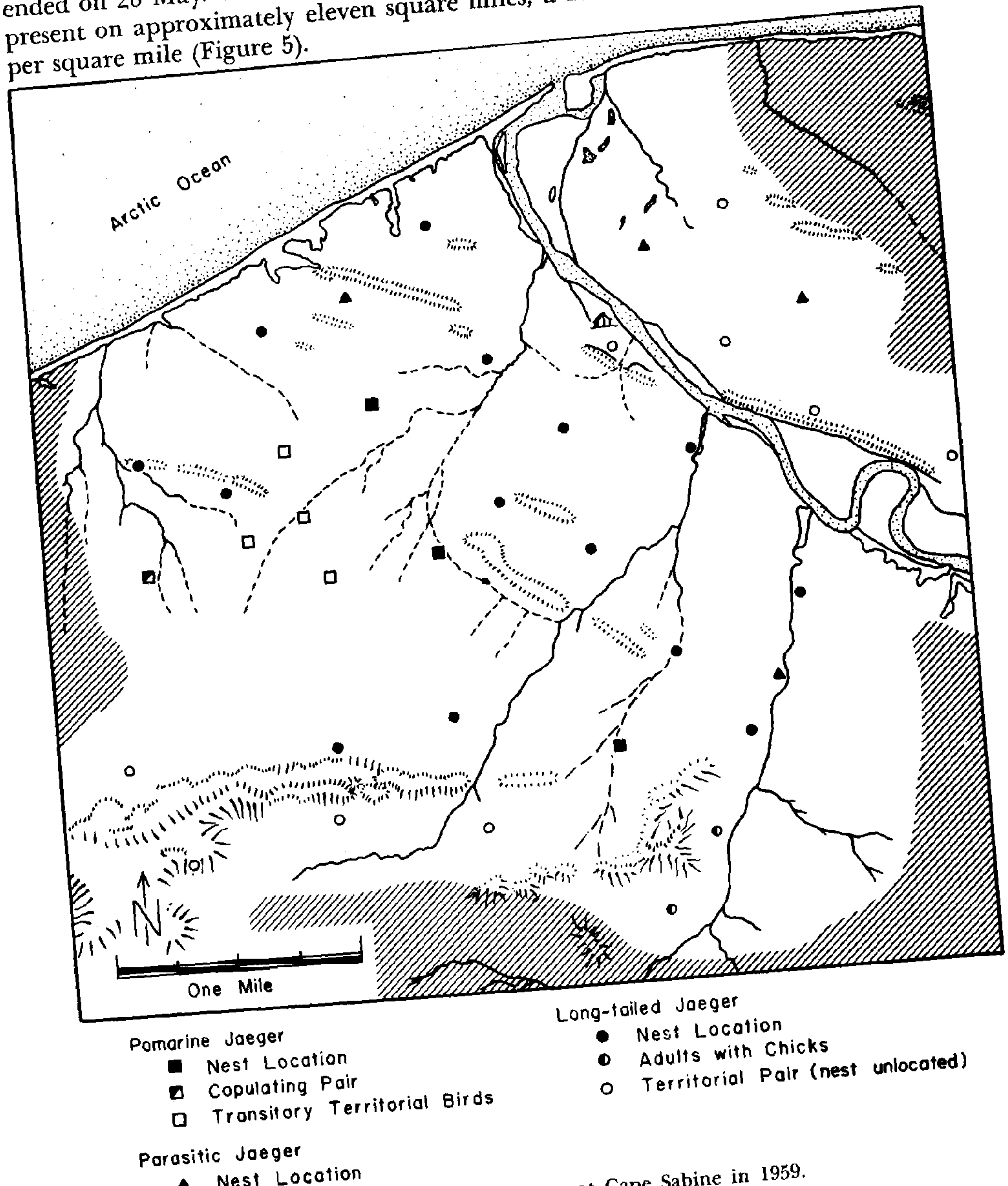

Figure 5. Map of breeding population of jaegers at Cape Sabine in 1959.

The Cape Sabine area is foothill tundra, much of which is unsuitable as nesting habitat for the pomarine jaeger. In the low, broad, grassy swales preferred by this species, pairs were spaced one mile apart, and the density in this habitat was about one pair per square mile.

A significant observation on behavior of transient pomarine jaegers was made in late June and July when a major westward movement of these jaegers occurred through Cape Sabine. A few pomarine jaeger pairs were noted moving westward through the area on 12 June. Six to eight jaegers a day were noted until the 24th. On that date a large number of transients were seen moving westward in small groups. The large movement continued through the 27th. Fifty to 55 jaegers were seen on the 25th, and an even greater number passed on the 26th. Many birds lingered on the area and hunted during these three days. Several individuals and pairs began defending territories. Pomarine jaegers were then abundant on the tundra, though most of them remained along the coast. Almost no jaegers were seen on the 28th and 29th when the weather was warm and clear, but they were again seen on the 30th when the weather turned cloudy.

Peak numbers were seen from 1 July through 3 July. Jaegers were heading westward continuously, and flocks of 50 to 60 birds roosted in the marshy areas of the study area at night. The number of jaegers declined on 5 and 6 July, and none were observed on the 7th and 8th. From 8 July until 11 August, when observations ceased, pomarine jaegers were seen only occasionally. Most of those seen were along the ocean; they were rarely seen over the tundra.

The observation is important because it is the only direct evidence for early departure of nonbreeding pomarine jaegers from northern Alaska and because it demonstrates the immediate response of the species to a suitable food supply.

In summary, in areas where there is a moderate to high population of lemmings as at Barrow in 1956 and 1960 and at Pitt Point in 1957, the pomarine jaeger population builds up rapidly to numbers in excess of the eventual breeding density. The surplus individuals typically remain in the area, roosting in flocks, and depart when breeding begins in the territorial population. The breakdown of flocks and the onset of territoriality can be delayed by adverse weather as at Barrow in 1956. The response of the arriving birds in low lemming years, for example, and the degree to which they tended to settle at Barrow from 1957 to 1959, were dircetly related to the level of the spring lemming population each year. In 1957 when the lemming population was lowest, transient jaegers did not stay at all but passed directly through the area.

The pomarine jaeger exhibits the widest year to year variation in breeding density of the three jaeger species. Breeding density in northern Alaska has ranged from 0.13 pairs per square mile to the mean high density of 19 pairs per square mile at Barrow in lemming high years. The extremes in density differ by 115-fold. Breeding densities are summarized in Table 3.

Duration of the pre-egg stage at Barrow: — The time elapsed from arrival to the beginning of egg-laying was used to estimate the duration of the pre-egg stage for the populations of Barrow in 1956, 1959, and 1960.

In 1956 the pomarine jaegers arrived on the tundra on 26 May. Territorial defense was general on 5 June, and egg-laying began on 14 June. Fifty per cent of the eggs laid were produced in six days, from 14 to 19 June inclusively. If the birds first established also laid their eggs first, then the pre-egg stage lasted from 9 to 14 days from the onset of territoriality, and approximately 21 days from the first arrival of the jaegers.

In 1959, jaegers arrived on 8 June. Egg-laying occurred in the period from 21 to 29 June, or 13 to 21 days after the arrival of the birds.

TABLE 3

Breeding densities and nesting success of the pomarine jaeger

Locality	*Year*	*Spring Lemmus density (no/acre)*	*No. of pairs*	*Area (square miles)*	*Average density (pairs/square mile)*	*Maximum density (pairs/square mile)*[a]	*Breeding success (per cent of eggs laid)*
Barrow	1952	15–20	34	9	3.8	5–6[b]	30–35[b]
	1953	70–80	128	7	18.3	25–26[b]	20–25[b]
	1954	<1	0	—	—	—	—
	1955	1–5	2	15±	0.13	—	0
	1956	40–50	114	6	19.0	22–23	4
	1957	<1	0	—	—	—	—
	1958	<<1	0	—	—	—	—
	1959	1–5	3	15±	0.20	—	—
	1960	70–80	118	5.75	20.5	25	55
Wainwright	1956		3	2±	1–1.5	—	?
	1957		3–4	4	1.0	—	?
	1958		0	—	—	—	—
	1959		0	—	—	—	—
	1960		4–5	?	2±	—	?
Pitt Point	1956		0	—	—	—	—
	1957	30–40	61	6	10.1	15	13
	1958		0	—	—	—	—
	1959		0	—	—	—	—
	1960		4–5	1–2	—	—	?
Cape Sabine	1957		0	—	—	—	—
	1958		0	—	—	—	—
	1959		4	11	0.36	1[c]	13
	1960		0	—	—	—	—

[a] Density on part of study area with greatest concentration of territorial pairs.

[b] Estimates provided by F. A. Pitelka; see Pitelka, Tomich, and Treichel, 1955a.

[c] In suitable nesting habitat.

In 1960 jaegers arrived on 24 May, territorial defense became general on 26 May, and egg laying began on 5 June. Fifty per cent of the eggs were laid in a six-day period from 5 through 10 June. Thus the pre-egg stage was 10-15 days from the onset of territoriality and 14 days from arrival on the nesting ground.

Other populations: — At Pitt Point in 1957 jaegers arrived about 20 May and the first eggs were laid on approximately 10 or 11 June, giving a pre-egg stage of 21 to 22 days. Jaegers arrived on 22 May at Cape Sabine, and egg-laying spanned 8 to 13 June, some 17 to 22 days later.

In all these instances the pre-egg stage lasted two to three weeks from arrival. The best information is for the 1956 and 1960 populations near Barrow. The pre-egg period was about three weeks in 1956, about two weeks in 1960. In both instances egg-laying began approximately ten days after territoriality was general in the populations. In 1956 the jaegers remained in flocks from 26 May to 5 June before establishing territories, while in 1960 the dispersal of the flocks was immediate. The delay in 1956 was associated with adverse weather conditions.

Egg-laying at Barrow: — Egg-laying was well synchronized in the 1956 Barrow population. Dates were recorded when 17 eggs were laid, and the dates for 54 additional eggs were estimated from known hatching dates and an incubation period of 26 days (Figure 6). Two pairs of jaegers re-nested after their first clutches were destroyed. The dates on which one second clutch was laid are known (Figure 6). The distribution of egg-laying is skewed to the left, approximately 50 per cent of the eggs being laid in the first six days, 14 to 20 June, and the remaining 50 per cent in the last 10 days of the egg-laying period.

The dates for the two clutches in 1959, calculated from known hatching dates, were 21 and 23 June for the first, and 27 and 29 June for the second.

Egg-laying began earlier and was more protracted in 1960 than in 1956, although the temporal distribution is again strongly skewed to the left (Figure 6). The dates are known when 37 eggs were laid. Forty-nine additional dates were calculated from hatching data. About 50 per cent of the eggs were laid in six days, 5 to 10 June, the remaining 50 per cent over 16 days. The distribution almost suggests a bimodal curve, the latter part of which could reflect the large influx of late arriving birds noted about 31 May.

Other populations: — Few data are available on the 1957 Wainwright population. One nest with two eggs was located on 6 July. The clutch was collected on 18 July when the eggs were within three to four days of hatching. They were probably laid about 26 June.

One complete clutch collected at Pitt Point on 14 June 1957 had not been incubated. Two females collected on 14 June had two ruptured follicles each, and two collected on 16 June had no follicles ruptured, the largest ovum being 14.2 and 6.4 mm, respectively. Two other females obtained on 21 June each had one ruptured follicle with the largest ovum being 15.0 in one and 6.3 mm in the other. The former bird would probably have ovulated in a day or two.

Egg-laying in this population must have begun at least on 10 or 11 June, since there is a one- to two-day interval between eggs, and must have extended at least from 10 to 22 June. The beginning of laying was approximately four days earlier than at Barrow in 1956.

The two clutches that hatched at Cape Sabine in 1959 were probably laid between 8 and 13 June. A third pair of jaegers was seen copulating on 17 June and was defending its territory on 23 June. The female may have laid about 18 June. Egg production in this population occurred between 8 and 18 June. The population bred a week earlier than the jaegers at Barrow in 1956 and only a few days ahead of the Pitt Point population of 1957.

First clutches of the pomarine jaeger are laid in June. Dense populations

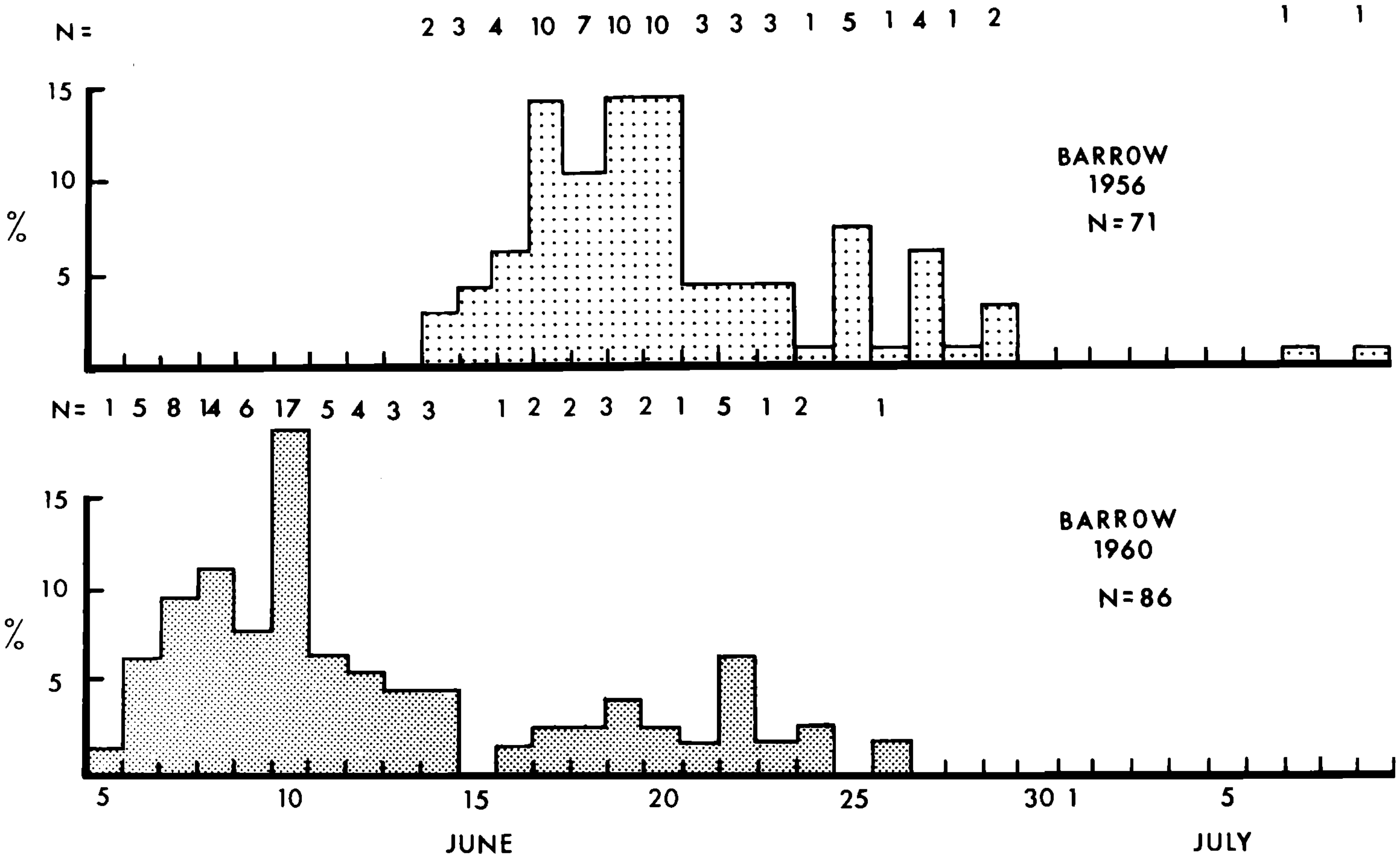

Figure 6. Distribution of egg-laying dates of the pomarine jaeger at Barrow in 1956 and 1960, both observed and calculated from known hatching dates.

show a very high degree of synchrony. Thus, half of the eggs at Barrow in 1956 were laid in six days from 14 to 20 June, and in 1960 half the eggs were laid in six days from 5 to 10 June. Eggs were laid in the first half of June at Pitt Point in 1957 and at Cape Sabine in 1959. The evidence from Barrow in 1959 and Wainwright in 1957 suggests that sparse pomarine jaeger populations breed one to two weeks later than dense ones.

Hatching at Barrow: — Hatching of 33 eggs in 1956 spanned 15 days from 10 July to 24 July; one egg of a second clutch hatched on 4 August (Figure 7). In 1960 the hatching of 67 eggs was either recorded or calculated from chicks one to two days old (Figure 7). Hatching spanned a 22-day period from 1 through 22 July. In both years the distribution is skewed to the left in the same manner as the egg-laying dates.

On 18 July 1959, one nest contained a downy chick, probably one day old, and one pipping egg that hatched the following day. The second nest had two pipping eggs on 19 July, and one of these hatched on 23 July; the second egg hatched, but the chick was found dead in the nest on 27 July.

Cape Sabine: — In 1959 the eggs in two successful clutches hatched on 4, 6, 7, and 9 July.

Hatching dates for all these pomarine jaeger populations are in the first three weeks of July.

Development of flight in the young at Barrow: — The first flying chick in 1956 was just able to fly when found on 15 August ten miles south of Barrow. The first flying chicks on the study area were two siblings noted on 18 August. All of the penned chicks were wing clipped in 1956; none fledged, and none yielded any useful data on the normal time of development for the species.

Only a little information was obtained in 1956 on the length of time that adults attend chicks. The success of this population was so low that most adults were gone before any chicks flew. The chick found on 15 August was not accompanied by adults. The two sibling chicks that could fly on 18 August were seen with both parents. Two other, unattended, flying chicks were seen on 20 August. An adult male was hunting near them, but there was no indication that it was associated with the chicks. This was the last observation indicating that adults and chicks were possibly still associated. On 21 August an unattended chick was found that could not fly. Another chick, which could just fly, was seen on that day, and again, no adults were present. No jaegers were seen on a survey of six to seven square miles of the study area on 24 August. E. Clebsch reported one adult on 27 August. On 30 August another unattended chick could just fly when found. On 31 August, the last day of observation, two adults were seen flying over the Naval Arctic Research Laboratory. Thus, it appears that those adults which did raise chicks in 1956 abandoned them by 20 August at the latest, when some were still unable to fly.

In 1960 most chicks flew well by 10 August, a week after the first flying chicks were seen, and by 12 August chicks began straying from their parents' territories. Adults were mildly aggressive towards strange chicks but restricted their aggression to territorial announcement (see section on territoriality). On 15 August a group of four adults and four chicks were associating amicably together, and on 18 August a chick that appeared to be completely independent was seen flying over the ocean. This was the first clearly independent chick seen in the entire course of study. A dozen independent juveniles and only one adult

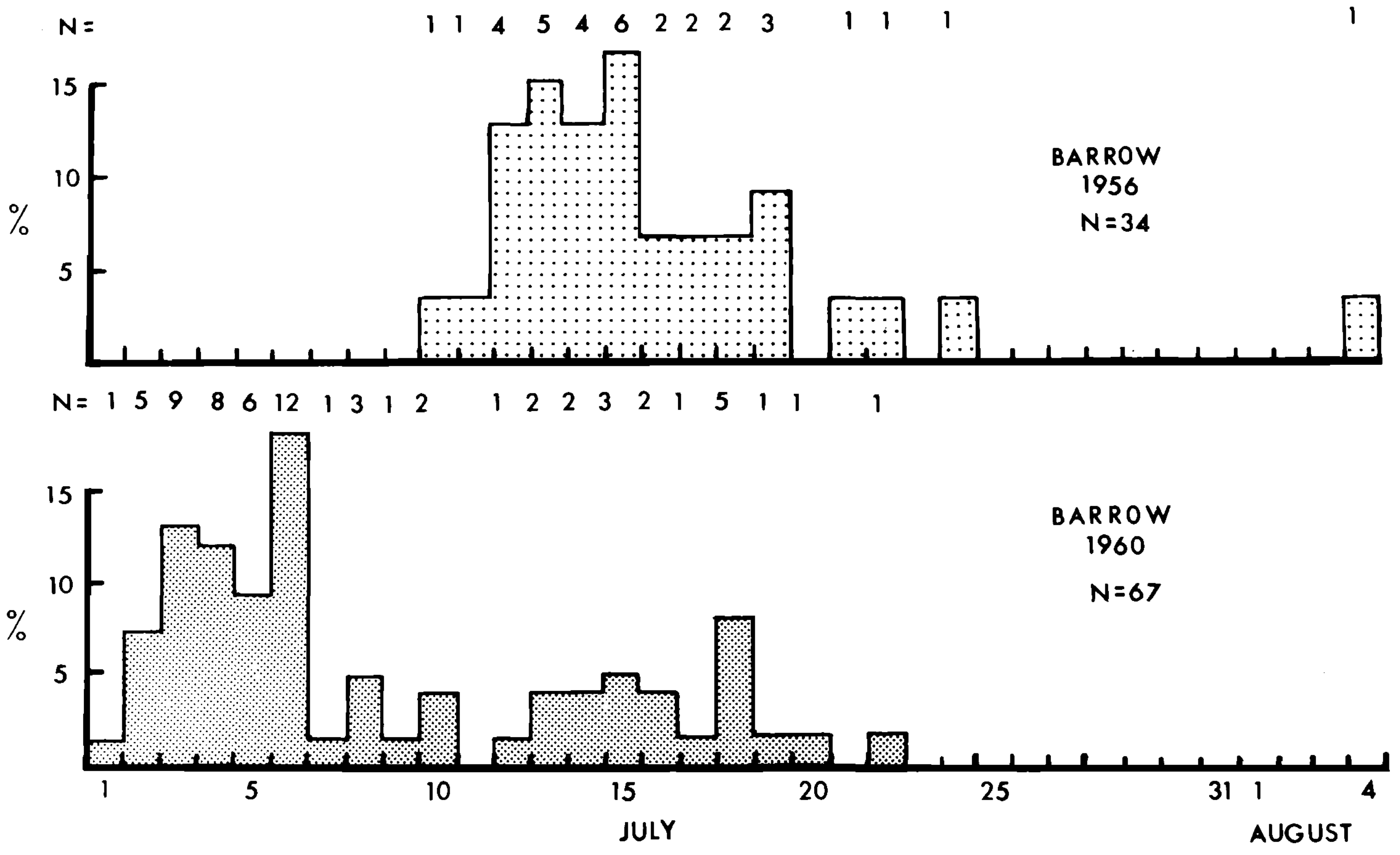

Figure 7. Distribution of hatching dates of the pomarine jaeger at Barrow in 1956 and 1960, both observed and calculated from chicks one or two days old.

jaeger were noted along the ocean on an eight mile trip to Point Barrow on 25 August. These included a flock of six juveniles worrying a group of four glaucous gulls (*Larus hyberboreus*). On 27 August, the last day of observation, some chicks were still attended by adults on the territories.

The chicks that were penned in 1960 were not pinioned and were able to fledge from their enclosures. Seventeen flew successfully in an average of 31.3 days from hatching. The extremes were 28 and 34 days.

Other localities: — The one chick raised to maturity at Cape Sabine in 1959 was able to fly over the one-foot enclosure on 10 August. It took 37 days to mature.

Pitelka *et al.* (1955b) suggested that young pomarine jaegers fly when they are five to six weeks, or 35 to 42 days old, and that they are dependent on the adults for at least a week or two longer. They did not determine the length of the period of dependence. My data indicate that pomarine jaegers begin to fly at 31 to 32 days of age on the average, though the time it takes to mature to the flying stage can be almost a week longer, as at Cape Sabine. Early to mid-August seems to be the normal time for pomarine chicks to begin flying. Fourteen days elapsed from the date when most chicks were flying until flocks of independent juveniles were seen, suggesting that the young are dependent on the adults for at least two weeks after they first fly.

Adult attendance of young: — Pitelka *et al.* (1955b) suggested that only one adult attends each chick once the chicks begin to fly. Observations at Pitt Point in late August 1957 indicated that one or both parents may attend the chicks. Fifteen chicks were seen, five of which were attended by two adults, five, by one adult, and one, not attended at all as far as could be determined. One adult was feeding two chicks, and one pair was attending two chicks. The chicks could fly at the time of this survey, though none of them appeared to fly well.

Observations in 1960 at Barrow also indicated that flying chicks were attended by either or both adults. However, watches on several pairs revealed that after the chicks were flying one parent frequently left the territory for long periods. This may explain the observation of single adults attending one or both chicks. There is no evidence that one sex is more attentive than the other to the chicks in this period, or that the adults were attending individual chicks.

Departure of breeding birds: — The unsuccessful population of 1956 gave little information on normal departure. Observations given in the next section detail the decline in the number of adults in August. Almost all were gone by the end of the third week in the month, and no groups of adults were seen on the tundra or along the ocean. The birds apparently left singly or in small groups as their nests failed.

In 1960 adults remained on the breeding ground until the fourth week in August, when groups of independent young were seen along the ocean (see above). It appears from the scarcity of adults along the coast at the same time that the adults depart on migration as soon as their young become independent. The juveniles apparently remain for a short additional period before also departing. Final departure of the population was not witnessed, as many adults were still attending chicks on territory on 27 August when observations ended.

Seasonal population trends and breeding success

Barrow in 1956: — Population changes on an area of five and one-half square miles were documented by five censuses. A total of 101 pairs established territories on the area early in the season, and two unmated pairs defended territories briefly in mid-June. Additional territorial males or pairs were probably present for brief periods but were not noted because of the difficulty of mapping the location of pairs before the snow melted and the confusion created by the excess birds early in the season.

Ninety-six pairs were still present when the population stabilized in late June, and this number was considered to be the initial breeding population. On 25 June when the first census was taken, only 71 of the 96 pairs had produced eggs (Table 4). Ninety-one of these pairs eventually produced at least one egg. Five of those that produced eggs laid only one; the remainder produced normal clutches of two eggs. Thus the initial reproductive effort by the 96 pairs was 177 eggs. Two pairs that renested in the season are counted as having nested once in this total.

TABLE 4

Change in the population of pomarine jaegers at Barrow in 1956

Date	*Pairs*	*Territorial* *males*	*females*	*No. Eggs*	*Eggs/pair* *two*	*one*	*none*	*Chicks*
June 25	96			137	66	5	25	
July 10	85 + 1?	1		154	73(66)[a]	8	5	
July 27–28	46	4	2	4	2[b]		1	79(24)
Aug. 9–10	15	9[c]	4					32(13)
Aug. 17–18	4							7

[a] Number in parenthesis is the number actually seen, the totals are estimated.

[b] One renest and one late nest.

[c] Includes two of questionable sex.

The nesting population remained relatively stable until the hatching period (10 to 24 July). Eighty-nine per cent of the nesting pairs and 88 per cent of the total number of eggs were still present on 10 July. The decline in population accelerated when the chicks were being fed. By late July only 48 per cent of the pairs were still present. Most were attending chicks; but two were incubating full clutches, and one pair, which had not produced any eggs, was also still present.

On 9 August the weather turned cold and windy. Two inches of snow fell and remained on the ground for several days. On 9 and 10 August, before any chicks had begun to fly, the nesting efforts of 84 per cent of the pairs had failed, and at least 82 per cent of the possible increment of young (based on 177 eggs) was already lost.

Only four pairs and seven chicks were present on the final census of 17-18 August. Three pairs had one chick each, and two surviving chicks of the fourth pair could fly. A fifth pair was possibly present as it was seen on 14 August; but only one chick was on its territory on 18 August. The seventh chick was unable to fly and apparently had been abandoned. No chicks were observed or reported to be flying before 18 August on the census area; hence none could have left the area. No independent juveniles were observed at any time in 1956.

Thus, when the first chicks were able to fly, only 4 to 5 per cent of the pairs were present, and only 4 per cent of the potential number of chicks, based on the number of eggs laid (Table 4). This is a production of 0.073 chicks per pair based on the 25 June census. Actually, as recorded in the discussion of the departure of the populations, it is doubtful whether more than two of the seven chicks actually survived to leave the area, and the most probable outcome was that no chicks left.

Population trends in areas near Barrow in 1956: — Local killing of jaegers by humans complicates the discussion of population trends in the Barrow population. It is thus desirable to examine events in areas not subject to this interference, in order to determine whether or not human interference contributed significantly to the events observed at Barrow.

Several overland trips were made 10-12 miles inland to South Barrow 3 (Figure 15) during the season to census the jaeger populations. The first, on 11 July, indicated that from Ikroavik Lake south jaegers were generally distributed but were slightly less abundant than in the Barrow area. On 1 August, the breeding pomarine pairs were still regularly spaced in this area. It was apparent that they had maintained themselves at a higher density than in the area around the laboratory. A trip on 15 August, after the cold weather and snow had reduced the Barrow population, confirmed that the weather had had the same effect on the population farther south. Only four adult pomarine jaegers were seen, and only two of these were in the area south of Ikroavik Lake (Figure 15). A lone flying chick, the first seen in the season, was found near the north end of the lake. E. Clebsch saw no jaegers at all on a similar inland trip on 29 August. It was concluded from this evidence that the factors responsible for the failure of the 1956 jaeger population near Barrow had affected the entire population of the region and that human interference at Barrow did not significantly influence the final outcome there.

Reconnaissance flights made in the last half of August in 1956 by several investigators connected with the Naval Arctic Research Laboratory indicate that the jaeger population suffered a similar fate over the entire area of the lemming high. On 22 August I made a flight around Teshekpuk Lake southeast of Barrow (Figure 1) at an average altitude of 175 feet. Only 11 pomarine jaegers were seen, mostly in the vicinity of the lake. No jaegers were seen on a flight south to the Meade River Coal Mine on 21 and 23 August (E. Clebsch, personal communication). None were seen also on a flight westward along the coast to Cape Sabine on 21 August at an altitude of 100 feet (W. Boyd, personal communication). And finally, Ira Wiggins (personal communication) saw no jaegers on 23 August on a reconnaisance flight southwest from Barrow over the Kaolak River and Meade River drainages.

Had there been any successful breeding on the area of the lemming high, some of the adults with young and some independent juveniles should have been present on the breeding area or along the coast when these trips were made. Since I requested information on jaegers from these investigators, the fact that they saw none is significant.

Barrow, 1960: — The dense jaeger population of that year was studied on the same general area as 1956. The census area of 5.75 square miles was slightly larger than that of 1956. The plot was censused four times in the season: 25 June, 3 to 10 July, 27 to 30 July, and 8 to 11 August.

On 25 June the population on the plot was 118 pairs; 110 pairs had two-egg clutches, seven pairs had one-egg clutches, and one pair had no eggs but later laid two. Hence, the initial maximum reproductive effort was 229 eggs produced by 118 pairs. Three pairs had already renested by 25 June. Their first clutches are not counted in the total above (Table 5).

TABLE 5

Change in the population of pomarine jaegers at Barrow in 1960

Date	Pairs	Territorial adults	No. Eggs	Eggs/pair			Chicks
				two	one	none	
25 June	118		227	110	7	1	
3–10 July	118		127	54	19		93(52)[a]
27–30 July	104	2	2		2		188(117)
8–11 Aug.	96	10	1		1		117

[a] Number in parenthesis is the number actually seen, the totals are estimated.

All pairs present on 25 June were still present from 3 to 10 July, during the hatching period. The total of chicks and eggs present was 220, only 7 less than on 25 June. Six eggs lost between the two censuses resulted from human interference; hence, excluding these six eggs from the initial egg total, 96.8 per cent of the eggs survived into early July. The population began to decline after hatching; but by 27-30 July, when chicks were one to two weeks old, 90 per cent of the pairs were still represented by at least one adult, and a maximum of 85 per cent of the eggs still survived as young chicks or well advanced eggs.

Eighty-five per cent of the pairs were present on the 8 to 11 August census, which was taken when most of the chicks were just flying. Reproductive success was between 52.4 and 75.8 per cent of eggs laid, or 0.99 to 1.43 chicks per pair. Since the chicks are bold and conspicuous at this time, and no independent juveniles had yet been observed, I believe the actual count of 117 chicks is nearly complete, and that the reproductive success was approximately 55 per cent (Table 3), or one chick per pair.

Population trends in areas near Barrow in 1960: — An overland trip to the Inaru River on 4 June (Figure 1) confirmed that the lemming high extended that far south and that the pomarine jaeger population inland was approximately as dense as it was near Barrow all the way to the Inaru River itself. On a second trip made 12 to 15 miles inland on 2 August, the number of jaegers was very high along the entire route, and their density was estimated to be at least as high as near Barrow. The first flying chicks were seen on this trip. It was concluded from these observations that the inland population was as successful as the population near Barrow.

Other populations: — Data on success of the jaeger population nesting at moderate density near Pitt Point in 1957 were obtained on two visits from 26 June to 2 July, and from 19 to 22 August.

The initial breeding density was estimated to be 10.2 pairs per square mile, based on 61 pairs on six square miles. The second census in late August revealed six pairs and six single adults attending chicks. Two territorial adults were apparently without chicks. Fifteen chicks found then were conspicuous and made no effort to conceal themselves. They were still dependent on adults, and their begging cries were heard frequently. All of them could fly reluctantly. Because of easy observability, the count of chicks is believed to be almost complete. The reproductive success was 13 per cent (Table 3), or 0.25 chicks per pair, based on the 61 pairs present in late June.

In 1959, four pairs of pomarine jaegers nested at Cape Sabine. Two failed during incubation, and two clutches hatched from 4 through 9 July. In one nest, both eggs were pipped on 6 July, and on 8 July one chick was hatched. The nest was found destroyed on 10 July. Both eggs hatched in the second nest. The older chick, which hatched on 4 July, successfully fledged on 10 August. The second chick hatched on 6 July and disappeared by 9 July. The nesting success of these four pairs was 0.25 chicks per pair.

The only data on reproductive success of a sparse pomarine jaeger population breeding in an area of low lemming density is from Barrow in 1959, when three pairs nested. One of the nests was fenced. One chick died shortly after hatching, the second survived until about 20 August; it was present in the enclosure on 19 August and absent on 21 August. The adults departed by the 26th. The chick could not fly when it disappeared, and it is presumed to have been taken by a predator. Several adult snowy owls roosting in the general vicinity of the nest may have accounted for its disappearance.

The history of the other nests is poorly known. Both eggs of one nest hatched, and the two chicks were seen on 19 July; they left the nest by the next day. One chick was banded 200 yards from the nest site on 23 July, but it was not seen again. The adults were not present later in the season, and presumably neither chick survived.

The third nest located on 14 July contained two eggs, which were found destroyed four days later.

The nesting success of the pomarine jaeger has varied considerably in both time and space in northern Alaska (Table 3). The per cent success is moderate at intermediate nesting densities, about 30 to 35 per cent. Nesting success varied from four per cent to approximately 55 per cent at the highest nesting densities. Success of breeding populations of low density is surprisingly low, and most of these failures appear to be caused by interference from non-breeding jaegers or other predators.

Mortality factors

Adult mortality at Barrow: — There was considerable mortality inflicted on the adult jaeger population in the Barrow area by humans, mainly hunters, particularly in 1956. It is necessary to assess this impact at the outset of any discussion of factors influencing population losses. The Eskimos do not normally take the pomarine jaeger for food. In seasons such as 1956, however, when the jaegers are abundant they shoot them and occasionally feed them to their dogs. Most of the adults shot are left where they fall. The eggs are taken and are considered good eating.

The shore of Elson Lagoon on the east edge of the study plot is a favorite duck hunting area (Figure 15). Ducks, mainly eiders on return migration, fly northwestward along the shore, across a narrow sandspit to the north of the study area, and then fly southwest along the ocean shore. The Eskimos occupy a small village site, Birnirk, at the neck of this spit for duck shooting, principally in the summer. Hunters from this camp spread along the coast of Elson Lagoon as far as Wohlschlag Slough or beyond, but the northeast corner of the plot is most often utilized. The departure of several territorial pairs located along the lagoon shore early in the season was probably the result of interference by hunters.

Sixteen adult jaegers were found dead and two crippled on the study area during the season. Six of them probably died of natural causes. Four of the remaining 12 were probably killed and two crippled by Eskimos. Six were probably killed by personnel of the government base.

Most kills were found along the edge of Elson Lagoon and along a beach ridge that runs northeast-southwest across the study area. This is a ridge of gravelly, well-drained soil, which provides easy footing in contrast to the adjacent tundra (Figure 3). It is a natural pathway along which hunters from Barrow Village walk to Elson Lagoon and is also readily accessible from the base.

Shooting of one member of a pair usually resulted in the departure of its mate shortly after. One mateless male, however, successfully fed a penned chick from 22 July until 10 August, and a female with a crippled wing was present on another territory from 29 July until 10 August. One chick of this female still survived on 17 August and is one of the few chicks that possibly fledged.

The total loss attributable to humans in 1956 was at least 10 pairs but not more than 15 to 20 pairs. Since the birds killed were in areas normally traversed by the Eskimo hunters and most accessible to personnel from the base, most of the study area was probably only slightly affected.

The cause of death of six adult jaegers found on the study area could not be determined. Territorial strife may result in the death of some adults, though I have no evidence. There were no indications of disease.

In 1960, there was less human interference with the jaeger population than in 1956. On the census area, only six adults were killed and one wounded by hunters or others. Four of the dead adults and the wounded one were found just south of Birnirk (Figure 15) and were probably shot by duck hunters. Approximately eight pairs and one member each of two other pairs disappeared from this same corner of the plot, suggesting that one third of all pairs that failed were killed by hunters. Thus, while human interference did not greatly affect the population in this season, it did account for a large proportion of the mortality that did occur.

Egg losses at Barrow: — In 1956, nine pairs lost full clutches of eggs. Two of these renested; the remainder departed. The cause of these losses could not be determined. In some instances it is not clear whether the eggs were destroyed before or after the adults had abandoned them.

Seven pairs lost one egg of a clutch, and five were lost after they began to pip. One pipping egg, which failed to hatch presumably from neglect, belonged to a pair with a crippled female. Two other eggs failed to hatch.

In 1960, nineteen eggs did not hatch. Three failed at hatching, and at least two had no embryos and were presumably infertile. Five other eggs were lost by three pairs that later renested. Six eggs were removed from the population by humans; one of these, which I collected, was abnormally small and did not contain an ovum. Three others disappeared from nests.

Chick mortality at Barrow: — Adult deaths accounted for few nesting failures. Most failures were the result of chick mortality followed apparently by departure of the adults.

In 1956, six chicks were found dead in the season. On 18 July, two newly hatched chicks were dead in one nest, one having died before its natal down had fluffed. The female was still on the territory. Death was possibly from exposure through failure of the adults to brood the chicks, though there was no apparent reason for the adults to neglect them. On 20 July, one of two newly hatched chicks was dead. A chick one-third grown was found dead and still warm on 28 July. There was no apparent cause for either death.

On 14 August, a dead and mutilated chick was found, and a Snowy Owl was seen carrying the remains of a jaeger chick on 24 August. The latter two observations were made after cold weather killed most chicks, and they may have been carrion.

I have evidence that jaegers may occasionally kill chicks of other jaeger pairs. On 13 July 1956, I. Deyrup and I. L. Wiggins observed an adult jaeger pecking at a live jaeger chick, while two other adults, presumably its parents, were attacking the first. The outcome of this encounter was not observed.

In 1960, there was very little obvious mortality of chicks. I have data on only three. One just hatched was crushed in the nest on 17 July, one was found dead on 27 July, and one was taken by Eskimo children on 1 August. Most of these observations on mortality of unpenned jaeger chicks are of young dead at or shortly after hatching. Chicks are killed by being crushed by the adults or die from neglect or for no apparent cause. Chicks that die later in the season are rarely found, and usually the cause of death cannot be determined.

Mortality at other localities: — At Pitt Point in 1957 there was almost no human interference with the jaegers after 2 July. Only two adults were shot between the two censuses. One abandoned clutch of two eggs was found. There was no known natural mortality of adults at Pitt Point, or in the 1959 Cape Sabine population.

While there is no information on the factors contributing to the decline of the jaeger population at Pitt Point in 1957, observations on several snowy owl nests by resident personnel are suggestive. One wrote as follows: "It may interest you to know that the death rate of young owls is very high. They did well while the lemmings were plentiful, but the lemming population has now been reduced to a point where we rarely see any. Dead owls surround each nest with only two healthy survivors to each nest" (R. Lemay, *in litt.*, 13 July 1957).

Apparently food shortage was the major factor contributing to the decline of this population, as it was at Barrow in 1956. However, judging from the reproductive success of this population, competition for food was less severe than at Barrow, and the Pitt Point jaegers did not experience any freezing weather in August such as that which disrupted the breeding population at Barrow in 1956.

At Cape Sabine in 1959, the destruction of one nest during incubation on 3 July, and the disappearance of another territorial pair at about the same time, were probably caused by the presence of numbers of transient jaegers that were hunting and roosting in the nesting area from 24 June to 6 July. The loss of a second nest at hatching, and of one chick of a third nest, occurred approximately when the movement of transient jaegers ended, but they are the probable cause of these losses too.

Mortality of penned chicks: — In 1956, nine pomarine jaeger nests were fenced. The nests included eight two-egg clutches and one single-egg clutch. All 17 of the eggs hatched. Five of the 17 chicks penned in 1956 died as a result of predation, human interference, or unknown causes. One found dead on 22 July had large bruises on its head, and there were breast feathers of an immature glaucous gull around the nest enclosure. When this happened, a large flock of non-breeding glaucous gulls was roosting in the vicinity of the nest. One brood of two chicks starved after the adults were killed by humans, and another brood of two chicks was destroyed by unknown causes.

Death of the remaining 12 resulted, directly or indirectly, from food shortage. Eight chicks lost weight in late July and early August. Sudden cold weather killed six immediately, one died a few days later, and one escaped from its enclosure when still unable to fly and was not seen again.

Four of the 12 chicks were killed and usually eaten by their siblings. Killing of one sibling by the other did not occur until one chick had gained a considerable weight advantage. The first chick hatches one to two days before the other, because incubation begins with the first egg. It is usually the older chick that survives, as the younger one rarely overcomes the disadvantage in size. This fratricidal strife occurs even when the food shortage is slight.

In 1960, fifteen nests were penned; fourteen of these were initially two-egg clutches, and one, a single-egg clutch. A second egg was transferred to the one-egg nest when it became apparent that the egg would not hatch; hence for discussion we can consider these as 15 complete clutches with a total of 30 eggs.

Five of the thirty eggs did not hatch, or the chick died at hatching. Seven of 25 chicks died after hatching in the penned nests. One was found dead five days after its rhamphotheca was torn off on the enclosure wire. One, which disappeared when about to fly, was probably taken by a predator; and one, which could not fly at the age of 44 days, is presumed to have died.

The remaining four died of no apparent cause; all lived 23 to 29 days, and all lost weight rapidly for a few days before dying. Two of these were of the same brood, and although in separate enclosures, one died a week before the other. The sibling of one other fledged successfully, and the sibling of the fourth is the chick presumed to have been depredated. All signs indicated an abundance of food for this population, so that it is difficult to attribute these deaths to starvation.

The chicks of three broods were put in separate enclosures in 1960, and chicks were left together in the remaining seven nests in which both eggs hatched, in order to determine whether or not food shortage had been responsible for the death of the younger siblings in 1956. Among chicks from separated broods, both chicks of one fledged, both chicks of another died a week apart, and one chick of the third brood died, while the other was depredated.

Of the seven enclosures with two chicks, both chicks fledged in four; one chick fledged from each of two others; and in the seventh one chick escaped from the enclosure at an early age, but both chicks ultimately fledged.

These results suggest that chicks can be raised normally in enclosures and presumably are fed normally. They also suggest that, if food is abundant, two chicks can be raised when confined together and, conversely, that the fratricidal strife between confined chicks in 1956 and 1959 was the result of food shortage. Finally, they support the conclusion that the deaths of the last chicks of the 1956 population were attributable to a failing food supply.

Population Biology of the Parasitic Jaeger

Breeding range in northern Alaska

The parasitic jaeger breeds on the entire North Slope of Alaska. It is known to nest in the mountains in Anaktuvuk Pass (Irving, 1960), in Howard Pass (Irving and Paneak, 1954), and at Peters and Schrader lakes. I have recorded it also in the foothills at Cape Sabine and on the Kaolak River. Nesting localities on the coastal plain include Barrow, Pitt Point, the Meade River Coal Mine, and the Colville River delta (Anderson, 1913, and T. Myres, *in litt.*). I studied populations of parasitic jaegers at Barrow, the Kaolak River, Cape Sabine, and lakes Peters and Schrader.

Population histories

Barrow: — The population at Barrow has varied from year to year and has never been high. Pitelka *et al.* (1955a) and Bailey (1948) considered the parasitic jaeger an occasional breeder in that area. Five pairs have nested at Barrow between 1951 and 1960. One pair nested in 1952 (Pitelka *et al.* 1955b), one in 1955, two in 1956, and one in 1957. None nested in 1951, 1953, 1954, 1958, 1959, and 1960 (Table 6).

In 1955 one pair of dark phase parasitic jaegers nested two miles south of the Naval Arctic Research Laboratory. The birds deserted on 30 June after one was trapped on the nest and banded. This pair was one of two that bred at Barrow in 1956. In that year the nest was located near the Naval Arctic Research Laboratory (Figure 3), approximately two miles from its location in 1955. Both were again dark plumaged birds, and the banded bird was netted to confirm the band number. The second nest that year was located four and one half miles south of the laboratory. In 1957 one pair nested approximately 200 yards from the site of the latter nest. Thus, the parasitic jaeger population at Barrow from 1955 to 1957 could have consisted of two pairs, one black phase pair that bred in 1955 and 1956, and a second pair that bred in 1956 and 1957.

A few transient parasitic jaegers occur over the tundra at Barrow each season. Two thirds of the records are in June, most in the first half of the month; slightly less than a third of the records are in July, and a few are in August. Mixed-species flocks of jaegers are occasionally seen in July. In 1954 a flock of 50 to 60 jaegers of all three species, as well as 15 to 20 immature glaucous gulls, fed in Central Marsh on 8 and 9 July. Two small flocks of parasitic and long-tailed jaegers were seen in July 1958; nine parasitic and two long-tailed jaegers, on 6 July, and two parasitic and six long-tailed jaegers, on 11 July.

A general picture of the movements of parasitic jaegers at Barrow seems to be as follows: After the first observation of the species in early June there are records of birds singly or in pairs travelling through the Barrow area in June and early July. These may be birds without established territories seeking a suitable breeding area; some of the later ones may be birds that failed earlier in breeding, though few from that period show any brood patch development (Figure 20). In July and August few birds are seen but occasionally mixed flocks of

TABLE 6

Breeding density and nesting success of the parasitic jaeger

Locality	*Year*	*No. of pairs*	*Area (square miles)*	*Density (pairs/ square mile)*	*Breeding success (per cent)*
Barrow	1955	1	15±	0.07	0
	1956	2	15±	0.1	0
	1957[a]	1	15±	0.07	?
Kaolak River	1957	3	9	0.3	75[b]
	1958	3	9	0.3	50–66
	1959	3	9	0.3	?
	1960	2–3[c]	9	0.2–0.3	?
Lakes Peters and Schrader	1958	2	—[d]	—	0
	1959	2	—	—	75
	1960	2	—	—	?
Cape Sabine	1957	1[e]	10±	0.1	50
	1958	0[e]	10±	—	—
	1959	4	11	0.4	50–75
	1960	1	10±	0.1	?

[a] None nested in 1958, 1959, or 1960.

[b] See breeding success.

[c] See population histories.

[d] An aereal figure is not possible because of the nature of the terrain.

[e] Data from Childs (1969).

all three jaegers occur. The jaegers, particularly the long-tailed and parasitic jaegers, appear to forage in loose mixed flocks during the summer. These are both non-breeders and birds whose breeding effort has failed.

Kaolak River: — The parasitic jaegers were studied from 1957 through 1960 on a nine square mile study area on the Kaolak River (see Table 1 for study periods). The area is described in a report on the avifauna as a whole (Maher, 1959).

Three pairs of parasitic jaegers nested in each of the years 1957, 1958, and 1959; and two, possibly three, nested in 1960 (Table 6, Figure 8). The same territories were occupied each year, though the nest sites were different each time. It appeared that the same pairs usually returned to the territories each year. My evidence for this is the color phases of the birds, the permanence of the territories, and the clustering of the nest sites on the territories.

The three pairs were designated as the "camp pair," the "eagle-bluff pair," and the "lake-basin pair," from the location of their territories. The camp pair

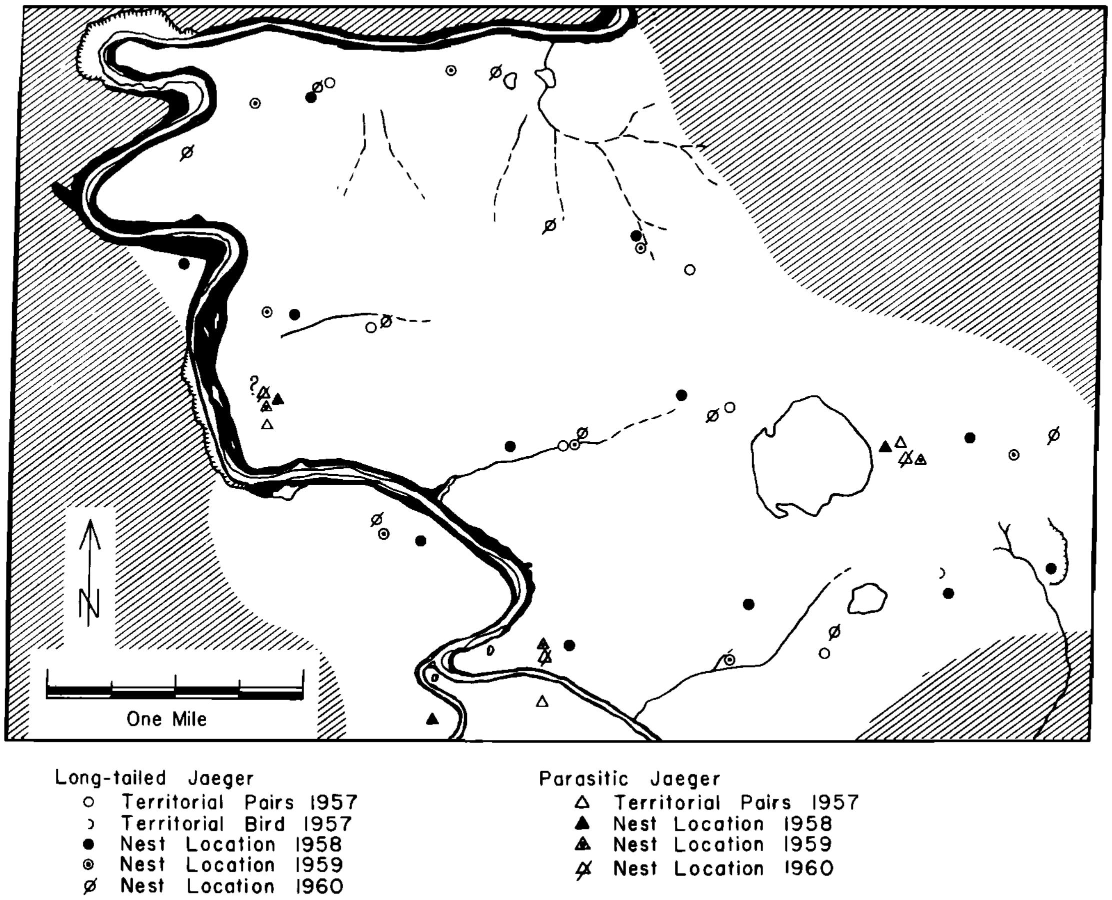

Figure 8. Map of breeding long-tailed and parasitic jaeger populations at the Kaolak River in 1957, 1958, 1959, and 1960.

(one light and one dark phase) bred in all four seasons and was recognized by the plumage of the birds and also by the behavior of the light phase bird, which was exceptionally vocal and called loudly and frequently whenever I was near the nest area. The "eagle-bluff pair" consisted of two light-plumaged birds in 1957 and 1958. In 1959 on two visits to the nest site in June, I saw only one bird of light plumage each time. The fact that the nest site was only 200 yards from the previous year's argues that it was the same pair. In 1960 a pair of light plumaged birds was seen on 27 June at the 1959 site, defending the area from a dark plumaged parasitic jaeger. The pair was not seen there on a later visit, and there was no nest. This may have been the regular pair, which had failed early in its breeding effort. The record of the "lake-basin pair" suggests that more than one pair occupied this territory during my study. In 1957 it was a pair of dark birds, in 1958 a pair of light birds, and in 1959 and 1960 a light-plumaged, and a dark-plumaged bird. The nest sites are close together (Figure 8). On the basis of the plumage records, the resident pair changed between 1957 and 1958, and at least one member of this pair changed between 1958 and 1959.

The distance between nest sites on each territory also supports the occurrence of a relatively permanent breeding population at the Kaolak River. Nest sites were not located in 1957, though the area in which the chicks were found suggest their probable location. The "camp pair" shifted its nest site most from year to year. Its nest in 1958 was 780 yards from the approximate area used in 1957; in 1959 it moved 880 yards, and in 1960 it nested 20 yards from the 1959 site. All sites were located about the junction of the two forks of the Kaolak River and could be included in a circle with a radius of 450 yards. The "eagle-bluff pair" in 1959 had moved 200 yards from its 1958 nest. The "pair" in the lake basin in 1959 was 200 yards from the previous site, and in 1960 it nested 100 yards from the 1959 site.

Lakes Peters and Schrader: — The only level marshy tundra in the vicinity of these two lakes is on two large alluvial fans, approximately one mile apart, at the mouths of Whistler and Coke Creeks. A pair of parasitic jaegers occupied each of these territories from 1958 to 1962. None nested in 1963. The combination of plumage phases in the pairs indicate that the pairs on each territory changed frequently between years. Whistler Creek fan was inhabitated by a pair consisting of a light phase and a dark phase mate in 1958, two dark phase birds in 1959, two light phase birds in 1960 and 1961, and two dark plumage birds in 1962. Coke Creek fan had two dark phase birds in 1958, and a light phase and a dark phase pair in 1959, 1960, and 1962. Only one bird (light plumage phase) was seen on this territory in 1961; but it was presumed that the pair of the previous year was present that year also. Thus it is possible that only two pairs of parasitic jaegers occupied Coke Creek territory in these five years; one of them for four consecutive years; while at least three, possibly four, pairs were on Whistler Creek territory in the same period. Data for 1960 to 1963 are from T. Cade (*in litt.*).

Cape Sabine: — Cape Sabine is the only other area in which a jaeger population was censused for more than one year (Table 6). The study area of 10-11 square miles was censused in 1957 and 1958 by Childs (1969). I was in this area in 1959 and briefly in 1960 (see Table 1).

In 1957 only one pair of parasitic jaegers nested, although transients were seen all summer. This pair of two light phased adults was seen on 5 August with one juvenile. No parasitic jaegers nested in 1958, though again occasional individuals were present through the season. Four pairs of parasitic jaegers bred in 1959. One was a pair of dark-plumaged birds, one a pair of light-plumaged birds and two pairs consisted of a dark and a light-plumaged bird.

One dark pair nested in 1960. The pair acted as if it had chicks on 5 July, although none was found. One transient pair was also seen on that date.

These records suggest that the parasitic jaeger tends to establish permanent territories, to which it returns yearly, as at the Kaolak River and lakes Peters and Schrader. There are apparently no resident pairs at Cape Sabine, while pairs at Barrow were disrupted by human interference. The fact that one pair apparently bred in two successive years at Barrow suggests that pairs would be permanently resident there if permitted to.

Schedule of breeding events

Arrival and breeding density: — Parasitic jaegers are usually seen singly, in twos, or occasionally in small groups in spring migration. Their arrival in an area is not as readily observed as the arrival of the pomarine jaeger, because the populations are dispersed and their numbers are low.

Irving (1960) reported that the arrival date of this species in Anaktuvuk Pass was between 21 May and 1 June. At the west end of the North Slope, at Cape Sabine, they arrived on 22 May in 1959. In that same year parasitic jaegers arrived at Peters and Schrader lakes on 27 May, in a flock of 10. They were observed from 2 June at Umiat in 1958, and at Nigisaktuvik River on 31 May in 1957. The arrival of the species at Barrow since 1954 has been in the first half of June. Barrow arrival dates are: 4 June (1954, 1956, 1957); 10 June 1958; 11 June 1959; and 6 June 1960. It probably arrives at the Kaolak River between 25 and 30 May, though I have never been there to witness it.

Parasitic jaegers appear to occupy their territories directly upon arrival in an area. At Cape Sabine in 1959 one pair was seen on its territory on 28 May, five days after the arrival of the species. This pair remained and bred. At lakes Peters and Schrader in the same year a pair was noted on its territory on 30 May, three days after the species was first seen in that area.

The breeding density of the parasitic jaeger population varies least of the three species, and it generally has the lowest breeding densities (Table 6). The highest density recorded for the species is 0.36 pairs per square mile at Cape Sabine. The population at the Kaolak River was constant for three years at 0.3 pairs per square mile, and at Peters and Schrader lakes two pairs nested in 1958 through 1962. The population density varied at Cape Sabine from 0.1 to 0.4 pairs per square mile, and at Barrow from 0.07 to 0.1 pairs per square mile.

The pre-egg stage and egg-laying: — The information I have on arrival and egg-laying of the parasitic jaeger in northern Alaska suggests that the pre-egg stage can be short. The best evidence is from Cape Sabine in 1959, where egg-laying began nine days after arrival on 22 May. The dates for four eggs determined from hatching dates were approximately 31 May, 3 June, 6 June and 8 June (Table 7). The pomarine jaegers which arrived in that area at the same time laid their eggs between 8 and 13 June.

Three dates were obtained for the 1958 Kaolak River population by extrapolating from growth curves of chicks. These estimates give 4 June, 8 June, 10

TABLE 7

Breeding data on the parasitic jaeger

Locality	*Year*	*Egg laying dates*	*Hatching dates*	*Fledging dates*	*Days to fly*
Barrow	1956	18 June[b]	15 July		
		20 June	17 July		
		14–15 June			
		15–17 June			
Kaolak River	1958	3 June	29 June[a]		
		4 June[b]	30 June[b]		
		8 June[b]	4 July[b]		
	10 June[b]		6 July[b]		
	1960	5 June[b]	30 June[c]		
Cape Sabine	1959	31 May[b]	25 June[b]	25 July	30
		3 June[b]	29 June[b]	28 July	29
		6 June[b]	2 July	1 Aug.	30
		8 June[b]	4 July		
Lakes Peters and Schrader	1959	8–9 June[b]	4–5 July[b]		
				7 Aug.	
		10 June[b]	6–7 July[b]		

[a] Egg was pipped on 27 June.

[b] Dates estimated from hatching or data on growth. They are considered accurate to one to two days.

[c] One egg of two-egg clutch pipped on 28 June.

June, as egg-laying dates. One other egg, pipped on 27 June, was probably laid on 3 June.

A pair of parasitic jaegers copulated at the Nigisaktuvik River on 31 May, 1957, the day that parasitic jaegers were first seen in that area.

At Barrow in 1956 parasitic jaegers were first seen on 4 June. One pair laid its first egg on 18 June, and a second pair had its first egg on 14 or 15 June. In comparison, pomarine jaegers first arrived on the tundra at Barrow on 26 May that season, and the peak of egg-laying for the population was from 14 to 19 June.

The first parasitic jaegers were seen on 27 May at lakes Peters and Schrader in 1959. The dates of laying one clutch calculated from hatching dates were 8 and 10 June.

The pre-egg stage of this species, as judged from these data, is usually shorter than that of the pomarine jaeger. Parasitic jaegers are most often seen in two's when migrating, and the fact that pairs appear to return and breed together for more than one season suggests that they may remain paired through the year or that the pairs meet before reaching the breeding area; however, members of the pair return to the territory seperately on Fair Isle (Williamson, 1965).

The observation of a pair copulating on the day of arrival at the Nigisaktuvik River in 1957 suggests that the males arrive in breeding condition and that the females are responsive, so that while breeding can probably be delayed by adverse environmental conditions, the species can begin breeding within a week or ten days of arrival on the nesting ground if conditions are suitable. The elimination of prolonged courtship each season has permitted the species to compress the pre-egg period.

Egg dates: — The dates on which 15 eggs were laid are known or were calculated from hatching dates and growth data (Table 7). There are 11 egg dates in the 11 days between 29 May and 10 June for Cape Sabine and the Kaolak River in foothill areas, and lakes Peters and Schrader, a mountain area. Four egg dates from Barrow were from 14 June through 19 June, a week later. Two eggs collected at Meade River Coal Mine on 16 June 1957, were considered by G. D. Hanna to be only slightly incubated, and may have been laid about 10 to 12 June. The lateness of egg-laying at Barrow in 1956 may have been caused by late arrival, the lateness of the spring season at Barrow, or severe competitive pressure from the high pomarine jaeger population in that season. The dates of five other nests found with eggs from coastal plain localities fall between 16 and 30 June.

Hatching: — In inland areas hatching takes place in the last week of June or the first week of July (Table 7). The extreme dates are 25 June and 6-7 July. The Barrow population appears to hatch later, though only two dates are known from this area, 15 July and 17 July.

Development time of the young: — Data on the development of the young are meager. The one chick studied at Barrow in 1956 and the chicks studied at the Kaolak River in 1957 were pinioned, so that fledging dates were not obtained. Three chicks were raised successfully at Cape Sabine in 1959. Two flew from enclosed nests in 27 to 30 days, and one in 26 to 29 days. These figures compare with Perry's (1948) finding that in 22 observations fledging varied from 27 to 33 days, with an average of 29 to 30 days.

Departure of breeding birds: — Little information was obtained on departure. Adults and young were still present at Cape Sabine in 1959 when I departed on 11 August. On 1 and 2 September of that year, two pairs were seen at the Kaolak River. One, the "camp pair," was still on its territory and defended it against a gyrfalcon. The begging call of a chick was heard several times.

At Peters and Schrader lakes in 1958, one pair with a chick was present in the week from 13 to 20 August. The chick was found dead on the 20th. The following year both pairs were present in the latter part of August. A pair and its one young were noted on 19 August; the other pair, whose two chicks were flying as early as 7 August, was still present on 21 August.

Except at Barrow, all observations on the nesting of this species indicate that the young are usually flying by the last of July or the first week in August. A period of two to three weeks of dependence seems to follow fledging. Normal departure is probably in late August and may be as late as the first week in September. Obviously more observations are needed at the end of the season, since it is possible that this phase of the nesting cycle can be abbreviated if necessary. The probability of severe weather increases after the middle of August.

Perry (1948) found that the chicks remained on Noss for an average of 28 days after fledging. The extremes were 21 and 33 days. Departure dates there are from 17 August to 4 September.

Breeding success

Data on nest success in these populations are scanty. All available information is in Table 6.

Barrow: — The 1955 nest was abandoned after one adult was trapped on the nest. In 1956 one nest was destroyed in the incubation period. This nest had one egg on 15 June and two on 21 June. On 27 June one egg was broken and lying four feet from the nest, the second egg was punctured but still being incubated. On 6 July the egg was gone, the male was present, and the carcass of the female, which had been shot, was nearby. I attribute the failure of this nest primarily to interference from nesting pomarine jaegers and flocks of non-breeding glaucous gulls. This pair had been observed under great pressure from these two species in the week previous to finding the eggs damaged.

The second nest in 1956 was enclosed and the chicks pinioned. The younger chick died on 21 July, at four days of age; the older grew rapidly and survived the snow and cold, which killed off all but two of the penned pomarine jaeger chicks on 8 August. On 11 August the banded member of this pair, the female, was netted, and her wing was accidently broken. The male was observed hunting on 13 August and continued to feed the chick. On 21 August the carcass of the chick was found buried in a mound 40 feet from the nest enclosure with one wing tip sticking out from the soil, presumably where it had been left by an arctic fox (*Alopex lagopus*). Foxes were common then. This chick should normally have fledged on 13 or 14 August, if its wings had not been clipped.

Kaolak River: — In 1957 the camp pair apparently had two chicks. One caught and penned on 22 July died two days later. On 9 August, the adults were seen circling over the camp accompanied by the second chick. One chick of the eagle-bluff pair was located and penned on 16 July. This chick died on 8 August, and the adults immediately departed. No other chick was seen on the territory. Nothing is known of the breeding success of the lake-basin pair in that year.

In 1958 the camp pair had two eggs, one of which was pipped on 27 June. One chick was penned on 12 July and taken captive on 11 August, when it was approximately 30 days old. No evidence of a second chick was ever noted. The eagle-bluff pair had two eggs both of which hatched. One chick was dead in the nest enclosure and partly eaten on 13 July. The second chick escaped when the enclosure was trampled by caribou. When it was recaptured on 12 August, one wing was broken and it had lost approximately 80 grams since 4 August. The lake-basin pair also had two chicks. One was dead on 17 July, the second one had disappeared between 26 and 29 July. The death of the former was apparently caused by food competition with the larger sibling. The disappearance of the larger chick was attributed to a large predator, possibly a fox, as there were no remains in the enclosure.

In 1959 only one pair, the camp pair, was still present on 2 September. The begging call of a chick was heard on two occasions on their territory, although the chick was not seen.

I can say little about nesting success of the Kaolak River population since much of the chick mortality is attributable to my activities in the area. In 1957 two pairs had three chicks, two of which died as the result of interference. In 1958 two of six chicks died natural deaths, and two died after being penned. The two which were successfully raised were taken captive, one with a broken wing. It is difficult to say whether the bird would have been injured if unconfined when caribou crossed the territory. In 1958, Childs (1959) witnessed a herd of caribou in the Pitmegea River area estimated at more than 100,000, a portion of which passed through a long-tailed jaeger territory. The chick on the territory survived in spite of severe trampling of the area.

Success in 1957 without interference might have been 75 per cent, and in 1958, 50 to 66 per cent.

Lakes Peters and Schrader: — In 1958, no chicks were raised by the two pairs, although they were not interfered with in that year. One chick seen flying a week previously was found dead on 20 August. In 1959 the two nests were enclosed. One chick fledged from one nest and two from the other; a 75 per cent nesting success.

Cape Sabine: — The history of three of the four 1959 nests is known, as they were fenced. Five of six eggs hatched. One egg of one nest was dented on 26 June. When revisited on 4 July only one chick was present, and presumably the damaged egg did not hatch. The one chick was fledged. The other two pairs each raised one chick successfully, but one chick of each brood died. The fourth nest had only one slightly damaged egg when found on 8 July. The pair was present and defensive on 8 August. The damaged egg probably did not hatch, but their presence in August suggested that they had a chick already hatched when the nest was found on 8 July. Assuming that this is correct, success for the four pairs was 50 per cent and, without interference, might have been as high as 75 per cent.

The nesting success of this species in northern Alaska would appear to be typically quite high, except at Barrow where the nests have been interfered with by humans. I estimate that success usually ranges from 50 to 75 per cent (Table 6).

Population Biology of the Long-tailed Jaeger

Breeding range in northern Alaska

The long-tailed jaeger is known to nest in the mountains in Anaktuvuk Pass (Irving, 1960), in Howard Pass (Irving and Paniak, 1954), and on the Okpilak River (J. Brown, personal communication, 1958). I have records for the foothills along the Ikpikpuk River, the Kaolak River, and Cape Sabine. Two nesting localities on the southern part of the coastal plain are the Ikpikpuk River, and the Meade River Coal Mine. The only nesting records from coastal areas are at Cape Sabine where foothill tundra abuts on the coast, a record by Bailey (1948) from Wainwright and records from 1967-1971 at Ocean Point (T. Cade, personal communication). Bailey records one egg taken 8 July 1922 by R. W. Hendee "while at Wainwright," which could possibly have been taken inland along the Kuk River near the foothills. Apparently the usual nesting habitat of this species in northern Alaska is in the mountains and foothills, as well as in the southern part of the coastal plain.

The long-tailed jaeger is typically allopatric with the pomarine jaeger and sympatric with the parasitic jaeger. The nesting of all three species in one area, as at Cape Sabine in 1959, is exceptional. The only previous record of such sympatry in Alaska is from Hooper Bay, Alaska, in 1924 (Brandt, 1943).

Breeding long-tailed jaegers were studied at the Kaolak River and at Cape Sabine. There are also some observations from the Meade River Coal Mine (see Table 1).

Population histories

Kaolak River: — The number of pairs breeding on the nine square miles of foothill tundra at the Kaolak River ranged between 6 and 12, and the density, between 0.66 and 1.3 pairs per square mile (Table 8). Figure 8 suggests also that there was a core of permanently established pairs present each season and that the fluctuations in population result from the nesting of additional pairs, which frequently do not return to the area the following year. Thus, there were five territories occupied in each of the four seasons, three that were occupied three times, one occupied twice, and five occupied only once each, four of the latter in 1958 alone. Only two of the six pairs that nested for the first time in 1958 appeared to have returned in 1959 and again in 1960.

Cape Sabine: — The population of long-tailed jaegers at Cape Sabine was studied in 1957 and 1958 by Childs (1969). In 1957 there were two nests on an area of 11 square miles, one of which fledged one chick successfully. The chick was just able to fly on 30 July, and it was seen again on 6 August, when it could fly well.

In 1958 there were again two nests on the area. One with two eggs on 10 June was found destroyed on 14 June; the second, also with two eggs on 7 June, was found destroyed on 12 June.

The 1959 population consisted of 25 pairs. The nesting density in this area then has varied from 0.18 pairs per square mile in 1957 to 2.3 pairs per square mile in 1959, an increase of 13-fold in 1959 over the density in the two previous years.

In 1960 three pairs were on the study area on 4-5 July, but only one pair appeared to be breeding.

The Cape Sabine long-tailed jaeger population has fluctuated more in numbers and density than the population at the Kaolak River. The evidence suggests either a very low permanent population or no permanent population at all. The high density in 1959, the highest recorded in this study, was apparently a response to an abundant food supply, a high population of *Microtus oeconomus*, encountered by migrating birds in the spring.

TABLE 8

Breeding density and nesting success of the long-tailed jaeger

Locality	*Year*	*No. of pairs*	*Area (square miles)*	*Density (pairs/square mile)*	*Breeding success (per cent)*
Kaolak River	1957	6[a]	9	0.66	?
	1958	12	9	1.3	16
	1959	8	9	0.88	?
	1960	10	9	1.1	?
Cape Sabine	1957[b]	2	10±	0.2	25
	1958[b]	2	10±	0.2	0
	1959	25	11	2.3	63–70
	1960	1	10±	0.1	?

[a] In 1957 one jaeger was defending an area in the upland lake basin. It is ignored in the density total.

[b] Data from Childs (1969).

Schedule of breeding events

Arrival and breeding density:—These jaegers usually travel in pairs or small groups rather than in flocks when migrating, and because nesting density is usually low, the build up of a population is not easily observed. In many instances the birds establish themselves quickly because they are returning to breeding territories used in former years.

At the Nigisaktuvik River this species was first observed on 30 May, the next day a pair was seen attacking two parasitic jaegers, and on 1 June the same pair was definitely defending the territory from parasitic jaegers. At Cape Sabine, long-tailed jaegers were first seen on 20 May when one pair was noted. A second pair was seen on 22 May, and on 23 May only two birds were seen during the day. On 25 May two pairs were already defending territories, two additional pairs were settled the following day, and two more on 27 May.

The long-tailed jaeger generally nests at higher density than the parasitic jaeger and exhibits greater variation in density between years than the latter does (Table 8). At the Kaolak River density varied two-fold, from 0.66 pairs per square mile to 1.3 pairs per square mile, while the parasitic jaeger population remained constant at 3 pairs. At Cape Sabine the variation was 12-fold from about 0.20 to 2.3 pairs per square mile; at the same time the parasitic jaegers varied from 0 to 4 pairs on the same 10-11 square miles.

The pre-egg stage and egg-laying: — The duration of the pre-egg stage is known only from Cape Sabine. In 1959, the jaegers were first seen on 20 May. On 25 May, two pairs were defending territories; several other pairs defending territories were noticed in the next three days. Egg-laying in this population began on 1 June and continued until 19 June. The pre-egg stage probably varied from one to two weeks. One pair that established a territory near camp and copulated on 28 May did not produce any eggs as far as is known.

Nineteen egg dates were determined at Cape Sabine in 1959. Five were observed, and the remainder were calculated from known hatching dates using a 25-day incubation period (see Breeding Biology). The 19 eggs were laid between 1 and 19 June. The distribution of the laying dates is remarkably uniform. No more than two eggs were laid on any one day; ten (53 per cent) were laid in the first 8 days, and the remaining nine eggs (47 per cent) were laid in the last 11 days.

At the Kaolak River, in 1958, four eggs were laid on 6 June, 8 June, 11 June, and 14 June. No data are available on egg-laying for 1957 or 1959. In 1960 one egg out of 17 was pipped on 27 June. This egg, laid probably on 4 June, was apparently the first one laid in the population.

The single egg of one pair was laid on 12 June 1957 at the Meade River Coal Mine. A nest with two eggs was found on 16 June, and on 17 June a single-egg clutch was collected by an Eskimo. This egg was one-quarter incubated according to G. D. Hanna, and was probably laid about 11 June.

Two nests were found along the Ikpikpuk River in 1958. One contained a single egg on 29 June, and the second, a one-day old chick on 7 July. The egg in the latter nest was probably laid about 12 June.

All of the egg-laying dates known for this species are between 1 June and 19 June. The lack of synchrony shown by the Cape Sabine population, which was nesting in response to a high of *Microtus oeconomus,* was surprising. There was no peak period of laying such as occurs in the pomarine jaeger population when that species is nesting at high density.

Hatching: — The eggs hatch in late June and early July. Hatching dates for 14 eggs were determined from Cape Sabine in 1959. The dates span 19 days from 26 June to 14 July. They are, of course, distributed in the same manner as the egg-laying dates, except that there is a concentration of hatching dates in late June and early July resulting from failure of two clutches in incubation and one egg that did not hatch. Thus 10 eggs hatched between 26 June and 3 July, and four hatched between 4 and 14 July.

At the Kaolak River in 1958, four chicks hatched on 1 July, 3 July, 6 July, and 9 July, the first three dates having been estimated from the age of chicks. Hatching dates for 1957 and 1959 are not known. In 1960 the egg found pipped on 27 June probably hatched on 29 or 30 June. A one-day old chick was found on the Ikpikpuk River on 7 July, 1958.

Development time of the young: — The number of days to flying was determined for four penned chicks, three at Cape Sabine in 1959 and one at the

Kaolak River in 1958 (Table 9). The median number of days was 25.

TABLE 9

Number of days to flying of penned long-tailed jaeger chicks

Locality	*Year*	*Hatching date*	*Date last in enclosure*	*Date missing from enclosure*	*No. days*
Kaolak River	1958	9 July	3 Aug.	6 Aug.	25–28
Cape Sabine	1959	1 July	25 July	28 Aug.	24–27
		8 July	31 July	3 Aug.	23–26
		12 July	3 Aug.	6 Aug.	22–25
Median number of days					25

Chicks usually begin flying in late July or the first week in August. At the Kaolak River in 1957 one young bird was seen flying on 6 August. A penned chick with its wings partially pinioned was flying on 8 August. In 1958 one, partially pinioned, penned chick escaped from its enclosure on 4 August. A second, unpinioned chick escaped on 6 August.

At Cape Sabine in 1957, Childs (1959) noted one long-tailed jaeger chick that could fly well on 6 August. In 1959 unpenned chicks were first seen flying as follows: On 29 July a pair with one chick, 30 July a pair with two chicks and a pair with one chick; on 4 August two pairs with two and one chicks respectively and on 5 August a pair with two flying chicks. The chicks generally flew well on these dates. The number of days from hatching until these chicks were seen flying ranged from 30 to 33 days with a median of 31 or 32.

Departure of breeding birds: — Pairs with chicks were still present when I left the Kaolak River on 9 August in 1957. In 1958 one pair with a chick was still present on 14 August. In 1959 no resident pairs of long-tailed jaegers were on the area from 30 August to 5 September, although several transient birds were seen.

At Cape Sabine long-tailed jaegers had essentially disappeared shortly after the first week in August (Childs, 1959). In 1959 the pairs were present when I left on 11 August. There were no jaegers on the area on 14 September when C. Thomas of the Naval Arctic Research Laboratory visited the area.

Departure dates from the territories are not precisely known but probably occur in late August, certainly before the first of September.

Breeding success

Kaolak River: — Six of the 11 long-tailed jaeger nests were fenced in 1958. Two of the fenced nests failed in the incubation period, but at least one chick was raised to flying age at each of four of them. The wings of all but one of these were clipped. Two wing-clipped chicks disappeared, along with the adults on 1 and 4 August, respectively, and are presumed to have been taken by a predator. One chick was captured after escaping from the enclosed nest on 4 August, and one chick not pinioned flew out between 3 and 6 August and was present on the territory with the adults on 12 August. The five unpenned nests were visited for the last time on 14 August, when only one pair with one chick was present. Only one flying young was seen on the study area during the season; hence, it is assumed that the remaining four pairs were unsuccessful. All four pairs had been present on 10 or 13 July, one with a single egg, the remainder presumably with chicks or a chick. One of the pairs had probably already failed judging by its reaction to my presence.

Assuming that three chicks fledged, including the one taken captive and the one present on 14 August, the breeding success of this population from 19 eggs laid was 16 per cent (Table 8).

Cape Sabine: — The nesting histories of 15 pairs are known from 1959. One pair did not produce any eggs. Four of the 14 nests were penned. The ten non-penned nests produced 19 eggs, of which nine chicks are known to have fledged, an additional two chicks probably fledged, and two more possibly so. If 11 chicks fledged, the unpenned nests were 58 per cent successful; if 13 fledged they were 68 per cent successful. Nesting success per pair, including the pair which did not lay eggs, was 0.73 to 0.87 chicks per pair.

The four enclosed nests had different fates. One failed during incubation; the other three produced five chicks, one egg not hatching. Three of the five chicks, one from each nest, fledged successfully. Two chicks were killed by their siblings; however in view of the high success among the unpenned chicks, I assume that they would have survived had they been unpenned. Hence, a total population of 19 pairs produced 18 nests with 27 eggs. A maximum of 17 to 19 chicks could have fledged giving a breeding success of 63 to 70 per cent, or .89 to 1.0 chicks per pair.

The long-tailed jaeger shows considerable variation in its reproductive success (Table 8), which was greatest at high density and lowest at low densities. In this respect its pattern of reproduction is very similar to that of the pomarine jaeger.

Mortality factors

Nests failed for several reasons at the Kaolak River in 1958. One complete clutch was either infertile or addled. One nest was found on 10 July with the enclosure broken down, apparently by migrating caribou, and the eggs and adults were gone. A lack of food remains about the nest indicated that the chicks had not hatched.

At Cape Sabine in 1959 the eggs and adults at three of the 18 nests disappeared from the territory during incubation. One egg that disappeared was abnormally large and was slightly cracked. The second egg of that clutch disappeared at hatching. A chick was dead at hatching on 26 June, and an egg of another clutch disappeared four or five days after one egg had hatched.

Summary and Discussion of Population Biology

The brevity of the Arctic summer suggests that critical adjustments are necessary in the relations of breeding populations to their food supply. The scheduling of breeding activities must insure that the chicks have sufficient time to develop and that their growth period occurs at a time when food supply is adequate. The three jaeger species have adjusted their breeding schedule to the arctic in different ways.

The pomarine jaeger differs from the parasitic and long-tailed jaeger in the way that the spring build up of its population takes place. At Barrow in 1956 and 1960, at Pitt Point in 1957, and at Cape Sabine in 1959, the pomarine jaeger population reached a peak in numbers shortly after arrival and then declined to a stable breeding population at the beginning of egg-laying. The surplus birds in the population were estimated to be between 25 and 50 per cent above the final breeding level at Barrow in 1956. Surplus birds were relatively fewer in 1960 and were estimated to be less than 25 per cent of the breeding population. A smaller mid-July decline was recorded on Victoria Island in a lemming year (Parmelee *et al.*, 1967).

Parasitic and long-tailed jaegers usually do not have such a spring peak in numbers. The presence of surplus birds that can breed given the proper circumstances was demonstrated, however, by the fluctuations of the long-tailed jaeger population at the Kaolak River and of both the parasitic and long-tailed jaegers at Cape Sabine, as well as by the reproductive data (see Gonad Cycle). At Cape Sabine, where all three species were present early in the spring, the pomarine jaegers built up to a population level of 10-12 individuals on one square mile and then declined to an overall breeding density of 0.72 individuals per square mile. Neither the parasitic nor the long-tailed jaegers showed a similar build up at Cape Sabine. Both of the latter species arrived in moderate numbers, established territories, and bred.

The difference in spring build up of the three jaeger populations appears to be related to their migratory behavior, which in turn is related to their different food supplies and territorial systems. The pomarine jaeger, in contrast with the other two species, migrates in loose, straggling flocks, which may contain up to 100 individuals. Their migratory path takes some of them from west to east, essentially across that part of the coastal plain where lemming highs occur. Large numbers are also known to come down the Colville River presumably after crossing the Brooks Range (T. Cade, *in litt.*). Movement in large groups seems to insure that lemming highs of any significant size will be discovered and that an excess number of jaegers will be present in such potential breeding areas.

Parasitic and long-tailed jaegers are seen migrating in pairs and in small groups. Many are returning to territories occupied in prior years. Both species can usually depend on an adequate food supply, because of their comparative versatility as predators. There is no obvious surplus in arriving populations.

The males of all three jaegers arrive in northern Alaska with testes almost fully enlarged, and the females, with the largest ovarian follicles enlarged to approximately 6 mm (see Gonad Cycle); yet the length of time before the eggs are laid differs among the three species. The pre-egg stage of the pomarine jaeger varies from ten days to two or three weeks. It appears to be longer and more labile than that of the parasitic and long-tailed jaegers.

Paludan (1951) found that the pre-egg stage averaged 37 days in five seasons for *Larus argentatus* and five to six weeks for *Larus fuscus*. For the former species it varied from 24 to 48 days. Most of this variation was the result of differences in the date on which the colony was first occupied. This varied by a maximum of 28 days, while the date of egg-laying varied by only seven days in the same sample period. He concluded from these facts that gulls were able to adjust egg-laying to compensate for variation in occupation of the colony site. Late occupation of colonies was attributed to alteration of the photoperiod by cloudiness.

Lack (1933) found a difference of 23 days in the dates of the first eggs in three colonies of the arctic tern, *Sterna paradisaea*, on Bear Island. He attributed this difference to variation in suitability of nest sites, as the nest sites in the last colony to begin laying remained water logged for a longer period than those in which nesting began earlier. There is no indication that factors related to nest-site condition or photoperiod were important to the jaeger populations under discussion, but weather conditions at arrival did influence the beginning of territoriality and courtship.

The parasitic and long-tailed jaegers, which tend to have permanent territories and presumably more permanent pair-bonds than the pomarine jaeger, may depend on more constant environmental cues to trigger breeding, such as arrival on the territory. This could account for the shorter pre-egg period in the latter two species. In this regard Perry's (1948) work on the parasitic jaeger in Great Britain is of interest, as he showed that at approximately 60° N., in a temperate maritime situation, the egg-laying dates were late May and early June with the peak from 28 May to 2 June, only a few days earlier than the egg dates of this species at 70° N. He also showed that the pre-egg stage of the parasitic jaeger was about three weeks; hence, it appears that in the arctic this portion of the nesting cycle is reduced by 30 to 50 per cent.

The pomarine jaeger has a strong tendency to synchronize egg-laying when breeding at high densities. Egg-laying at Barrow in 1956 and 1960 spanned the last half of June and mid-June, respectively. In both years 50 per cent of the eggs were laid in the first six days of the egg-laying period. Data for other pomarine jaeger populations are not as complete, but this species produces its eggs any time from the end of the first week in June until the end of the month. Sparse populations seem to lay their eggs later than dense ones. The tendency for the pomarine jaeger to arrive in a breeding area in large numbers, and to set up territories and undergo courtship simultaneously, probably contributes to the synchrony of egg-laying in the population. The parasitic jaeger lays its eggs in the foothills in late May or the first week in June. At Barrow eggs are laid about a week later. Egg dates of the long-tailed jaeger are usually in the first half of June. The long-tailed jaeger seems, on the basis of these data, to produce its eggs a few days later than the parasitic jaeger. At the Kaolak River and Cape Sabine, the laying dates within the population on the average showed no sign of synchrony. This was especially noticeable at Cape Sabine, where the dates of 19 eggs spanned 1 to 19 June.

Hatching dates for the pomarine jaeger range from 1 to 24 July. In 1956 at Barrow they were from 10 to 24 July, in 1960 from 1 to 22 July, and at Cape Sabine in 1959 from 4 to 9 July. Parasitic jaeger hatching dates range from 25

June to 17 July. These, like the egg-laying dates, are later at Barrow than they are in the foothills or mountains. Eggs of the long-tailed jaeger hatch out in late June to Mid-July. The inclusive dates are 26 June to 14 July.

It is in the development time of the chicks that the most significant difference in breeding cycles of the three species is found. The pomarine jaeger chicks fledge in 30 to 35 days; the parasitic jaeger, in 27 to 30; and the long-tailed jaeger, in 22 to 28 days. There is thus an average difference of eight days in the mean development time between the smallest and largest species.

Pomarine jaeger chicks first flew in late August at Barrow in 1956 and early August in 1960. A chick was flying at Cape Sabine on 10 August in 1959. In 1957 at Pitt Point all the chicks were flying on 21 August. It seems that early to mid-August is the usual time for this species to finish fledging. The parasitic jaeger finishes in the last week of July and the first week of August. At Barrow its young would probably fly in mid-August, though I have no records of chicks that completed fledging there. Young long-tailed jaegers fly in late July and early August. The chicks of all species are dependent on the adults for two to three weeks after first flying.

From this discussion, it appears that the pomarine jaeger is at a disadvantage compared with the parasitic and long-tailed jaegers. It is the largest of the three species with a more specialized food requirement, and because of its size, the chicks take a longer time to mature than those of the other two species. Hence, the pomarine has the longest nesting cycle of the three jaegers. In spite of this fact, it lays its eggs later than the other two species, and as a result its chicks do not fly much before the end of August, at which time the parasitic and long-tailed jaegers have usually departed from their breeding grounds. This fact may be significant in determining northern limits of breeding of the pomarine jaeger and certainly gives the long-tailed jaeger an advantage in areas where the potential breeding season is critically short. Indeed in northeast Greenland, and northern Ellesmere Island, the long-tailed jaeger nests at a higher latitude than is known for either of the other two species (Bird and Bird, 1941; Parmelee and MacDonald, 1960).

Territoriality

The Pomarine Jaeger

General characteristics: — The general characteristics of pomarine jaeger territories have been described by Pitelka *et al.* (1955a, p. 93) as follows:

> "Jaegers arriving on breeding grounds become territorial any time from the last week of May through the first two weeks of June (or even later, in a minor part of the population, as in 1953). Members of a breeding pair defend their areas by calling and chasing and are persistently alert for intrusions of both resident neighbors and local vagrants. In a breeding population, and particularly in the dense one of 1953 [and both 1956 and 1960], the pattern of territories is diagrammatic, as Manniche (1910) also remarks for the long-tailed jaeger. The pairs are spaced out with remarkable regularity, and the nest is generally placed in the approximate center of the defended area."

Thus the pomarine jaeger territory is a "large breeding area within which nesting, courtship and mating, and the most food-seeking usually occur" (Hinde, 1956), and fits type A of the classification of Nice (1941) and Hinde.

The kind of spatial organization associated with the "all-purpose" territory was generally maintained at all densities; but, under some circumstances, when breeding at low density the pomarine jaeger departs from this type of spatial organization. One such variation was observed from 5 to 8 July, 1957 at Wainwright, where there was a sparse breeding population of pomarine jaegers estimated at one pair per square mile. The lemming population was generally low, but lemmings appeared to be locally abundant along a ridge behind Wainwright Village. Jaegers hunted along this ridge, and the hunting birds performed territorial announcements to each other.

Pomarine jaegers perform territorial announcements in flight by giving a characteristic nasal call and flapping their wings more slowly and with greater amplitude than normally. This behavior may develop into a more intense form of display, in which the bird calls and glides with wings held up at a sharp "V" angle, the so-called "V-glide." The bird may glide to the ground in the latter position. Pomarine jaegers also announce on the ground by raising their wings to a "V" position and calling. This display is exactly like the ground announcement of the larger skuas (Stonehouse, 1956), but the other jaegers do not perform it.

There was no nesting pair near where the territorial announcements were made at Wainwright, and different individuals were involved in each observation. Nesting pairs were apparently foraging away from their territories, because of the low food supply, and responded to passing jaegers by territorial announcement and by defensive actions.

The nesting density of the Cape Sabine pomarine jaeger population was similar to that at Wainwright in 1957; but, in this instance the spatial organization of the population was typical in the first half of the season, with pairs occupying large exclusive territories on which foraging took place. Two differences from the Wainwright situation should be noted. The food base of the population at Cape Sabine was an abundant supply of *Microtus oeconomus,* which appeared to be uniformly distributed and available on all territories, and there was competition for space and food from breeding long-tailed and parasitic jaegers, as well as from a number of transient pomarine jaegers that briefly established territories on the area in late June and early July. It seems probable that with food evenly distributed and territorial competition high, the tendency to occupy and defend a territory, i.e. the normal territorial behavior of this species, would not break down even at low densities.

Pomarine jaegers defend their territories against several species. In addition to other pomarine jaegers, they announce to parasitic and long-tailed jaegers, glaucous gulls, short-eared owls (*Asio flammeus*), snowy owls, arctic loons (*Gavia arctica*), and arctic foxes. The opponent was recorded in 143 territorial displays in 1956 and 256 in 1960. Eighty-nine per cent of them were against other pomarine jaegers in 1956 and 99 per cent in 1960. Most involved neighboring pairs, 47 per cent in 1956 and 62 per cent in 1960. Eleven per cent of total defenses in 1956 and 1 per cent in 1960 were directed at other species. The remaining displays were against transient pomarine jaegers.

Territory size: — The pomarine jaeger populations, except at Cape Sabine, have nested on coastal plain tundra, all of which is acceptable nesting habitat. In lemming high years the nests have tended to be spaced with remarkable regularity (Figures 3 and 4), and all of the tundra has been occupied by territorial pairs, at least at the beginning of the season. The nest is usually near the center of the territory, as Pitelka *et al.* (1955a) have pointed out, so that mean territory size for populations that occupy all available habitat can be approximated by using the average nesting density per square mile (Table 10). Mean territory size has varied about five-fold, from 31 to approximately 170 acres, in such populations. The variation between years and areas suggests that the pomarine jaeger can greatly extend its territory against population pressure when lemmings are not super abundant.

TABLE 10

Mean area occupied by pairs of pomarine jaeger at different population densities

Population	*Density (pairs/ square mile)*	*Territory area (acres)*
Barrow 1952	3.8[a]	168
Barrow 1953	18.3[a]	35
Barrow 1956	19.0	34
Barrow 1960	20.5	31
Pitt Point 1957	10.1	63

[a]Data from Pitelka, Tomich and Triechel 1955 a.

The Cape Sabine population of 1959 was the only one in which suitable nesting habitat for the pomarine jaeger was discontinuous and in which several pairs nested whose territories did not abut or abutted only on one edge. Three nests were situated approximately one mile apart (Figure 5). One nest failed early, and the size of the territory defended by this pair was not determined. The defended territory of the remaining two pairs was marked on aerial photographs, one from 16-17 hours of observation on 22 through 24 June, the second from 6 hours of observation on 30 July and 2 August (Figure 9). The area defended by a single transient bird was also mapped on 10 July, after I observed a series of defenses and boundary patrols. The territory areas were $\frac{1}{3}$, $\frac{1}{2}$ and $\frac{1}{2}$ square miles, approximately 200-300 acres, respectively. The nest was located well toward one end of one territory and was approximately in the center of the other. The irregular outline of two of the territories appeared to result from the jaegers using topographic features as boundaries. If we regard these as approximately maximum-sized territories, then the total range in size of the average pomarine jaeger territory in populations of different density is from 25 to 300 acres, a 12 fold variation.

Variation within and between high populations: — Mean territory diameters can be used to compare variation in territory size within and between the 1956 and 1960 Barrow populations. In 1956, 72 nests on approximately four square miles of tundra adjacent to the Naval Arctic Research Laboratory were mapped with alidade and plane table. In 1960, 45 nests on approximately 2.5 square miles were mapped in the same manner. Mean territory diameters were determined by using the mean distance from each nest to all of its neighbors. The number of measurements per nest ranged from two to nine. Peripheral pairs with less than one half of their territories on the sample area were not included, and were arbitarily determined if their nests were outside a line connecting the nests of two adjacent neighbors on the periphery. Exceptions were made for the nests along the east and south sides of the plot that bordered on Elson Lagoon and Wohlschlag Slough.

The results suggest a normal distribution of territory diameters in 1956 with a mean of 1069 feet, and extremes of 690 and 1515 feet (Figure 10). The 1960 results are very similar to those of 1956; the mean is 1164 feet, and the extremes are 735 and 1693 feet, although the distribution is not as smooth as in 1956. The difference in distribution may be the result of the smaller 1960 sample. The similarity of the samples is shown by statistical test ($t_{95} = 2.38$, $p = .98$).

Territory diameters varied by 2.3 and 2.5 within these two high years. If we assume for comparison that these territories are circles, then the areas range from 8.5 to 40 acres in 1956 and from 8 to 45 acres in 1960, thus indicating a maximum size range of about five-fold in territory size in a high year. These comparisons strongly indicate that population density, mean territory size, and the range of territory sizes were essentially the same in these two high years.

We can compare these data with some from the 1953 high population (Pitelka *et al.*, 1955a). The 1953 data are distances between pomarine jaeger pairs nesting on and adjacent to three census plots. Plot 1 is a forty acre plot, two acre-lengths wide and 20 acre-lengths long on an old beach ridge; plot 2 of 20 acres is an area of low tundra; and plot 3 of 86 acres is marshy flat tundra. Plots 1 and 3 are shown on Figure 4. I do not know the location of plot 2.

Forty-nine measurements taken to the nearest 100 feet were made between pairs on the plots and from each of these to all of their adjoining neighbors off the plots and between pairs along the periphery (Pitelka *et al.*, 1955a). Similar measurements in 1956 for plots 1 and 3 gave 48 distances taken with an alidade and plane table and accurate to within 20 feet.

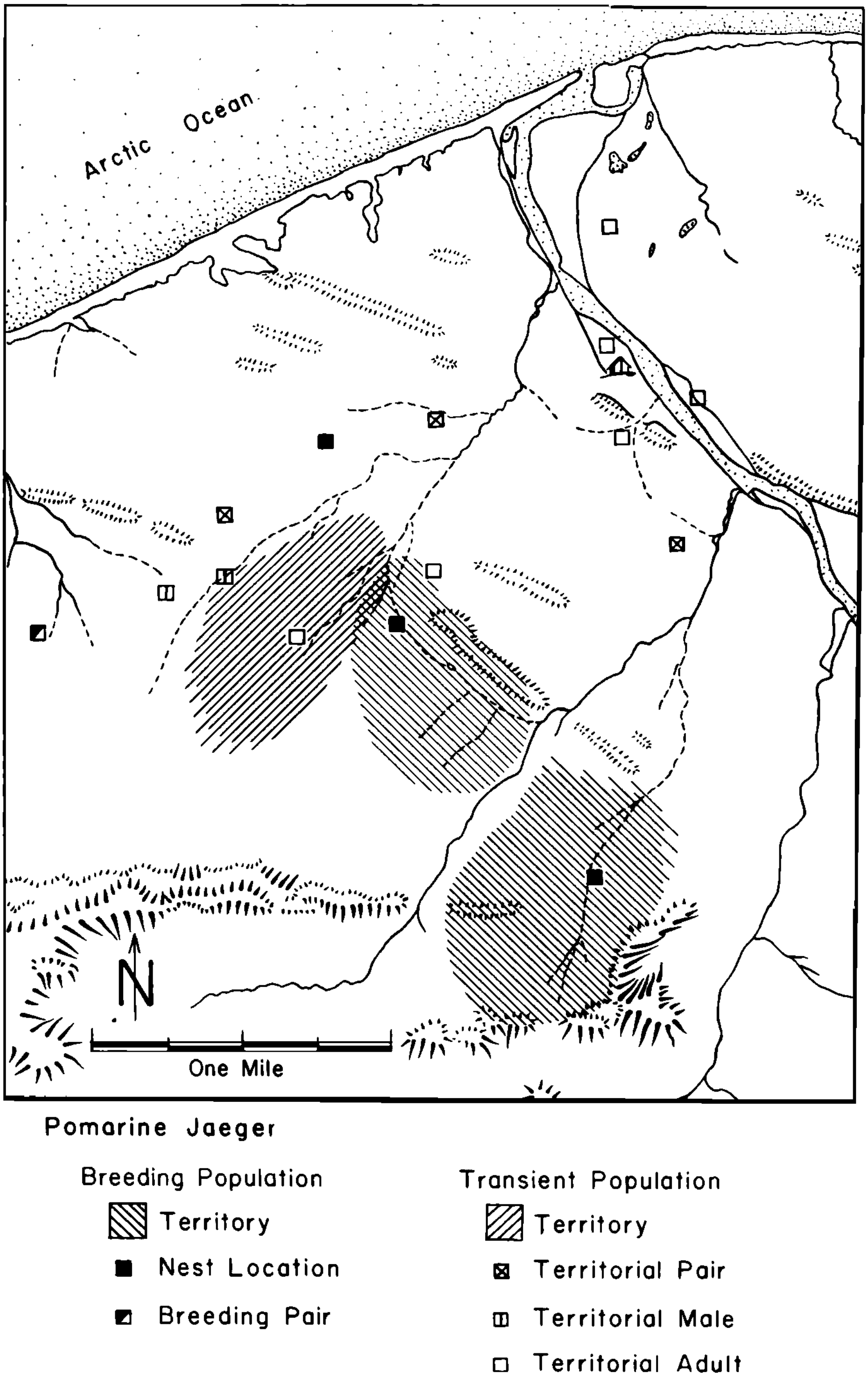

Figure 9. Map of breeding and transient pomarine jaeger populations at Cape Sabine in 1959. Hatching indicates observed territory areas.

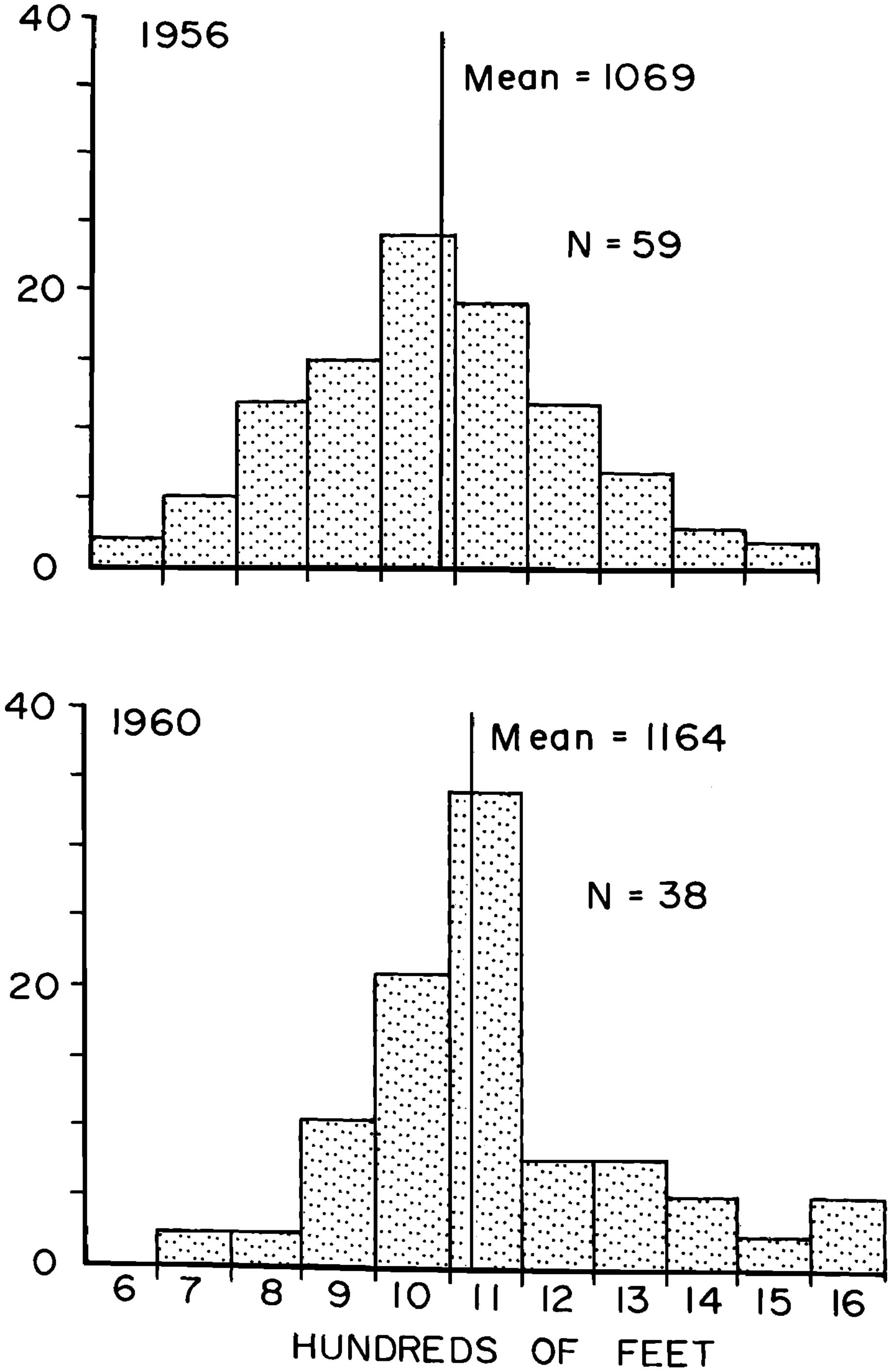

Figure 10. Distribution of mean territory diameters of pomarine jaegers at Barrow 1956 and 1960.

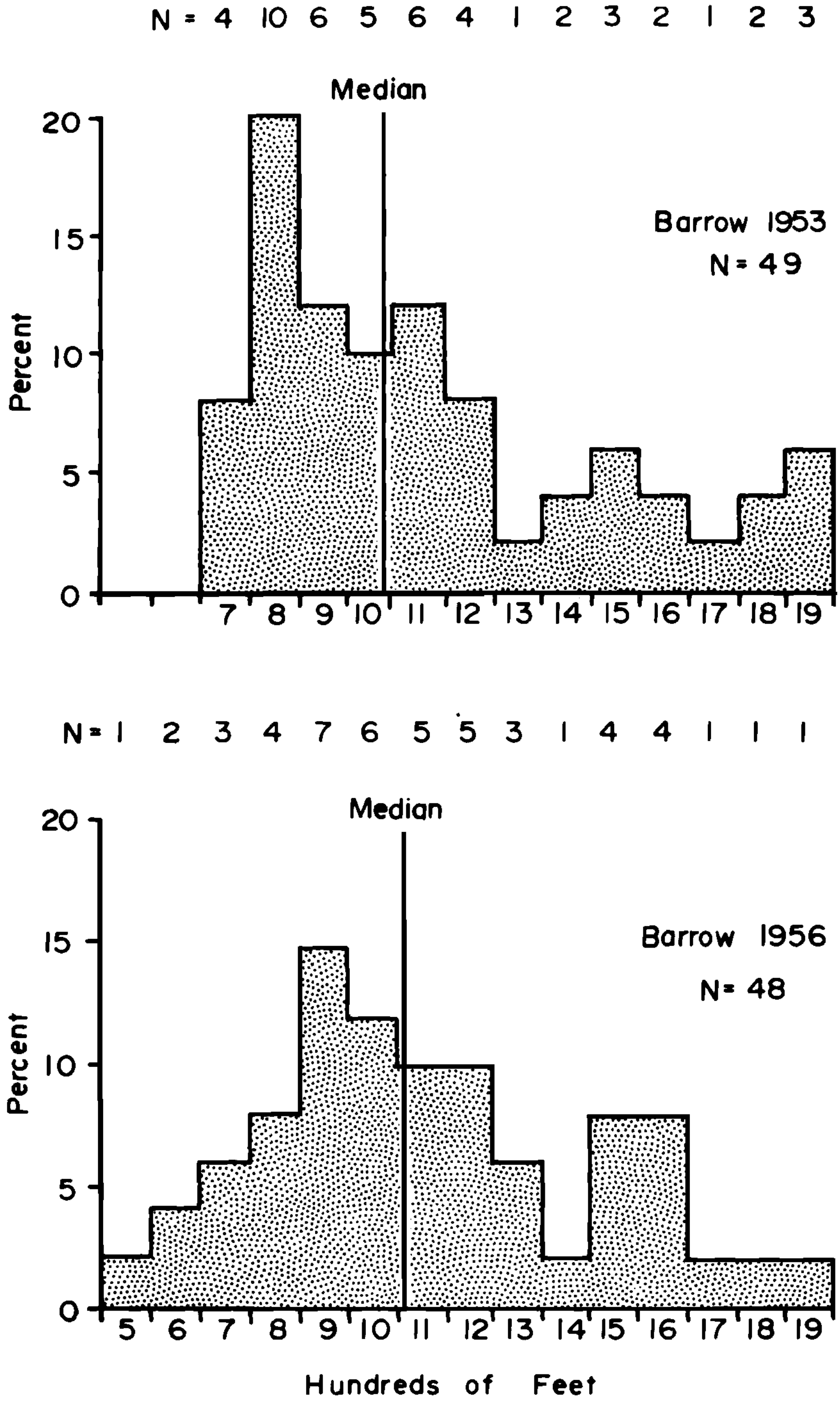

Figure 11. Comparison of inter-nest distances of the pomarine jaeger populations at Barrow in 1953 and 1956.

The per cent frequency distributions for the inter-nest distances of the 1953 and 1956 populations are very similar (Figure 11). The medians for both years are between the 1000-foot and 1100-foot classes. The distributions are skewed to the left and peak at the 800-foot class (1953) or the 900-foot class (1956). Distances ranged from approximately 700 to 1900 feet in 1953 and from 500 to 1900 feet in 1956. The slight differences in distribution in these two years are attributed to the different methods of measurement.

Thus the evidence very strongly supports the conclusion that pomarine jaeger density in the 1956 and 1960 lemming high years was essentially the same. Comparison of the frequency distributions of distances among the subsample of nests from 1953 and 1956 indicates that their spacing may be different. The average densities of breeding pomarine jaegers in those two years (Table 3) are so close, however, as to justify concluding that the densities in all three years were essentially the same.

Seasonal changes in foraging area: — Exclusive occupation of territories had a tendency to break down in the latter part of the season both in the dense population at Barrow in 1953, and also in the intermediate population of 1952 (Pitelka *et al.*, 1955a).

The tendency toward breakdown of territoriality and enlargement of the foraging area was also noted in 1956 and 1960. In 1956, population pressure was maximal, and faced with a failing food supply jaegers immediately absorbed the territories of neighboring pairs that departed. For example, on 10 July one pair was missing from its territory, the eggs were punctured, and the contents had been eaten apparently by a jaeger. The neighboring pair flew over and called in exactly the same manner as territorial birds when I was in the vicinity of the nest. At about this time, in early July, it became evident that some of the birds were leaving their territories to forage. One or both members of a pair would be absent during my visits to enclosed nests. On 29 July, a polar tomcod (*Boreogadus saida*), was found in one enclosure. On 10 August a chick caught on the tundra cast up a piece of fish. Thus, it was evident that some of the birds were foraging along the ocean, probably as a result of food shortage on the tundra.

In 1960 this tendency to forage away from the territory was also noted, though it seemed relatively uncommon. Remains of eight fish (in a total of approximately 2500 prey items) were found in late July. Adults were also noted as being absent from their territories toward the end of the season.

A similar situation was seen in 1959 at Cape Sabine, where one pair defended a large territory and apparently obtained most of its food from the territory until the last part of July. On 28 July the only food found in the chick enclosure consisted of a few small fish, and fish continued to occur in the diet along with other food items until the chick flew on 10 August. The jaegers were apparently obtaining food either by scavenging along the beach or by robbing kittiwakes (*Rissa tridactyla*), which were common along the shore at this location. At Cape Sabine the critical factor was not absolute shortage of food, but decreasing prey availability caused by the growth of the tall dense vegetative cover of that region. In this instance, as in 1953 and 1956, the change in food habits also coincided with the interval of rapid growth of chicks.

Seasonal decline of territoriality: — Pitelka *et al.* (1955a and 1955b) noted the last territorial defense in 1952 on 30 August. In 1953 territories were still being defended when observations ended on 24 August.

Territorial defense waned earlier at Barrow in 1956 than in the more successful years studied by Pitelka *et al.* The last territorial defense was observed on 10 August, though a few territories were occupied until 21 August when a pair of adults and a chick were still on their territory. The adults apparently abandoned this chick, as it was found alone, just able to fly, and still within its natal territory on 25 August.

In 1956, the difficult circumstances of a declining food supply were aggravated as demands by growing chicks increased. The chicks could not be fed sufficiently, and in the latter part of the season their begging cries were heard frequently. One consequence of the food shortage was that the chicks did not mature at a normal rate (see Growth). The chick found abandoned on 25 August, for example, could not fly well even at that late date. The major factor considered responsible for the ending of territorial defense was shortage of prey and starvation of chicks. The failure of chicks to mature at a proper rate may also have resulted in waning of the adults' feeding drive and caused abandonment of some live chicks.

In 1960, on the other hand, there was no apparent food shortage, and territorial defense was still strong on 12 August. On 15 August a group of four adult and four young jaegers were associating with no apparent strife. This observation apparently marked the beginning of the breakdown of territoriality, as small groups of adults and chicks were noted on the tundra on subsequent days. The first fully independent juvenile was seen over the ocean on 18 August.

A comparison of the number of territorial defenses per hour by pairs in 1956 and 1960 shows the difference in the persistence of defenses in the two seasons (Table 11). The decline of the number of defenses in August of 1956 as compared with August 1960 probably reflects both the declining adult population of the former year as well as the lessened interest in territory by adults still present in August of that year.

TABLE 11

Pomarine jaeger territorial defenses per hour of observation in two lemming high years

Dates	*No. of defenses*	*Hours of observation*	*Defenses/ hour*
1956			
13 June–2 July	66	13	5.0
7–8 July	95	24	4.0
20 July–4 Aug.	34	16	2.1
1960			
18–19 June	137	24	5.7
7–8 July	83	24	3.5
23–24 July	109	24	4.6
13–14 Aug.	112	24	4.7

Toward the end of the 1956 season territorial boundaries underwent a marked reorganization. Many of the pairs still remaining had moved from their original territories onto adjacent territories. They still defended a territory but the area was apparently centered around the chick and not necessarily related to the territory originally established. Movement of pairs was made possible by the very high percentage of breeding failures and the number of abandoned territories. Pairs were identified by plumage notes made on each pair earlier in the season. Accurate records on movement of six pairs were obtained. The distances moved ranged from 675 to 1050 feet and averaged 850 feet, less than the diameter of an average territory. All of these pairs moved just after the snow and cold weather that caused a large number of nesting failures in the population.

Events in 1960 indicated that such widespread shifting of territorial boundaries was not usual in a successful breeding year, primarily because most territories were still occupied and defended until mid- or late August. In general in 1960 boundaries appeared to remain stable as long as territories were defended. On 12 August, one pair moved onto the territory of an adjacent pair that had lost its nest, and about twelve pairs were noted to have shifted their territories on the 8 to 11 August census. Change of territorial boundaries was especially noticeable in the northeast part of the study plot where several pairs had been shot by Eskimo hunters.

Early in August of 1960 chicks on adjacent territories were observed gathering in groups of four and six. These groups usually moved unchallenged across territorial boundaries, although the adults remained territorial with respect to each other and some adults were seen announcing to neighboring chicks when the chicks strayed across the boundary. Shortly afterwards groups of both adults and chicks were seen as territoriality began to break down.

Initiation of territorial behavior: — The environmental factor or factors responsible for triggering territorial behavior of a nomadic species, such as the pomarine jaeger, is of theoretical interest. Food supply suggests itself as the responsible factor for a species that is not returning to a fixed territory when migrating over breeding terrain in the spring and that is seeking an area with a food supply adequate for breeding. The territorial behavior of transient pomarine jaegers at Cape Sabine in 1959, as well as a comparison of breeding and nonbreeding populations at Pitt Point and Barrow in 1957 (see Gonad Cycle), and the behavior of arriving birds in the springs of 1957, 1958, and 1959 at Barrow, all suggest that "recognition" of a suitable food supply could trigger territorial behavior in this species.

I have discussed previously the large westward passage of pomarine jaegers through Cape Sabine in late June and early July 1959. Several of these transient birds remained in the area apparently because of the high *Microtus* population and began defending territories. Ten territories were defended, seven by single adults and three by pairs. It is not known whether these pairs were formed on the territory or whether the birds were paired when they arrived. Incipient courtship behavior witnessed between one defending male and a transient female suggests that the pairs were formed on the territories.

The earliest of these territories was occupied on 21 June, and it was defended for at least a week (Figure 9). The latest one to be occupied was seen for the first time on 10 July and was defended at least until 12 July. All transient territories were abandoned by 20 July. On 17 July a pomarine jaeger defended part of a caribou carcass near camp. This bird performed all the typical territorial defense activities, calling, announcing on the wing, and chasing. It departed the next day. All transients occupied low, comparatively level, marshy ground, which was the same habitat occupied by the breeding pairs in the area.

The Parasitic Jaeger

General characteristics: — The parasitic jaeger in northern Alaska occupies a large all-purpose territory, which is not, however, completely defended for the entire nesting season in the manner of the pomarine jaeger, and in this respect it differs from the all-purpose territory as defined by Nice (1941) and Hinde (1956). In a relatively stable situation, as at the Kaolak River, pairs of parasitic jaegers and long-tailed jaegers are widely dispersed on the tundra, and the pattern of dispersion suggests that they are spaced with reference to each other as uniformly as the terrain and habitat permit. During most of the nesting season the parasitic jaegers do not defend all of the area that appears to be occupied. Instead, they defend at all times a central core of territory that is variable in size. The outer portion of the territory is defended only to the extent that another jaeger hunting in that area is challenged. In these features the territoriality of parasitic jaegers best fits the model proposed by Cade (1960) for the peregrine falcon (*Falco peregrinus*). Foraging is done in the core area, on the remainder of the territory, and away from the territory.

The size of the defended core varied for the same pair; but, an area within a radius of 200 to 300 yards of the nest is an appropriate estimate of an average core size. This species forages in the defended core of the territory, but most foraging is done farther away from the nest area. The degree to which the birds leave their territory to forage in the outer portions of other territories is not known. Territorial displays are witnessed frequently at places far removed from a nest, and these are presumed to result from a nesting bird meeting another adult on its territory. A marked male foraged at least two miles from the nest on Victoria Island (Parmelee, *et al.*, 1967).

Some variation in this general picture should be mentioned. The pair that nested at Barrow in 1956 occupied an isolated area near the Naval Arctic Research Laboratory (Figure 3) and defended it from pomarine jaegers; however, the birds did very little foraging for food on the territory. The very small amount of *Lemmus* in their food remains suggested that most foraging was done along the ocean shore (see Food Habits and Predation, beyond).

Parasitic jaegers usually hunt in pairs in the period when the chick is being fed. Pairs were observed to depart from the nest area together and were observed cooperating to chase birds to the ground, although frequently they returned to the nest area separately. As a result, the parasitic jaeger chicks are deserted for long periods of time. Observations totalling 16 hours at nests on the Kaolak River area in 1957 and 1958, on 24 July and 10 August, showed that both adults leave the chick for about 50 per cent of the time, both were present 27 per cent of the time, and one was absent about 23 per cent of the time (Figure 12). Perry (1948) also observed that the chicks were abandoned for long periods on the Isle of Noss.

The observations were compared with similar ones made at long-tailed jaeger nests. The parasitic and long-tailed jaegers differed significantly in the pro-

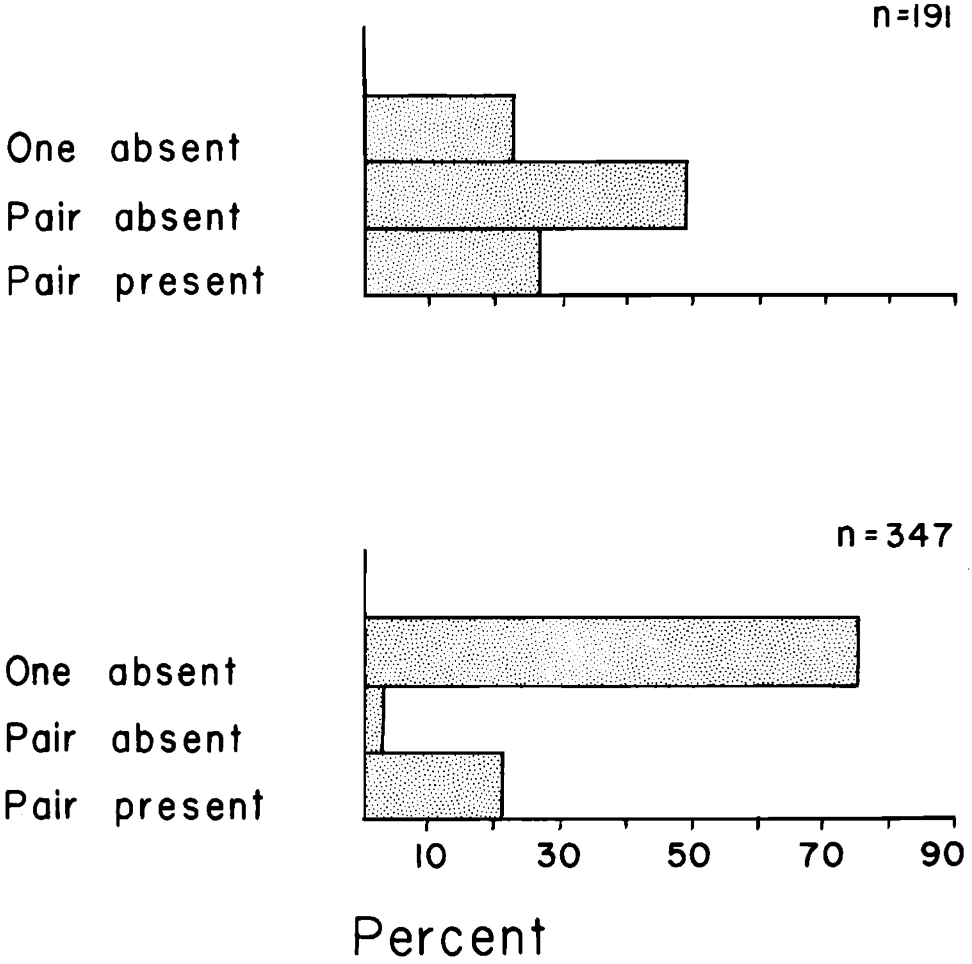

Figure 12. Presence of adult long-tailed (lower figure) and parasitic jaegers (upper figure) near the nest during the period of rearing chicks, Kaolak River 1958.

portion of time both adults were absent from the nest area (Chi-square = 168.9, p = 0.005), and in the proportion of time that only one adult was absent from the nest area (Chi-square = 136.1, p = 0.005). The two species did not differ significantly in the proportion of time in which both adults were present at the nest (Chi-square = 2.15).

Parasitic jaegers have been observed defending their territories against several species including pomarine and long-tailed jaegers, glaucous gull, snowy owl, arctic fox, and caribou.

Territory size: — Distances between parasitic jaeger nests are usually large. At the Kaolak River the distances between the three nests in 1958 and 1959 and between the two nests in 1960 ranged from 2400 and 4500 yards (Figure 8). At Cape Sabine in 1959 the distances between four nests ranged from 1200 to 4100 yards. These figures do not reflect the territory sizes of the birds, however, as the parasitic jaegers were nesting in association with long-tailed jaegers at the Kaolak

River, and with both long-tailed and pomarine jaegers at Cape Sabine. Only once were the territories of two pairs of parastic jaegers adjacent. In this instance, at Cape Sabine, the two nests were 1200 yards apart. Parmelee *et al.* (1967) found them nesting 3 to 4 miles apart in 1962 and 1 to 2 miles apart in 1966 on Victoria Island.

The average distance from parasitic jaeger nests to neighboring long-tailed jaeger nests, discussed below, can be used for a crude estimate of the size of the total area occupied by breeding pairs. Assuming that the average distance (approximately 1350 yards at the Kaolak River) is the mean diameter of a circular territory, the average territory is about 300 acres or approximately one half square mile. The average distance to all neighboring nests at Cape Sabine was approximately 800 yards, giving an average territory of approximately 100 acres. These are probably conservative figures.

Thus, territories of the parasitic jaeger are larger than those of the pomarine jaeger and average less than one half square mile in area. They also differ from the pomarine jaeger in that only a central core some four to six hundred yards in diameter is defended at all times in the season.

The Long-tailed Jaeger

General characteristics: — In general, territorial organization by the long-tailed jaeger in northern Alaska is similar to that of the parasitic jaeger. The long-tailed jaeger occupies a large area and completely defends the central portion, which can be considered the core of the territory. The remainder of the territory is defended only when another jaeger is encountered on it while foraging, and the outer part of the territory is not patrolled. The core area is estimated to average 400 to 600 yards in diameter, approximately the same as the core of a parasitic jaeger territory. Long-tailed jaegers at the Kaolak River frequently nested in the bottoms of shallow swales, and in these situations the edges of the swales were the boundary of the core area.

The adults of this species usually hunt singly in the period of feeding chicks, and usually one member of a pair remains near the nest so that the chick is rarely left alone. The species obviously guards the chick as the return of one adult to the nest is usually the signal for the other to leave. Thirty-seven hours of observation on 14 July 1957 and 31 July through 12 August 1959 indicate that the long-tailed jaeger chicks are left alone only 3 per cent of the time (Figure 12). One adult was absent 75 per cent of the time, and both adults were present 22 per cent of the time. The proportion of time in which one adult is absent and both are absent is significantly different from similar observations made at parasitic jaeger nests (See the section on the parasitic jaeger for level of significance of differences.).

Territory size: — Inter-nest distances of the long-tailed jaeger have varied more than those of the parasitic jaeger because of greater variation in nesting density. In 1958, 1959 and 1960 at the Kaolak River the nests ranged from 700 to 2600 yards apart with a mean distance for all measurements of approximately 1450 yards. At Cape Sabine inter-nest distances ranged from 670 to 1470 yards with a mean of 970 yards. Using these means as territory diameters the territory areas are 340 and 170 acres respectively, or one half square mile to slightly more than one quarter square mile. The average of four long-tailed jaeger territories in Northern Sweden was approximately 220 acres with extremes of 200 and 250 acres (Andersson, 1971). These estimates give minimal figures that can be compared with the territorial areas of parasitic and pomarine jaegers.

Interspecific territoriality among jaegers

The three species of jaegers when breeding are hostile to each other as well as to their own kind. Territorial announcement and defenses are made toward all jaegers of any species when individuals trespass. This fact suggests that they maintain exclusive territories with respect to each other. However, evidence that a species is hostile to another does not establish the fact of interspecific territoriality, since jaegers are hostile to several other predators as mentioned above. The significant factor in establishing interspecific territoriality is whether individual pairs of the species respond spatially to each other, by maintaining mutually exclusive areas. Inspection of the maps of breeding populations at the Kaolak River (Figure 8) and Cape Sabine (Figure 5) show that the nests are in fact spaced regularly regardless of species.

Distances between the nests of the three species when nesting together were examined for possible clues to differences in territorial response among them. The distances between all long-tailed jaeger nests at the Kaolak River in 1958, 1959 and 1960 were compared with the distances between each parasitic jaeger nest and all of its neighbors (Table 12).

TABLE 12

Distances in feet between long-tailed jaeger nests and from parasitic jaeger nests to neighboring nests

	Long-tailed Jaeger			*Parasitic Jaeger*		
Year	*Mean*	*Range*	*N*	*Mean*	*Range*	*N*
1958	1353 ± 132	708–2478	15	1156 ± 111	590–1652	10
1959	1686 ± 168	1357–2596	7	1534 ± 207	649–2419	10
1960	1429 ± 98	866–1870	12	1420 ± 137	842–1832	6

The similarity of the distances between these groups emphasizes the tendency toward uniform spacing within and between the two species and suggests that they are comparably territorial with respect to each other. Indeed, statistical comparision of the long-tailed jaeger inter-nest distances and distances from parasitic jaeger nests to their neighbors within all three years shows no significant differences (1958, $t = 1.05$, 23 d.f., $P = 0.2$; 1959, $t = 0.33$, 15 d.f., $P = >0.5$; 1960, $t = 0.04$, 11 d.f., $P = >0.9$).

Frequency distributions of the combined measurements of each of the two groups for all three years further emphasize the similarity of the samples but also suggest a piling-up of measurements at the shorter distances between parasitic jaeger nests and neighboring long-tailed jaeger nests (Figure 13). This skew-

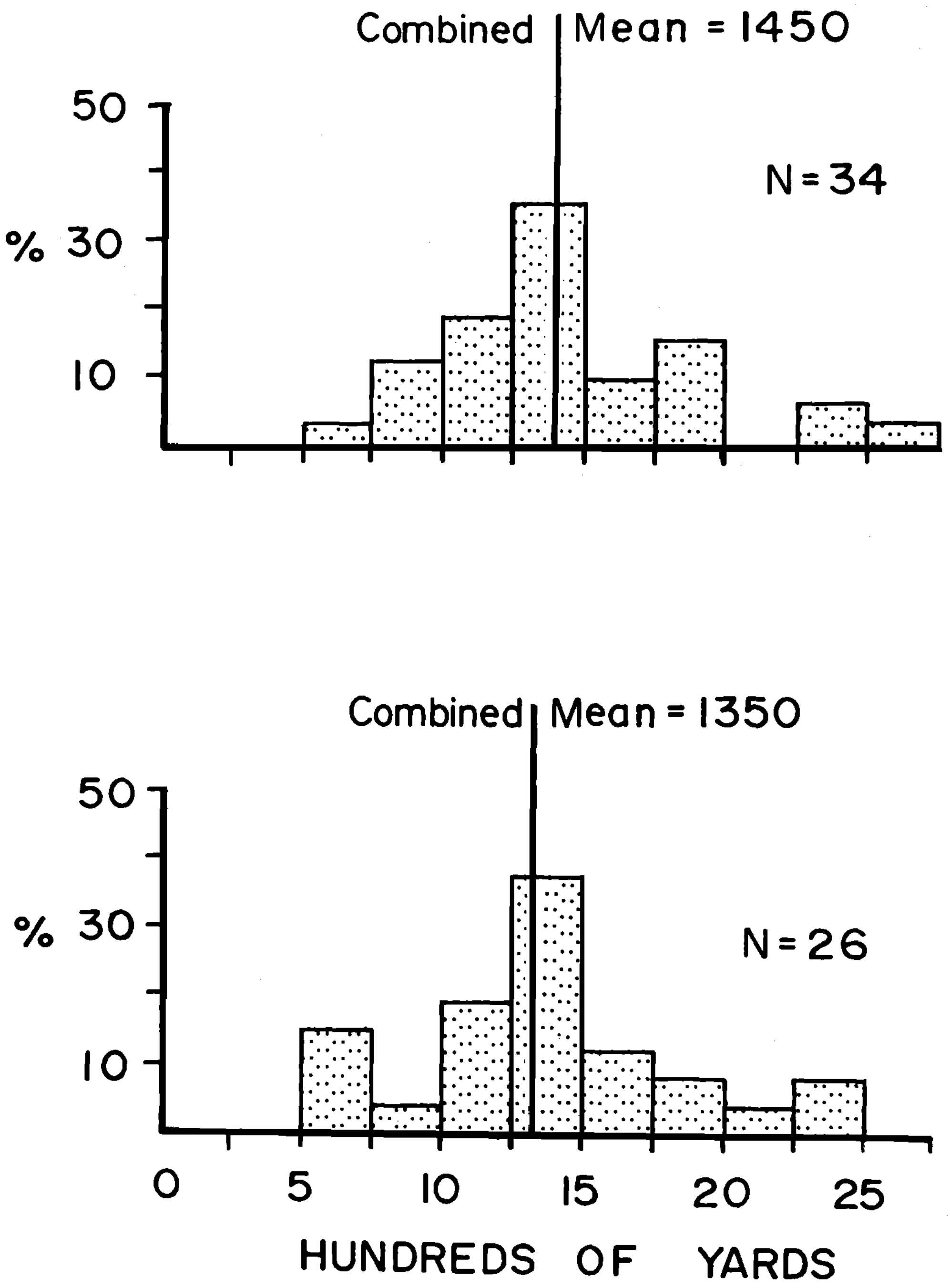

Figure 13. Comparison of all long-tailed jaeger inter-nest distances (upper figure), and the distance of all parasitic jaeger nests to neighborhing long-tailed jaeger nests (lower figure) at the Kaolak River.

ing leads to the suggestion that the difference between the two groups of inter-nest distances may result from a greater intolerance of the parasitic jaeger to long-tailed jaegers at close distances than individual pairs of the latter species have among themselves.

A similar analysis was made for the Cape Sabine populations, where the distances from each of three pomarine jaeger nests to its neighbors were compared with the distances between long-tailed jaeger nests and neighboring long-tailed jaegers and between four parasitic jaeger nests and their neighbors (Figure 14). Pomarine jaeger neighbors were usually long-tailed jaegers but included the other pomarine jaeger nests and one parasitic jaeger nest. Parasitic jaeger neighbors were also usually long-tailed jaegers but included one pomarine jaeger nest and one parasitic jaeger nest (Figure 5).

Distances in these three groups were as follows: the distance from long-tailed jaeger nests to neighboring long-tailed jaegers averaged 969 ± 61 yards (extremes 672 and 1471, N = 16); parasitic jaeger nests to all neighboring nests averaged 784 ± 89 yards (extremes 440 and 1181, N = 8); and the distances from pomarine jaeger nests to all their neighbors averaged 1153 ± 81 yards (extremes 556 and 1899, N = 17).

The three groups are statistically similar when compared among themselves. The inter-nest distances of long-tailed jaegers compared with the distances from pomarine jaeger nests to their neighbors are not significantly different ($t = 1.79$, 31 d.f., $P = .9$ to .95), and they are not different when compared with the distances from each parasitic jaeger to its neighbors ($t = 1.73$, 22 d.f., $P = .9$). However, the distance to neighbors from pomarine jaeger nests and from parasitic jaeger nests are possibly different ($t = 2.68$, 23 d.f., $P = 0.02$). Thus, spacing within and among the three species at Cape Sabine seems to be more uniform than between the parasitic and long-tailed jaegers at the Kaolak River and here firmly supports the similarity of the interspecific territorial response.

It is not necessary, however, to show that the birds maintain similar territory sizes or to insist on similar inter-nest distances in order to establish the fact of interspecific territoriality. The three species show differences in preferred nesting habitat, although there is broad overlap in the types of situations in which they are found nesting. Non-uniform distribution of habitat types, then, would result in uneven distribution of the species. Also, the species could be interspecifically territorial and still not be evenly spaced. In other words, the parasitic jaeger, for example, could demand and exact a greater spatial response from a long-tailed jaeger than the latter does with its own kind, as suggested by the comparison of inter-nest distances of these two species at the Kaolak River.

My data do indicate a remarkable degree of uniformity in size of territory among the three species when they associate as nesting birds, and the fact of interspecific territoriality among these species is well established.

Summary and Discussion of Territoriality

All three species of jaegers maintain large exclusive territories upon which mating, nesting, and most food gathering take place. The territories are thus classifiable into the type A category of Nice (1941). However, the three species do differ in the way in which territories are utilized and defended, and in the degree to which exclusiveness of the territory is maintained through the season.

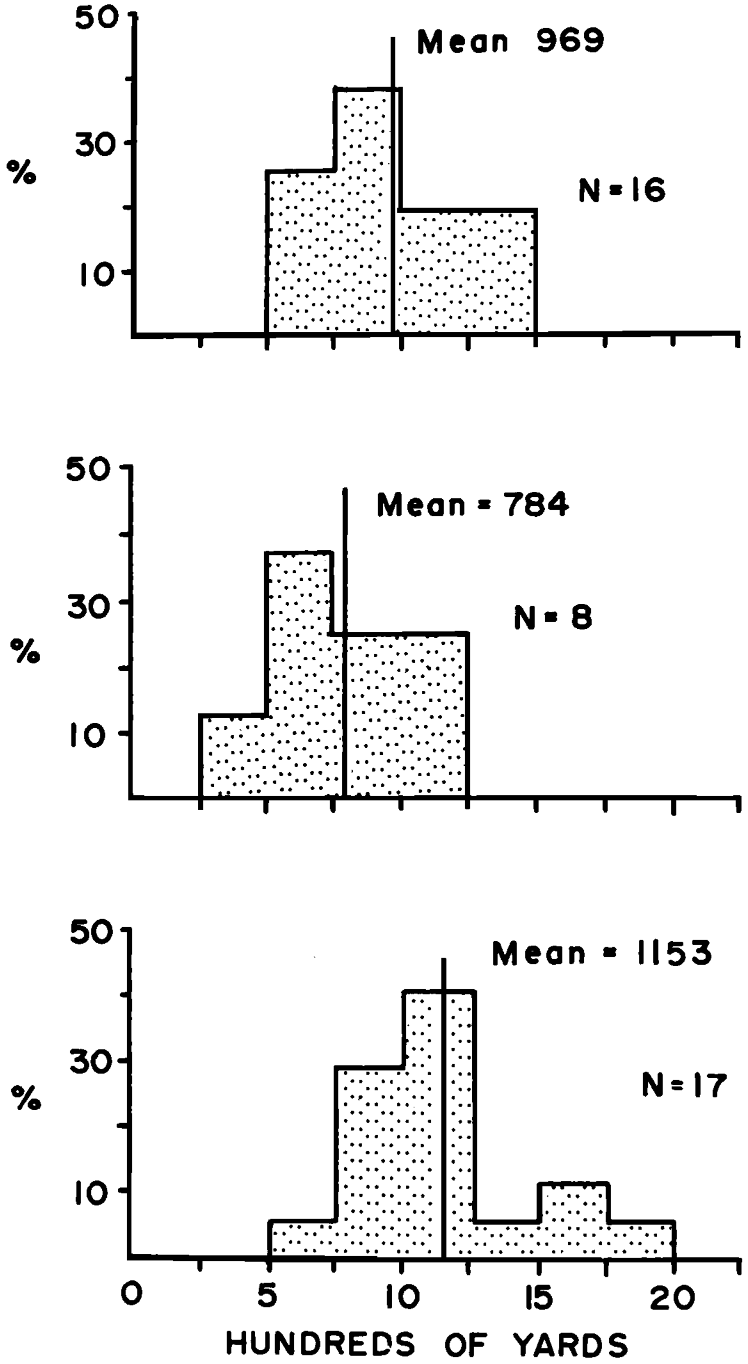

Figure 14. Inter-nest distances among long-tailed jaeger nests (upper), from parasitic jaeger nests to all neighboring jaeger nests (middle), and from pomarine jaeger nests to all neighboring jaeger nests (bottom), Cape Sabine 1959.

All three species are aggressive to each other, and all respond spatially to inter- and intraspecific aggression, so that interspecific territories are maintained when any of the species occur together on the breeding grounds.

The pomarine jaeger maintains a territory that is completely exclusive for the entire nesting season, except under special circumstances of extreme food shortage. The pomarine jaeger territory is relatively small, average 30 to 35 acres, in years of maximum breeding density. The entire territory is defended at all times, and the species appears to be basically adapted to this kind of small exclusively defended area, as suggested by several attributes of its territorial behavior. It defends the territory by frequent patrols of the boundary, and this patrolling apparently serves an announcement function. It is also the only species of this genus to have a ground display for territorial announcement. This is a signal that functions at short distances, and it is shared in the Stercorariidae only by the skuas (*Catharacta*), which nest in semi-colonial aggregations in the north Atlantic and south temperate and polar regions and which defend small nest territories within breeding groups (Stonehouse, 1956).

The territorial system of the pomarine jaeger seems to be primarily adapted to function at or near maximum population density. At Cape Sabine the few pairs, which were maintaining large territories, persisted in defending an exclusive territory and in making boundary patrols and thus spent a greater amount of time in territorial defense than the pomarine jaegers nesting at Barrow at maximum density in the same part of the season (10 vs 4.5%).

The size of the pomarine jaeger territory varies inversely with the density of its main prey, the brown lemming, and was minimal and approximately the same average size in three lemming high years of 1953, 1956 and 1960 at Barrow. This was true despite the fact that the estimated density of lemmings in those three years was considerably different. Breeding success of the species in high lemming years was not consistent and varied from mildly successful in 1953, to complete failure in 1956, to high success in 1960. This pattern of success accorded with estimates of the relative density of lemmings in the three highs, which were moderate in 1953, low in 1956, and high in 1960. Breeding success in the sparse nesting jaeger populations in low lemming years is usually poor; but even if it were not poor, the very high numbers of jaegers that breed in northern Alaska in high lemming years, presumably a large proportion of the population, suggest that on a population basis these are the significant reproductive efforts. The small, exclusive territory the species maintains then, and the behavioral means by which it does so, all suggest that the size of pomarine jaeger territories has evolved as a means to exploit the abundance of prey during the periodic high lemming years.

Territories of the parasitic jaeger and the long-tailed jaeger are similar in that, compared with that of the pomarine jaeger, they are relatively large and the spacing of the pairs and nests in mid-season suggests that exclusive areas are maintained early in the season, although not later on. I did not study the early establishment of any population in northern Alaska in detail and cannot say by what means this spacing is accomplished, but brief observations of the build up by the long-tailed jaeger population at Cape Sabine in 1959 suggest that territories were exclusively maintained in late May by the usual means of aerial announcements and frequent defense.

The periphery of the territories are not defended during nesting and rearing of young. At that time absolute defense is confined to a core area of territory around the nest, approximately 400 to 600 yards in diameter in both species. These jaegers appear to forage both on their own territories and on the outer fringe of other territories. Territorial announcements were frequently observed in such fringe areas, a fact suggesting that both species defend this part of their territories to the extent that they announce to another jaeger which they encounter there. Neither of these species was observed patrolling the boundaries of their territories, and neither uses a ground announcement display. Both species seem to be adapted to defending a moderately large territory.

Parasitic jaegers, unlike the other two species, frequently hunt in pairs, and the chicks are left alone. Also, the core of the territory is undefended while the adults forage. The mates cooperate in capturing small birds, and presumably their foraging in pairs is an adaptation for this means of hunting. At the Kaolak River they were observed hunting over the willow shrubs along the river when flocks of fledgling passerines were congregated in that habitat. The behavior was not a significant proportion of their foraging, and most food was apparently obtained on upland tundra.

Territoriality in the long-tailed jaeger is similar to that of the pomarine jaeger in that both species are adapted to exploit microtine rodent populations, as indicated by the readiness with which they adjust their population density to exploit these rodents. However, the long-tailed jaeger appears to require a larger territory than the pomarine jaeger, and its average territory at maximum density is 5 to 6 times larger than that of the pomarine jaeger at its maximum density. They also differ in that the long-tailed jaeger lacks a ground announcement in territorial defense, and for most of the season, only a central area of the territory is completely defended. This method of defending a territory economizes on the time and energy spent in these activities. Manniche (1910) observed this species nesting in conjunction with a high population of the collared lemming (*Dicrostonyx groenlandicus*) in northeast Greenland. While he gives no information on the density at which they nested, his comments clearly indicate that the territories were exclusive and suggest that they were nesting at a density higher than any witnessed in northern Alaska. As yet we do not know the degree to which this species can compress its territory.

At Cape Sabine, in 1959, all three species of jaegers nested at an overall density of 33 pairs on 11 square miles, or three pairs per square mile. Territorial defense by the long-tailed jaeger in this situation did not appear more intense than at the Kaolak River and, in general, the characteristics of the areas defended remained as described above. An exception to this generality was noted where one long-tailed jaeger nest was close to the edge of a pomarine jaeger territory, and a long rocky ridge was defended as an absolute boundary by both pairs.

Although the territorial systems of the pomarine jaeger and the long-tailed jaeger show adaptations for exploiting microtine rodent highs, there is an important difference between them in the tendency to establish permanent territories. Manniche (1910) described territorial and incipient breeding behavior in a long-tailed jaeger population in northeast Greenland in a year following a lemming high. The birds occupied and defended territories as they had in the high year, but soon departed without attempting to breed. I observed similar incipient breeding by long-tailed jaegers on Banks Island in 1963 (Maher, 1970b).

The pomarine jaeger did not exhibit this behavior at Barrow in 1957, and the birds which arrived in the spring passed through without pause. In 1958, an initial spring population build-up of 7 to 10 individuals per square mile was followed by the departure of the entire population, and in 1959 there was a similar response except that three pairs remained and bred. The difference in behavior of the two species in post-lemming high years suggests an important difference in their territorial systems.

Manniche's (1910) observations in Greenland, my own observations on northern Ellesmere Island and Banks Island (Maher, 1970b), as well as the population studied at Kaolak River, all document a tendency for the long-tailed jaeger to establish permanent territories; yet the species is also able to concentrate and to take advantage of microtine rodent highs, as at Cape Sabine. These facts suggest the following model for the territorial system of the long-tailed jaeger.

Long-tailed jaegers tend to return to an established territory, particularly if breeding was successful in the previous year. Among spring migrants there will be some jaegers without an established territory and some that have failed for one or more seasons and that consequently have a weak territorial attachment for a specific area. These birds would make up an opportunistic segment of the population, able to take advantage of a suitable area with a high food supply by settling to breed.

The pomarine jaeger, on the other hand, appears to be completely nomadic in that it does not form any territorial or even regional attachment that lasts beyond one season. The difference in the response of the species at Barrow in 1957, 1958, and 1959 from the response of long-tailed jaegers in low lemming years suggests that it establishes a territory only in association with an abundant food supply and that the population response is directly related to the distribution and density of that food supply. This point is also supported by the observations on the transient pomarine jaegers at Cape Sabine.

Evidence regarding the attachment of parasitic jaegers to a territory is ambiguous. In the temperate maritime population on Fair Isle the pairs return to the same territory each year (Williamson, 1965). Evidence from northern Alaska suggests that some pairs will repeatedly return to the same territory, or at least the same area as at Barrow; but in other instances the evidence of plumage combinations of the pairs suggests that pairs occupying a territory are frequently changed between years.

In some years on Fair Isle more than 50 per cent of newly established pairs failed to remate the following year (Williamson, 1965). The high divorce rate of young birds was attributed to asynchronous return to the colony site by inexperienced individuals. Williamson (1965) also noted a very high (20 per cent) failure to return among birds that had bred only once, compared with approximately 10 per cent failure to return among more experienced birds.

The rapid turnover observed on some territories in northern Alaska thus could be a reflection of occupation by inexperienced birds. Asynchronous return and failure to return could break up or eliminate such pairs at a high rate until a pair gained experience, after which territorial occupancy should stabilize for a few years.

Some Aspects of Breeding Biology

The Pomarine Jaeger

Habitat and nest sites: — The relationship of the pomarine jaeger population to the spring density of the brown lemming has already been indicated (Table 3). Clearly the level of the lemming population when pomarine jaegers arrive influences whether or not they breed and the density at which they breed. Factors other than food supply, however, also seem to influence the selection of territories.

Throughout its breeding range the pomarine jaeger prefers marshy areas as nesting habitats (Brandt, 1943; Pitelka *et al.*, 1955b, and Dement'ev *et al.*, 1951). In their study of the pomarine jaeger at Barrow in 1952 and 1953, Pitelka *et al.* (1955b) found that "breedings pairs may settle almost anywhere, but they settle in greatest density where marshy flats or poorly drained lowlands are most extensive. This is the habitat of their chief prey, the brown lemming."

In 1956 and 1960 I studied the rate of population build up on different habitats at Barrow. In 1956 two areas were censused in early June; one was a representative part of the main study area (Figure 15) and consisted of Central Marsh and adjacent polygonal tundra. The second area was one and one half square miles of well drained (mesic) tundra four to five miles south of the Naval Arctic Research Laboratory (Figure 15). In 1960 four areas were censused; the area used in 1956 on the main study plot was subdivided into a polygonal tundra area and Central Marsh, the mesic tundra area was reused, and also a second marsh off the main study area.

The results in 1956 (Table 13) indicated a slower build up of population density on the mesic tundra than in the marsh habitat. The final breeding density of 17 to 18 pairs per square mile on mesic tundra was less than the breeding density on the marshy area used for comparison but only slightly less than the average density on the entire area. The rate of population build up on the four different habitats in 1960 appeared to be approximately the same (Table 14), except for Central Marsh, which, however, included flocks of roosting pomarine jaegers. An early uniform occupation of the tundra is indicated in contrast with 1956.

The early preference for marsh habitat in 1956 and the lack of any clear preference in 1960 can be explained by the difference in spring lemming density in the two seasons. Lemming density was estimated to be considerably higher in 1960 than in 1956 (Table 3); furthermore, Thompson (1955) found in 1953 that spring lemming density was lowest on mesic tundra (36 per acre) and highest in marsh (71 per acre). This situation may have occurred in 1956, although there is no direct evidence for it, and the slow build up on mesic tundra could be related to a low food supply. In 1960, in contrast, the lemming population was obviously much higher than 1956 in all habitats, so that jaegers occupied all habitats at the same rate.

In both years the data emphasize that jaegers roost in flocks on the snow-covered lake surfaces and the level surfaces of low-lying marshy areas upon ar-

TABLE 13

Establishment of pomarine jaeger pairs on two types of tundra, Barrow 1956

Date	*Central Marsh and polygonal tundra*	*Mesic tundra*
June 9	15–20[2]	1
13	25–30	—
15	30	4–5
25	25	—
27	—	17–18

[2] pairs per square mile.

TABLE 14

Establishment of pomarine jaeger pairs on three types of tundra, Barrow 1960

Date	*Central Marsh*	*Marsh*	*Polygonal tundra*	*Mesic tundra*
26 May	7 ±[a]	11	9–10	12–13
28	11–12	11–12	16–17	10–11
31	40–41[b]	10–11	—	9
1 June	49[b]	—	12	—
2	30[b]	10–11	22	10
6	33[b]	8	14–15	11–12
Breeding population	22		24	

[a] Pairs per square mile.

[b] Includes some flocks of jaegers.

rival in the Barrow area. This preference for low level expanses is clearly indicated by the nesting sites chosen at Cape Sabine. At Cape Sabine the topography is rolling, with long, narrow, stony ridges connected by broad, shallow swales with wide *Carex* meadows at the bottom. The three breedings pairs of pomarine jaeger established in the swale bottoms. A fourth pair had its territory in the same habitat. Transient pomarine jaegers, which defended territories there briefly in July, also occupied low marshy areas. At Barrow the earliest territories occupied were situated along topographic features such as the beach ridge or Wohlschlag Slough (Figure 15), where the local relief provides prominent mounds. Such prominences are the first spots to be clear of snow and seem to function in habitat selection by providing elevated situations from which the territory can be surveyed, or on which a defending bird can make itself conspicuous.

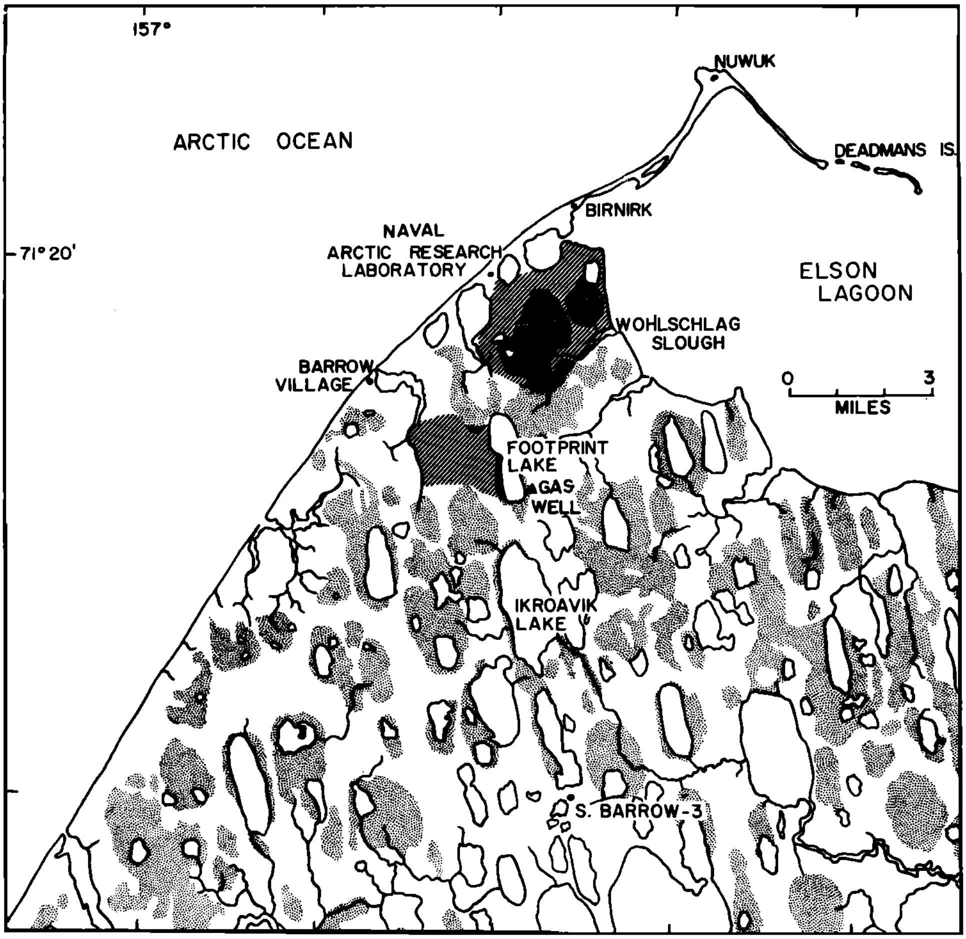

Figure 15. Map of the Barrow area. The main study plot used in 1956 and 1960 is the upper area with diagonal shading. The shaded area west of Footprint Lake is mesic tundra used in 1956 and 1960 to study establishment of the pomarine jaeger population in that habitat. Marshy areas are stippled.

In summary, the proximate stimuli that seem to govern the selection of a nesting area by the pomarine jaeger are: (1) The presence of a sufficient food supply, the chief requisite in this regard being a sufficiently dense population of *Lemmus,* or rarely another microtine rodent; (2) broad flat areas, such as swales in regions with rolling topography, or drained lake beds and marsh flats on the coastal plain; and (3) some mounds that provide lookout sites on which the birds are conspicuous.

Nest situation and construction: — The nest is usually situated on a slight elevation. In marshy areas they are on ridges that rim the low-center plygons, or on sphagnum mounds (Pitelka *et al.,* 1955b). In better drained sites they are sometimes located on level ground.

The nest bowls are made in a manner similar to that employed by the kittiwake and other larids (Paludan, 1955). Nest construction was observed several times, always at a considerable distance so that full details were not obtained. Both sexes have been observed constructing nests. In all instances the bird sat down with an exaggerated posture with the breast thrust forward as if settling down on a clutch of eggs. It then squirmed from side to side several times as if scraping out a nest hollow. This was usually repeated several times, the bird standing up and turning so as to face in a different direction each time. One female that was observed making a nest bowl followed the scraping motion by standing and turning around in the nest bowl as if trampling it. Another female, while standing between scraping bouts, rocked from side to side as if using her feet in alternate scraping motion. The use of the feet to push material outward in the manner of the kittiwake (Paludan, 1955) was not confirmed.

A male that was observed nest-making followed the scraping operation by "mewing" (Tinbergen, 1959) and was joined by the female who also "mewed." The female then sat in the nest, and the male began tossing grass blades at her over his shoulder while standing facing away from the nest. This grass tossing was observed frequently in the incubation period as part of the nest relief ceremony. It is probably the source of much of the loose grass lining in some nests. Jaegers were never seen carrying nesting materials to the nest sites. However, I observed one nest in 1960 situated in a marshy site that was definitely built up with hay by the jaegers in an apparent attempt to elevate the nest in the melt-off period.

Time of egg-laying and interval between eggs: — The time of egg-laying was determined in only three instances at Barrow in 1956. One was known to have been laid between 1900 on 17 June and 1000 on 18 June. Two others were known to have been laid in midday. One was found freshly laid with a few drops of uncoagulated blood on the shell at 1130 on 19 June, and another was laid between 1000 and 1630 of the same day. The observations suggest no definite period of the day in which the eggs are laid in this species.

The interval between eggs in a clutch averaged 1.7 days for ten clutches in 1956 and 2.2 days for ten clutches in 1960. The mean for both seasons was 1.95 days. Observations were made every 12 hours in 1956 and every 24 hours in 1960. The greater margin of error in 1960, because of less frequent nest visits, probably accounts for the different intervals in the two years. Three day intervals recorded in that year are actually between two and three days, and more likely are nearer to two days.

Renesting: — Pomarine jaegers rarely renest, although I have several records for Barrow. Two pairs renested in 1956. One pair had its second clutch by 25 June; the second pair apparently produced its second clutch in mid-July. This nest, found on 20 July, was destroyed in incubation.

Three pairs also renested in 1960. A pair with one egg on 8 June had the egg smashed on 9 June. The pair established a new nest site on the territory and produced two more eggs, the first one of which was found on 11 June. A second nest with one egg on 8 June was flooded by melt water on 16 June; a clutch of two eggs was produced about 22 June, also on the same territory. The third pair had two eggs on 16 June, which were found smashed on 25 June. A second complete clutch was produced, one egg of which was laid on 26 June.

Pomarine jaegers will also desert their nest if disturbed during egg-laying. One pair disturbed by erection of a blind near the nest after one egg was laid abandoned the nest and laid the second egg at a new site on the same territory.

This species will also remate, although rarely, if one mate is lost. One male remated in 1956 after his first mate was found dead on 28 June. A second female was on the territory the next day, and on 30 June a third female with very dusky plumage was on the territory. The male mated with the latter female, and a nest with two eggs was found on 9 July. By extrapolation from hatching dates, the dates of these eggs were 7 and 9 July, nine and eleven days after the first mate was lost.

Abnormal eggs: — Only one clutch of obviously aberrant eggs was noted in approximately 300 sets. In 1956, at Barrow, one female produced a clutch in which the usual olive brown color was missing; the eggs were white with some sienna speckling. One of these eggs was also abnormally large. A similar condition is known to occur in eggs of herring gulls (*Larus argentatus*), in which the olive brown pigment layer is missing and the egg appears light greenish blue (Tinbergen, 1953). The condition may be genetic, as the same gulls produced these atypical eggs in successive years.

The second egg of one pair in 1960 was less than one half normal size and contained only albumin; thus the female ovulated only once. No other egg was laid.

Clutch size: — The normal clutch of the pomarine jaeger is two eggs, though one egg clutches occur occasionally. Clutches of three eggs have been reported, but their validity has been rightly questioned by Pitelka *et al.* (1955a). Pitelka found no single egg clutches in 1952, and estimated that, five to ten per cent of the nests contained a single egg in 1953.

Single egg clutches occurred in five (4 per cent), of the 125 nests seen at Barrow in 1956. In 1960 adequate clutch size data were obtained for 119 clutches, 113 of which were complete, and six of which (5 per cent) consisted of one egg. In the total sample of 17 clutches from Pitt Point in 1957 only two (12 per cent) contained one egg.

Single egg clutches did not occur in any of the sparse populations studied.

Incubation: — The incubation period of this species had not been determined accurately before this study. Pitelka *et al.* (1955b) estimated it to be 27 or 28 days on the basis of three admittedly incomplete records. The date of laying of either the first or second egg was considered the beginning of the incubation period for that egg, since incubation apparently starts as soon as the first egg is laid. The incubation period until the egg was pipped averaged 23.6 days (extremes 23 and 25 days) for 14 eggs, and it averaged 25.9 days (extremes 25 and 27 days) for 11 eggs until the egg hatched.

As has been pointed out by Pitelka and others, both sexes share equally in the incubation.

The Parasitic Jaeger

Habitat and nest sites: — The parasitic jaeger utilizes a wider range of habitats than the pomarine jaeger, and thus it is difficult to analyze the factors to which the birds respond when selecting a territory.

I have records of four parasitic jaeger nests at Barrow. One was located in an area of low polygons in an extensive marsh, two were situated on high polygons on the rim of a marsh, and the fourth was in a polygonized area behind the Naval Arctic Research Laboratory, isolated from the adjacent tundra by an extensive junk pile on the south and west and by a lake on the east (Figure 3).

This site was occupied in 1956, a year of maximum pomarine jaeger density, and probably the dense pomarine population was at least partly responsible for use of this peripheral location.

A nest at the Meade River Coal Mine in 1957 was on a sphagnum mound four feet high situated in a wet *Carex* meadow at the margin of a pond. One at Pitt Point in the same year was on a sedge slope 100 yards from the edge of a slough.

Three territories were occupied by parasitic jaegers at the Kaolak River in the years 1957 to 1960. Two were on river terraces, the third was in a drained lake basin on the upland (Maher, 1959). All three were marshy areas with low center polygons, sphagnum mounds, and frost hummocks. Another river terrace with similar drainage and topography was occupied by long-tailed jaegers in these same years.

At Peters and Schrader lakes, two large alluvial fans were each occupied by a pair of parasitic jaegers. The fans are level and marshy, and both have some polygons developed. They are the only two areas of marshy land in the vicinity.

One of four nests at Cape Sabine in 1959 was on a well-drained terrace along a tundra stream, one was in an area of wet *Carex* marsh on a river terrace, a third in *Carex* meadow on a slope, and the fourth was located in *Carex* meadow just below the crest of a rocky ridge.

In general in northern Alaska, the parasitic jaeger seems to prefer marshy situations near a body of water for a nesting habitat, an elevated site for the nest, and either one or more mounds or a nearby slope to serve as an observation post. These are the situations in which it was nesting at Peters and Schrader lakes, Meade River Coal Mine, the Kaolak River, and at Barrow in 1955 and 1957. Parasitic jaegers show a greater affinity for bodies of water than the other two jaegers. The presence of open water, a lake, pond, or river, may be a decisive factor for this species in areas with well developed drainage. This is suggested by the two pairs at lakes Peters and Schrader, and the nest sites chosen by the species at the Kaolak River and at the Meade River Coal Mine. However, when nesting in competition with a very dense population of pomarine jaegers, as at Barrow in 1956, or when competing with moderately dense populations of pomarine jaegers and long-tailed jaegers as at Cape Sabine, it appears to show greater latitude in its habitat selection.

Parasitic jaegers nested in the marshy river valley of the Kuskokwim delta (Brandt, 1943) and in wet tundra on Victoria Island (Parmelee *et al.*, 1967).

Nest situation and construction: — The nest is situated on a slight eminence, from a few inches to several feet above the surrounding terrain. Typically the raised edge of a low center polygon, or the top of a frost hummock is used. Exceptionally, in well drained featureless terrain, it may be on level ground. The nest is a shallow unlined scrape or depression.

I have one observation suggesting that nest-building is accomplished in the same manner as by the pomarine jaeger.

Renesting: — Perry (1948) reported that one pair of parasitic jaegers, which lost its first clutch, produced a second clutch nine days later. Renesting was not observed in this study.

Clutch size: — Perry (1948) found that three of 28 clutches contained one egg, 25 or 90 per cent, contained two eggs. I have records of 21 parasitic jaegers nests, 18 with two eggs and three with one egg. Most of these, including the three single-egg nests, were found late in the incubation period. From this sample we can say that at least 85 per cent, and possibly more, of the clutches contained two eggs. Williamson (1965) noted two females that produced clutches of three eggs on Fair Isle.

Incubation: — I have been able to determine the incubation period for only one egg. The second egg of the pair nesting at Barrow in 1956 was laid between 1330 and 1900 on 20 June. The egg was pipped in the evening of 13 July, and the chick was hatched, dry and almost fluffed at 1000 on 17 July. The incubation period was 26.5 days. The time to pipping was 23 days, the hatching interval 2.5 days. Perry (1948) reported the incubation period to be 25 to 26 days for 16 observations. Both sexes share equally in incubation like the pomarine jaeger.

The Long-tailed Jaeger

Habitat and nest sites: — It is difficult to differentiate the nesting habitat of the long-tailed jaeger from that of the parasitic jaeger in northern Alaska. The three nests that I have seen on the southern part of the coastal plain have been in low center polygons, in high center polygons, and on a marshy river terrace. These are the same kinds of situations utilized by parasitic jaegers on the coastal plain. At the Kaolak River there appeared to be some separation of the two species with regard to the nest sites used. In this area eight territories were used three or four times in four successive seasons. Six of these were near the top of the sloping sides of the upland, four were associated with swales, one in an area of barely perceptible slope at the top of a drainage, and one was in a drained lake basin. Only two were on river terraces; one was a very marshy low-center polygon area, the same habitat utilized by two of the three parasitic jaeger pairs, and the second was on a high river terrace with tussock vegetation on it. Five additional territories were occupied once. Two were in the upland lake basin, two in a high center polygon area on river terraces at the base of slopes, and the fifth, in a very marshy low-center polygon area at the northeast end of the plot. In general at the Kaolak River it appeared that the long-tailed jaeger prefers situations that are more elevated and drier than situations the parasitic jaeger prefers, and that long-tailed jaegers prefer a situation on or near a slope. They differ from parasitic jaegers in that they seem to show no attachment to bodies of water in selecting a nest site.

Cape Sabine has more diverse habitat than the Kaolak River. The population of the long-tailed jaeger in 1959 was 25 pairs on 11 square miles. Here the species showed a preference for elevated situations just below the rocky tops of ridges or on the slopes below. Drainages, which here were broad wet sedge meadows, were usually avoided.

Nest situation and construction: — The nest of the long-tailed jaeger, like that of its two congeners, is an unlined bowl usually situated on a mound that elevates it slightly above the immediate terrain. I have never observed a long-tailed jaeger constructing its nest, though it is presumably done in the same manner as the pomarine and parasitic jaegers.

Interval between eggs: — Little information was obtained on this point. For two clutches it was approximately 48 hours.

Renesting: — No long-tailed jaeger pair renested at either the Kaolak River or Cape Sabine after its first nest was destroyed. There is a record of one pair renesting on Ellesmere Island (Maher, 1970b).

Abnormal eggs: — The first egg laid by a pair at Cape Sabine was almost twice as long as a normal egg and appeared to have a thin shell. The egg disappeared in the incubation period.

Clutch size: — Nine of 48 clutches (19 per cent) consisted of one egg (Table 15); 39 (81 per cent) consisted of two eggs. All clutches from the Kaolak River (28 of the 48) were located between 22 and 30 June, well towards the end of the incubation period. Since eggs are occasionally lost during incubation, it is not certain that nests located late with one egg have not lost a second egg. Two of the one-egg clutches in the Kaolak River area were produced in 1958 and 1959 on the same territory and presumably by the same female.

TABLE 15

Clutch size of the long-tailed jaeger

Locality	*Year*	*One egg*	*Two eggs*	*Total*
Meade River Coal Mine	1957	2	1	3
Kaolak River	1958	3	8	11
Kaolak River	1959	2	6	8
Kaolak River	1960	1	8	9
Cape Sabine	1957[a]	0	1	1
Cape Sabine	1958[a]	0	2	2
Cape Sabine	1959	1	13	14
Total		9	39	48

[a] Data from Childs, 1969.

Incubation: — Information on the incubation period of this species is scant. Manniche (1910) says that it is 23 days. Parmelee *et al.* (1967) observed an egg that hatched in 23 to 25 days. Maher (1970b) reported a mean incubation period of 24.2 days for five eggs on Ellesmere Island.

The incubation period was not determined in this study, although the incubation time to pipping was determined for one egg, which was still wet when found on 15 June 1959 at Cape Sabine. On 9 July it was pipped. The following day the chick punctured the shell and was still alive; on 11 July it was gone. The time from laying to pipping was 24 days. The egg may have hatched late on 10 July, which would have given a 25-day incubation period. I used 25 days as the incubation period in extrapolating egg-laying dates.

Both sexes share equally in the incubation.

Summary and Discussion of Breeding Biology

The breeding biology of the three jaegers is very similar. Considerable overlap is shown in the nesting habitat utilized, but pomarine and parasitic jaegers tend to occupy marshy areas, while the long-tailed jaeger tends to use drier more elevated situations. In addition, the parasitic jaeger prefers to nest near bodies of water, especially in the foothills and mountains. This may be a significant difference in habitat requirements between the parasitic and long-tailed jaegers in these areas. All three species locate the nest on an eminence, however slight. Nests are shallow unlined scrapes. Materials such as dry grass and vegetation, or lichens, which are sometimes found in the nest bowl, appear to accumulate from nest-inviting and incubation-relief ceremonies, in which the inviting or relieved bird stands before the nest, facing away from it, and tosses scraps of loose vegetation back over its shoulder toward the partner on the nest.

None of the three species shows much inclination to renest following the loss of a first clutch. There are two records of the pomarine jaeger renesting at Barrow in 1956 and three from 1960, but none for the parasitic or long-tailed jaeger. Perry (1948) recorded one parasitic pair renesting, and Maher (1970b) reported one pair of long-tailed jaegers renesting on Ellesmere Island. Clutch size for the three species is normally two, occasionally one. One-egg clutches for the pomarine jaeger were estimated by Pitelka *et al.* (1955b) to be 5 to 10 per cent in 1953. They were about 5 per cent in the combined populations at Barrow in 1956 and 1960 and at Pitt Point in 1957. Fifteen per cent of clutches laid by parasitic jaegers contained one egg and 19 per cent of those laid by long-tailed jaegers. Perry (1948) found 10 per cent single-egg clutches of the parasitic jaeger. A difficulty with the Alaska sample is that many clutches were found late in the incubation period, and hence a few may be nests from which one egg had been lost. Egg losses are generally low, however, and these figures are probably reasonably correct.

The incubation period for the three species appears to be about the same. The pomarine jaeger takes 23.6 days until the egg is pipped and 26 days to hatch. The parasitic jaeger (one determination) takes 23 days until the egg is pipped and 26.5 days to hatch, and the long-tailed jaeger (also only one determination) takes 24 days until the egg is pipped, and probably an average of 24 to 25 days to hatch.

In all three species both sexes share equally in the incubation.

Gonad Cycle

The reproductive cycle of the three jaegers was studied because the size of the gonad, of the male particularly, provides information on the length of the period of sexual activity and because the presence or absence of a brood patch is an indicator of the recent reproductive status of an individual.

Seasonal changes in the size of testes or ovarian follicles have been widely used as a means of studying the reproductive cycle of birds. In this study the left testis was measured in each specimen. This has been the usual procedure in studies of male reproductive cycles since Johnston's (1956) study of the reproductive cycle of the california gull (*Larus californicus*) demonstrated its validity. In rare instances when the left testis was destroyed by shot, the measurement of the right testis was used. The diameter of the largest follicle was used for the study of the ovarian cycle. Measurements made early in 1956 were made with a millimeter rule; all others were with a pair of calipers. Volumetric measurements of testes are considered ideal, although in practice volume is usually calculated from measurements of length and width (Blanchard, 1941; Johnston, 1956) as was done here.

In 1956 and 1960, particularly in the early part of the season, I collected many of the specimens myself and measured gonads shortly after death. Most of the specimens collected later in those seasons were birds found dead of natural causes or killed by humans. In 1957, 1958, and 1959, the jaeger population was sampled with the help of Eskimos and others, and the specimens were kept frozen at the Naval Arctic Research Laboratory and examined at the end of the season.

The Pomarine Jaeger

Testis cycle: — Testes volumes from breeding and non-breeding populations are analyzed separately. The sample from breeding populations includes specimens from Barrow and vicinity in 1956 and 1960, Wainwright in 1956, and Pitt Point in 1957. The non-breeding populations were from Barrow and vicinity in 1957 and 1958, and Wainwright in 1957.

Means were calculated for both breeding and non-breeding populations for specimens taken up to 15 June, and for specimens taken from 16 to 30 June to compare the testis size of arriving birds (Figures 16 and 17).

Several conclusions can be drawn from these data. Male pomarine jaegers arrive in northern Alaska with their testes already at or near maximum size in both breeding and non-breeding years. The means for the first half of June, 1023 mm^3 for non-breeding populations, and 1167 mm^3 for the breeding populations, are not significantly different ($t_{27} = 0.85$, $p = .5$). The means for the latter part of June, normally the egg-laying period, show a considerable difference. The mean testes volume of the breeding birds declined slightly to 1130 mm^3 while that for the non-breeding birds declined significantly to 602 mm^3 ($t_{18} = 2.4$, $p = .05$). The decline continues through the season in both populations at what appears to be a constant rate, though specimens from July and August from breeding populations are few. The variation in testes volume in the population is greatly increased in the latter part of the season.

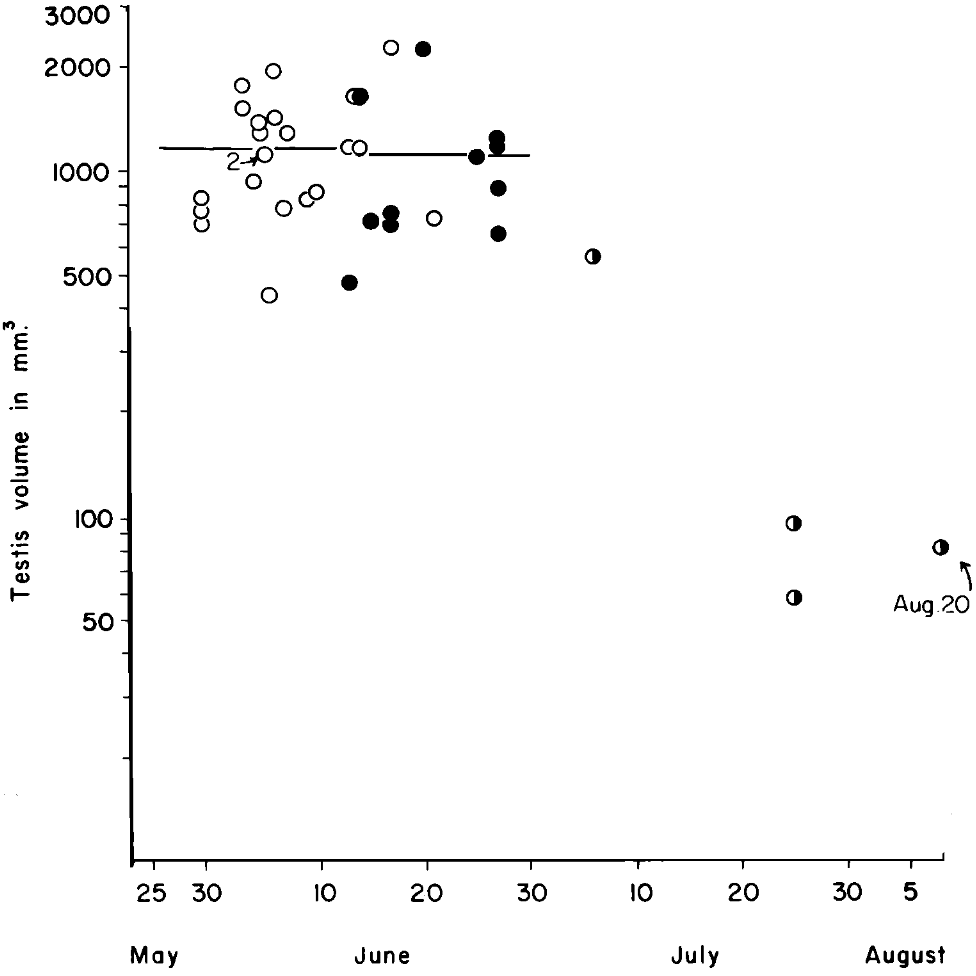

Figure 16. Testis volume of breeding pomarine jaegers at Barrow. The two horizontal lines indicate mean testis volume for the period spanned. Solid symbols indicate the presence of a brood patch; half-solid symbols, a regressing brood patch.

The question arises as to whether these two populations are of the same age composition and hence directly comparable. The plumage characteristics of jaegers seen in northern Alaska are variable. Pitelka *et al.* (1955a) considered that only two plumage classes were represented in the Barrow population of 1952 and 1953 and suggested a two-year plumage cycle for the species. However, the matter is complex, and detailed studies of the plumages of the pomarine jaeger remain to be done. The important point is that individuals of all the plumage types that have been observed on the breeding grounds are represented in breeding populations, and it is probable that all jaegers that migrate to arctic breeding grounds in summer are of breeding age.

Ovarian cycle: — Specimens from breeding and non-breeding populations are graphed separately (Figure 18). The data from 1957 are plotted to contrast

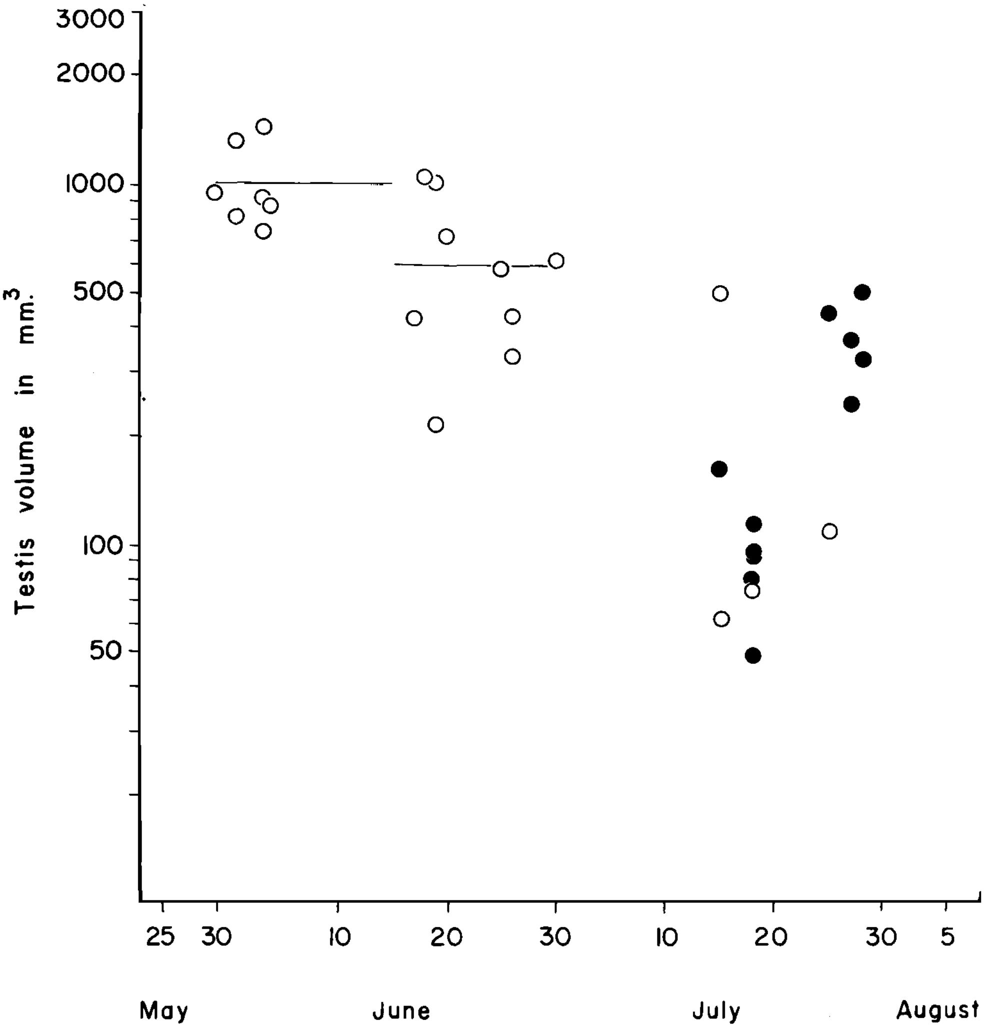

Figure 17. Testis volume of transient pomarine jaegers from coastal localities, either non-breeding or unsuccessful at breeding. The two horizontal lines indicate mean testis volumes for the period spanned. Solid symbols indicate evidence of a brood patch.

data from Barrow and Wainwright, where there was no breeding, with data from the breeding population at Pitt Point (Figure 19).

Breeding and non-breeding females show the same general trend in the development of the ovarian follicles as males do in the development of the testes. Females arrive in northern Alaska each year with ovaries at approximately the same stage of development, as indicated by the size of the largest follicle. The follicles of females that do not breed decline gradually in size through the season. The follicles of birds from breeding populations, however, show a rapid increase in size, already underway at the end of the first week in June. Too few data are available on breeding birds from the latter part of the season to compare follicle resorption with that of non-breeding birds.

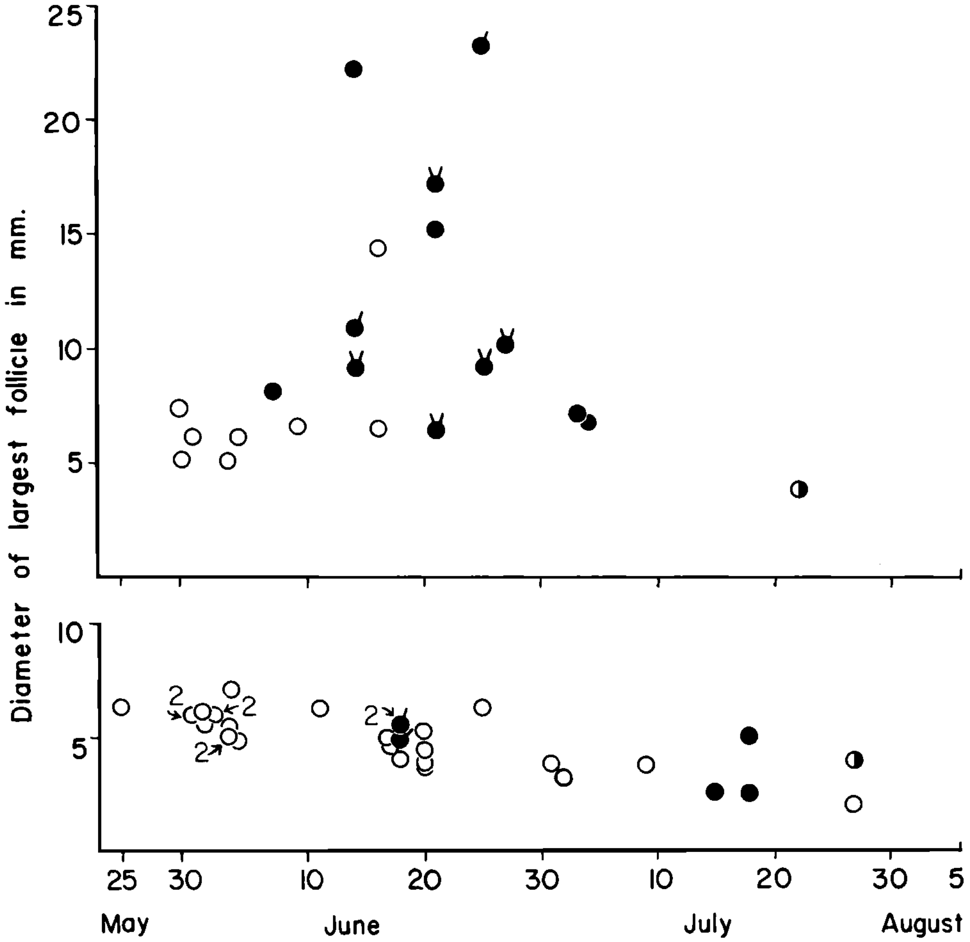

Figure 18. Diameter of largest follicle of locally settled, breeding (upper figure) and transient (lower figure) pomarine jaegers. Solid symbols indicate the presence of a brood patch; half-solid symbols, a regressing brood patch. Tags on symbols are the number of ruptured follicles.

The size of some follicles in ovaries with two follicles already ruptured indicate that more than two of them enlarge in the pre-egg period. In one such specimen the third follicle reached a diameter of 17 mm, in three others it ranged from 9 to 10 mm. Ova are more than 20 mm in diameter at ovulation.

The pomarine jaeger can replace eggs lost in the egg-laying season, as the herring gull does (Paludan, 1951), but it is not usual for it to do so. I have only one observation of a bird producing more than two eggs in one egg-laying cycle. One pair in 1960 produced a clutch of two eggs immediately following the destruction of their first egg. Several instances of clutch replacement are cited in the section on breeding biology.

Paludan (1951) notes that collapsed follicles were resorbed in the herring gull in at least nine days. Johnston (1956) states that they are resorbed in the California gull "rather rapidly, probably within a week." Resorption of col-

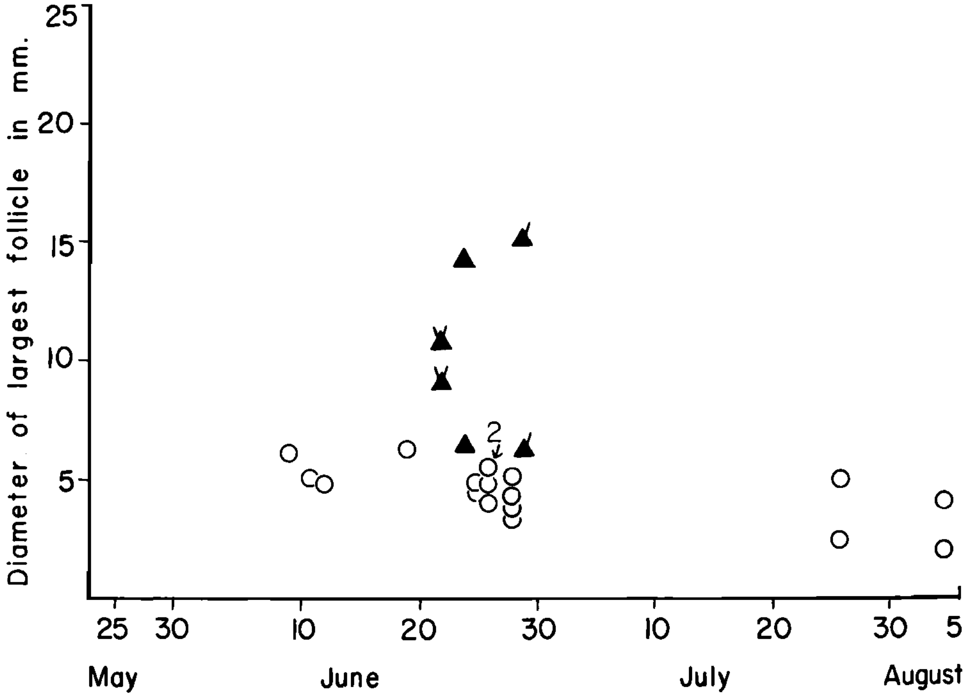

Figure 19. Comparison of diameter of largest follicle of pomarine jaegers at Pitt Point (triangles) and Barrow and Wainwright (circles) in 1957. Tags on symbols are the number of ruptured follicles.

lapsed follicles of the pomarine jaeger seems also to be very rapid. Two breeding female pomarine jaegers taken in early July had no visible collapsed follicles. One of these, which had two eggs on 18 June, was taken on 3 July, and the second one, dead about two days when found on 6 July, had had two eggs on 28 June. One collapsed follicle was plainly evident in a female taken 25 June with two eggs in the nest; the second had already been resorbed so much that it could not be identified macroscopically.

Brood patch: — Both male and female jaegers incubate, and both sexes develop a pair of oval bilaterally placed brood patches. These develop mostly in the apterylae between the axillar and abdominal branches of the ventral feather tract. The apterylae are normally covered with down, and the first external indication of a brood patch is the loss of the down. When fully matured the patch expands into the ventral feather tracts on either side and several adjacent rows of contour feathers are shed. This final phase of development occurs after the first egg is laid, since white contour feathers are frequently found then around the nests. The fully developed patch averaged about 60 by 40 mm on nine specimens. Regression of the patch is marked by the appearance of contour pin feathers in the pterylae and of down feathers in the apterylae. The replacement of the patch seems to have no relation to the annual molt.

The brood patch begins to develop just before the eggs are laid. The earliest specimen showing a developing patch in 1956 was a female taken on 7 June with a follicle 8 mm in diameter. A brood patch was not evident on two males taken on 7 and 9 June, nor on a female found dead on 9 June. This latter bird was probably dead for several days, for its largest follicle was only 6.5 mm. A female taken on 14 June with no ruptured follicles and an ovum 22 mm in diameter had a brood patch. A male taken on the same date did not. All adults collected after 21 June at Barrow in 1956 had signs of a brood patch. All of five birds taken on 27 June at Wainwright had brood patches.

At Pitt Point in 1957 two collected females which had ovulated one and two ova, respectively, had brood patches on 14 June. Two females that had not ovulated did not have brood patches on 16 June. The ova of these birds were 14.2 and 6.4 mm in diameter. Two females collected on 21 June had brood patches. One had ovulated twice, the other not at all; its largest follicle was 15 mm in diameter.

Five of the above specimens were females collected before they had ovulated. Two of the five had begun to develop brood patches, and three had not. The degree of enlargement of their largest follicle did not correlate well with the presence or absence of a patch. Thus, specimens with ova of 8 and 22 mm diameter had brood patches, and individuals with ova 6.5, 6.4, and 14.2 mm in diameter did not.

Most specimens taken after 10 July in both breeding and non-breeding populations had brood patches, indicating that they had attempted to breed earlier in the season (Figures 16, 17, and 18). The proportion of non-breeding birds declines after the end of June, and relatively few are present in the latter half of July.

These observations suggest that in years of low breeding effort by the pomarine jaeger population, the birds that do not breed leave the Arctic Slope early, or at least those parts represented by my samples. Further evidence of this departure is the absence of jaegers in the latter half of the summers of non-lemming years in various areas visited by investigators, and the westward movement of pomarine jaegers at Cape Sabine in 1959 in the latter part of June and early July.

Some breeding must occur in every season, as most adults along the coast after mid-July of all seasons have brood patches and presumably have attempted to breed but have failed. No individual in this sample was taken late enough to suggest that it had bred successfully, except one taken 20 August 1956. However, it should also be noted that no juveniles are represented in the samples, and none were ever observed until August 1960.

The Parasitic Jaeger

Because of the relative scarcity of parasitic jaegers, it was not feasible to collect breeding specimens. All of the material used in this study was obtained from Eskimos in coastal areas, except for five spring migrants from inland localities and one chick taken at the Kaolak River in 1958.

Testis cycle: — The testis volumes of all specimens are plotted in Figure 20. Only two specimens were taken early enough to be considered representative of arriving birds. These had the greatest testis volumes in the sample, and the trend in testis size for the remainder of the season is steadily downward. The sample indicates the comparatively late arrival of the species in the Barrow area and coastal localities in general. Few of them, even late in the season, had attempted to breed, as indicated by the small number with brood patches.

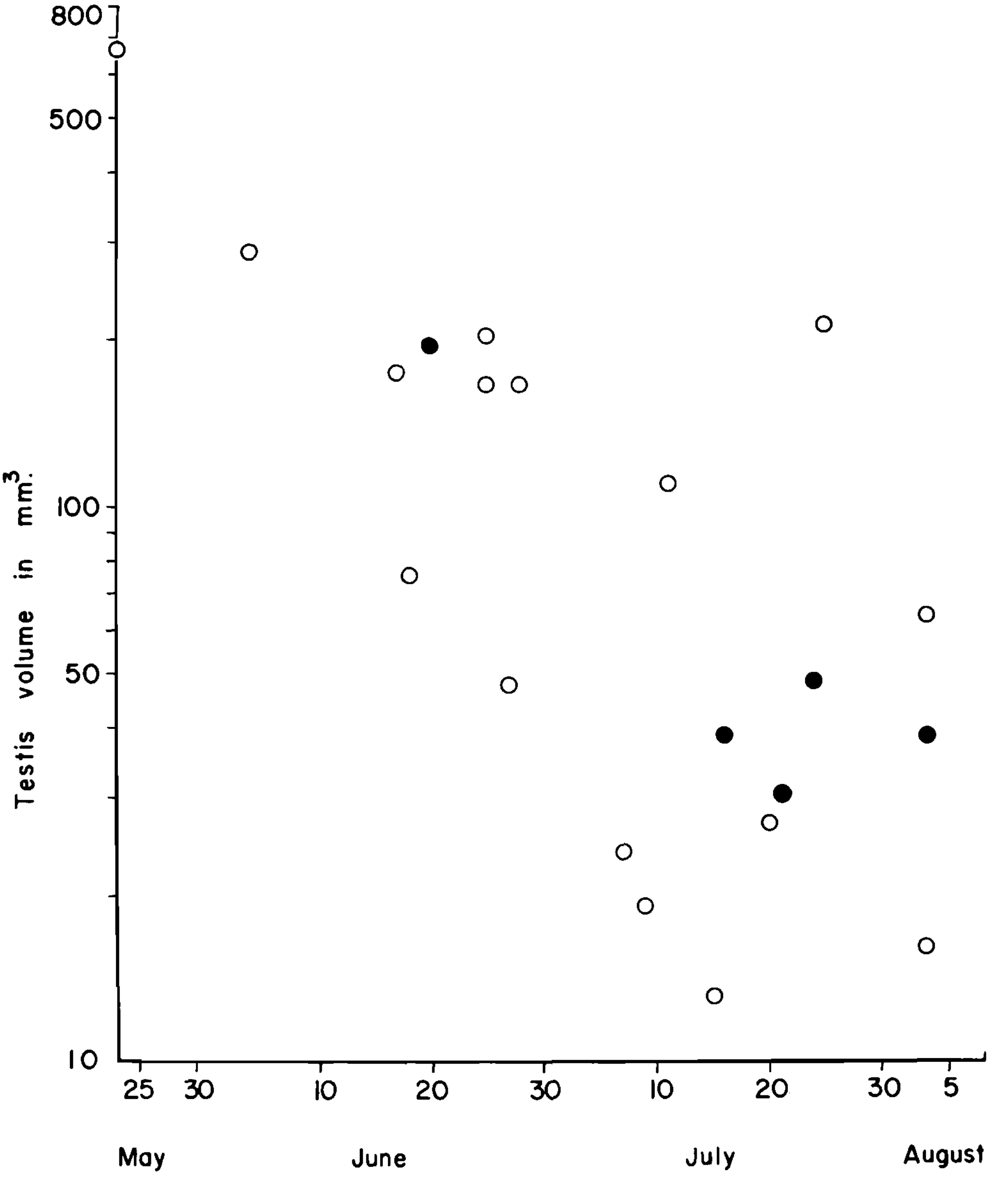

Figure 20. Testis volume of transient parasitic jaegers from coastal localities in 1957, 1958 and 1959, except one early June migrant from 20 miles south of Barrow. Solid symbols indicate evidence of a brood patch.

Ovarian cycle: — Only one of the female specimens is a spring migrant (Figure 21). This individual, collected at the Nigisaktuvik River on 31 May 1957, had ova enlarged to 6.4 mm in diameter. The six specimens from later in the season indicate a steady decline in follicle size.

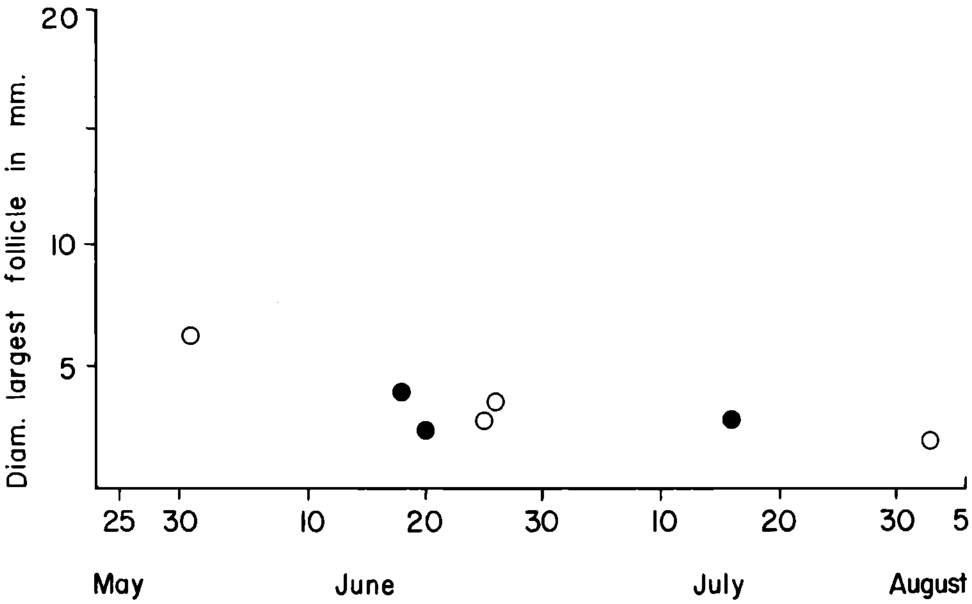

Figure 21. Diameter of largest follicle of transient parasitic jaegers from coastal localities in 1957 and 1958, except one late May migrant from 40 miles south of Barrow. Solid symbols indicate evidence of a brood patch.

The Long-tailed Jaeger

Few breeding long-tailed jaegers were collected. One pair was taken at the Meade River Coal Mine on 8 June 1957. Three other specimens were from inland; the remainder were non-breeding birds from coastal localities.

Testis cycle: — The testis cycle is similar to that of the parasitic jaeger (Figure 22). The testis is largest in newly arrived birds (one specimen) and decreases in size through the season. A large proportion of birds taken late in the season had had brood patches. None was collected late enough to have bred successfully.

Ovarian cycle: — The trend in size of the largest follicle of the female birds is similar to that of the parasitic jaeger (Figure 23). The arriving birds have ova above 6 mm in diameter. One breeding bird, which had produced two eggs, had a third ovum more than 6 mm in diameter. The data show a steady decline in size of ova through the season. The presence of brood patches indicated that a large proportion of the specimens had attempted to breed.

Summary and Discussion of Gonad Cycle

All three jaeger species arrive on the breeding grounds in breeding condition. In breeding populations, as exemplified by the pomarine jaeger, the male testes remain enlarged or even increase in size slightly in the egg-laying period, and then they regress at a more or less constant rate. The testes of non-breeding birds regress from their size at arrival, also apparently at a constant rate.

In females of all three species the largest follicles are about 6 mm in diameter at arrival on the breeding grounds. The follicles of breeding birds enlarge

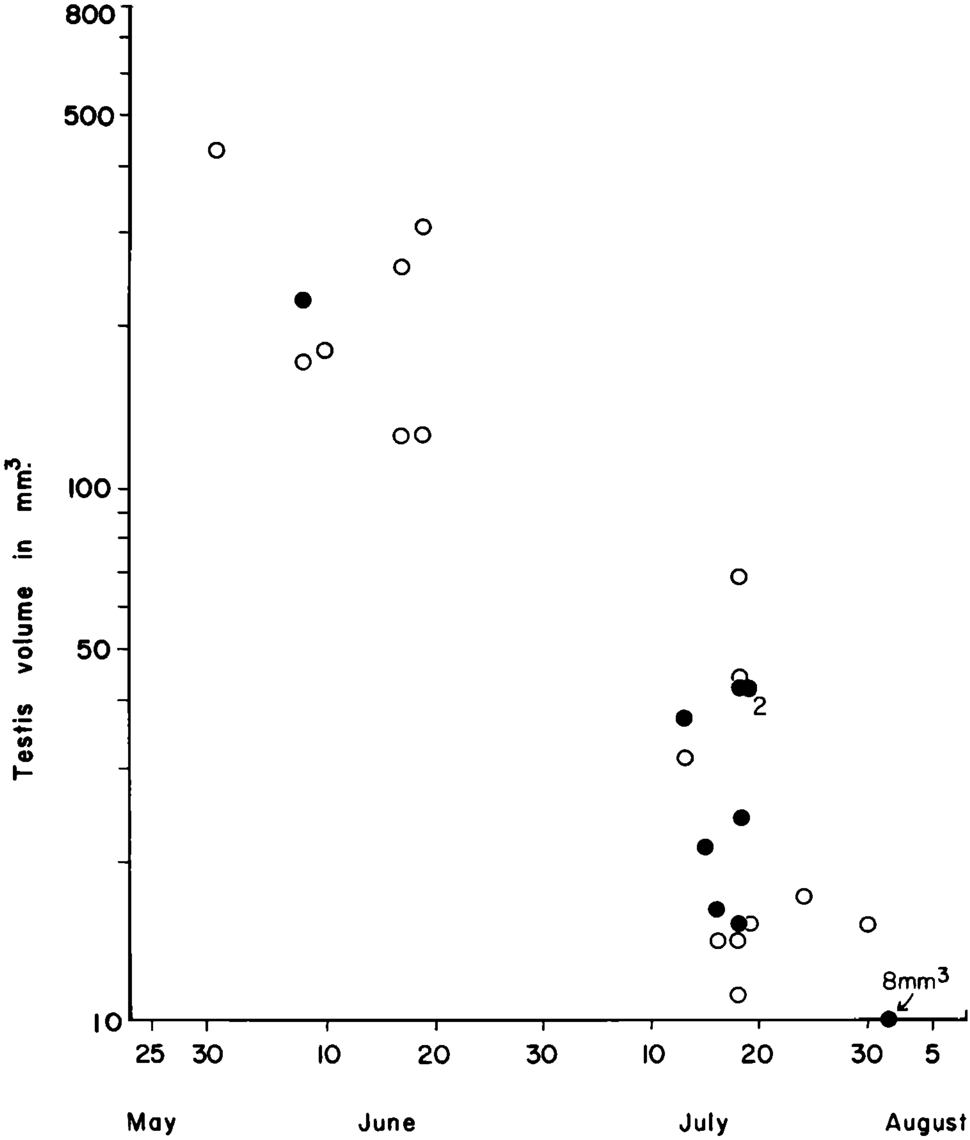

Figure 22. Testis volume of long-tailed jaegers, mostly transients from coastal localities in 1957 and 1958. Four early June specimens are from 40 to 60 miles south of Barrow. Solid symbols indicate evidence of a brood patch. Tags on symbols are the number of ruptured follicles.

rapidly and then decline after ovulation. More than two follicles begin to enlarge, but the production of more than two eggs is uncommon. The follicles of non-breeding birds decline in size through the season. Samples of breeding and non-breeding pomarine jaegers obtained simultaneously from Pitt Point and Barrow in 1957 showed this similarity in follicle size in all arriving birds.

The question of the factor or factors responsible for further development of the follicle and the production of eggs by the pomarine jaeger after arrival is an

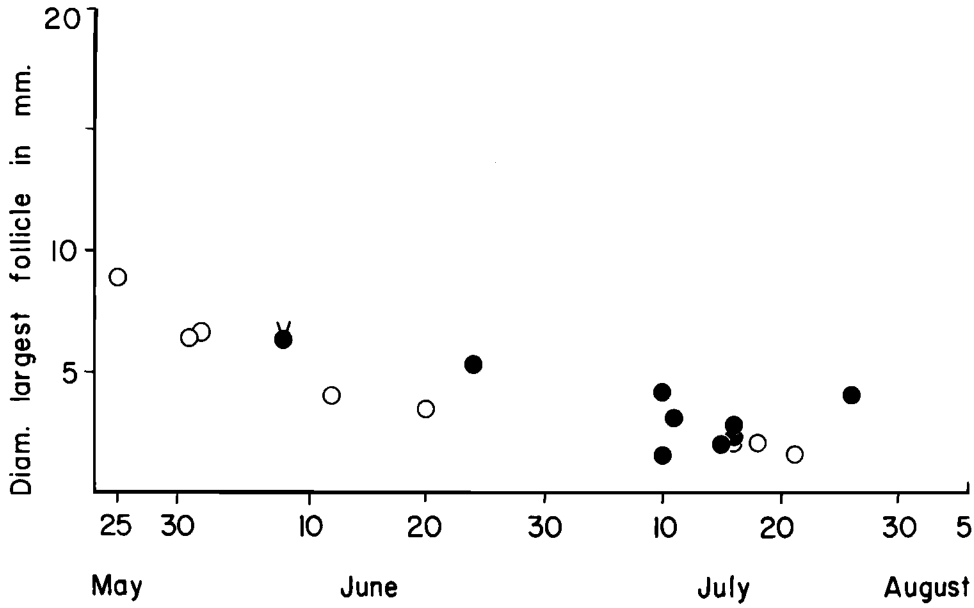

Figure 23. Diameter of largest follicle of long-tailed jaegers, mostly transients and migrants from coastal localities in 1957 and 1958. One late May migrant is from 40 miles south of Barrow, and one breeding bird is from the Meade River Coal Mine. Solid symbols indicate evidence of a brood patch. Tags on symbols are the number of ruptured follicles.

important one, and comparison of the populations at Barrow and Pitt Point in 1957 can clarify the factors responsible for it. A high population of *Lemmus trimucronatus* occurred at Pitt Point in 1957, while at Barrow, where a cyclic high had occurred in 1956, there were essentially no lemmings in 1957. No jaegers bred at Barrow that year, but a moderately dense population of pomarine jaegers bred at Pitt Point. In considering the different reproductive responses of the Barrow and Pitt Point populations in 1957, the influence of day length and climate can be ruled out as the two areas appear identical in these respects. For the females a difference between the two areas was the presence of territorial males at Pitt Point and, for both sexes, the availability there of an abundant food supply. It seems in this situation clearly to be food that stimulated reproductive activity, either directly in each sex or by stimulating the females indirectly through the aroused territorial behavior of males. The territorial response of transient pomarine jaegers to the high microtine rodent population at Cape Sabine was also clearly stimulated by food, even as late as early July.

Growth Characteristics

Growth rates can provide significant information on many environmental problems of a species, as well as the manner in which it has solved them. The growth rate of an arctic species, for example, must allow the chick to mature in the relatively short nesting season, and the growth period must be timed so that adequate food is available for the chick. The period in which the chicks are growing seems to be the critical one in the scheduling of breeding events in the north. Adjustments to the arctic regions, or any other environment with a restricted breeding season, involves the timing of other events in the annual cycle, particularly egg-laying and molt, so that the young may mature within the available time and so that the energetic demands of the population are optimally distributed in relation to seasonally changing food supplies.

Also, the rate at which an animal grows can provide insight into its ability to compete with co-existing species that occupy similar niches. Since the three species of jaegers treated here are all important predators in arctic ecosystems and since overlap is apparent in their ecological requirements, determination of their growth rates was an important aspect of this study.

Weights of penned wild chicks were used to study growth characteristics (see General Methods). Data on the pomarine jaeger are from Barrow in 1956 and 1960, and from Cape Sabine in 1959. Parasitic jaeger growth data are from Barrow in 1956 and Cape Sabine in 1959. Long-tailed jaeger growth curves are from the Kaolak River in 1958 and Cape Sabine in 1959.

Weights of the pomarine jaeger from 1956 and 1960 were averaged by age with the day of hatching as "day one." Mean daily weights, weight increments, and per cent instantaneous relative growth rates were calculated for each day or weighing interval. Standard deviation and standard error were calculated when there were five or more weights in the sample. All data are plotted on semilogarithmic grids. Data from different seasons and areas are treated separately.

The formula given by Brody (1945) was used for the calculation of the instantaneous relative growth rate in intervals between weighings. It is assumed that the growth rate between weighings is logarithmic even in the part of the curves where the growth rate is actually declining. This is the same method used by Dawson and Evans (1957) and Banks (1959).

The Pomarine Jaeger

The pomarine jaeger chicks grew rapidly for approximately the first ten days (Tables 16, 17; Figure 24). The mean growth rate steadily declined afterward, resulting in a weight curve that leveled off as growth essentially ceased. No true logarithmic growth phase is evident. Although growth approaches a constant rate from about day three to day ten, the growth curve appears to be sigmoid. The rate steadily accelerates from day one to day four, and a decline in rate is evident by day five, slight at first but gradually increasing. For the first day or two some chicks show a lag in growth, which probably reflects adult delay in feeding them.

TABLE 16

Growth of young pomarine jaegers at Barrow in 1956

Age (days)	*N*	*Mean Wt (gm)*	*Gm gained*	*Per cent growth rate*	*Range in Weight*		*S*	$S\bar{x}$
					Min	*Max*		
1	18	45			39.9	50.7	3.43	0.81
2	17	51	6	12.4	43.1	60.0	4.16	1.01
3	15	61	10	17.9	47.8	72.5	8.11	2.09
4	14	79	18	25.8	55.7	94.9	10.3	2.74
5	15	96	17	19.5	65.3	113.6	11.6	2.99
6	15	120	24	22.3	68.4	150.4	20.1	5.18
7	12	144	24	18.2	97.5	172.0	19.7	5.70
8	10	172	28	17.7	118.6	200.6	24.3	7.68
9	10	202	30	15.8	139.5	243.8	32.2	10.2
10	8	221	19	8.9	146.0	269.0	33.9	11.3
11	7	276	55	22.1	253.4	304.0	24.1	9.09
12	8	282	6.0	2.1	232.8	333.3	33.3	11.8
13	6	328	46	15.0	261.0	357.0	38.3	15.6
14	6	341	13	18.9	272.6	381.0	37.1	15.2
15	5	343	2	0.5	291.0	395.0	42.5	19.0
16	3	393	50	13.6	354.0	438.0		
17	3	395	2	0.5	386.0	402.0		
18	3	407	12	3.0	302.0	472.0		
19	3	395	−12	−3.0	353.0	420.0		
20	3	455	60	14.0	386.0	557.0		
21	3	449	−6	−1.4	356.0	523.0		
22	3	431	−18	−4.1	417.0	454.0		
23	2	447	16	3.7	402.0	493.0		
24	3	474	27	5.8	410.0	510.0		
25	2	475	1	0.2	383.0	568.0		
26	1	525	50	9.9	—	—		
27	2	440	−85	−17.7	383.0	497.0		
29	1	521	81	8.3	—	—		

TABLE 17

Growth of young pomarine jaegers at Barrow in 1960

Age (*days*)	*N*	*Mean Wt* (*gm*)	*Gm gained*	*Per cent growth rate*	*Range in Weight*		*S*	$S\bar{x}$
					Min	*Max*		
1	7	42			34.7	47.0	5.0	1.9
2	8	50	8	17.5	49.0	56.5	3.8	1.3
3	14	59	9	16.6	53.5	70.0	5.5	1.5
4	10	83	24	34.0	65.0	103.5	11.7	3.7
5	14	101	18	19.5	83.5	131.0	15.5	4.1
6	10	127	26	23.0	97.0	142	14.8	4.7
7	14	152	25	17.9	126	178	16.6	4.4
8	10	185	33	19.5	161	209	16.9	5.3
9	14	214	29	14.5	180	244	21.0	5.6
10	8	240	26	11.5	165	271	35.1	12.4
11	15	279	39	15.2	229	332	32.1	8.3
12	8	333	54	17.5	272	370	29.5	10.5
13	14	342	9	2.8	270	391	37.5	10.0
14	7	381	39	10.8	358	423	21.7	8.2
15	12	399	18	4.6	319	495	50.3	14.5
16	10	435	36	8.5	367	499	42.8	13.5
17	12	466	31	6.9	368	565	51.6	14.9
18	8	488	22	4.6	371	563	58.7	20.8
19	10	508	20	4.1	374	630	85.8	13.5
20	9	544	36	6.9	452	568	43.2	14.4
21	9	550	6	0.9	308	680	102.4	34.1
22	6	564	14	2.5	315	718	132.8	54.2
23	10	593	29	5.6	447	724	72.1	22.8
24	7	637	44	7.1	572	697	49.2	18.6
25	11	610	−27	−4.4	409	737	96.5	29.2
26	9	618	8	1.4	359	768	115.0	38.3
27	8	618	0	0.0	336	764	132.2	46.9
28	10	590	−28	−4.6	329	724	145.1	45.9
29	6	680	90	14.0	544	847	99.6	40.6
30	11	564	−116	−18.6	277	712	140.9	42.6
31	5	692	128	20.5	660	718	20.8	9.3
32	6	652	−40	−5.9	590	752	63.6	26.0
33	2	638	−14	−2.1	617	662	—	—
34	3	619	−19	−2.9	569	705	—	—

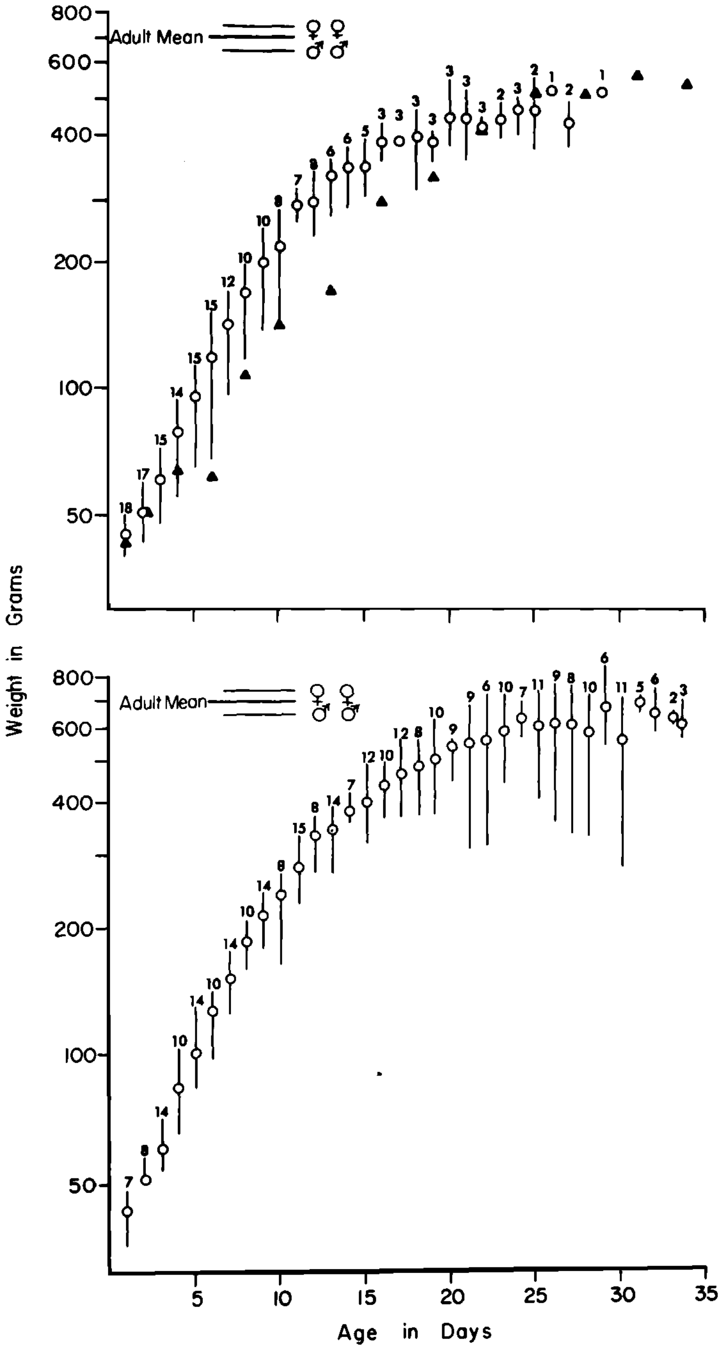

Figure 24. Growth of pomarine jaeger chicks at Barrow 1956 (upper figure) and 1960 (lower figure). Growth of one chick at Cape Sabine in 1959 is shown by triangles (upper figure). Vertical lines through daily mean weights indicate the sample range.

The chick weight curves from 1956 and 1960 are similar but show important differences. In both years growth in the first ten days is rapid. The average instantaneous relative growth rate in 1956 was 17.6 per cent from day one to day ten; in 1960 it was 19.3 per cent for the same period. Hence, the 1960 chicks did appear to grow more rapidly on the average in this period. The most important difference between the two seasons is the weight at which growth leveled off. In 1956 it was approximately 450 grams, in 1960 it was 600 to 650 grams; some 150 to 200 grams higher.

The weight curve of the pomarine jaeger chick that fledged at Cape Sabine in 1959 (Table 18, Figure 24) has an average instantaneous relative growth rate for the first ten days of 13.6 per cent, a rate slower than the mean growth of Barrow chicks. Its weight in the second week is well below the extremes of the 1956 or 1960 chicks, although the growth curve eventually leveled off at a higher weight than the 1956 chick population (550 grams vs 450 grams). This chick took longer to reach a constant weight than chicks of either Barrow population. It fledged successfully in spite of its slow development.

TABLE 18

Growth of one pomarine jaeger chick at Cape Sabine, 1959

Date	*Age (days)*	*Weight (gm)*	*Gm gained*	*Per cent growth rate*
4 July	1	43.0	—	—
5	2	50.9	7.9	16.8
7	4	64.3	13.4	11.5
9	6	61.5	− 2.8	− 2.3
11	8	108.5	47.0	28.3
13	10	143.5	34.0	13.8
16	13	172.0	28.5	6.0
19	16	281.0	109.0	16.3
22	19	325.5	44.5	4.8
25	22	424.5	99.0	8.7
28	25	510.5	86.0	6.0
31	28	516.5	6.0	0.5
3 Aug.	31	576.0	59.5	3.7
6	34	546.0	−30.0	− 1.8

TABLE 19

Growth of two parasitic jaeger chicks

Age (days)	*Wt (gm)*	*Gm gained*	*Daily Per cent growth rate*	*Wt (gm)*	*Gm gained*	*Daily Per cent growth rate*
	Barrow, 1956			*Cape Sabine, 1959*		
1	37.5			—		
2	40.0	2.5	6.4	43.6		
3	45.2	5.2	12.2	57.6	13.4	26.7
4	64.4	19.2	35.4	—		
5	72.9	8.5	12.4	88.1	31.1	21.6
6	91.0	18.1	22.1			
7	108.0	17.0	17.0	136	47.9	21.8
8	137	28.6	23.5			
9	153	16.0	11.0	162	26	8.5
10	174	20.9	12.9			
11	201	27.1	14.5	234	72	18.4
12	—					
13	267	66.9	14.3	278	44	8.5
14	—					
15	340	72.5	12.0	328	50	8.3
16	—					
17	352	12.5	1.8			
18	—			340	12	1.2
19	380	27.5	3.7			
20	—					
21	428	48.0	6.0	380	40	3.9
22	—					
23	424	− 4.0	− 0.5			
24	—			435	55	4.4
25	418	− 6.0	− 0.7			
26	—					
27	444	26.0	3.0	402	−33	− 2.5

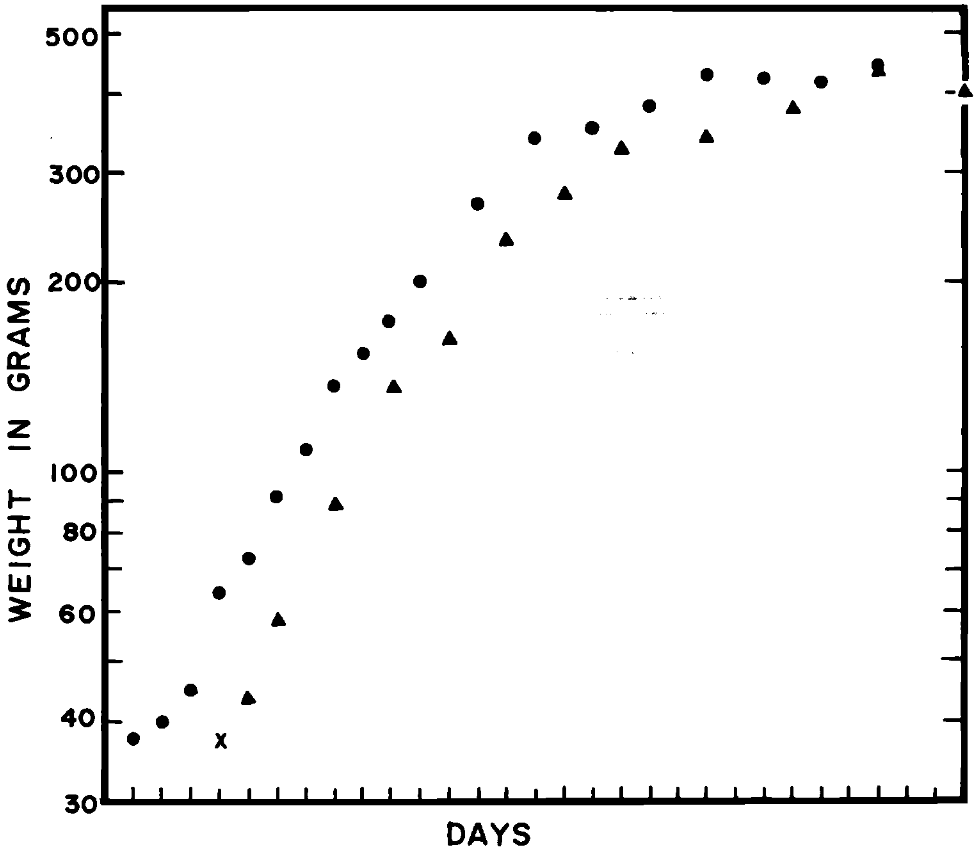

Figure 25. Growth of one parasitic jaeger chick at Barrow 1956 (left) and one at Cape Sabine 1959. First weight of right curve is estimated (X). Each curve begins on day one.

The Parasitic Jaeger

Only two complete weight curves of the parasitic jaeger were obtained (Table 19, Figure 25). The growth curve of one chick at Barrow in 1956 is slightly sigmoid with an accelerating growth rate to day four, an almost logarithmic growth phase to day nine, followed by a decelerating rate of growth as the curve levels off. The mean instantaneous relative growth for the first ten days was 15.1 per cent. One chick at Cape Sabine in 1959 grew at a logarithmic rate from hatching with an average instantaneous relative growth rate of 19.6 per cent in its first nine days. Thus, two complete weight curves of this species give 15.1 and 19.6 per cent as the instantaneous relative growth rate in the rapid phase of growth. All of the parasitic jaeger chicks weighed 400 to 450 grams at fledging. Weight curves in the late phases of growth were relatively smooth in contrast to the curves of the pomarine jaeger.

TABLE 20

Growth of five long-tailed jaeger chicks

Age (days)	*Mean weight (gm)*	*N*	*Range*		*Mean gm gained*	*Mean daily per cent growth rate*
			Min	*Max*		
1	29.0[a]	3	24.4	31.5	5.4[b]	—[c]
2	34.9	3	32.3	37.0	7.4	25.9
3	49.8	2	49.6	50.0	8.7	25.4
4	55.0	2	53.6	56.5	10.9	20.8
5	75.6	3	67	81	15.6	22.0
6	90.5	1			22.5	24.2
7	122	3	118	126	23.0	22.8
8	134	1			23.1	16.9
9	172	2	170	173	23.3	16.4
10	192	1			19.7	11.3
11	208	2	206	210	20.2	10.1
12	219	1			18.5	7.9
13	266	1			16.5	6.9
14	258	2	256	259	14.5	5.8
15	256	2	239	274	11.0	4.0
16	321	1			14.7	5.2
17	269	1			10.1	3.7
18	308	1			10.1	3.7
19	320	1			1.0	0.3
20	282	1			1.7	0.6
21	291	1			0.7	0.2
22	328	1			− 2.1	− 0.8
23	282	1			− 2.8	
24	261	1			− 2.8	
25	279	1			4.5	

[a] Last three data points of chick which died (right curve, Figure 26) were not used in table.

[b] Mean of average daily weight gain of all chicks.

[c] Mean of daily per cent growth rate of all chicks.

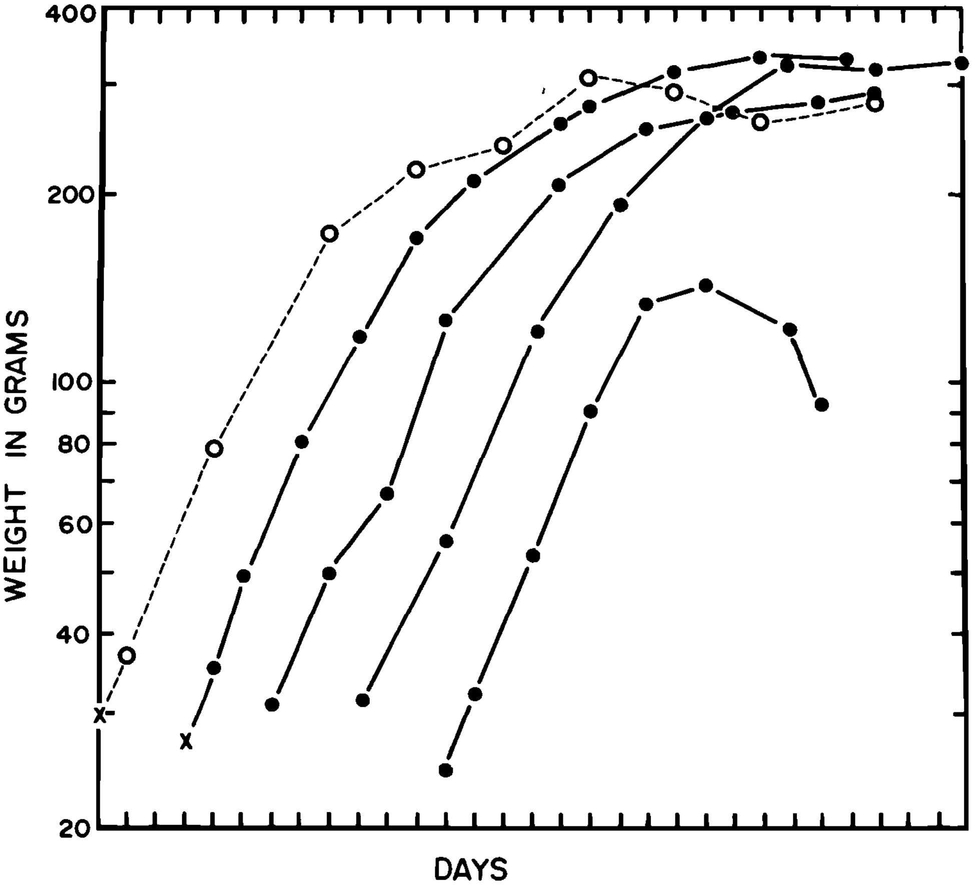

Figure 26. Growth of long-tailed jaeger chick at Kaolak River 1958 (open symbol) and four chicks (closed symbol) at Cape Sabine 1959. Values marked (X) are estimated. Each curve begins on day one.

The Long-tailed Jaeger

Growth of the long-tailed jaeger was studied at three enclosed nests with five chicks at Cape Sabine in 1959. Per cent instantaneous relative growth rate of four chicks for the first seven to eight days of growth range from 20.1 to 22.6 per cent with a mean of 21.2 per cent (Table 20, Figure 26). All four grew at an almost logarithmic rate from hatching. One complete weight curve was also obtained from the Kaolak River population in 1958. It had a slope of 22.4 per cent in the first eight days when growth was logarithmic, compared with the mean of 21.2 per cent for the Cape Sabine population.

Summary and Discussion of Growth

The per cent instantaneous relative growth rate of the three jaeger species in the rapid phase of growth is similar. There is no size correlated trend toward increased or decreased growth rates evident in the genus. The high rate shown by the small sample (five) of long-tailed jaeger chicks is not considered to be significantly different from the rates of the other jaegers, and I conclude that the three species are capable of a maximum growth rate that is essentially identical. Evidently, from the data on the pomarine jaeger, the average growth rate of chicks that fledge successfully can show considerable variation.

Rates of growth are expressed as instantaneous weight gain per unit of body weight already attained, without reference to adult weight. The three arctic species of *Stercorarius* differ markedly in weight at maturity, and hence when growing at identical rates, the species take different lengths of time to mature. This alone gives the long-tailed jaeger an advantage over the pomarine jaeger, for example, and small size may be either an adaptation of the long-tailed jaeger to the high arctic or a preadaptation that allowed it to occupy high latitudes.

The wide variation in growth rate within the pomarine jaeger populations and between the populations is related to problems of food supply. The 1956 lemming population at Barrow declined rapidly through the summer, and towards the end of July the jaegers' food supply became critically short. This is reflected in wide fluctuations in weights of individual chicks, in the comparatively low average weight at which growth ceased that year, and in high chick mortality. In 1960 at Barrow the lemming population remained relatively high through the summer, chick mortality was low, and the asymptote of the mean weight curve was 150 to 200 grams higher than in 1956.

The very slow growth rate of the Cape Sabine chick reflects a difference in the availability of food in that area. The area is characterized by relatively tall dense vegetation, and as a consequence of rapid vegetative growth the availability of *Microtus oeconomus* was restricted early in the nestling's growth. To compensate for this disadvantage the adult pomarine jaegers resorted to foraging along the ocean, and fish became a major component of the diet in the latter part of the season. The protracted development of this chick is probably the result of a restricted food supply, which was sustained, however, through the season. The chick fledged successfully.

Variation in development associated with food supply, as was found for the pomarine jaeger, was also noted by Sumner (1933), who was able to keep young barn owls in the downy stage for several months beyond the normal period by reducing their food supply.

There is then apparently no adjustment of growth rates among the stercorariids for living in an arctic environment. Because growth rate can vary greatly in a species in response to changes in food supply, adaptation to arctic conditions must occur in such population characteristics as the timing of the breeding cycle in relation to food supply, shortening of the pre-egg stage, and postponement of molt until breeding has concluded.

Food Habits and Predation

The Pomarine Jaeger

The pomarine jaeger utilizes a variety of foods, although most items occur rarely in its diet, and there are few kinds of prey it can obtain in quantity. This is partly because within the prey-size range of the pomarine jaeger there are few species that are abundant and easily obtained, and partly because the pomarine jaeger is a very specialized predator that depends on one class of prey, microtine rodents, for most of its food. The pomarine jaeger, in fact, does not attempt to breed unless there is a substantial microtine rodent population (usually brown lemmings) for a food supply.

This extreme specialization on rodent prey and dependence on them for breeding is particularly evident when the foods of breeding and non-breeding jaeger populations are compared.

Non-breeding jaegers were sampled at Barrow and Wainwright in the low lemming years of 1957 and 1958 (Table 21). The total sample of 65 specimens includes nine individuals collected inland from Barrow in the spring of 1957 and whose stomachs contained *Lemmus*. These stomach samples are not included in Table 21 because similar early samples from inland are not available for the parasitic and long-tailed jaegers and including them biases comparison with these species. They do show that migrating jaegers feed on lemmings and that even in a low year like 1957 there are lemmings locally available in the spring. Including them raises the percentage of microtine rodents from 41 to 49 per cent.

Birds occurred in 25 per cent (14) of the stomachs; passerine bird remains occurred only once. Four of five shorebirds were red phalaropes (*Phalaropus fulicarius*) and one was either *Calidris melanotos* or *C. alpina*. Other remains included unidentified large birds and at least one ptarmigan. Carrion included caribou and the remains of a seal, *Phoca* sp. Miscellaneous items were squid, polychaete worms, and unidentifiable remains.

This diet suggests that the pomarine jaeger is largely opportunistic in its food gathering when microtine rodents are not available and that it forages along the ocean shore and near Eskimo villages, as well as over the tundra.

The proportion of major food items in pellets was determined for breeding populations at Barrow in 1956, 1959, and 1960, and at Pitt Point in 1957 (Table 22). One jaeger population was low (Barrow, 1959), and the remaining three were moderately high to high. The very strong preference of the pomarine jaeger for *Lemmus* when breeding at both low and high density is apparent. The small number of food items used other than *Lemmus* is also significant.

Breeding pomarine jaegers utilize food other than lemmings when available, particularly if lemmings become scarce. In 1956 the lemming population did not remain high enough through the season to support the jaeger population. Use of food items other than *Lemmus* increased in July and August. There is a trend from only *Lemmus* in the pellets in May and June to the occurrence of other food items in 15 per cent of the pellets in August, reflecting the decline in availability of *Lemmus* to this population in the latter part of the season. The per cent of non-lemming food items actually used in August was probably higher,

TABLE 21

Food of transient pomarine jaegers, 1957 and 1958

Food items	*Number of stomachs*	*Per cent occurrence*
Avian, total	14	25
Passerines, total	1	2
Charadriiformes, total	5	9
Calidris sp.	1	
Phalaropus fulicarius	4	
Lagopus sp.	1	
Unidentified bird	7	
Mammalian, microtine rodent, total	23	41
Lemmus trimucronatus	19	
Dicrostonyx groenlandicus	1	
Unidentified microtine	3	
Carrion, total	8	14
Pinniped	1	
Rangifer	3	
Unidentified	4	
Bird egg, total	11	20
Phalaropus fulicarius	2	
Unidentified egg	9	
Insect, total	5	9
incidental	3	5
predominant	2	3
Fish	7	12
Marine invertebrate	2	3
Number of stomachs	56	

because all pellets were collected at random on the tundra, and those collected late must have included some from early in the season.

Adult jaeger food pellets were not collected from the tundra in 1960 in the latter part of the season. The low incidence of food other than *Lemmus* in the diet of the 1960 population suggests that there was no significant trend towards use of other food items (Table 22). The fact that such food items did occur in spite of the high lemming population, however, indicates again the opportunistic nature of the pomarine jaeger's predatory habits.

The remaining three breeding populations for which I have data are low populations at Barrow and Cape Sabine in 1959, and a moderate population at

TABLE 22

Food items of breeding pomarine jaegers

	Barrow			*Pitt Point*
Food items	*1956*	*1959*	*1960*	*1957*
Total microtine rodent	98.6[a]	100[a]	97.8[b]	100[a]
Other food	8.5	27	2.2	3
Total bird	0.9	9	1.9	1
Bird eggs	1.2	12	3[c]	2
Fish	0.2	3	0.3	
Insects (incidental)	6.2	3	1[c]	
Number	432	75	2500	206

[a] Per cent occurrence of food items in pellets.

[b] Per cent occurrence of food items in total number of prey items.

[c] Total occurrences in pellet samples, not included in total of prey items.

Pitt Point in 1957 (Table 22). These data show that, even when jaegers nest at low density with a low lemming population, *Lemmus* still makes up most of the diet of the pomarine jaeger. There is a significant increase in the occurrence of other food items (birds' eggs and fish) and a decline in the occurrence of insects, in the low population of 1959 at Barrow, compared to their occurrence in the high populations.

The food of the Cape Sabine population is analysed as per cent of occurrence in the total number of food items found exclusive of insects and fish, because each sample of pellets from nest enclosures was analyzed as a unit (Table 23). The total number of microtine rodents eaten was based on the number of jaws. The data include several pellets of adult jaegers and stomach contents of an adult.

The results indicate a heavy reliance on *Microtus oeconomus;* however, the number of *Microtus* remains in the enclosure declined as the vegetation developed. On 28 July the only food remains were several partly eaten small fish (*Ammodytes hexapterus*, the Sandlance), and on 31 July no pellet material was found. Since pellets will not be ejected unless there is undigestible material in the food, and also since there were fish vertebrae in five of the eleven pellet samples, fish not reflected in these figures were probably forming a significant portion of the diet. The important point is that *Microtus* was the bulk of the food that the jaegers were able to obtain on the tundra.

The data from Barrow in 1959, recalculated on the same basis as the Cape Sabine data, show a similar composition of food items, with the exception of fish (Table 23).

Tables 22 and 23 illustrate clearly the specialized food requirements of the pomarine jaeger when it breeds. In each situation in which it has been studied at high and low nesting densities, this jaeger has been shown to exploit a single food source to a very large extent. When this food source fails, as it did at Bar-

TABLE 23

Food items in pellets and stomachs of pomarine jaegers at Barrow and Cape Sabine in 1959

Food items	*Per cent occurrence in Total No. Items*[a] *Barrow*	*Cape Sabine*
Microtine rodent, total	83	88
Other food	17	12
Bird, total	7	12
Passerine	3.5	9
Shorebird	3.5	1.5
Other	—	1.5
Bird eggs	10	—
	Per cent occurrence in Pellets or Stomachs	
Fish	3	5[b]
Insects, incidental	3	2
Number of pellets and stomachs	89	68

[a] Exclusive of fish and insects.

[b] Occurrences in the eleven samples of pellets analyzed.

row in 1956 and also at Cape Sabine in 1959, ability to use alternative foods appears to be limited. In the latter instance, however, the failure was not caused by a shortage of food *per se* but rather by the growth of vegetation that provided effective cover for *Microtus*. At Cape Sabine, when nesting near the coast, the pomarine jaeger was able to obtain fish. Many of them probably came from windrows of capelin (*Macrotus villosus*), washed up on the beach, and some were possibly obtained by robbing kittiwakes, which occur along this stretch of coast. In this situation the one chick fledged successfully.

At Barrow in 1956, on the other hand, the jaegers were unable to exploit other foods effectively, though they attempted to do so. The occurrence of food items other than *Lemmus* increased as the season progressed. Several other observations in 1956 suggest desperation in the attempt to find food. On 13 July the remains of 17 adult red phalaropes were found near one nest. This occurred when female phalaropes were in dense pre-migratory flocks. Three eaten short-eared owls, one adult pomarine jaeger, and one adult glaucous gull (all probably carrion) were found in the course of the season. One chick was being fed polar tomcod (*Boreogadus saida*) on 10 August. In spite of this attempt to exploit alternate foods, the population failed to breed successfully (see Population Biology).

Alternate foods in 1960 made up only 2.2 per cent of the total food items (Table 24). The nature of these foods is not unusual and does not suggest any desperate attempt to get food as the incidental food items suggest in 1956. Young

TABLE 24

Food items in pellets of pomarine jaegers, Barrow, 1960

Food item	*Number*	*Per cent*	*Remarks*
Lemmus trimucronatus	2444	97.8	*Lemmus* jaws
Other food	56	2.2	
Total Bird	47	1.9	
Anseriform chick	6		
Shorebird, adult	4		
Shorebird, chick	26		
Passerine, adult	1		
Passerine, chick	2		
Unidentified chick	7		
Unidentified adult	1		
Mammal (sans *Lemmus*)	1	0.04	*Mustella rixosa*
Fish (prs. of otoliths)	8	0.03	
Birds egg fragments	3[a]		
Insects (incidental)	1[a]		
Grand total prey	2500		

[a] Occurrences in samples of pellets, not included in total number of prey items.

shorebirds made up almost 50 per cent of the total, but adults occurred only four times. There was no evidence that the jaegers fed on carrion in 1960.

The main conclusions to be drawn from these data on the qualitative food habits of the pomarine jaeger are: (1) The pomarine jaeger requires a microtine rodent population of sufficient density to provide the bulk of the food for successful breeding, even at low densities; (2) the ability of the pomarine jaeger to exploit alternate foods is limited. It apparently cannot subsist on avian prey; but when microtine rodents are not available, it depends mainly on carrion and fish for alternate foods. (3) Because of its dependence on microtine rodents, and its specialized hunting methods, it is limited as to suitable breeding areas by the nature of the vegetative cover and the substrate.

The Parasitic Jaeger

Breeding parasitic jaegers have more specialized food habits than non-breeding ones, although the contrast between breeding and non-breeding birds is not as extreme as for the pomarine jaeger. Breeding parasitic jaegers are widely dispersed over the North Slope, and most must nest well inland away from the ocean. Non-breeding birds and birds whose breeding effort have failed, however, usually forage in coastal areas, as the other non-breeding jaegers do.

The stomach contents of 32 speciments collected at Barrow, Wainwright, and Point Lay in 1957 and 1958 show that non-breeding birds take a large num-

TABLE 25

Food of transient parasitic jaegers, 1957 and 1958

Food items	*Number of stomachs*	*Per cent occurrence*
Avian, total	9	28
Passerine, total	1	3
Charadriiformes, total	2	7
Ereunetes pusillus	1	
Phalaropus fulicarius	1	
Unidentified bird	6	
Mammalian, microtine rodent, total	7	22
Lemmus trimucronatus	3	
Unidentified microtine	4	
Carrion, total	2	7
Phoca hispida	1	
Unidentified	1	
Bird egg, total	9	28
Phalaropus fulicarius	1	
Unidentified	8	
Insect, total	10	31
incidental	7	22
predominant	3	9
Fish	7	22
Marine invertebrate	2	7
Seeds	2	7
Number of stomachs	32	

ber of different food items (Table 25). Birds, mammals, and bird eggs each occurred in 28 per cent of the stomachs, and fish, in 22 per cent. Eight of the nine birds are non-passerines. Insects occurred in 10 of the stomachs and were the bulk of the contents of three stomachs (nine per cent). These food items emphasize the opportunistic nature of the non-breeding populations of jaegers.

The breeding birds specialize either on birds or on birds and microtine rodents. The parasitic jaegers at the Kaolak River had an average of 82 per cent birds and 16 per cent microtine rodents in their diet in the three seasons from 1957 to 1959 (Table 26). The per cent of passerine birds in the total number of prey items varied from 45 in 1957, to 66 in 1958, and 75 in 1959. The per cent of shorebirds decreased correspondingly from 20 to 10, and finally to 7 in 1959, while the total number of birds taken was 75 per cent of all food items in 1957, 81 in 1958, and 88 in 1959. Mammalian prey was predominantly three species of

TABLE 26
Food items in pellets of parasitic jaegers, Kaolak River

	1957		*1958*		*1959*		*Totals*	
Food items	*No.*	*Per cent*	*No.*	*Per cent*	*No.*	*Per cent*	*No.*	*Per cent*
Avian, total	58	75	130	81	109	88	297	82
Passerine, total	35	45	107	66	93	75	235	65
Acanthis "hornemanni"	4		6		2		12	
Charadriiformes, total	15	20	15	10	9	7	39	11
Pluvialis dominica	4		2				6	
Calidris melanotos	4		8		2		14	
Limnodromus scolopaceous	3				1		4	
Ereunetes pusillus	2		2		1		5	
Lobipes lobatus	1		1				2	
Stercorarius parasiticus			2		1		3	
Unidentified	1				4		5	
Lagopus lagopus, adult	6		1				7	
Lagopus lagopus, chick			4		3		7	
Anatid, chick					4		4	
Anatid, adult	1						1	
Unidentified bird	1		3				4	
Mammalian, microtine, total	16	21	28	17	14	11	58	16
Lemmus trimucronatus	6		8		11		25	
Dicrostonyx groenlandicus	2		9		2		13	
Microtus oeconomus	1		5		1		7	
Unidentified	7		6				13	
Mammalian, non-microtine, total					1	1	1	0.5
Mustela rixosa					1		1	
Carrion, total	3	4	2	2			5	1
Total food items	77		160		124		361	
Miscellaneous foods								
Lagopus eggs	1[a]		2		2		5	
Bird eggs, total	7		3		2		12	
Insects	9		6				15	
Salmonberry			7				7	
Blueberry			3				3	
Seeds			1		1		2	

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[a] Occurrences.

microtine rodents and comprised 21 per cent of the food items in 1957, 17 per cent in 1958, and 11 per cent in 1959.

The food data for 1957 are from pellets collected from mounds in the vicinity of parasitic jaeger nests, while pellets for 1958 and 1959 are mostly from nest enclosures. The difference might bias these data, because the samples of pellets from the territories would be from the entire season, while food items from nest compounds are only from July and early August. Nevertheless these data suggest the sort of shifts in year-to-year availability of prey that would be expected to show up in the changing composition of the jaegers' diet.

The parasitic jaeger is primarily a bird predator in this area and concentrates most heavily on passerine species. Microtine rodents are an important 11 to 21 per cent of their prey, carrion and insects are of minimal importance. Only a few fragments of insects were found in six different samples of pellets.

Blueberry (*Vaccinium uliginosum*) and salmonberry (*Rubus chamaemorus*) were significant food items in the latter part of the 1958 season. Both appeared in food remains on 26 July, when the berries were beginning to ripen. A large quantity was eaten. On 1 and 4 August the total food remains at one nest consisted of a large mass of blueberry and salmonberry pulp, predominantly the latter. From 26 July to 4 August, the remains of only eight passerine birds and one microtine rodent were found at this nest, in addition to the berry pulp.

The 1959 Cape Sabine population nested in association with a peak population of *Microtus oeconomus* and breeding pomarine and long-tailed jaegers. Food items from three enclosed nests, plus a few food items from a fourth nest, are in Table 27. The food of the parasitic jaegers at Cape Sabine differed surprisingly little from that of the Kaolak River population. The per cent of microtine rodents increased to 25; but birds still comprised 75 per cent of the food, and most of the birds taken were passerines.

The Cape Sabine data are detailed enough to indicate seasonal trends in numbers and kinds of prey (Table 28). The number of passerine birds seemed to reach a peak in the second half of July, coinciding with their peak of abundance. The number of *Microtus oeconomus*, on the other hand, remained constant through the season. There is a suggestion of a downward trend in number of *Microtus* taken per day from mid-July onward.

The two pairs of parasitic jaegers nesting at lakes Peters and Schrader were preying almost entirely on birds (Table 29). Eighty-seven per cent of the 245 food items identified were passerine birds, and six per cent were shorebirds, a total of 93 per cent avian food items. Four species of shorebirds were taken; ptarmigan remains were not found. Habitat for microtine rodents is more restricted in the mountains than in foothill tundra, and this may account for the low representation of rodents in the jaegers' diet.

One pair of parasitic jaegers bred in association with the lemming high and the dense pomarine jaeger population at Barrow in 1956. Forty food items were found on the territory, only 14 of them in the nest enclosure (Table 30). Birds made up 22 per cent and mammals, 78 per cent of the entire sample, while in the nest enclosure birds were slightly more than half, and mammals (mostly *Lemmus*) constituted the remainder of the food items. Three nests at Cape Sabine yielded 151, 64 and 57 food items in a season; thus these 14 remains could represent at most 20 per cent of the food fed to the chick. It is assumed from the lack of remains, and from the fact that the chick grew normally, that the adults were

TABLE 27

Food items in pellets of parasitic jaegers, Cape Sabine 1959

Food items	*Total number*	*Per cent*
Avian, total	208	74
Passerine, total	201	72
Acanthis "hornemanni"	1	
Charadriiform, total	5	2
Pluvialis dominica	1	
Calidris melanotos	2	
Ereunetes pusillus	1	
Unidentified	1	
Anatid, chick	1	
Unidentified bird	1	
Mammalian, microtine rodent, total	70	25
Microtus oeconomus	70	25
Mammalian, non-microtine, total	1	1
Sorex arcticus	1	
Mammalian, total	71	26
Total food items	280	
Miscellaneous foods		
Bird egg	1[a]	
Insect, tipulid	4	
Coleoptera	1	
Seeds	1	

[a] Occurrences

feeding largely on carrion or more likely on fish. The lack of emphasis on lemmings in a high year is significant, as the territory apparently had a *Lemmus* population of average density. The lemming remains were probably from early in the season, when lemmings were very abundant.

These data all indicate clearly that the parasitic jaeger is primarily a predator on birds when breeding. Passerine birds make up the bulk of its diet; shorebirds, primarily chicks, and microtine rodents usually make up less than one fourth of the total. This was true regardless of the availability of microtine rodents, as at Cape Sabine, where *Microtus oeconomus* was abundant and available and was used preferentially by pomarine and long-tailed jaegers breeding in the same area.

Age classes of non-passerine prey: — The remains of 50 non-passerine birds taken by parasitic jaegers included unidentified duck chicks, ptarmigan, and

TABLE 28

Food items from three parasitic jaeger nests, Cape Sabine 1959

Food items	*July* 6	*8*	*10*	*12*	*14*	*16*	*19*	*22*	*25*	*28*	$\bar{E}$	*Per cent*
Avian, total											43	75
Passerine, total		10	8	7	10	2	3	1	0	0	41	72
Charadriiform, total						1					1	
Unidentified bird			1								1	
Mammalian, total											14	25
Microtine rodent, total		2	2	1	2	2	0	1	2	1	13	23
Sorex arcticus			1								1	
Total food items											57	
Insect, tipulid					1[a]						1	
Avian, total											50	78
Passerine, total	2	4	4	7		16	10	6			49	77
Charadriiform, total								1			1	1
Mammalian, total											14	22
Microtine rodent, total		1	2	1		3	2	4	1		14	22
Total food items											64	
Insect, tipulid	1[b]										1	

	July 5	*7*	*9*	*11*	*13*	*16*	*19*	*22*	*25*	*25*[c]	$\bar{E}$	*Per cent*
Avian, total											112	74
Passerine, total	20	9	8	8	9	15	5	10	1	23	108	72
Charadriiform, total						1				2	3	2
Anatid, chick										1	1	
Unidentified bird						1					1	
Mammalian, total											38	25
Microtine rodent, total	5	4	7	4	2	4	2	5	1	4	38	25
Total food items											151	
Bird egg	1[a]										1	
Insect, tipulid		1		1							2	
Coleoptera	1										1	
Seeds				1							1	

[a] Occurrences.

[b] A pellet of tipulid eggs.

[c] Pellets collected from the territory

TABLE 29

Food items in pellets of parasitic jaeger, lakes Peters and Schrader 1958

Food items	*Total number*	*Per cent*
Avian, total	228	93
Passerine, total	214	87
Acanthis "hornemanni"	17	
Eremophila alpestris	16	
Unidentified	180	
Charadriiformes, total	14	6
Pluvialis dominica	1	
Calidris bairdii	11	
Calidris minutilla	2	
Mammalian, microtine rodent, total	17	7
Lemmus trimucronatus	5	
Dicrostonyx groenlandicus	4	
Microtus oeconomus	8	
Total food items	245	100
Bird egg	1[a]	
Fish	1	
Insect	2	

[a]Occurrences

TABLE 30

Food items in pellets of parasitic jaegers, Barrow 1956

Food items	*July 29*	*August 8*	*14*	*21*	*Totals*	*Per cent*
Avian, total					9	22
Passerine, total	3	2	2	1	8	20
Ereunetes pusillus	0	1	0	0	1	
Mammalian, total					30	75
Lemmus trimucronatus	3	2	0	25	30	75
Carrion, total					1	3
Unidentified mammal, large	0	0	1	0	1	
Total food items					40	
Insects (tipulid)	1[a]	—	—	—	1	

[a]Occurrences.

eight species of shorebirds. Shorebird remains included: *Pluvialis dominica, Calidris melanotos, C. bairdii, C. minutilla, Limnodromus scolopaceus, Ereunetes pusillus, Phalaropus fulicarius, Lobipes labatus,* and the remains of two unidentified juveniles. Sixty-eight per cent of all remains were of juveniles. They included all the anatids (5), four of five ptarmigan, and 62 per cent of 40 shorebirds. The most commonly taken shorebirds were *C. melanotos* (11), *C. bairdii* (11), and *E. pusillus* (7). Larger species, *P. dominica* and *C. melanotos* were taken only as juveniles, while smaller species were taken only as adults (*P. fulicarius* and *L. lobatus*), or in approximately equal numbers of adults and juveniles (*C. bairdii, C. minutilla* and *E. pusillus*). The only exception to the trend for large species to be taken as juveniles was the remains of one adult *Limnodromus scolopaceus.* The adult ptarmigan was identified from the foot of a winter bird and was obviously carrion.

Predation on passerine birds: — It is difficult to identify passerine birds because the most common skeletal remains, the humerus, cannot be identified to species in many cases. Redpolls (*Acanthis "hornemanni"*) and horned larks (*Eremophila alpestris*) can be identified because no passerine present overlaps them in size. The large passerines in northern Alaska, raven (*Corvus corax*), robin (*Turdus migratorius*), and northern skrike (*Lanius excubitor*), could also be identified by size, but none was found.

The relative abundance of the passerine species that breed in the four areas studied are in Table 31. The estimates from lakes Peters and Schrader are from T. J. Cade (personal communication) who was there from 31 May to 16 June 1959. Data from Cape Sabine are from Childs (1969) and my own notes. Unidentifiable passerines among prey items could include any of 11 species at lakes Peters and Schrader, six species at the Kaolak River, nine or possibly eleven species at Cape Sabine, and two species at Barrow. Most of these are usually rare or restricted in habitat, so that they are probably seldom in the parasitic jaeger's diet. The number of common passerines in the study areas are four, three, two and two species respectively (Table 31). The Lapland longspur (*Calcarius lapponicus*) is the most abundant passerine in all four areas, as it is on the entire North Slope. The snow bunting (*Plectrophenax nivalis*), a cavity nesting species, is common on rock slopes of the mountains and about human refuse and habitations at Barrow; it is rare in foothill and coastal plain tundra. The savannah sparrow (*Passerculus sandwichensis*) is abundant in foothill tundra where low shrubs provide the cover that this species prefers in contrast with the longspur. The redpoll (*Acanthis "hornemanni"*), probably the second most common passerine on the North Slope, requires willow shrub one to several feet in height in order to nest. Hence, it is virtually absent at Cape Sabine, though abundant a few miles inland. Nesting records of this species at Barrow are rare. The water pipit (*Anthus spinoletta*), is common in the mountains at lakes Peters and Schrader, absent at the Kaolak River, and uncommon at Cape Sabine, where it occurs on bare hilltops.

The relative number of passerine species in all identifiable bird remains should be an index to the ratio of the species in the total diet, assuming that each bird eaten has an equal chance of leaving an identifiable part. Such parts are bill, skull, lower jaw, and tail. Forty-five identifiable parts were found, twenty-eight of which, or 62 per cent were lapland longspur. Water pipit remains occurred five times, yellow wagtail (*Motacilla flava*) four times, horned

TABLE 31

Relative abundance of breeding passerine birds on study areas in northern Alaska

Species	*Lakes Peters and Schrader*	*Kaolak River*	*Cape Sabine*	*Barrow*
Sayornis saya	uncommon	—	rare	—
Eremophila alpestris	uncommon	—	rare	—
Corvus corax	uncommon	—	rare	—
Turdus migratorius	uncommon	—	—	—
Oenanthe oenanthe	uncommon	—	—	—
Luscinia svecica	—	uncommon	rare(?)	—
Motacilla flava	rare	rare	rare(?)	—
Anthus spinoletta	common	—	uncommon	—
Lanius excubitor	uncommon	—	rare	—
Acanthis "hornemanni"	common	common	uncommon	rare
Passerculus sandwichensis	uncommon	common	abundant	—
Spizella arborea	uncommon	uncommon	uncommon	—
Zonotrichia leucophrys	uncommon	uncommon	uncommon	—
Calcarius picta	uncommon	—	—	—
Calcarius lapponicus	abundant	abundant	abundant	abundant
Plectrophenax nivalis	common	—	uncommon	common

lark, wheatear (*Oenanthe oenanthe*) and savannah sparrow each twice, and redpoll and snow bunting once.

Passerine prey items from each area tended to be the common species. Lapland longspur and snow bunting were the only species taken at Barrow, three species, redpoll, savannah sparrow, and Lapland longspur, were taken at the Kaolak River, and only the longspur occurred in prey remains from Cape Sabine. The remaining four passerine species plus the longspur were from lakes Peters and Schrader.

Savannah sparrows and redpolls seem very much under-represented in the samples from foothill tundra where they are relatively abundant. This may be because both occupy habitats that provide more cover than that of the Lapland longspur, and because the savannah sparrow is secretive and remains in the vegetation more than the longspur does. Redpoll adults travel and feed in flocks over the tundra through the season, and the nomadic flocking habit may serve to reduce predation by jaegers. The yellow wagtail occurs in a higher proportion of the lakes Peters and Schrader prey items than would be expected from its abundance there. This species is in foothill tundra, and this habitat is extensive to the north of lake Schrader where the jaegers may forage.

The Long-tailed Jaeger

Long-tailed jaegers typically nest well inland in the southern coastal plain, the foothills, or the mountains, and rarely nest near the coast except, as at Cape Sabine, where foothill tundra is close to the sea. Nonbreeding birds and breeding failures, however, move to the coast and forage along the shore and on adjacent tundra. Breeding and nonbreeding individuals take very different kinds of prey.

Stomach contents of forty birds collected in 1957 and 1958 at Barrow, Wainwright, and Point Lay show that the long-tailed jaeger, like the other jaeger species, takes a large variety of food when not breeding (Table 32). Most interesting is the occurrence of insects in 62 per cent of the stomachs and as the bulk of the contents in 52 per cent of the stomachs. Compared with non-breeding parasitic jaegers, the long-tailed jaeger takes a lower percentage of birds (10 vs 28), the same per cent of small mammals (22), a higher per cent of carrion (22 vs 7), and a lower per cent of bird eggs (7 vs 28).

Breeding birds at the Kaolak River in 1957, 1958, and 1959 were more specialized than the non-breeding jaegers (Table 33). Birds were more than half of the total prey in 1957 and 1959 and slightly less than half in 1958. Microtine rodents, which were the remainder of the diet, fluctuated accordingly. One least weasel (*Mustella rixosa*) and one shrew (*Sorex* sp.) were found.

Comparing the long-tailed jaeger food habits with those of parasitic jaegers in the same area shows that the former takes slightly fewer birds, and a lower proportion of shorebirds. A consistently larger per cent of the long-tailed jaeger's food consists of microtine rodents.

The occurrence of the bar-tailed godwit (*Limosa lapponica*) in the diet of the long-tailed jaeger is interesting, because the godwit nests in close association with the long-tailed jaeger in this area (Maher, 1959) and is more aggressive towards the parasitic jaeger than to the long-tailed jaeger; yet these were the only godwit remains in the food of any jaeger.

Insects occurred in 32 per cent of 65 pellets in 1957 and in 21 per cent of 154 pellets in 1958. They seemed to be less frequent in 1959. Insects were never a significant proportion of any pellet.

Salmonberries and blueberries were eaten in quantity only in 1958, as they were by the parasitic jaeger. Very few were found in the 1959 Kaolak River sample, and none in the 1957 sample. Salmonberry seeds occurred in 20 per cent of the long-tailed jaeger pellets in 1958, and samples from two nests on 1 August and 4 August consisted mainly of salmonberry seeds. The long-tailed jaeger seemed to eat fewer blueberries than the parasitic jaeger. They only occurred in the feces of one chick on 29 July.

The 1959 Cape Sabine population was nesting in an area with a peak population of *Microtus oeconomus* and breeding populations of the pomarine and parasitic jaegers. In these circumstances, the long-tailed jaegers obviously concentrated on *Microtus oeconomus* as a principal food (Table 34). Ninety-one per cent of 391 food items were mammalian, one of these was *Sorex arcticus,* three were *Lemmus trimucronatus,* the remaining 387 were *Microtus oeconomus.* Bird remains were 9 per cent of the total, shorebirds (3 items) constituting less than 1 per cent. Insects occurred in 15 per cent of 285 pellets, and avian egg shell fragments, in one per cent. The per cent of the different food items was consistent among the three nests for which a season's total is available. No change in the

TABLE 32

Food of transient long-tailed jaegers, 1957 and 1958

Food items	*Number of stomachs*	*Per cent occurrence*
Avian, total	4	10
Passerine, total	1	2.5
Charadriiformes, total	2	5
Ereunetes pusillus	1	
Unidentified	1	
Mammalian, microtine rodent, total	9	22
Lemmus trimucronatus	1	
Unidentified microtine	8	
Carrion, total	9	22
Phoca hispida	1	
Unidentified	8	
Bird egg	3	7
Insect, total	25	62
incidental	4	10
predominant	21	52
Fish	1	2.5
Marine invertebrates	3	7
Total number of stomachs	40	

number or type of food could be detected during the season (Table 35). There was no evidence of a decline in the proportion of microtine rodents taken, as was noted for the parasitic jaeger in the same season.

Age classes of nonpasserine bird prey: — Seven species of shorebirds made up the identified non-passerine prey of the long-tailed jaeger. Species represented were: *Pluvialis dominica, Calidris melanotos, Limnodromus scolopaceus, Ereunetes pusillus, E. mauri* (?), *Limosa lapponica,* and *Lobipes lobatus. C. melanotos* was the most common (8 of 24 remains), followed by *Lobipes lobatus* (4) and *Limosa lapponica* (2), while the remaining four species were each represented once. Six remains were unidentified. *C. melanotos* was the only adult of the 24 remains, a fact suggesting that this jaeger cannot take adult shorebirds except in rare instances. The parasitic jaeger, in contrast, took 30 per cent adult shorebirds, primarily adults of relatively small species.

Predation on passerine birds: — Passerine birds comprised 44, 31, and 56 per cent of the total food items of the long-tailed jaeger at the Kaolak River. The humeri were used as indicators of the number of passerines in the prey total, and these with the exception of the redpoll could not be identified to species. Only six redpolls were found in a total of 232 passerines; all in the 1958 sample.

TABLE 33
Food items in pellets of long-tailed jaegers, Kaolak River

	1957		*1958*		*1959*		*Totals*	
Food items	*No.*	*Per cent*	*No.*	*Per cent*	*No.*	*Per cent*	*No.*	*Per cent*
Avian, total	84	64	76	41	123	59	283	54
Passerine, total	58	44	57	31	117	56	232	44
Acanthis "hornemanni"			6				6	
Charadriiformes, total	16	12	14	8	4	2	34	6
Pluvialis dominca	3				2		5	
Calidris melanotos	7		3				10	
Limnodromus scolopaceus	2		1				3	
Ereunetes pusillus	2				2		4	
Limosa lapponica			2				2	
Lobipes lobatus	1		4				5	
Stercorarius longicaudus	1		1				2	
Unidentified			3				3	
Lagopus, adult	5		1				6	
Lagopus, chick	4		2		2		8	
Unidentified	1		2				3	
Mammalian, total	47	36	110	59	84	41	241	46
Microtine rodent, total	46	35	110	59	83	40	239	46
Dicrostonyx groenlandicus	3		33		11		47	
Lemmus trimucronatus	19		50		36		105	
Microtus oeconomus	14		24		36		74	
Clethrionomys rutilus			3				3	
Unidentified microtine	10						10	
Sorex sp.					1		1	
Mustella rixosa	1						1	
Total food items	131		186		207		524	
Bird egg	5[a]	8	3	2				
Carrion, *Rangifer*	4	6						
Insect	21	32	33	21	Few[b]			
Rubus			30	20				
Vacinium			7	5				
Seeds					Rare			
Total pellets	65		154					

[a] Occurrence in pellets.

[b] Estimates of amount present.

TABLE 34

Food items in pellets of long-tailed jaegers, Cape Sabine 1959

Food items	*Total number*	*Per cent*
Avian, total	40	9
Passerine, total	37	9
Charadriiform, total	3	1
Calidris melanotos	2	
Ereunetes pusillus	1	
Mammalian, total	391	91
Microtine rodent, total	390	90
Lemmus trimucronatus	3	
Microtus oeconomus	387	
Sorex arcticus	1	
Total food items	431	
Bird eggs	2[a]	1
Insects	43	15
Number of pellets	285	

[a] Occurrence in pellets.

These were only half of the proportion of redpolls in the parasitic jaeger's diet. All ten identifiable passerine birds in the food remains were Lapland longspurs. This passerine, the most abundant species in foothill and coastal plain tundra, seems to be the most frequently taken bird by both the long-tailed and the parasitic jaegers.

These data all indicate clearly that the long-tailed jaeger is by preference a microtine rodent predator, which is also able to prey successfully on birds, primarily passerines and some juvenile shorebirds. In inland areas of northern Alaska, the microtine rodent and passerine bird populations provide a dependable food supply from year to year and consequently support a relatively stable breeding population of long-tailed jaegers.

TABLE 35

Food items from three long-tailed jaeger nests, Cape Sabine 1959

	July						*August*			
Food items	*16*	*19*	*22*	*25*	*28*	*31*	*3*	*6*	$\bar{E}$	*Per cent*
Avian, total									4	5
Passerine, total	0	2	0	1	0	1	0	0	4	5
Charadriiform, total									0	
Mammalian, total									81	95
Microtine rodent, total	2	13	12	8	17	12	10	7	81	95
Total food items									85	
Bird egg		1[b]							1	2
Insects	1	13	8						22	41
Number of pellets									53	

	July											
Food items	*6*	*8*	*10*	*12*	*15*	*16*	*19*	*22*	*25*	*28*	$\bar{E}$	*Per cent*
Avian, total											18	12
Passerine, total	1	1	3	2	2	1	4	0	1	1	16	11
Charadriiform, total			1		1						2	1
Mammalian, total											133	88
Microtine rodent, total	9	11	24	22	20	7	12	8	18	2	133	88
Total food items											151	
Insects				1[b]		2	2	1	2	2	10	10
Number of pellets											105	

	July											
Food items	*11*	*13*	*15*	*19*	*22*	*25*	*28*	*31*	*3*	*25*[a]	$\bar{E}$	*Per cent*
Avian, total											14	11
Passerine, total	0	1	2	0	3	0	4	1	0	2	13	10
Charadriiform, total				1							1	1
Mammalian, total											112	89
Microtine rodent, total	10	7	10	18	8	9	14	8	9	19	112	89
Total food items											126	
Insects	1[b]			1	1					1	4	5
Number of pellets											81	

[a] Pellets collected from the territory.

[b] Occurrences in pellets.

Summary and Discussion of Food Habits

The parasitic and pomarine jaegers both breed on the northern part of the coastal plain, while the parasitic and long-tailed jaegers breed on the southern coastal plain, in the foothills, and in the mountains. Rarely, as at Cape Sabine in 1959, all three jaegers breed in the same locality. Modern competition theory suggests that the three species cannot occupy the same niches, and feeding is one of the adaptations most immediately responsive to competition among sympatric species (Huxley, 1942).

Except in rare instances when the three jaegers breed in the same area, the only way to compare food habits directly is to study the non-breeding birds that do occupy similar environments. Non-breeding jaegers forage in coastal areas and on adjacent tundra, and they are rarely seen inland in the breeding season. The three species occasionally forage in large mixed flocks, especially in non-lemming years, when large numbers of non-breeding pomarine jaegers form the nucleus of such aggregations.

The similarities in the diet of the three jaegers when foraging in the same areas are much greater than any differences. All three are omnivorous feeders, consuming small percentages of birds, small animals, and carrion, with almost no significant difference in relative amounts apparent among them.

The one difference in food habits that seems significant is the degree to which the three species utilize inverbebrate prey, particularly insects. The pomarine jaeger stomach samples had 83 invertebrate items of 13 taxa, an average of 2 items per stomach; the parasitic jaeger stomachs had 215 items from 7 taxa with an average of 7 items per stomach; while the long-tailed jaeger stomachs contained 1811 items from 37 taxa, an average of 55 items per stomach. Insects were more than half of the contents of 52 per cent of the long-tailed jaeger stomachs. They were a significant proportion of the contents of only a few parasitic jaeger stomachs (9 per cent) and of no pomarine jaeger stomach.

Jaegers thus appear to be potential competitors for food in years when they do not breed. The long-tailed jaeger seems to be able to use insects as an important part of its diet in such years and thus escapes partly from competitive pressure from the two larger species. Its relatively small size allows it to use such small particles of food more efficiently than the other jaegers. Competition for the limited food supply in these years may, however, be ultimately responsible for the early departure of non-breeding jaegers from the North Slope.

Food habits of breeding jaegers are significantly different. The pomarine jaeger is an obligate predator on the brown lemming and other microtine rodents. At Pitt Point in 1957, and at Barrow in 1956 and 1960, when the lemming population was at least moderately high, *Lemmus* occurred in 100 per cent, 98.6 per cent, and 97.8 per cent of the pellets respectively. Data from Barrow in 1959, when the lemming population was low, showed that the pomarine jaeger also took lemmings almost exclusively. The data from Cape Sabine support these observations, where almost 100 per cent of the food that the pomarine jaeger was able to obtain from the tundra was *Microtus oeconomus*. The pomarine jaeger not only requires small rodents as a food supply, but can obtain them efficiently only when the vegetation is low and the rodents are accessible. The observation that the pomarine jaegers at Cape Sabine resorted to the ocean for most of their food, coincident with the growth of vegetative cover, indicates that tall vegetation can interfere with the hunting effectiveness of the largest jaeger.

The parasitic jaeger is primarily a predator on small birds. In the mountains at lakes Peters and Schrader 93 per cent of its food was avian, and 94 per cent of that was passerine birds. At the Kaolak River the quantity of birds in the diet was variable and ranged from 75 to 88 per cent in the three seasons, and again most (65 per cent) were passerines. The remainder of the food was mostly microtine rodents. At Cape Sabine, the parasitic jaeger (and also the pomarine and long-tailed jaegers) bred in numbers in excess of their numbers in the previous two years, apparently in response to a high *Microtus oeconomus* population. Yet the percentage of birds in the diet of the parasitic jaeger was 75, and *Microtus oeconomus* was only 25 per cent. This is an increase of only a few per cent of rodents over the average at the Kaolak River. There could hardly be a better illustration that the breeding parasitic jaeger is primarily a bird predator than the fact that it took predominantly birds even in the presence of an abundant microtine prey. Ninety-six per cent of the birds taken were passerine. The food habits of one breeding pair at Barrow in 1956 are also interesting. This pair selected a territory isolated from the dense pomarine jaeger population of that year. Though the territory supported a *Lemmus* population, almost no *Lemmus* remains were found in the nest enclosure, and only a few *Lemmus* remains were picked up on the territory. The chick grew rapidly and steadily, so that the 14 food items found in the nest enclosure must have represented a small fraction of its food. Presumably this pair fed on fish or carrion, which would explain the lack of undigested remains at the nest. Both *Lemmus* and birds were an insignificant part of this pair's diet. The low breeding populations of birds in high lemming years at Barrow may be the reason for the paucity of avian remains in the food in this pair.

In lemming years, many nesting attempts by both shorebirds and passerines fail because of physical disruption of nests by lemmings and probably also because of predation by pomarine jaegers.

The food habits of the parasitic jaeger at Cape Sabine in 1959 raise the question of why they bred there that year if they did not utilize the *Microtus* population. One possibility is that the birds responded to the microtine population early in the season and then switched to their preferred prey, birds, by the time the chicks had hatched. This change would not be detectable from food remains at nests. It is also possible that they were stimulated to breed by the high population of long-tailed and pomarine jaegers establishing territories in the area.

The long-tailed jaeger is primarily a microtine rodent predator, as is the pomarine jaeger. Unlike its more ponderous relative, however, it is able to exploit alternative food when breeding. This is best illustrated at the Kaolak River, where it exploited both birds and small rodents with almost equal success. Birds varied from 41 to 64 per cent in the long-tailed jaeger's prey in the three seasons, and the per cent of microtine rodents varied accordingly. They took more birds than rodents on the whole but nevertheless took a higher proportion of rodents than the parasitic jaeger in the same area. At Cape Sabine, however, 91 per cent of the food items were microtine rodents, and the remainder were birds, thus illustrating that when it is possible they are preferentially microtine rodent predators.

Both the parasitic and long-tailed jaegers prey to a significant extent on birds, predominantly passerine birds. Seventy-nine to 96 per cent of the birds taken by the parasitic jaeger at the Kaolak River and Cape Sabine were passerines, as were 82 to 92 per cent of the birds taken by the long-tailed jaeger in the same areas. Shorebirds, which are the other major bird group preyed on, make up 2.4 to 13 per cent of the birds taken by the parasitic jaeger, and they are 7 to 12 per cent of the birds taken by the long-tailed jaeger. The 2.4 per cent shorebirds was the proportion taken by the parasitic jaeger at Cape Sabine, the percentages at other localities were 6 per cent at lakes Peters and Schrader, 11 per cent at Barrow, and 13 per cent at the Kaolak River.

While the two jaegers take a similar proportion of shorebirds among their avian prey, the age classes of shorebirds differ. The parasitic jaeger takes 32 per cent adult shorebirds and 68 per cent juveniles, while 96 per cent of the shorebirds taken by the long-tailed jaegers are juvenile. Usually only the small shorebirds (Baird's sandpiper and semi-palmated sandpiper) are taken as adults by the parasitic jaeger.

The Lapland longspur was sixty-two per cent of identifiable passerine remains among the parasitic jaeger's prey, and all ten identifiable passerines among the long-tailed jaeger's prey. Thus the evidence suggests that the commonest and most conspicuous passerine on the North Slope is the major avian prey of both of these jaegers.

In summary, we can generalize on the predatory habits of jaegers when breeding by saying that the parasitic jaeger is primarily a bird predator, while the pomarine and long-tailed jaegers are primarily microtine rodent predators. The pomarine jaeger, however, is an obligate microtine rodent predator as it is unable to exploit alternative prey to a significant degree. The long-tailed jaeger, a smaller and more agile bird, can and does exploit avian prey to a considerable degree and is further able to augment its food supply with insects. Thus it is able to inhabit areas where microtine rodent populations do not build up to superabundant "highs." Both of the two smaller jaegers prey on birds to a significant degree. Passerine birds, predominantly the Lapland longspur, are the major avian prey of both species.

General Discussion

Competition

When congeneric species come into geographic contact after having evolved in isolation they usually compete. The evolutionary and ecologic results of such contact were first put forth by Gause (1934), Mayr (1942), Huxley (1942), Lack (1944, 1947) and subsequently discussed by several authors, including Gibb (1954), Hamilton (1962), Orians and Willson (1964), Schoener (1965) and Lack (1971). The general conclusions are that several stable conditions can eventually result from this competition: One species may eliminate the other completely; the two species may continue to occupy separate but contiguous geographic regions; they may occupy different habitats in the same region; and they may live in the same habitat and region but eat mainly different foods. The last two steps involve evolution of sympatry and separate ecologic niches. When sympatry is achieved the two species may differ significantly in size, the size difference being associated with differences in food (Huxley, 1942). The evolution of sympatry may also involve an intermediate situation manifested as interspecific territoriality. The subsequent evolution of separate niches, which allow over-lapping territories, will also result in reduction or virtual elimination of interspecific strife. Thus selection tends toward reduction of interspecific competition as sympatry evolves.

The different body sizes of the three jaegers, their geographic distribution, and their habitat preference suggest that they have been in geographic and ecologic contact for a long time and that they have evolved separate ecologic niches. Their territorial relationships and particularly their food ecology, however, indicate that some competition does occur among them.

Geographic Distribution: — The ranges of the three jaegers in northern Alaska are detailed in an earlier section. Briefly, the pomarine jaeger breeds along the coast and in the northern apex of the coastal plain, in an area approximately coincident with the region in which the brown lemming population undergoes extreme cyclic fluctuations. The long-tailed jaeger breeds in the southern coastal plain, foothills, and mountain valleys; while the parasitic jaeger breeds over all of the North Slope and is sympatric with both of the other species.

All three jaeger species have broad, almost circumpolar breeding ranges in arctic and subarctic regions; but in spite of differences in their breeding ranges there are large areas of geographic overlap. The parasitic jaeger has the most southerly range of the three jaegers with a significant portion of its population breeding in subarctic, maritime regions, where it does not compete with either of the other two species. The long-tailed jaeger breeds farther north than either of the other two species and thus is also without competition on part of its range. The pomarine jaeger, with a range that is the most latitudinally restricted of the three, is a potential competitor with both of the other species over its entire range. Thus potential competitive relationships occur among the three jaegers over a large part of the ranges of all three species as well as in northern Alaska.

Habitat preferences and overlap: — The three jaegers do show different habitat preferences in northern Alaska. The pomarine jaeger roosts and nests on low lying marshy tundra in coastal areas. The long-tailed jaeger definitely prefers upland situations and usually nests on ridge tops or on the upper parts of long slopes. It does occasionally establish territories in marshy areas similar to situations utilized by the parasitic jaeger. The habitat preferences of the parasitic jaeger are the most difficult to define precisely. It breeds on marshy tundra near Barrow and in marshes along river courses in the foothills. It shows an affinity for bodies of water and frequently nests near large lakes, as at lakes Peters and Schrader and at the Kaolak River. In its preference for wet tundra it seems closest in habitat affinity to the pomarine jaeger. While it chooses wet areas in which to nest, such habitat is limited in the southern coastal plain and foothills, and parasitic jaegers typically hunt over mesic tundra where the long-tailed jaeger also seeks its prey.

The three species occupy similar habitats in other parts of their range. The pomarine jaeger breeds in the marshy river valley in the Kuskokwim Delta (Brandt, 1943), in wet tundra on Victoria Island (Parmelee *et al.*, 1967), and on low plains near the sea in western Greenland (Salomonsen, 1950). In the Old World it nests on coastal tundra primarily, but also along lakes and rivers, and is found in both dry and boggy situations (Dement'ev *et al.*, 1951).

The long-tailed jaeger nests only on the upland tundra in the Kuskokwim Delta (Brandt, 1943). In Greenland it breeds on the dry tundra of the high arctic (Salomonsen, 1950), where it is found on plains and slightly sloping hillsides up to an altitude of approximately 2500 feet. It does not breed in islets and skerries as does the parasitic jaeger, but prefers the interior where it may exist independently of the sea. It has similar habitat preferences on Ellesmere Island (Maher, 1970b) and presumably elsewhere in the high arctic. In the Old World arctic it breeds on tundra south to the forest boundary, prefering dry stretches, and in the hilly interior of Lapland and Norway (Dement'ev *et al.*, 1951).

Elsewhere in the arctic the parasitic jaeger prefers low grassy or mossy tundra with preference for water bodies, as it does in northern Alaska (Brandt, 1943; Godfrey, 1966; and Dement'ev *et al.*, 1951). In Greenland it also breeds in isolated pairs or small colonies of up to 20 pairs on islets or on the mainland. Colonies of up to approximately 70 pairs occur on Fair Isle (Williamson, 1965), from 10 to 150 pairs in the Faeroes (Dement'ev *et al.*, 1951), while Lovenskiold (1964) records one colony of 9 pairs on Spitzbergen.

Colonial pairs defend rather large territories so that the colonies are dispersed (Salomonsen, 1950), but there is little exact information on territory size. Dement'ev *et al.* (1951) mention that nests are 50 to 100 meters apart. Nests are more dispersed on Spitzbergen, so that it becomes difficult to consider groups as colonies. Lovenskiold (1964) records a group of 9 nests with one kilometer between nests, while later he says that there is "always at least several hundred meters between nests."

Food overlap: — Indices of food overlap among the three species of jaegers were calculated using the overlap index of Orians and Horn (1960). The indices are based on food data presented previously and are calculated for both breeding and nonbreeding populations. Indices for breeding populations were calculated separately for each locality where at least two jaeger species are sympatric. Insects and invertebrates were not included in the food of the breeding populations, because they were usually unidentifiable fragments and because such remains were an insignificant part of the total food. Data from nonbreeding populations were combined from several coastal localities. Separate indices for vertebrate and invertebrate prey were calculated, because the sample is mostly stomach contents rather than regurgitated food remains, and the invertebrates were, therefore, identifiable and, also, because such prey was evidently important in the diet of nonbreeding birds, particularly the long-tailed jaeger.

The results for breeding populations (Table 36) show that there is no strong food overlap between the pomarine and parasitic jaegers either at Barrow or Cape Sabine. The overlap is higher at Barrow (.64 vs .41) where there were fewer avian prey than at Cape Sabine. Parasitic and long-tailed jaegers have a very high index of overlap at the Kaolak River (.89) where both species took similar proportions of microtine rodent and avian prey, but they have a very low index of overlap at Cape Sabine (.41) where the parasitic jaeger took mainly avian prey and the long-tailed jaeger took mainly microtine rodents. The degree of overlap between parasitic and pomarine jaegers and parasitic and long-tailed jaegers at Cape Sabine are very close (.42 vs .41). Finally the long-tailed and pomarine jaegers at Cape Sabine have an overlap index of .9993.

TABLE 36

Index of food overlap of breeding jaeger populations

Species	*Locality*	*Index of overlap*
Pomarine vs parasitic	Barrow	0.6394
	Cape Sabine	0.4189
Parasitic vs long-tailed	Kaolak River	0.8896
	Cape Sabine	0.4123
Pomarine vs long-tailed	Cape Sabine	0.9993

Only food obtained from the tundra was used in calculating these indices. In most instances this was all or almost all of the food; but the parasitic jaeger at Barrow in 1956 and the pomarine jaeger at Cape Sabine in 1959 were both apparently obtaining a significant proportion of their food from the ocean. Thus, the very high overlap of pomarine and long-tailed jaegers at Cape Sabine is somewhat biased.

Non-breeding jaegers foraging in coastal areas show variable amounts of food overlap, and also variation in the degree of overlap between vertebrate and invertebrate prey, as would be expected (Table 37). Indices of overlap of vertebrate prey among nonbreeding populations show that the overlap between the pomarine and long-tailed jaeger is less than between these species when breeding at Cape Sabine (.76 vs .99). The overlap index (.53) for nonbreeding long-tailed and parasitic jaegers is considerably less than the overlap of the breeding populations at the Kaolak River (.88); but it is higher than the overlap between these species at Cape Sabine (.41).

All of the nonbreeding jaegers seem to eat a higher proportion of insects than the breeding populations; but the long-tailed jaeger is the only species for which insects appeared to be a significant bulk of the total food. The parasitic and long-tailed jaegers showed greatest overlap in composition of invertebrate food.

TABLE 37

Index of food overlap of non-breeding jaeger populations from coastal localities

Species	*Index of food overlap* *Vertebrate prey*	 *Invertebrate prey*
Pomarine vs parasitic	0.8542	0.5836
Parasitic vs long-tailed	0.5308	0.9459
Pomarine vs long-tailed	0.7643	0.6840

I have no quantitative index of habitat overlap among the three species. Habitat preferences discussed earlier, particularly in discussion of foothill tundra, were based on the kind of situations in which the birds prefer to nest — that is, where the core of the territories was located. In fact, the parasitic jaegers forage far from their nest sites, and in situations like the Kaolak River and Cape Sabine overlap in foraging habitat between the species is very high. At the Kaolak River both long-tailed and parasitic jaegers were seen commonly on the upland and over marsh. The long-tailed jaeger was not seen foraging along the riparian willow shrub as the parasitic jaeger was; and anatid chicks never showed up in the food remains of the long-tailed jaeger, a fact suggesting that the long-tailed jaeger did not forage about the lakes and ponds as the parasitic jaeger did. With these minor exceptions, the foraging area of the two species appeared to be the same, so that the index of food overlap probably closely represents the total ecologic overlap. Foraging overlap on tundra between the pomarine and parasitic jaegers at Barrow must be total, as habitat differences are negligible in that area. The topography at Cape Sabine allowed some habitat separation among the jaegers. Pomarine jaegers established their territories in the broad marsh swales and appeared to confine themselves almost entirely to such areas in foraging, except late in the season when they foraged along the ocean. Long-tailed and parasitic jaegers nested and foraged in more mesic parts of the area. Thus overlap in foraging habitat between the parasitic and long-tailed jaegers was very high — nearly total, as at the Kaolak River, and overlap of either with the pomarine jaeger was comparatively slight.

Discussion: — The two jaegers with the highest index of food overlap, the long-tailed and the pomarine, are also the two species with the clearest habitat separation and the most clearly separated geographic ranges in northern Alaska. The pomarine jaeger appears to be the dominant competitor of the two, as it evidently excludes the long-tailed jaeger from an area in which they come into direct contact. It seems reasonable to conclude that the long-tailed jaeger has been excluded from the northern part of the north Alaska coastal plain, or at least prevented from colonizing it, by the interaction with the larger species. The pomarine jaeger, however, appears to be restricted in geographic range and habitat by the nature of its specialized adaptations as a predator on the brown lemming. Its highly efficient method of catching lemmings requires shallow peaty soil and low vegetation, while it is too ponderous to exploit birds effectively as alternate prey when breeding. In the region it does inhabit there is no alternate microtine rodent that occurs regularly in significant numbers. Its southward spread in northern Alaska, therefore, seems to be limited by the lack of the kind of substrate on which it can function effectively as a lemming predator. The northern limit of its range may be set by attenuation of the habitat of the brown lemming, by interaction with the long-tailed jaeger, or by the length of its breeding cycle, which is significantly longer than that of the long-tailed jaeger. Possibly all three factors operate. Nothing is known of the species and its relations with the long-tailed jaeger at the northern edge of its range.

The long-tailed jaeger is preferentially a microtine predator, but because of its small size and great agility it can exploit passerine birds as alternate prey; and it is the only jaeger that is able to use insects as a significant food source in nonbreeding years. It usually preys on microtine rodents and passerine birds in almost equal proportions in northern Alaska, and this habit has allowed it to occupy foothill tundra south of the coastal plain inhabitated by the pomarine jaeger. It is the only jaeger that breeds in central Alaska (Gabrielson and Lincoln, 1959). The long-tailed jaeger is apparently very dependent on lemmings in the northern part of its range, but this may be partly because passerine birds are relatively scarce on the high arctic tundra (Maher, 1970b).

Selection for interspecific territoriality should not occur until the degree of overlap between two species is great enough that it becomes advantageous. Ecological overlap of this magnitude seems to occur more readily in areas with simple vegetative substrates (Orians and Willson, 1964). It is not surprising that the long-tailed and pomarine jaegers are interspecifically territorial when they breed in proximity, considering the almost complete overlap of food that they take from the tundra as well as the simplicity of tundra vegetation. Yet it is obvious from the habitats utilized by the two species that they have partitioned their food initially by exploiting different kinds of habitats and that they only breed in proximity where the topography produces an environment with intermixed patches of marsh and upland tundra.

An alternative to partitioning food supply by habitat is partitioning it by body (and food) size (Schoener, 1968), and it might at first glance seem as if these species, which are the smallest and largest members of the genus, have done so. The almost total degree of overlap of the vertebrate food they exploit from the tundra, however, is evidence that they have not, at least as far as their food supply on the breeding grounds is concerned. Such partitioning as there is seems to involve a greater amplitude in the food niche of the long-tailed jaeger compared with that of the pomarine jaeger. The former can (as at the Kaolak River) subsist to a significant extent on birds in addition to microtine rodents; or as at Cape Sabine or in the high arctic (Maher 1970b), it can subsist almost entirely on rodents when they are sufficiently abundant. The long-tailed jaeger also makes significant use of insects as food when not breeding, and insects may be a critical supplement to the diet of chicks at times (Maher 1970b). In spite of these differences in feeding niche, both species seem to be primarily adapted as microtine rodent predators, as they both have their greatest recorded breeding densities and greatest breeding success when nesting in association with a rodent high.

Partitioning of food by size would seem to offer the possibility of complete geographic overlap and habitat sharing between the pomarine and long-tailed jaeger; but there is no obvious alternative mammalian prey abundant enough and sufficiently different from the lemmings in size that either one of these species could specialize on it. Thus the present relationship between the two species does not seem to be a temporary stage in the evolution of sympatry but a stable situation resulting from lack of a suitable alternative food source that would allow partitioning of food by size rather than the present partitioning by habitat. The two species are thus constrained by the low ecologic diversity of the tundra ecosystem.

Other avian predators on lemmings, such as the snowy owl, regularly occur with the pomarine jaeger in northern Alaska and also exploit the brown lemming population highs. Certainly the jaeger is aggressive toward the snowy owl; but the latter does not respond spatially to the harassment, and presumably the superabundant food supply usually present in lemming high years allows both to utilize it together (Lack, 1946).

Competitive relations of the parasitic jaeger with the pomarine jaeger in northern Alaska are obscure, because I was only able to study two instances in which both species bred in the same area; at Barrow in 1956 and at Cape Sabine in 1959. Food overlap indices suggest greater potential competition at Barrow (overlap .64) than at Cape Sabine (overlap .42). In lemming highs, breeding by ground nesting birds is greatly reduced because of interference by lemming activity and predation by pomarine jaegers, so that avian prey for parasitic jaegers is probably below normal levels. Thus the increase in food overlap between these two jaegers at Barrow over that at Cape Sabine could be the result of reduction of the parasitic jaegers' preferred prey, forcing them into greater competition with the pomarine jaeger. In this instance the parasitic jaeger was able to solve the problem at Barrow by resorting to feeding from the ocean in the latter part of the season; however, there is evidence from Victoria Island that pomarine jaegers exclude parasitic jaegers when they breed. Parmelee *et al.* (1967) noted that parasitic jaegers were more abundant during two lemming low years when no pomarine jaegers bred than they had been in a lemming high in 1960 when both species bred.

There is more information on the ecological relationship of the parasitic jaeger with the long-tailed jaeger. The two species coexist over large areas of northern Alaska where they maintain exclusive territories and take approximately the same prey. Breeding habitat of the two species broadly overlaps in the northern Alaska foothills. The parasitic jaeger seems to prefer nesting in swamp areas near bodies of water, and the long-tailed jaeger, at the top of slopes or ridges; but in the foothills they tend to forage over the same areas, and overlap of foraging habitat is greater than nest habitat.

The short-eared owl is the only other ground nesting predator that regularly inhabits these northern foothills, although it is usually widely dispersed. In coastal areas of the foothills, as at Cape Sabine, microtine rodent populations occasionally reach peak numbers, and there the short-eared owl coexisted with the three jaeger species.

I have assumed that in typical foothill tundra the parasitic and long-tailed jaegers are unable to separate their niche requirements completely, particularly their food requirements, and that under these circumstances there is a selective advantage for development of interspecific territorial behavior (Orians & Willson, 1964). Furthermore, the broad overlap of food habits, as well as the lack of suitable alternative prey for either species, suggests that the development of completely separate niches is not possible and that the present relationship will remain stable for a long time, as with the pomarine and long-tailed jaegers.

The northern limit of the parasitic jaeger's range corresponds approximately with the northern extent of the range of its most important prey, the Lapland longspur. This may be partly coincidental, yet the food habit studies suggest that passerine birds are the most important component in the diet of this species and that most passerines eaten are longspurs. The other important dietary component consists of shorebirds, which are usually taken as chicks; and these, because of the short season of abundance, could not be a dependable food supply by themselves. Hence, it is not unreasonable to expect a decline in the density of parasitic jaegers northward as the density of tundra passerines in general, and the longspur in particular, declines. Towards the northern edge of the parasitic jaeger's range, inland populations should also experience intensified competition with the long-tailed jaeger as the population at Barrow did with the pomarine, since passerine birds are an important alternate prey for the long-tail, and lemmings are an important alternate prey for the parasitic jaegers.

It is difficult to reconcile the coexistence of the long-tailed jaeger and the parasitic jaeger in foothill tundra with modern thinking on competition, but Hutchinson (1957) has suggested several cases in which the Volterra-Gause principle is unlikely to apply. He suggested that a fluctuating environment may prevent competition from going to completion and allow competing species to coexist. In this case, fluctuations in relative proportions of microtine rodents and passerine birds in foothill tundra may allow both jaeger species to remain, by frequently tipping the balance to favor the reproductive success of one or the other jaeger population. A pair of either species once established on a territory could maintain it against aggression from individuals of both species, as they apparently do. The proportion of new permanent territories established by the two species each year would be related to the proportion of each species among the spring migrants that are ready to establish territories and the relative abundance of either microtine rodent or avian prey. The proportion of the two jaeger species in the migrants each spring would relate to the average reproductive success of each species in previous years and to their survival in winter quarters.

Alternatively a competitive disadvantage of one species could be masked by continued inflow of juveniles produced on other parts of the species range.

Function of territories

Several aspects of territories among the jaegers suggest that they are adapted primarily to insure that nesting pairs have enough food for the breeding season. This is particularly true of the long-tailed and pomarine jaegers, in which territory size has been shown to vary directly with microtine rodent density.

Schoener (1968) compared regressions of avian type A territory size with body weight for species grouped according to the amount of animal food (vertebrate or insect) in their diet. Herbivores and some omnivores had the smallest territory size for their weight, while predatory birds had the largest. He concluded that territory size was correlated with food supply, as his results were probably related to the relative food densities for the different diet categories.

A regression of body weight and territory size of birds that feed on almost all meat or insects gave a positive slope of 1.31 ± 0.06 for predatory and insectivorous birds (Schoener, 1968). Figure 27 shows the data and the regression line with

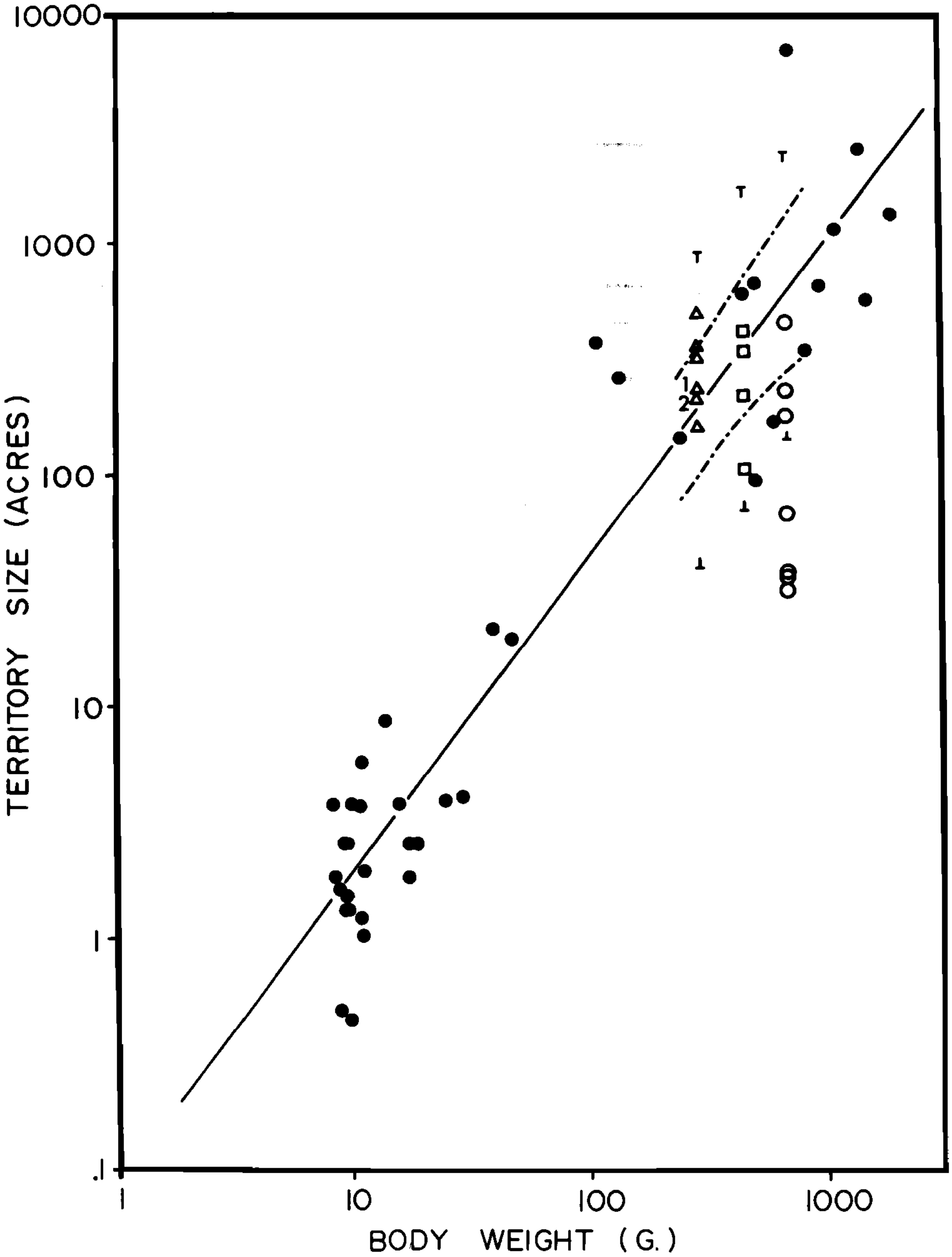

Figure 27. Regression of body weight and territory size of carnivorous birds with all-purpose territories (from Schoener, 1968). Territories of long-tailed jaeger (triangle), parasitic jaeger (square), and pomarine jaeger (open circle) have been added with 95 per cent confidence limits (dash dot line) and 95 per cent prediction limits (T). Numbers 1 and 2 are long-tailed jaeger territory sizes from northern Sweden and Ellesmere Island respectively.

the mean territories of jaegers for different years and areas added. Ninety-five per cent confidence limits and 95 per cent prediction limits for the values of X equal to mean jaeger weights compared with the number of data points for each jaeger species are also shown.

The mean territory values from northern Alaska for the long-tailed jaeger fall within the 95 per cent confidence limits as do most of the points from individual years and areas. Two of these points are above the 95 per cent confidence limits but within 95 per cent prediction limits. Average territory sizes from Norway (Andersson, 1971) and Ellesmere Island (Maher, 1970b) are also within 95 per cent confidence limits. The average territory size of the long-tailed jaeger is above the regression line, suggesting a territory size slightly larger than normal for its size.

The mean territory sizes of parasitic jaegers are almost on the regression line, and the data points are distributed symmetrically about it. Only one point is outside the 95 per cent confidence limit but is within the 95 per cent prediction limit. These data suggest that the parasitic jaeger territory is approximately average in size for a predatory bird of its weight.

The pomarine jaeger territory size is well below the expected value for a predatory bird of its size. All seven data points are below the regression line, only one is within the 95 per cent confidence limits, and only two others are within the 95 per cent prediction limits. The four lowest points, well below the 95 per cent prediction limits, are mean territorial values for the four lemming high years. The upper one is from Pitt Point, a moderate high, and the other three points are from Barrow.

The territory sizes of the long-tailed and parasitic jaegers are predictable by Schoener's regression and are therefore consistent with the sizes of territories of other predatory species. The pomarine jaeger on the other hand has a similarly predictable territory size only at its lowest recorded breeding densities, and thus appears to be a special case especially when breeding at maximum density. Schoener (1968) showed that the home ranges of some Wyoming raptors varied inversely with the number of prey per area. The relatively small size of the pomarine jaeger territory seems to accord with the conclusion that its size is correlated with the very high density of its prey species, the brown lemming.

Both long-tailed and pomarine jaegers feed on prey of similar types and size range when exploiting lemming highs. The difference in territorial response between them can be explained on the basis of their foraging behavior, and the resulting foraging efficiency in addition to the absolute density of prey. I have no data on prey density in any of these highs, but on the basis of the vegetative destruction by the overwintering microtine population it seems clear that the brown lemming high in the Barrow region reached considerably higher peaks than either the *Microtus* high at Cape Sabine or the *Dicrostonyx* high at Lake Hazen (Maher, 1970b). Moreover, the nature of the marsh vegetation and peat substrate allows the pomarine jaeger to dig lemmings from their burrows. Thus a lemming that has been detected but escapes to its burrow is still vulnerable to pomarine jaegers. In contrast, the tall complex vegetation at Cape Sabine and the hard mineral soil at Lake Hazen did not permit the long-tailed jaegers to dig lemmings out of their burrows, so that once a rodent reaches a burrow system it is no longer available to the long-tailed jaeger. Indeed, as discussed beyond, the long-tailed jaeger has not developed the digging behavior as the pomarine jaeger has. The result of these factors is that the pomarine jaeger seems to be more efficient at exploiting microtine rodents than the less specialized long-tailed jaeger, and this difference is reflected in a reduced territory size for the larger species.

Origins

The range of the long-tailed jaeger extends from the southern arctic to the northern limits of land. Viewed on this scale the north Alaska population is near the southern edge of the total range. The ecology of the species is best known, however, from the high arctic of Greenland and Canada, and there its association with the fluctuations of the varying lemmings has been described by Maniche (1910), Johnsen (1953), Maher (1970b) and others. Nothing like these high arctic breeding concentrations have been described from other parts of its range.

The pomarine jaeger on the other hand, is essentially a low arctic species with a latitudinally restricted range. In the North American arctic it is most abundant in the marshy tundra of northern Alaska and possibly Banks and Victoria islands. Its dependent association with the brown lemming fluctuations and with marshy tundra have been previously summarized by Pitelka *et al.* (1955a and 1955b) and more recently by Maher (1970a).

In northern Alaska the long-tailed jaeger prefers uplands, especially on slopes near the top of ridges. It breeds in similar situations on Ellesmere Island (Maher, 1970b) and Greenland (Salomonsen, 1950). The pomarine jaeger utilizes low marshy areas for its territory. The two species coexist only where topographic diversity brings their respective habitats into proximity as at Cape Sabine or the Kuskokwim delta (Brandt, 1943).

The habitat preferences of these two jaegers suggest that the two species evolved in different parts of the arctic, each in association with one of the two lemmings. Lemmings of the genus *Dicrostonyx* have a more northerly distribution than the genus *Lemmus* and extend to the northern limit of land over all of the arctic. Their habitat is mesic to dry upland tundra. *Dicrostonyx groenlandicus* is rare in the north Alaskan coastal plain because its habitat is also very rare. The brown lemming (genus *Lemmus*) extends farther south in the new and old world arctic than *Dicrostonyx* does, and in North America it is absent from the high arctic north of Lat. 75°N. Its preferred habitat is wet marshy tundra.

Refugia available to jaegers in the arctic for adaptation to tundra ecosystems during the last glaciation were in the high arctic of northeast Greenland, Beringia, and a series of nonglaciated areas in the old world in northern European Russia, in western Siberia about the mouth of the Ob, the central Siberian Plateau, and a large refuge or series of refuges in eastern Siberia separated from Beringia by the Chuckchi Peninsula (Johansen, 1956).

I suggest that the long-tailed jaeger adapted to breeding in the high arctic of northeast Greenland where it evolved as a lemming predator on the only microtine rodent probably present, *Dicrostonyx* (Macpherson, 1965). As sea birds which feed, at least in part by robbing other sea birds of their food, adaptation to a tundra community probably involved a first stage as a predator on birds. This may have been true of both the long-tailed and pomarine jaegers initially, and adaptation to preying on rodents was a subsequent development.

The pomarine jaeger still breeds on the last remnants of the Beringian coastal lowlands, in northern Alaska; and certainly nothing like the numbers and extent of the breeding that occurs there in lemming high years has been reported from elsewhere in the arctic. The refugium most likely to have had extensive marshy lowlands and a cycling population of *Lemmus* was Beringia, and I suggest that it is the probable area of origin of the pomarine jaeger.

The parasitic jaeger which still has a large maritime population in the north Atlantic probably originated in that area at the same time. Retreat of the Wisconsin and other glaciers permitted expansion of the ranges of the pomarine and long-tailed jaeger and brought them into contact. Habitat differences imposed on them in isolation by their primary prey species probably allowed geographic overlap to proceed rapidly, while ecological factors discussed above prevented niche expansion of either species and kept their contact to the marginal one it is.

The comparatively small size of the long-tailed jaeger may also have evolved as an adaptation to breeding in the high arctic, although the body sizes of the jaegers may be more directly related to partitioning of food or victims for robbing while away from the arctic breeding grounds. The advantages of large body size (reduced surface/volume) of homeothermic animals in cold climates is well known, and many groups illustrate the evolutionary response of increased body size and reduction of the size of extremities with increased latitude. However, there may be countervailing advantages to reduced size for a migratory predatory bird such as the long-tailed jaeger. The high arctic summer is very short; annual rainfall and the productivity of the tundra are low. This low productivity is reflected in low average density of lemmings and passerine birds, the major food supply of the jaeger. The advantages of smaller body size in these circumstances would be smaller energy requirement to produce the clutch, a more efficient relationship to the sparse food supply, and a shorter development time for the young, and hence a shorter breeding period.

The parasitic jaeger has probably colonized the arctic more recently than its congeners, as suggested by its southerly breeding range and generally low density in the arctic. If, as suggested here, the pomarine and long-tailed jaegers were already present in the arctic and adapted to their roles as lemming predators when the parasitic jaeger spread northward, it is difficult to imagine a third similar niche being available. The niche of a bird predator, therefore, was the inevitable one for the parasitic jaeger, because it was available and because the parasitic jaeger feeds by robbing other sea birds in the south. An avian predator niche was the simplest one for the parasitic jaeger to fill in colonizing the arctic.

Adaptations of Jaegers to the Arctic

The introductory section on the environment of northern Alaska has detailed the features of the arctic to which birds must adapt in order to colonize arctic communities successfully. Tundra vegetation is comparatively simple, and average productivity of arctic ecosystems is low. The productive season is short, and mean temperatures, even in mid-summer, are not far above freezing. Large differences in temperature between seasons greatly affect the time of snow melt, annual productivity, and avian food supplies. Moreover, the predatory jaegers have particular problems concerned with the nature of their food supplies. The brown lemming, which is essential for the pomarine jaeger when breeding, is abundant enough to support breeding in only one or two years out of four.

Other microtine rodent species, which are important to the long-tailed and parasitic jaegers in the foothills, do not fluctuate as widely in numbers as does the brown lemming, but collectively they seem to vary in abundance from year to year. The brown lemming, in high years, is typically most abundant when the snow melts and may either decline in numbers through the season, remain approximately constant in numbers, or, rarely, even increase in numbers. Young passerine birds and shorebirds, which are important prey of parasitic and long-tailed jaegers, are most available in mid-July, and their numbers gradually decline afterwards.

The three jaeger species have been conspicuously successful in adapting to this environment. In this discussion I will consider attributes of jaeger ecology and behavior that suggest themselves as adaptations to the arctic and compare them with breeding adaptations of their closest relatives, the gulls and terns.

Timing of the breeding cycle: — The length of the breeding cycle of the three jaegers differs. The long-tailed jaeger takes approximately 50 days from egg-laying until the chicks fly, while the pomarine jaeger takes approximately 60 days. When a two- to three-week period of chick dependence and a one- to two-week pre-egg period are added, the minimal time required for breeding is 80 to 90 days for the long-tailed and 90 to 100 days for the pomarine jaeger. The parasitic jaeger is intermediate between these two species.

There is little leeway for the jaegers to modify or vary their breeding cycle because of its length and the short arctic summer. An important adjustment for arctic breeding by jaegers has been the abbreviation of the initial phases of the cycle — occupation of territory and courtship. For the parasitic jaegers nesting on the Isle of Noss (Perry, 1948), this period is almost twice as long as it is for the species in northern Alaska. It is also characteristically long for temperate gulls (e.g., California gull, Johnston, 1956). The pomarine jaeger has the longest breeding cycle of the three jaegers; but on the other hand its food supply, a high lemming population, does not typically have a mid-season peak to which the pomarine must adjust. It is able then to arrive on the breeding grounds just at snow melt-off and begin breeding immediately. This results in the synchrony observed in the populations, although the beginning of breeding can be protracted somewhat in high years among some members of the population, and breeding by entire populations can be delayed by inclement weather.

The pomarine jaeger seems to have a slightly longer pre-egg stage than the other two jaegers, possibly because the population is nomadic with no apparent areal or territorial attachment from year to year. Since there appears to be no other means of facilitating remating of adults, establishment of territory and courtship are repeated each time the population breeds.

The mid-July generation of *Lemmus* has been suggested as an event that influences the timing of the pomarine jaeger's breeding (Pitelka *et al.*, 1955a). I do not consider it important in this regard, as the initial biomass contributed to the lemming population when this generation emerges is comparatively small and not then a significant addition to the pomarine jaeger's food supply. However, the size of this cohort does become important later in the season, because as the lemmings grow their increased biomass sustains the jaegers' food supply during the latter part of their breeding cycle as the chicks are reaching maturity.

The parasitic jaeger begins breeding immediately upon arrival. Pairs frequently reoccupy territories used previously, and this habit may facilitate rapid remating and breeding. In foothill tundra the chicks appear on the average to be a little ahead of the long-tailed jaeger chicks and are almost full-sized when their food supply peaks. Being very dependent on juvenile passerine birds, the parasitic jaegers characteristically have a sharp temporal peak in the availability of their food. Timing of breeding seems adjusted so that maximum demand of the pairs coincides with this peak. Microtine rodents are used as alternative food.

The long-tailed jaeger seems to have the most ecological amplitude of the three jaegers. It can exploit microtine rodent populations as at Cape Sabine, or bird and microtine populations as at the Kaolak River. A comparatively short breeding cycle and its flexibility in prey types apparently allow this species more freedom in timing than the other two jaegers. These differences may explain the lack of synchrony in egg-laying observed at Cape Sabine, as well as the tendency to breed a little later than the parasitic jaeger at the Kaolak River. Lack of synchrony in breeding was also observed in the high arctic (Maher, 1970b). Another factor that may reduce pressure on the long-tailed jaeger's breeding schedule is that in foothill tundra it exploits microtine rodent populations that are apparently not subject to great fluctuations from year to year and that also provide a more consistent food source for an entire breeding season than do juvenile passerine birds.

Timing of adult molt: — Molt is an energy-demanding process that must be performed at a time when sufficient food is available. In temperate zone and arctic birds the timing of molt in relation to food supply and the breeding cycle is an important ecological adjustment. Many arctic birds, including such large predatory species as the snowy owl, the short-eared owl (Pitelka *et al.*, 1955a) and the glaucous gull, molt on the breeding grounds. The passerines and many shorebirds separate the energy demanding molt and breeding cycles, but the larger forms broadly overlap molt with breeding. Most arctic shorebirds appear to molt on the breeding grounds immediately after breeding although some, as the pectoral sandpiper (Pitelka, 1959), molt after leaving the breeding grounds. All three jaegers, however, appear to postpone major molt until after they have left the breeding grounds. Pitelka *et al.* (1955a) reported that molt got underway in the pomarine jaeger population in late July or early August, but I have not observed this in subsequent seasons.

Examination of 114 jaeger skins from northern Alaska, including 79 pomarine jaegers, 23 long-tailed jaegers, and 12 parasitic jaegers, demonstrated that molt on the breeding ground consists almost entirely of adventitious replacement of contour feathers on the head and throat. Of 37 birds in the series showing signs of molt, only three were replacing rectrices (one pomarine and two long-tailed jaegers), and none were replacing any remiges. Examination of a series from temperate areas showed that molt of flight feathers can begin in August in birds away from the breeding ground but that generally molt of the flight feathers does not begin until mid-September or later.

The jaegers, then, have essentially by-passed the problem of molt on the breeding grounds, and unlike the other large avian predators mentioned above, they have avoided the additional energy drain this would entail in the period when the chicks are maturing and food supplies generally are dwindling.

Concealment and defense of brood: — Jaegers utilize some of the behavior patterns of ground nesting gulls to protect their nests and young. Breeding adults are very wary, and when a predator approaches they usually fly up while it is still a considerable distance away. As in the herring gull (Tinbergen, 1953), this habit must be associated with the fact that the nest and eggs are cryptically colored and difficult to locate.

The parasitic jaeger frequently performs an elaborate distraction display. It is characterized by plaintive calling and by a leading or luring movement away from the nest or young while the wings are extended and beaten spasmodically. The intensity varies directly with breeding density and with the phase of the breeding cycle (Williamson, 1949). Neither of the other jaegers performs this display, although elements of it are present in their behavior under the same circumstances. Both the pomarine and long-tailed jaegers will occasionally land near an intruder and run or walk away from the nest or young, sometimes calling and holding their wings up in an incipient flight position. Only once in approximately two thousand visits to pomarine jaeger nests, did I see an adult make a complete distraction display like that of the parasitic jaeger, and I have seen one or two distraction displays by long-tailed jaegers. The behavior is extremely rare, although incipiently present, in these two species in contrast to the parasitic jaeger. Distraction displays do not occur among the ground nesting gulls, probably because this would be an inappropriate and ineffective defense by colonial species, which depend instead on aggression towards predators and intruders (Cullen 1957).

All three jaegers attack predators and intruders near the nest or chick. They do this by repeated swoops and dives accompanied by loud calls. As they approach the intruder, they lower their feet and will strike with the feet as they swoop past. The parasitic and long-tailed jaegers attack by rapidly repeated dives. Long-tailed jaegers are sometimes so frantic in attacking an arctic fox that they will fly a vertical circle between dives going around the top upside down. Both members of the pair take part, when present. The pomarine jaeger frequently approaches an intruder by flying at him at eye level and swooping up at the last minute. The large size of the bird makes this a very intimidating display. In my experience the parasitic jaeger is the most aggressive of the jaegers toward a human intruder and the most likely to strike, the pomarine jaeger is slightly less aggressive, while the long-tailed jaeger rarely strikes an intruder.

Williamson (1949) noted that colonial parasitic jaegers were much more aggressive than isolated pairs. I noted the same correlation of aggression with density in the pomarine jaeger. Parasitic jaegers also seemed more aggressive when breeding in association with a high density of pomarine jaegers than in other situations. In all species aggressiveness varies individually.

The most effective predator of eggs and young jaegers in northern Alaska, and probably elsewhere in the arctic, is the arctic fox (*Alopex lagopus*); and it is harassed relentlessly by all three species in a nest area. The pomarine jaeger seems particularly effective in driving a fox, probably because of its large size. It is my impression that harassment by jaegers does fluster a fox and probably does reduce its effectiveness in locating jaeger chicks or eggs.

The virtual absence of a distraction display in the pomarine and long-tailed jaeger suggests that it is not as effective against arctic fox (or even wolf) predation as is aggression. There is some evidence that the distraction display of the parasitic jaeger may also be ineffective against an intelligent canid like the arctic fox. Observers who have witnessed arctic foxes depredating parasitic jaeger nests (S. W. Speller, *personal communication*) report that the fox ignored the display-ing adults and went directly to the nest. If the distraction display is not as effective against the arctic fox as aggression, then its retention by arctic populations of parasitic jaegers may be the result of selection in the southern maritime populations of the species. Williamson (1949) reported a much more rapid development of the display in colonies of jaegers than in isolated pairs. He also reported cooperation in distraction displays and observed groups of up to five birds "groveling and whimpering . . . at a radius of from thirty to fifty yards." The effectiveness of this display against a mammalian predator may be enhanced by the confusion created by the participation of neighboring pairs, making it an effective anti-predator device in the portion of the species range where it does nest in groups. The parasitic jaegers breeding in colonies, it should be remembered, are greatly dispersed in comparison with gulls breeding colonially, and Cullen's observation (cf above) about the effectiveness of aggression rather than distraction in the colonial nesting gulls is probably valid. The distraction display of the parasitic jaeger needs more investigation from a functional point of view.

Young jaegers exhibit cryptic behavior in response to intruders as do young ground nesting gulls (Cullen, 1957). Jaeger chicks conceal themselves under vegetation or other cover if possible, flatten themselves on the ground, and remain motionless while the adults give the alarm call. Although the plain grey or blackish natal down is not cryptic, as is the natal down of young gulls, the territorial system of jaegers, which results in wide dispersion of the young, may render cryptic color itself unnecessary. The juvenile plumage, which becomes visible when the chick is a couple of weeks old, is a cryptic mottling of black, brown, and tan and may contribute to concealment.

Pomarine jaegers protect their entire territory and attack intruders on any part of it. The parasitic and long-tailed jaegers, however, defend only a core area of some 500 yards diameter (40 ± acres) during incubation and rearing of chicks. One or both adult long-tailed jaegers is almost always at the nest area to defend it and the chick. Adult parasitic jaegers frequently leave the chick and nest area unguarded while they hunt together. As mentioned previously, the difference between the latter two species in this behavior is highly significant. The behavior of both species, guarding or not guarding the chicks, seems successful in north Alaska. This may be because the vegetation structure is so complex that the chicks are always well concealed. Long-tailed jaeger chicks are very conspicuous on the bare tundra of the eastern and high arctic where the species is more abundant than in northern Alaska. The parasitic jaeger chick on Fair Isle is usually guarded by one adult while the other adult forages (Williamson, 1965).

Foraging and food supply: — (a) Clutch size. The clutch size of altricial birds appears to be adjusted to the number of young for which the adults can, on the average, find enough food (Lack, 1954). This should apply to the semi-precocial gulls, terns, and jaegers since the adults provide most of the food the chicks require until fully fledged. Clutches in gulls are usually three, and in terns, usually two or three. Clutches smaller than normal in these groups seem to occur in species that are offshore (rather than inshore) feeders, are partially scavengers, or that breed in situations demanding a very compressed breeding cycle (Lack, 1968). Among the arctic nesting *Larus* gulls (*L. argentatus, L. thayeri, L. glaucoides* and *L. hyperboreus*) three-egg clutches are normal (Smith, 1966), as also in Sabine's gull (*Xema sabini*). The cliff-nesting, off-shore-feeding kittiwake (*Rissa tridactyla*) and the ivory gull (*Pagophila eburnea*), a partial scavenger, normally lay two eggs. Thus most gulls in the arctic lay the normal three egg clutch of the family with the two exceptions mentioned. Among terns, three eggs are most common in the clutch. The clutch of two in the arctic tern is slightly smaller than the typical number. The clutch of two eggs in all the Stercorariidae is small in comparison with the related gulls and terns, and the small clutch may possibly be an adaptation to breeding in the arctic as well as to food supply.

(b) Asynchronous hatch. Incubation begins with the first egg in the Stercorariidae, and since the eggs are laid 2 to 3 days apart, hatching is also asynchronous. Asynchronous hatching is said to be an adaptation to bring family size into a more refined adjustment to food supply (Lack, 1954). It occurs commonly among raptorial birds and other groups, and its occurrence suggests that clutch size is close to the limit set by food for the young when food is plentiful (Lack, 1968).

(c) Hunting methods. Behavioral responses to their food supply seem to be the most significant way in which the jaegers have adapted to the arctic. They are predators on microtine rodents, passerine birds (primarily juvenile), and shorebirds (primarily chicks). Jaegers are not specially equipped morphologically for predation so that the adjustments to their arctic food supply have been largely behavioral.

In a lemming high year the lemmings are very vulnerable to an avian predator early in the season. The vegetation is typically cut down to the ground, and their burrow systems are frozen or flooded so that they have little cover. The pomarine jaeger then hunts by flying over the tundra approximately 20 feet off the ground. When it sees a lemming it lands quickly and usually grabs the rodent in the thoracic region and kills it by squeezing and vigorously shaking its head while holding the lemming in its beak.

If the lemming escapes before being grabbed, the jaeger chases it on the ground by running, holding its wings up, sometimes using them to aid progress. If the lemming gets into a burrow the jaeger attempts to dig it out using the bill to grab tufts of peat and to toss them aside with a shake of the head. The preferred habitat of the brown lemming is marsh where the soil is a soft peat and where the ground thaws only to a maximum of approximately 8 inches in a season. The lemming burrows are therefore shallow, and sometimes are little more than a trench with a thin, even incomplete, roof of peat fibers. The burrows are easily dug into by jaegers. Later in the season the pomarine jaeger depends primarily on digging to get lemmings. This was particularly true in 1956 when lemming numbers were exceptionally low in the latter part of the season. In that year the jaegers spent hours digging, and extensive areas were pockmarked with their digs. They appear to depend on momentary sightings of a lemming to direct them to an area. Sometimes they appear to use hearing as they will suddenly stop digging, dash a short distance and begin digging again. Such audible cues could only function at short range.

Neither the long-tailed jaeger nor the parasitic jaeger is as easily observed foraging in northern Alaska as the pomarine jaeger is, because of their relative scarcity and because their territories are usually large. Another reason their feeding is difficult to observe is the complexity of the vegetative substrate in tussock-heath tundra where they hunt.

The long-tailed jaeger, for example, spends large amounts of time walking about among the tussocks completely invisible to an observer. I have also observed them on Ellesmere Island (Maher, 1970b), where the vegetation is very low and sparse. They usually hunt alone as the pomarine jaeger does; but I have seen pairs of long-tailed jaegers chasing passerine birds. These jaegers locate lemmings by sight, either while flying or while on the ground standing on a slight elevation. The jaeger then flies down and grabs the lemming. They kill in the same manner as the pomarine jaeger. I have never observed the long-tailed jaeger dig after its prey and believe they do not do so. The complex vegetative substrate in the Alaska foothills would seem to be nearly impossible for a jaeger to dig in, and the deep burrow systems of the collared lemming are inaccessible to the jaeger in the mineral soil of the high arctic. Long-tailed jaegers hunt birds singly, also, and because of their agility they follow them easily.

Both adult parasitic jaegers leave the nest area and the chick for long periods of time in northern Alaska. The fact that they usually leave the area together and frequently return together suggests that they hunt in pairs. I have also observed pairs hunting together over the willow shrub along the river and have observed a pair cooperate to kill a juvenile passerine bird. The pair chased the bird until it was exhausted and dove into the vegetation; then they landed and grabbed the bird. Parasitic jaegers also forage alone, and I do not know what proportion of their hunting is done cooperatively.

Generally jaegers breeding in the arctic obtain all or most of their food from the tundra. The only place in northern Alaska where jaegers were observed feeding from other sea birds was near Cape Sabine. Here kittiwakes from a colony near Cape Lisburne occasionally fed offshore and were pursued by pomarine and parasitic jaegers on three occasions. A parasitic jaeger was also observed once pursuing an arctic tern. Some of these observations coincided with a coastal migration of pomarine jaegers and probably involved non-breeding transients.

In more southerly parts of their breeding ranges the jaegers do feed at least partly by robbing other birds. The parasitic jaeger appears to be the most dependent on robbing other birds for its food. Subarctic and temperate latitude breeding populations of this species obtain most or all of their food in this way. This has been reported from Fair Isle (Williamson, 1965), Greenland (Salomonsen, 1950), Svalbard (Lovenskiold, 1964), the Murman coast of Russia (Dement'ev *et al.*, 1951), and Iceland (Grant and Nettleship, 1971). In Greenland the pomarine jaeger gets some of its food from gulls, chiefly the kittiwake (Salomonsen, 1950). The long-tailed jaeger apparently does not rob other sea birds as frequently as the other jaegers and generally fishes for itself in a tern-like manner (See, Lovenskiold, 1964 and Salomonsen, 1950).

All of the jaegers are observed in temperate latitudes chasing other sea birds and forcing them to regurgitate their crop contents, which the jaegers eat. It is apparently an important means of feeding by all the jaegers away from the breeding grounds. The extent to which they are dependent on this behavior is unknown (Fisher and Lockley, 1954), and as mentioned above seems to differ among the three species. The pomarine jaeger, for example, fishes for itself (c.f. above) and has been observed killing a phalarope at sea (Bent, 1924), suggesting that it can partly subsist without robbing other species. Gulls and terns are the jaegers' principal victims inshore, but most of these species would not be available to them on their wintering grounds (Fisher and Lockley, 1954).

To the degree that jaegers prey on birds in their arctic breeding grounds they are using in a new situation commonly employed chasing techniques that were originally adapted for parasitizing other sea birds. Such a transition would seem to be the easiest way for them to adapt to the role of predator in terrestrial ecosystems and may have been the first stage of adaptation to the arctic tundra for all three species.

Adaptation to feeding on microtine rodents involves more complex changes to a new kind of prey image and to the habits of a different kind of prey. In the pomarine jaeger this adjustment involves also the behavior of digging the prey from burrows and the probable use of auditory cues, as well as the complex adjustments in its variable territorial system. Adaptation of the long-tailed jaeger to preying on rodents is similar to that of the pomarine jaeger in that it has adjusted to a new class of prey item with attendent differences in habits and habitat. The long-tailed jaeger has adjusted its territorial system to exploiting this kind of prey in the same manner but not to the same degree as the pomarine jaeger.

(d) Prey handling. Adaptation to the arctic has also involved new methods of manipulating the prey and feeding the young. After killing a lemming or bird, all three jaeger species either swallow it entire, head first, or, less commonly, carry it in their bill to the nest area. While single adults can thus swallow the prey intact it must be dismembered to feed the chick and is frequently dismembered and shared by the adults in courtship and afterward presumably to reinforce the pair bond. Food is dismembered by a "food-tug" in which both adults grab the prey and have a tug-of-war. When this is done near the chicks, the chicks eat the smaller pieces the adults drop between pulls and also peck at the internal organs of the prey. The adults frequently swallow the last pieces. The importance of this behavior was demonstrated in an instance in 1956 when a female at an enclosed nest was killed, and the prey brought by the male accumulated because the chicks were unable to eat.

All the jaegers have adopted this habit of cooperating to tear large prey apart, as I have observed parasitic jaegers dismembering birds in this manner; and presumably they treat any large prey the same way.

One additional adaptation, perhaps, by the long-tailed jaeger, results from its small size relative to the larger lemmings among its prey. Observation of them swallowing lemmings suggests that they have difficulty with the larger ones, and frequently a number of tries are necessary before they can be swallowed. Long-tailed jaegers disembowel such prey, sometimes pecking at the abdominal cavity between attempts to swallow it, in a manner suggesting that the behavior is adaptive. Pomarine jaegers occasionally disembowel lemmings early in the season when they seem surfeited with food but not in connection with unsuccessful attempts to swallow them.

The chicks of all three jaegers feed on insects. There is little evidence on the importance of this adaptation, but there are some observations suggesting that it may be important to long-tailed jaeger chicks when other food is scarce and may be of minor importance to chicks of the other jaegers as well. Insects occurred much more frequently in the food remains of long-tailed jaegers from chick enclosures than in the other two jaegers in northern Alaska. On Ellesmere Island a chick that had stopped gaining weight in a nest enclosure gained 41 grams in 3 days after being released. The chick was observed picking up insects after release, and I attributed the weight gain to that factor (Maher, 1970b).

Summary

The ecology of the pomarine, parasitic, and long-tailed jaegers was studied in the summers of 1956 through 1960 in northern Alaska. Areas where populations were studied in detail were situated on the coastal plain (Barrow, Wainwright, and Pitt Point), in the foothills (Kaolak River and Cape Sabine), and in the Brooks Range (Peters and Schrader lakes).

The three jaegers differ in size; the pomarine jaeger, the largest, averages 694 grams in weight, the parasitic jaeger, 465 grams, and the long-tailed jaeger, 296 grams. They differ in their breeding ranges and in details of their breeding biology and population phenomena, but broad areas of similarity suggest that competition actually or potentially occurs among them. The pomarine jaeger nests along the northern edge of the coastal plain, the long-tailed jaeger nests from the mountains north to the southern part of the coastal plain, and the parasitic jaeger nests over all of the North Slope of Alaska. The pomarine and long-tailed jaegers normally do not overlap in their breeding distributions, while the parasitic jaeger overlaps with both of them.

The clutch of all species normally consists of two eggs. Their incubation periods are essentially the same, 25-27 days, although that of the long-tailed jaeger may be on the average a day shorter than the other two species.

Two significant differences in breeding biology are the length of the pre-egg stage (shortest in *parasiticus*), and the development time of the chicks (shortest in *longicaudus*). The pre-egg stage of the pomarine jaeger seems to be several days to a week longer than that of the other species, apparently because the pomarine jaeger must establish a territory and undergo complete courtship activities when it breeds, while the long-tailed and parasitic jaegers appear to develop some attachment to set territories, which facilitate remating. Pomarine jaegers fledge in 30 to 35 days, parasitic jaegers in 27 to 30 days, and the long-tailed jaegers in an average of 25 days.

Characteristic nesting density differs among the three species, and it differs in each species in different years and in different areas. The pomarine jaeger density has varied 150-fold from 0.13 pairs per square mile to a mean of 19 pairs per square mile; the greatest range of variation in the group. The parasitic jaeger, in contrast, varies little in nesting density; it was constant for four seasons at 0.33 pairs per square mile at the Kaolak River, and ranged from zero to 0.36 pairs per square mile at Cape Sabine. The long-tailed jaeger density varied two-fold, from 0.66 to 1.3 pairs per square mile at the Kaolak River; and 11-fold, from 0.20 to 2.3 pairs per square mile at Cape Sabine.

Population phenomena of the pomarine jaeger differ from the other two species in that its population characteristically builds up to peak numbers shortly after arrival on the breeding grounds, and a portion of this peak density, ranging from 25 to 50 per cent of the total, usually departs without breeding. Egg-laying in the pomarine jaeger population usually shows a high degree of synchrony not matched by either of the other species.

Nesting success of the pomarine jaeger has been low at low breeding densities, moderate at intermediate densities, and very low to high at high densities. In the sparse populations of the parasitic jaeger observed, breeding success has

been high, while the success of the long-tailed jaegers varied from low at the Kaolak River to very high at Cape Sabine.

Jaegers defend large, mutually exclusive, all-purpose territories, which vary in size with different nesting densities. The average diameter of the pomarine jaeger's territory varied eight-fold in different years. Inter-nest distances of the long-tailed jaeger averaged 1448 yards and 969 yards at the Kaolak River and Cape Sabine respectively. The inter-nest distances of the parasitic jaeger do not indicate territory size, because they nest at low densities and their territories are rarely adjacent. Distances from parasitic jaeger nests to their neighbors (long-tailed jaegers) averaged 1362 yards at the Kaolak River. At Cape Sabine two adjacent parasitic jaeger nests were 1180 yards apart.

Mutually exclusive territories are indicated by the similarity of mean inter-nest distances among the species when they nest in association. Mean distances between long-tailed jaeger nests, and mean distances from parasitic jaeger nests to all neighboring long-tailed jaeger nests at the Kaolak River, were 1448 and 1362 yards respectively. At Cape Sabine the mean inter-nest distances among all long-tailed nests, from parasitic jaeger nests to their neighbors, and the mean distances from the pomarine jaeger nests to their neighbors were also similar; 969, 784, and 1153 yards respectively.

Differences in manner of defense of territories were found between the pomarine jaeger, on the one hand, and the parasitic and long-tailed jaegers on the other. The pomarine jaeger maintains totally exclusive territories, even when the territories are of large size, while the parasitic and long-tailed jaegers maintain only the central core of the territory as an exclusive area, at least in mid-season and later, and they permit other jaegers to cross the outer part of their territories. The spacing of these species suggest early season exclusiveness. This difference in territorial defense suggests that the pomarine jaeger is adapted to defending smaller territories than the long-tailed and parasitic jaegers and also that the pomarine jaeger is specialized for nesting at high densities.

Two adaptations of jaegers for nesting in the arctic are recognized: (1) shortening the pre-egg-laying portion of the breeding cycle, and (2) postponement of the annual molt until the birds have left the breeding grounds.

Jaegers arrive on the breeding grounds physiologically ready to breed. At that time testes of males have usually recrudesced to full size, and ovarian follicles of females have begun to enlarge. The testes and ovarian follicles of non-breeding birds decline in size through the summer season. The testes of breeding males (of the pomarine jaeger) begin to regress after the egg-laying period.

Growth curves for the three species of jaegers are basically sigmoid in shape but have an early phase in which the relative growth rate is rapid and almost constant, followed by a period in which the growth rate declines steadily. The mean rates of the three species in the early growth phase are similar.

The pomarine jaeger is an obligate lemming or microtine rodent predator when breeding, as indicated by the facts that its diet consists almost entirely of *Lemmus* in both high and low lemming years and that dense breeding populations occur only where *Lemmus* is the prevalent and periodically abundant microtine. It is unable to exploit avian prey effectively. The parasitic jaeger is primarily a small bird predator and utilizes this prey predominantly in all situations studied, even where the local microtine rodent population was high. The long-tailed jaeger is a microtine rodent predator; but unlike the pomarine jaeger, it is also able to take avian prey effectively. Birds constitute half or more of its prey at the Kaolak River, while *Microtus* constituted over 90 per cent of its food at Cape Sabine.

The pomarine jaeger is limited in its distribution by its specialized food habits and hunting methods, and by the length of its breeding cycle. The long-tailed jaeger is considered to have been excluded from the pomarine jaeger's breeding area by competition. The parasitic jaeger can co-exist with both pomarine and the long-tailed jaegers because of its specialization on avian prey. The long-tailed jaeger and the parasitic jaeger compete where they nest together, but competition does not exclude either form. It is suggested that random fluctuations in the numbers of the major prey classes (microtine rodents and passerine birds) result in shifts in the balance of reproductive success and, hence, in the competitive advantage of the two species, in the long run allowing both forms to persist.

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