

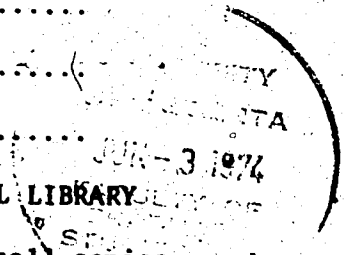
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 JAEGER AND SNOWY OWLS ON BATHURST ISLAND N.W.T.
 EMPHASIZING THE LONG-TAILED JAEGER*.....
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THE UNIVERSITY OF ALBERTA

SUMMER POPULATION AND FOOD ECOLOGY
OF JAEGER AND SNOWY OWLS
ON BATHURST ISLAND N.W.T.
EMPHASIZING THE LONG-TAILED JAEGER

by

© PHILIP SCOTT TAYLOR

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

SPRING, 1974

THE UNIVERSITY OF ALBERTA
FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Summer Population and Food Ecology of Jaegers and Snowy Owls on Bathurst Island, N.W.T. Emphasizing the Long-tailed Jaeger submitted by Philip Scott Taylor in partial fulfilment of the requirements for the degree of Master of Science.

Date... April 22, 1974.....

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ABSTRACT

I gathered baseline demographic data on a high arctic population of long-tailed, parasitic, and pomarine jaegers and snowy owls during the summers of 1968 to 1971 near the National Museum of Natural Sciences' High Arctic Research Station on Bathurst Island, N.W.T. Numbers of lemmings, the birds' major prey, were very low, high, moderate, and high, respectively, each year.

Long-tailed and parasitic jaegers bred each season, though success was poor to nil each year: long-tailed jaegers raised most young (5% of their eggs) in 1971. I found single-egg clutches of long-tailed jaegers in 1968, and second nests of other species in 1971; otherwise two-egg clutches were usual for both species. The eggs hatched asynchronously, the elder chick surviving longer than its younger sibling. Both species resided on their respective territories from mid-June to mid-August, and used the same territories in subsequent summers. Long-tailed jaegers maintained higher breeding populations than parasitic jaegers in all years but 1968. Large numbers of non-territorial long-tailed jaegers moved into the study area each July, for a few days.

Pomarine jaegers and snowy owls bred only in 1969 and 1971. The jaegers did not produce young, but the owls did in 1969 when their breeding population was ten times greater than in 1971. Owl clutches, significantly smaller than in many other areas, averaged 5.8 eggs, and hatched asynchronously. Older owlets survived longer than younger siblings.

Adults of both species left their territories when their eggs or young were destroyed. Additional male snowy owls arrived in the study area in July, 1971, and August, 1970, staying for a few weeks. Many losses of eggs and young, of jaegers particularly, resulted from arctic fox predation.

I also studied the food habits of territorial long-tailed jaegers, finding a remarkable separation of foraging niches between the sexes. Males spent 92% of their foraging time hunting lemmings, while females spent 81% of their foraging time hunting arthropods. Length of hunting periods and hunting success varied with habitat and time of season, which reflected differences in abundance and vulnerability of prey species. Males made all the observed lemming kills and probably took an average of 3.5 lemmings per day in 1971. Major foods found in pellets cast by adult jaegers, ranked according to frequency, were lemmings (over 99%), arthropods (over 1%), and birds (under 1%). Arthropod remains were much more frequent in pellets cast by chicks. A pair of long-tailed jaegers consumed an estimated 24-29% of their total body weight in food per day. Most of their food was lemmings, however, for a period in July, arthropods provided an estimated 10% of the pair's food - at least 18% of the female's food. The jaegers foraged mostly within their territories.

The results are discussed as adaptations which optimize the exploitation of fluctuating prey populations in the arctic while minimizing inter- and intraspecific competition.

ACKNOWLEDGMENTS

The opportunity to study jaegers and snowy owls in the Canadian Arctic came while I worked as a summer assistant to Stewart D. MacDonald, Curator of Vertebrate Ethology, National Museum of Natural Sciences, Ottawa. His untiring efforts instrumental in establishing the N.M.N.S. High Arctic Research Station on Bathurst Island and in providing funds for my research each season, his supervision and his friendship, for which I am indebted, receive my special thank you.

I would also like to thank the other museum personnel, principally W. Earl Godfrey, for their assistance. The help and companionship of the people at the Research Station over the four summers from 1968 to 1971 made work there a pleasure. I thank, especially, David A. Gill, David R. Gra . Pierre Lamothe, Harold F. Mayfield, and David F. Parmelee who lent much to this study even after the field work was completed.

Logistic support was provided each season in large part by Polar Continental Shelf Project, Department of Energy, Mines, and Resources, coordinated by E. F. Roots. The PCSP personnel in Resolute Bay, particularly E. Chapman, and the pilots who made flying both safe and rewarding, I heartily thank.

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Finally, for warmly encouraging my interests in biology from the beginning, I am most grateful to my parents. I cannot adequately thank my family, and now my wife, for their support.

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INTRODUCTION

The relationship between avian predators and their prey has been the subject of many studies (for reviews see Craighead and Craighead 1956, Errington 1967, The Wildlife Society 1972). Nevertheless, long term studies, and those concerning non-breeding segments of the population, are still relatively uncommon. In the North American arctic, Rausch (1950), Pitelka, Tomich and Treichel (1955a and b), Sutton and Parmelee (1956), Watson (1957), and Maher (1970a) have documented numerical and functional responses in populations of breeding snowy owls (Myctea scandiaca) and pomarine jaegers (Stercorarius pomarinus) to changing numbers of their prey, primarily lemmings, Lemmus trimucronatus and Dicrostonyx groenlandicus, showing these birds to be obligate lemming predators. Parasitic jaegers (S. parasiticus) appear to be less dependent upon lemmings as a primary food source, utilizing birds extensively in many areas (Sutton 1932, Parmelee et al. 1967, p. 226, Russell unpubl. MS). Information on the food habits of long-tailed jaegers (S. longicaudus) is incomplete and inconsistent. Maher (1970b, p. 124) reviews the food habits of this species and suggests "that the (long-tailed) jaeger in the High Arctic is an obligate lemming predator adapted to exploit lemming

population highs and that it must have sufficient lemmings to provide most of its food in order to breed." Yet he includes considerable evidence for extensive use of alternate foods, and refers to the results of others (Løppenthin 1943, Parmelee and MacDonald 1960). Manning et al. (1956, p. 87) suggest that long-tailed jaegers on Banks Island and, in some years, Prince Patrick Island, are less affected by lemming scarcity than other jaegers, apparently because "caterpillars and spiders, sometimes form much of the food of Long-tailed Jaegers".

The long-tailed jaeger is a circumpolar species, as are parasitic and pomarine jaegers, and snowy owls. It differs from them all in being smaller in size, and being more northern in its summer distribution over large parts of its range than the other jaegers (Godfrey 1966).

The opportunity to study the relationships between the three species of northern jaegers, and the snowy owl and their prey arose while I worked as a field assistant in 1968 at the High Arctic Research Station of the National Museum of Natural Sciences of Canada, on Bathurst Island, N.W.T. In 1969, I studied mainly snowy owls; in 1970, emphasis was switched to jaegers because of the sudden disappearance of owls: major emphasis was placed on the relationship between long-tailed jaegers and their prey. The study of jaegers

was continued in 1971.

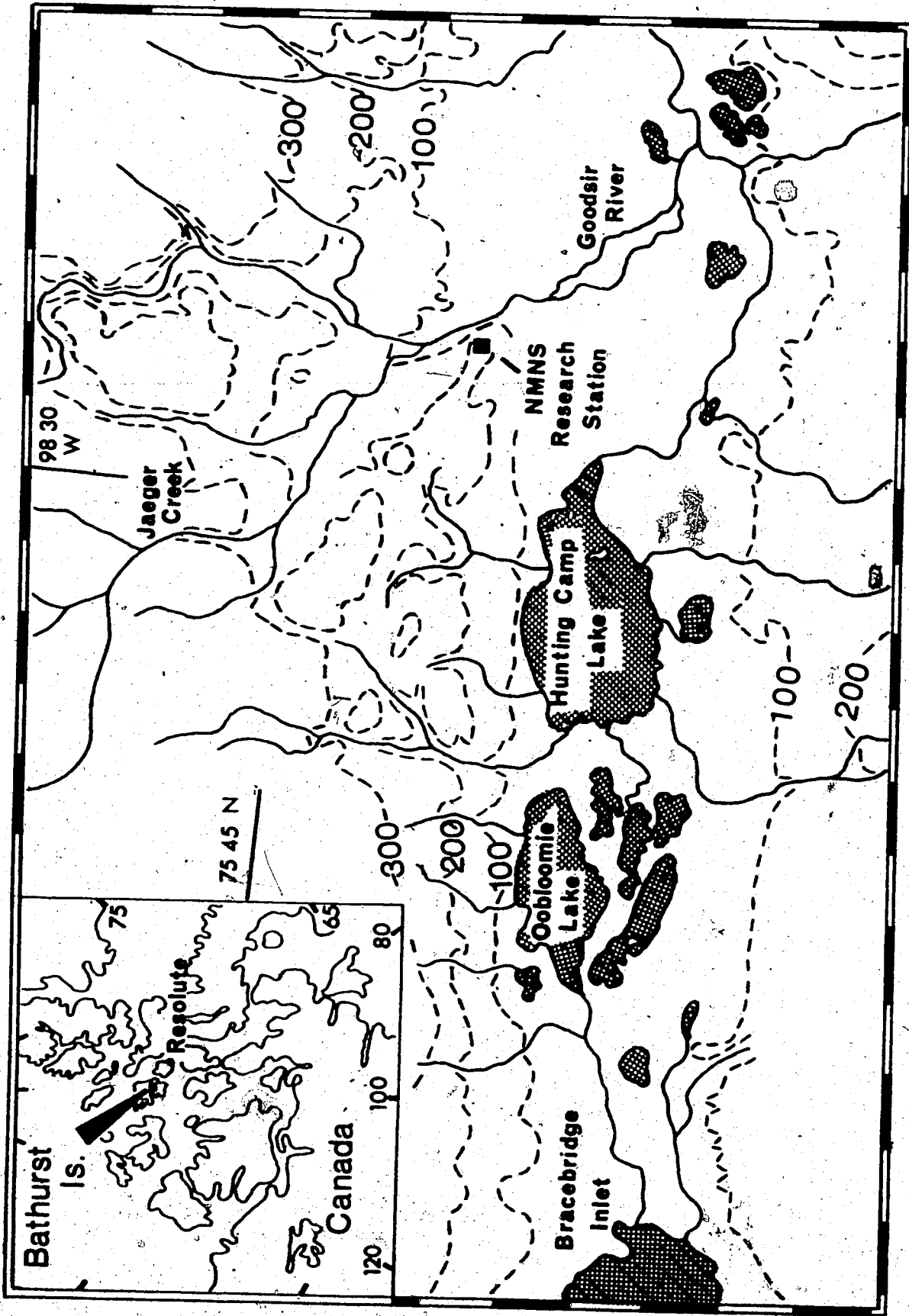
One objective was to record demographic parameters for all four species each summer. I also examined the summer food habits of territorial long-tailed jaegers in various habitats and collected similar information for snowy owls, pomarine and parasitic jaegers when the presence of these birds in the study area permitted me to do so. I estimated prey abundance among major prey species.

STUDY AREA

The location for this study, Bathurst Island, Northwest Territories, is of particular interest for a number of reasons. While much of its flora and fauna are representative of many of the high arctic islands (Porsild 1964, Danks and Byers 1972), parasitic, and pomarine jaegers are breeding at the northern limits of their ranges (Godfrey 1966). Competition with other predatory birds is minimal since peregrine falcons (Falco peregrinus), gyrfalcons (F. rusticolus), and ravens (Corvus corax) are transient, and rough-legged hawks (Buteo lagopus), Thayer's (Larus thayeri), and glaucous gulls (L. hyperboreus) breed in small numbers. The only microtine rodent present as prey for avian predators is the collared lemming, Dicrostonyx groenlandicus. The area has remained relatively undisturbed from intensive human activity throughout the study.

The National Museum of Natural Sciences' High Arctic Research Station (Latitude $75^{\circ}43'N$, Longitude $98^{\circ}25'W$) was used as base camp for the field research. The station is located midway between Goodsir and Bracebridge inlets on the northern edge of a broad, flat valley known as Polar Bear Pass, and is approximately 145 km WNW of Resolute (Figure 1).

Figure 1. Map of Polar Bear Pass, Bathurst Island, N.W.T., Showing Topography and Location of the NMNS Research Station. Map Border is Divided into 1 km Segments.

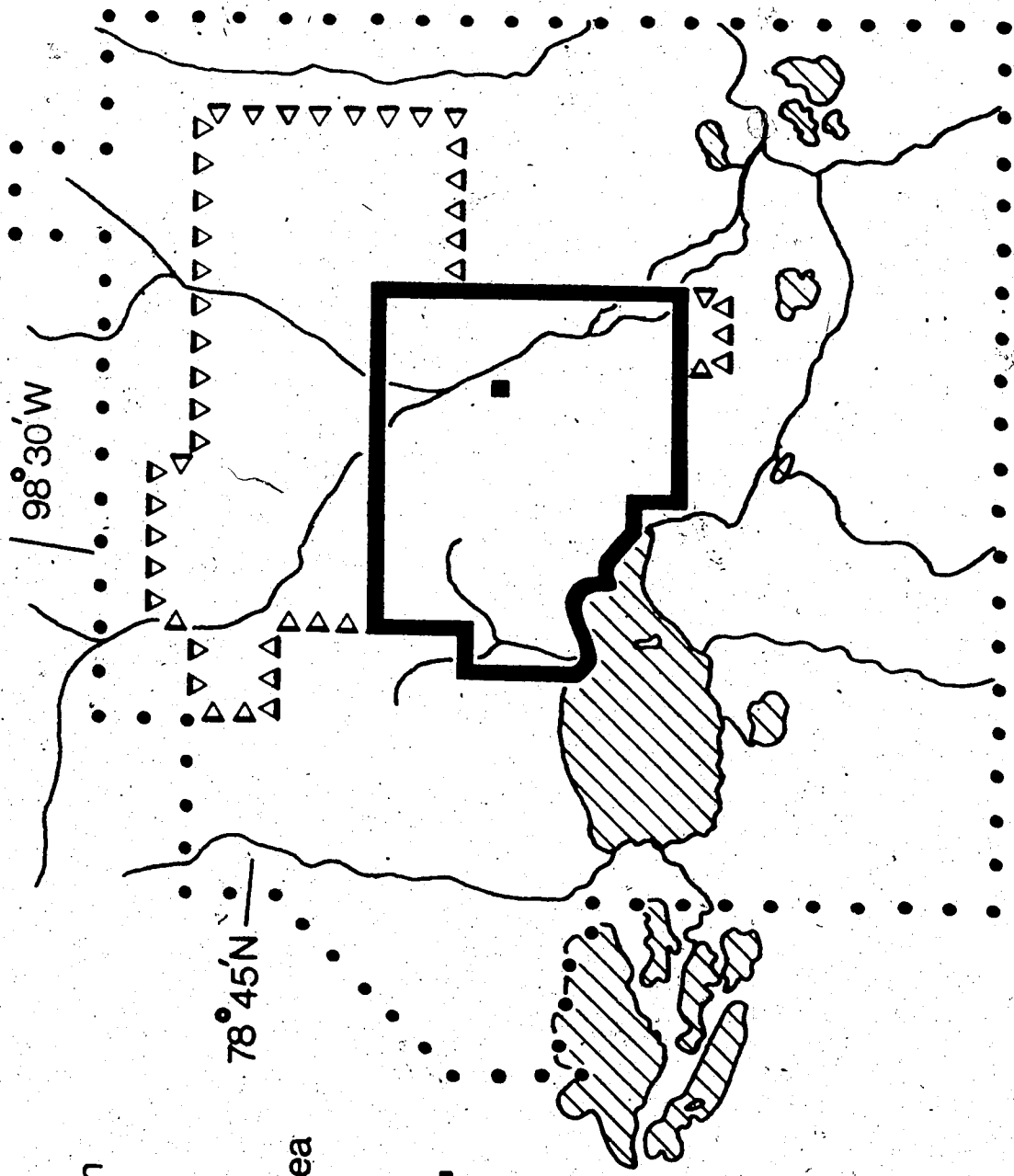


An area of 13.5 km² of tundra was chosen for an intensive study of populations of snowy owls and three species of jaegers: pomarine, parasitic, and long-tailed. Further information was gathered within two areas encompassing 16.5 km² and 84.5 km² adjacent to the main study area (Figure 2).

Bathurst Island, seven neighboring smaller islands, and numerous islets form a group of islands totalling some 18,000 km² (7000 mi²). Bathurst Island itself has a very irregular coastline and, despite its size, no part of its rolling interior is more than 24 km (15 miles) from the Arctic Ocean (Fortier et al. 1963). They state that the low rounded hills, plateaus, and ridge systems, comprising most of the island, are composed of Devonian and Silurian sandstones, limestones, and shales which are relatively well-drained but poorly vegetated. Elevations are generally below 365 m (1200 feet) but heights of 460 m (1500 feet) are to be found.

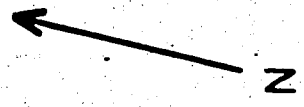
Bathurst Island lies within the zone of continuous permafrost, the active layer being less than 1 m thick (Bird 1967). The permafrost inhibits drainage in the lowlands and depressions, resulting in well-vegetated, pond- and lake-filled tundra. One of the most extensive and best vegetated lowlands on this island is Polar Bear Pass, which is 25.5 km (16 miles) long, and up to 4.8 km (3 miles) wide.

**Figure 2. Map of Study Areas in Relation to the NMNS
Research Station.**



- Research Station
- ▬ Core Study Area
- Owl Study Area
- ▲▲ Jaeger Study Area

Scale:  2 KM



I used a combination of the life form of vegetation and the physical characteristics of terrain to classify some of the major habitats found within the study area. Descriptive terms conform, as nearly as possible, to those of Porsild (1964) and Bird (1967). This procedure follows Kessel and Cade (1958, p. 11) who state that "with few exceptions, there seems to be little meaning in fine delimitations of plant associations as far as the ecology and distribution of birds are concerned. Rather, more inclusive categories . . . based primarily on life-form, have more significance", and Wiens (1969).

The following are distinctive types:

1) Desert-like stoney barrens, hereinafter called barrens, covered an estimated 45% of the upland and lowland sections of the study area. On the ridges and hills of the northern and western part of the study area, widely separated tussock or rosette-forming plants such as Saxifraga oppositifolia, Draba spp., and Papaver arctica, grew commonly. In the valleys, the flood plain deposits and fluvial fans from secondary tributaries, banked along the ridge bottoms, supported tussock plants too. However, in the latter location the density of plants was greater, and Dryas integrifolia and Salix arctica were more abundant. The barrens were probably the single most important summering habitat for

lemmings; they were important forage areas for muskoxen (Ovibos moschatus) and caribou (Rangifer tarandus) and important nesting areas for many birds (ptarmigan, shorebirds, waterfowl).

2) Large snowbanks and melt water seepage areas associated with them were found on the steeper slopes of ridges and creek bottoms, and commonly persisted well into summer. Some were regular enough in their size and location to inhibit most plant growth under them. Carpets of sodden mosses grew around and below these places. Such areas, which are referred to as snow melt or snow bed communities (Porsild 1964), were estimated to cover less than 10% of the study area. These, as well as deep snow in low lying areas, were wintering areas for lemmings.

3) A special type of wet tundra, referred to as tundra hummocks (Bird 1967), was present along the edges of many creeks and low lying regions in the study area. I estimated tundra hummocks to cover less than 10% of the study area. Each hummock was usually less than 30 cm in height and diameter. Lateral drainage channels from creeks often intersected this type of tundra, leaving a system of level hummock tundra subdivided intricately by deep mossy creek bottoms, 1-3 m deep. A complex variety of plants, none of

which seems to form a pure stand, grew in this habitat. Mosses grew around the bases of the hummocks, along with Oxyria digyna, Juncus biglumis, and Saxifraga oppositifolia which might all extend up the hummock sides to the top where lichens were often abundant. Lemmings were present here in the summer, and waterfowl frequently nested in this habitat.

4) Marshy meadows covering approximately 30% of the study area were most extensive in the poorly drained depressions of the uplands and the valleys. A number of species of Carex, Eriophorum, and other monocotyledenous plants grew over the level or tussocky tundra, and around the numerous shallow tundra ponds and lakes. In the low areas, moss formed an almost continuous cover between these plants.

Large frost mounds, up to 3 m in height, covered with similar species, plus Draba spp., and Saxifraga spp. were found in most of the habitats. These, as well as isolated mats of monocotyledenous plants, were included in the meadow habitat type. The low meadows were devoid of lemmings in the summer but the mounds and grass mats of the barrens were favored summer denning sites. The mounds were used extensively as perches by owls and jaegers. The marshy

meadows were used for nesting by many shorebirds and for feeding by many other bird species as well as muskoxen.

Other habitats, comprising less than 10% of the study area, included fluviatile and the large lacustrine waters (seldom exceeding 1.5 m in depth), scree, outcrops, and tors (Bird 1967).

The vertebrate, and known arthropod fauna recorded on the study area was typically high arctic in quantity and diversity. Forty-two species of birds have been recorded for Bathurst Island, of which at least 22 have bred near the Research Station (Appendix 1). Seven species of terrestrial mammals have been recorded (Appendix 1). Terrestrial arthropods, so far recorded, suggest lower numbers than on some neighboring islands (Danks and Byers 1972).

Bathurst Island, being in the north-central portion of the Canadian Arctic Archipelago, has a continental, high arctic climate which is somewhat modified by the Arctic Ocean during winter and summer (Thompson 1967). The weather at the NMNS Research Station was similar to that recorded at Resolute, the nearest permanent Ministry of Transport weather station, but was less influenced by the ocean

(Thompson 1971).

Snowfall accounts for over half the annual precipitation, which totals less than 5 inches (Atlas of Canada 1957). Most snowfall occurs in spring and fall. Large snow drifts which accumulate along creek bottoms and in the lee of hills persist well into summer.

The period of 24 hour daylight begins in late April, and extends to the middle of August. Wintery and below freezing temperatures continued into late April, and early May. The daily mean temperatures recorded at the N.M.N.S. Research Station during June, July, and August approached or exceeded 32°F, but were usually prevented from rising above about 45°F by persistent fog, and low cloud cover. Most rain fell in late July, and August. The combination of spring melt water and thawing permafrost often gave the impression that it was a very wet region.

A lack of good weather information from the Research Station during 1968 and 1969 prevented detailed comparison between all years. However, some important differences in the trends of spring and summer weather over the four years of this study were observed. Comments on these are of interest:

1968: The latest spring. Floodpeak on Goodsir River reached about 9 July, and the shortest, coolest summer recorded, with much wind, cloud, and rain.

- 1969: Spring was earlier. Flood peak on Goodsir River reached on 3 July, and, except for a very cold wet two weeks in late July and early August, a longer, warmer summer than 1968.
- 1970: Spring earlier than previous two years. Flood peak on Goodsir River reached 30 June, summer longer, and warmer than 1969.
- 1971: Earliest spring recorded. Flood peak on Goodsir River reached on 28 June. Warmest June recorded with daily mean 3.2°F higher than 1970. August was slightly cooler, and wetter than 1970.

The spring melt did not occur evenly over the whole area; some areas where early melt occurred, usually were clear one to two weeks before the surrounding region; these were located at the base of slopes along extensive upland hills, and ridges. Dust and debris, blown from these areas onto the snow-covered valley, hastened the melt. Early melt areas were important as feeding sites for all early-arriving birds, including jaegers, as well as for herbivorous mammals, such as muskoxen.

METHODS

I. General.

I spent most of June, July, and August of all four summers (1968 to 1971) on Bathurst Island, and, in 1969 and 1970, I arrived before the end of April (Table I). I was on the island each spring before most of the migrant birds arrived, including jaegers.

In 1968, general reconnaissance indicated that the tundra surrounding the station was readily accessible for research purposes, since the ridge system there facilitated travel by foot, even during the spring melt. This was the core of my study area. After 1968, use of snowmobiles enabled me to search for snowy owl nests over a much larger area until mid-June, when the spring melt restricted travel. By preference, most travelling thereafter was by foot, for then birds were most easily seen, and heard.

I made notes and sketches while in the field and used binoculars (7 X 35), and telescopes (15-25 X) as observational aids throughout the study.

II. Marking and Identification.

The three jaeger species were separable in the field by plumage as well as behavioral differences. Field identification of jaegers could be made at considerable distances

Table 1. The Period of Time which I, and Other Researchers Spent at the NMNS Research Station, Bathurst Island.

Year	Duration of my field season	Duration when other observers present
1968	20 May to 14 August	20 May to 14 August
1969 ^a	29 April to 14 August	29 April to 27 August
1970	21 April to 19 August	12 April to 31 December
1971	12 June to 27 August	1 January to 27 October

^a In 1969 I was not at the Research Station from 29 June to 9 July.

when the bird's flight pattern and its reaction to other jaegers were visible. Jaegers which held territories during the summer usually bred and were distinguishable from non-territorial transient jaegers by behavioral patterns.

Territorial jaegers displayed to trespassing individuals of the same species and evicted the other species (Andersson 1971).

Seven territorial long-tailed jaeger adults were banded and color marked in 1970, and one in 1971. Combinations of Canadian Wildlife Service aluminum leg bands, colored plastic leg bands, and green, gold, and red spray paints were used for marking. Birds were caught by hand (one), by padded steel traps set near carrion (three), and by snaring incubating birds with a 20 m cord (four). Only one adult of a pair was banded, and marked. This successfully prevented nest desertion which has been experienced by other workers when both adults were marked (Maher 1970b). The spray paints lasted only one season, with red being the most visible. Young long-tailed jaegers were identified as individuals either by banding them immediately after hatching, or by punching unique combinations of holes in the webs of their feet before they were banded (Wing 1965, p. 79).

Territorial pomarine, and parasitic jaegers were not marked. Plumage variation, and behavior helped me identify

certain individuals of these two species. This method has been used successfully in Alaska with pomarine jaegers (Pitelka et al. 1955a, Maher 1970a), and in Europe for parasitic jaegers (Venables and Venables 1955, p. 331).

Adult snowy owls were not banded, and most could not be identified as individuals by either plumage or behavioral patterns. Young owls from a number of nests were identifiable after color dyes ("Magic Marker" felt pens) were placed on their legs until they reached banding age (12-14 days). In 1969, 26 young owls were banded with Canadian Wildlife Service lock-on bands and seven of these were uniquely color marked on the wings and tail, with orange and green spray paint. The marked sexual dimorphism in adult snowy owls did allow me to separate males with their immaculate white plumage from the larger, darker females. Some birds, apparently non-territorial, and considered to be adult females, may have been juveniles of either sex. All adult owls were classified as territorial or non-territorial. The criterion used for the former was attendance of nests or young. Non-territorial owls were either non- or unsuccessful breeders, thus the numbers in these two categories could change over the season as territorial birds became non-territorial.

III. Demographic parameters.

A. Territorial jaegers and owls.

The number of territorial pairs of jaegers and owls was determined each year on an extensive study area which varied in size annually (Table 2); nevertheless, a core area of 13.5 km² yielded most of the data on all four species. I plotted the location of each pair with the help of air photographs, and could then establish crude density figures for each species. Territorial pairs of birds and their nests were visited at least weekly, others, less regularly. Information on the length of time territories were held, the time and number of eggs laid, and their fate, and faithfulness to territories during the season and between years, was kept.

Table 2. Study Area Size in Square Kilometers (km²), 1968 to 1971.

Year	Core	Adjacent Area		Total	
		Jaeger	Owl	Jaeger	Owl
1968 ^a	13.5	6	6	19.5	19.5
1969	13.5	16	84.5	29.5	98
1970	13.5	1.5	84.5	15	98
1971	13.5	13.5	84.5	27	98

^aFor the 1968 population, only breeders studied.

B. Non-territorial jaegers and owls.

I made weekly surveys of non-territorial jaegers within an 8.5 km² area, and non-territorial owls within a 53.5 km² area each summer. The counts were made from three observation points on ridge tops beside the NMNS Research Station, usually between 1800 and 2400 hours when the birds were most active, the wind speed was least, and the visibility best. By slowly scanning the census area with a telescope, from one side to the other, I recorded the total number of individuals visible. If more than one census was taken during a week, or if a greater number of birds was counted within the census area at a time other than during the census period, the highest count was used. Sunny days provided the best survey conditions, and were therefore chosen for the counts whenever possible.

IV. Food habits of long-tailed jaegers.

A. Hunting activity.

In 1971, I observed pairs of territorial long-tailed jaegers, tabulating over 81, and 80 hours of activity by males and females respectively, on 30 days from 16 June, to 13 August. I observed birds between 1200 and 2400 hours (C.D.T.) with most observations falling between 1500 and 1800 hours. The sequence of jaeger activities, time of observation

and termination of each activity, and sex of the birds were noted. Additionally, for hunting and feeding activities of this species, the habitat utilized, number of capture attempts and kills were recorded whenever possible. Most observations were of two pairs of long-tailed jaegers which were accessible and easily seen throughout their territories. Observations were usually made from one of two blinds, each located on upland ridges affording maximum visibility of the two jaeger territories. Observations of less than 30 minutes duration were omitted. This eliminated activity sequences on birds the identity of which was not known. In 1970, after making spot observations throughout the 24 hours, I concluded that long-tailed jaeger activity patterns did not differ markedly between 0000 and 1200 hours, and 1200 to 2400 hours - a conclusion also reached by Andersson (1971).

B. Pellets, specimens, and droppings.

I collected 1052 pellets from the territories of long-tailed jaegers. For each pellet, placed separately in a plastic bag, I recorded date, jaeger territory, age of jaeger casting the pellet (if known), and whether the pellet itself was fresh, or old. I collected most pellets cast by adult jaegers in 1971 from frost mounds, and other favored perches within the birds' territories. Pellets gathered from young

jaegers in 1970 and 1971 were in the immediate vicinity of the nests, and were smaller than pellets cast by adult jaegers. The presence of a shiny mucus coating (Maher 1970b) was useful in separating new pellets from old pellets.

I analyzed each pellet for the quantity and quality of its contents. Vertebrate remains were identified to species, and invertebrate remains to family when possible. I assumed the number of individual vertebrates present per pellet to be one, unless skeletal remains (usually lower jaws) indicated otherwise (Rusch et al. 1972).

The number of pellets cast by other species and included in this analysis was minimal because:

- 1) other jaeger species, snowy owls, and gulls were present only in low numbers in the areas where pellets were collected, 2) the aggressiveness of the territorial long-tailed jaegers toward these species was sufficient to keep most individuals out of their territories, 3) pellets cast by other species averaged larger than long-tailed jaeger pellets, and were usually separable on that basis, and 4) any pellets of obviously questionable origin were excluded from the analysis.

The contents of 116 droppings from territorial long-tailed jaegers, collected in 1971, plus the anterior gastrointestinal tracts from an additional ten birds, collected

during the four years, also were analyzed for food remains.

An estimate of the total number of insects contained in each of two stomachs was made by counting the number of pairs of insect wings in one-tenth of the contents. The total stomach contents were suspended in 100 ml of water by stirring vigorously, then one-tenth was drawn off for inspection.

In 1970, the nests of five long-tailed jaegers were fenced, following a method described by Maher (1970a). Corrals of wire mesh (1 inch diameter) three feet high, enclosed approximately 80 square feet of tundra. Upon hatching, the young jaegers remained inside the corral, where they were protected from arctic foxes. I was able to measure the rate at which pellets were regurgitated, and growth of the chicks. This procedure was not repeated in 1971 since it produced only meager results.

V. Food habits of parasitic and pomarine jaegers and owls.

I collected information on the food habits of snowy owls, parasitic, and pomarine jaegers whenever possible. This included observations of food items brought to nests and young, the hunting techniques of the adults, and analysis of some pellets.

VI. Estimates of prey abundance.

I sampled arthropod populations in 1971 to provide an

index of arthropod abundance that could be compared with feeding activity, and habitat selection of long-tailed jaegers. From 15 June, to 26 August three sites on the barrens, and three on the marshy meadows were sampled eight times, unless they were snow covered. For comparison, eight additional sites were sampled periodically. Sunny, calm days were chosen for sampling. Samples were collected with a 15 inch diameter sweep net. Either 100, or 200 sweeps were taken low over the substrate in each habitat type. I recorded the sample site, number of sweeps, and date, before preserving the sample in 70% alcohol. Later, arthropods in the sample were counted and identified to family, where possible. The Chironomidae, and Muscidae were each separated into two different size classes (either shorter or longer than 3 mm).

David A. Gill estimated lemming density within the study area in 1970, and 1971 from trapping records. I estimated lemming numbers in other years, based on a subjective comparison with 1970, and 1971. Personnel at the NMNS Research Station kept records of all breeding birds within the study area each year. From these records, an estimated density was established.

RESULTS

I. Demographic parameters of territorial and non-territorial jaegers and owls.

A. Numbers of territorial and breeding pairs.

1. Long-tailed jaegers.

The number of pairs of long-tailed jaegers which established territories on various parts of the study area on Bathurst Island did not differ significantly for three of the four summers (Table 3) and exceeded the combined numbers of pairs of parasitic jaegers, pomarine jaegers, and snowy owls for the same area each year.

In 1968, though there were more territorial pairs of long-tailed jaegers present in the study area than the two which attempted to breed, their exact number is unknown, preventing a complete comparison of data between all four years. The number of territorial birds did not differ significantly in 1969, 1970, and 1971, from expected values, and respectively 94% (n=14), 78% (n=7), and 83% (n=14) of the pairs bred, showing no significant differences between years. Densities of pairs in core and adjacent areas were not significantly different in any year. The numbers of pairs holding territories compared to the proportion which bred were not significantly different in any year. The number

Table 3. The Number of Pairs of Long-tailed, Parasitic, and Pomarine Jaegers and Snowy Owls which Established Territories on the Bathurst Island Study Area from 1968 to 1971.

	Observed Numbers		Crude Density: Pairs per 100 km ²	
	<u>Core Area^b</u>	<u>Adjacent Area^c</u>	<u>Territorial</u>	<u>Breeding</u>
Long-tailed jaeger:				
1968	? (0) ^a	? (2) ^a	?	10
1969	8 (8)	7 (6)	51	47
1970	7 (6)	2 (1)	60	47
1971	9 (8)	8 (6)	63	52
Parasitic jaeger:				
1968-1971	1 (1)	0 (0)	<3	<3
Pomarine jaeger:				
1968	0 (0)	0 (0)	0	0
1969	4 (4)	2 (0)	20	14
1970 ^d	0 (0)	0 (0)	0	0
1971	5 (3)	3 (1)	30	15
Snowy owl:				
1968 ^e	0 (0)	0 (0)	0	0
1969	2 (2)	13 (13)	0	15
1970 ^f	0 (0)	1? (0)	0	0
1971	0 (0)	1 (1)	0	1

^a Figures in parentheses are number of pairs that bred after having established a territory,

^{b, c} The size of the core area was 13.5 km² but the adjacent area varied, being 6 km² in 1968, 16 km² in 1969, 1.5 km² in 1970, and 13.5 km² in 1971 (see Table 2),

^d In 1971, there were 2 to 4 territorial pairs immediately south of the study area, but none apparently bred,

^e One pair, seen 32 km (20 miles) N.W. of the study area possibly bred,

^f One male seen courting in late June in the adjacent area, did not nest.

of breeding birds in 1968 was significantly lower than in 1969 ($p < 0.05$), 1970 ($p < 0.08$), 1971 ($p < 0.01$), but other years did not differ from one another.

These data suggest that a fairly stable population of long-tailed jaegers existed for at least 3 years.

In all years, long-tailed jaegers were at least twice as abundant as any other avian predator in the study area.

2. Parasitic jaegers.

The number of parasitic jaegers establishing territories on the study area was the same each year (Table 3). At least 2.3 km separated nests of adjacent pairs of parasitic jaegers. Despite their low density, parasitic jaegers were an important predator for they bred in 1968 and 1970, when pomarine jaegers and snowy owls failed to breed.

3. Pomarine jaegers.

The number of pairs of pomarine jaegers which established territories on the study area varied greatly between years (Table 3). I believe these figures reflect fairly accurately general population trends in the Polar Bear Pass region of Bathurst Island in all years but 1970, when densities were greater outside the study area. In 1969 and 1971, similar numbers of territorial pomarines

were present and pairs bred. In 1970, territorial birds did not establish themselves on the study area, but two to four territorial pairs located immediately to the south, periodically flew into the study area. I do not know if these pairs nested.

Densities in 1969 and 1971 were not significantly different, but were both significantly higher than either 1968 or 1970.

4. Snowy owls.

The number of snowy owls which established territories on the large study area varied between years (Table 3), and the changes appeared to be more irregular and unpredictable than any fluctuations in the jaeger populations. I recorded maximum numbers of territorial owls in 1969 when they exceeded by more than ten times recorded numbers in other years. I recorded no territorial owls in 1968 and 1970 on the study area. However, a few isolated pairs of owls may have bred on other parts of Bathurst Island. One pair of owls bred on the study area in 1971.

The 1969 density of owls was significantly higher than all other years which did not show significant differences between one another.

The presence or absence of territorial and breeding

jaegers and owls was apparently related to food levels rather than seasonal differences in weather (i.e., the warming trend over the four summers).

B. Breeding success.

1. Long-tailed jaegers.

The low reproduction rate of the territorial long-tailed jaegers in 1968 preceded three years with increased numbers of breeding pairs and greater egg production per pair (Table 4). In 1968, both clutches (100%) were of single eggs. The incidence of two-egg clutches was high in 1969, 1970, and 1971, when an average of at least 94% of all initial nests from those three years combined (n=28) contained two eggs. This increased proportion of two-egg clutches in the last three years was statistically significant ($p < 0.025$: Fisher Exact Test). The first clutches normally laid in the last week of June, or the first week of July, showed no marked synchrony between pairs. In 1971, the jaegers laid their first eggs nine days earlier than in 1970, and five days earlier than in both 1968 and 1969. This is probably a reflection of the early spring melt in 1971.

Renesting of some pairs of long-tailed jaegers occurred. There was no renesting in 1968, and there was no direct evidence of its occurrence in either 1969 or 1970. However,

Table 4. Clutch Size of Long-tailed Jaegers Nesting on the Study Area from 1968 to 1971.

Year	Number of Eggs in:		Mean Egg Production Per Pair
	First Clutch 1	Second Clutch 2	
1968	2 (100) ^a	0	1.0
1969	0-1 (0-7)	13 (93)	1.9-2.1 ^b
1970	1 (14)	6 (86)	1.9
1971	0	9 (100)	2.2

^a Figures in parentheses are percentages of the number of eggs laid,

^b Range dependent upon whether single egg nest was a re-nest or a first clutch of one egg.

a nest with a single egg located on 12 July, 1969, and a chick less than three days of age outside the study area on 9 August, 1970, perhaps came from renesting attempts. Two pairs of those intensively studied in 1971 renested soon after losing their initial clutches to predators. One pair laid the first egg of a second clutch eight days and approximately 20 hours after incubating the initial clutch for 15 days. In each renesting attempt, the female jaeger laid only one egg. The early spring of 1971 possibly facilitated renesting, since the renesting occurred within the normal period of first clutches.

Increasing arctic fox predation on jaegers resulted in a smaller expectancy of successful hatching (Table 5), many nests being found early in incubation; this probably allowed for renesting of some pairs in 1971. Of the three intensively studied nests in 1969, all hatched; that is, they survived the 24.5 day incubation period. The average length of survival for first clutches in both 1970 (n=7) and 1971 (n=7) was about 22 days, while the average survival time for those nests destroyed before they hatched was 15 days in 1970 (n=4) and only 10 days in 1971 (n=4). The two repeat clutches recorded in 1971 survived 8 and 13 days, respectively.

The nesting success of long-tailed jaegers was very low

in all years (Table 5), despite changes in the number of eggs laid. In 1968 and 1970, no young reached fledging age on the study area. In 1969, I watched closely three of 14 nests located, and while all six eggs hatched only one chick survived to, at least, near fledging age. That is, 0.33 chicks per pair survived. In the other 11 nests, no chicks survived to approach fledging age. Thus, the 1969 population of jaegers was successful in raising only 3.7% of the eggs produced; that is, 0.07 chicks per pair. The nine pairs studied intensively in 1971 raised one chick to fledging (5% of eggs produced), or 0.11 chicks per pair. Eight additional pairs of jaegers raised only one chick to fledging, 6% of eggs produced, or 0.13 chicks per pair, assuming they laid 18 eggs.

A trend of increasing egg loss, resulting almost entirely from arctic fox predation, can be seen from 1970 to 1971. The proportion of eggs surviving to hatch decreased as a result, yet jaeger chicks seemed to survive equally well in both years. Generally, nests with eggs appeared more vulnerable to changing predation pressures than did the chicks. That the chicks leave the nest a day or two after hatching, to wander over the tundra, probably lessens predation pressure upon them.

I gathered detailed information on the rates and causes

Table 5. The Total Number and Fate of Eggs Laid by Long-tailed Jaegers Nesting on the Study Area from 1968 to 1971.

Year	EGGS				CHICKS			Last Seen Alive
	Number Laid	Fate Unknown	Eaten or Disappeared	Abandoned or Failed to Hatch	Hatched	Disappeared as Young		
1968	2	1	0	1	0	0	0	0
1969	6	0	0	0	6 (100) ^a	5 (83)	1 (17)	0
1970 ^c	13	0	7 (54)	0	6 (46)	5 (38)	0	0
1971 ^d	20	0	14 (70)	0	6 (30)	4 (20)	1 ^e (5)	1 ^e (6)
	18 ^b	-	-	-	-	-	-	-

^a Figures in parentheses are percentages of the number of eggs laid.

^b Eggs for which only partial information was available.

^c One chick found dead on 26 July, 1970. Cause of death unknown (Appendix IV).

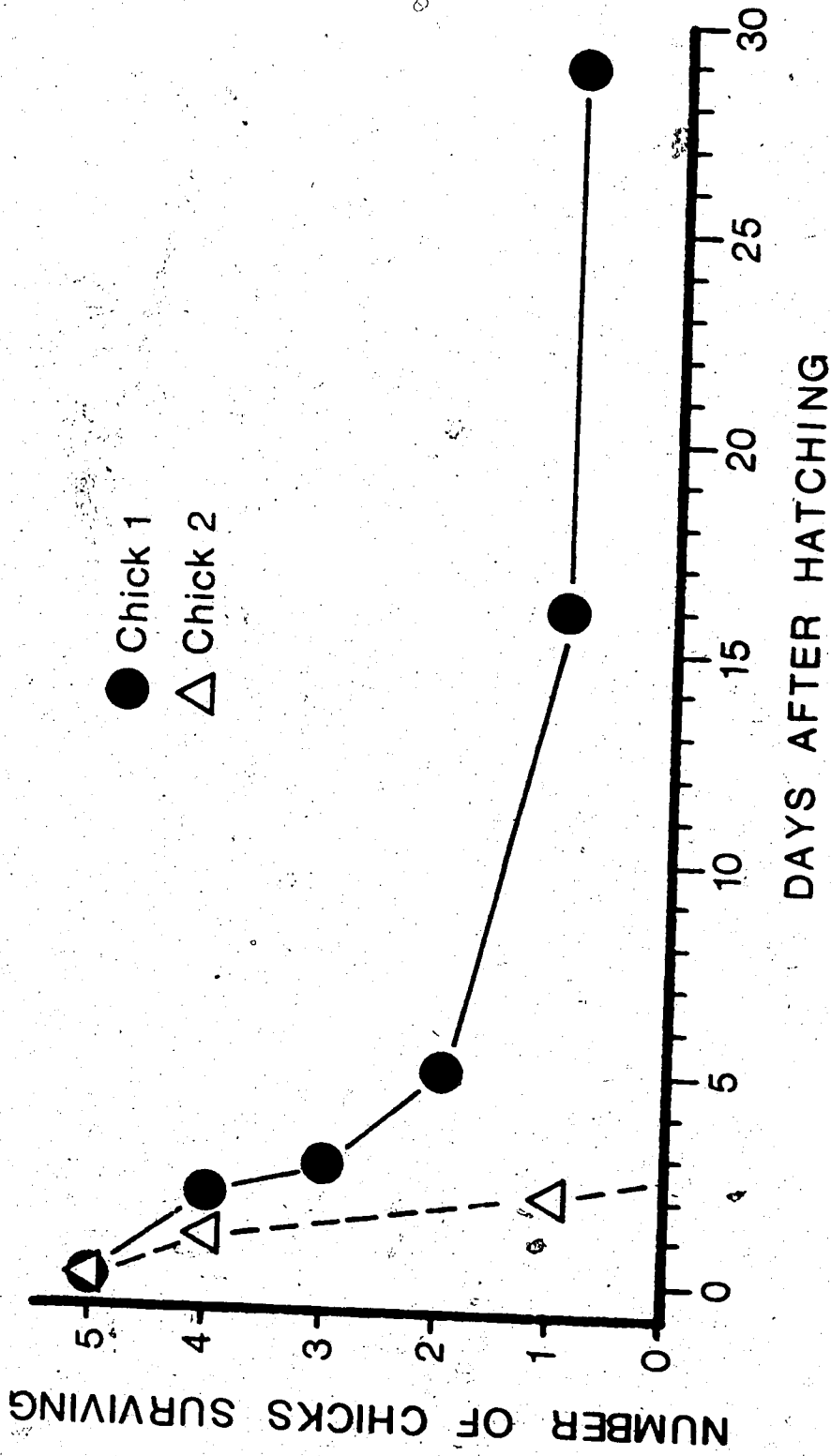
^d One chick collected on 28 July, 1971 (Appendix IV).

^e Known to have fledged.

of pre-fledging mortality for ten individually marked long-tailed jaeger chicks (Figure 3). Differential mortality occurred within broods; the older chick, hatched two days earlier because incubation commenced with laying of the first egg. The older chick appeared to have a distinct advantage over the younger, particularly after the older chick was three or four days of age. Of six chicks penned at three nests in 1970, a fox ate one (the older), I found one (the younger) dead apparently from chilling, and parent or sibling jaegers probably ate four. The latter supposition is supported by pellet content. Whether the chicks were killed and then eaten, or were eaten after dying from chilling, I do not know. In 1971, I do not know the extent of cannibalism; predation was possibly higher than in 1970. Because these chicks are precocial, they left the nest at two or three days of age and usually remained separated thereafter, perhaps reducing cannibalism. In all nests except one, the older chick survived longer than the younger. Survival of the older chicks was apparently facilitated by hatching two days before the younger, and thus being larger and presumably stronger than it.

I removed the older chick (two days old) from one brood leaving only the newly hatched second chick. This latter chick survived to fledge. This indicates that the second

Figure 3. Survival of Ten Long-tailed Jaeger Chicks after Hatching, from Five Nests (Three Corralled Nests in 1970 and Two Unconfined Nests in 1971).



chick is capable of surviving if the first chick is not present.

2. Parasitic jaegers.

The number of eggs laid by parasitic jaegers in the study area was the same each year (Table 6), but success was generally low. These jaegers started clutches between 24 and 29 June, with 1968 and 1971 being the years of earliest initiation. In 1968, when both chicks hatched, the elder survived until we collected it at 16 days of age. The youngest died before it was eight days of age. In 1969, no young survived. Although their exact fate is unknown, the single clutch probably hatched before being lost to arctic fox. In 1970, the clutch disappeared 20 days after being initiated. In 1971, the nest remained intact less than three days before an arctic fox took it. This trend to earlier nest loss may have resulted from an increasing arctic fox population in the study area and the greater predation pressure.

3. Pomarine jaegers.

Pomarine jaegers were not successful in fledging any young from the study area, despite more eggs being laid in 1969 and 1971 (Table 7). Clutches in 1969 survived up to 17 days before arctic foxes ate them, but in 1971, none lasted.

Table 6. The Total Number and Fate of Eggs Laid by Parasitic Jaegers Nesting on the Study Area from 1968 to 1971.

Year	Clutch size	EGGS		CHICKS	
		Fate Unknown	Eaten or Disappeared	Hatched	Eaten or Disappeared
1968	2	0	0	2(100) ^a	1(50)
1969	2	2	?	2?	0
1970	2	0	2(100)	0	0
1971	2	0	2(100)	0	0

^a Figures in parentheses are percentages of the number of eggs laid.

Table 7. The Total Number and Fate of Eggs Laid by Pomarine Jaegers Nesting on the Study Area from 1968 to 1971.

Year	Number of Eggs Laid	Eaten or Disappeared	Hatched
1968	0	0	0
1969	6 + 1	6 + 1(100) ^a	0
1970	0	0	0
1971	7 + ?	7 + ?(100)	0

^aFigures in parentheses are percentages of the number of eggs laid.

longer than four or five days, some not even the day of laying. I found clutches of one, and more often, two eggs.

Laying began in 1971 eleven days earlier than in 1969.

4. Snowy owls.

More pairs of snowy owls attempted to nest in the study area in 1969 than any other summer (Table 8), and 13 of them (87%) completed clutches. Snowy owls laid 16 times as many eggs on the study area in 1969 as in 1971, the only other year in which they bred on the study area.

In 1969, the owls laid most eggs during the last week of May and the first week of June (Figure 4). In that year, owls started the first clutch 24 days earlier than in 1971, the only other year for which comparable data were available. Seasonal differences in weather do not explain the delay in laying in 1971, since 1971 was an earlier spring than 1969. Also, lemming populations were comparable in 1969 and 1971.

The mean clutch size in 1969 was not significantly different from that produced in 1971 (Table 9). Clutch size varied from three to nine eggs.

Snowy owls bred successfully in only one year (1969) when 54 of 83 (65%) eggs laid, hatched (Table 8). Of these 54, at least 54% died of natural causes (not collected) before fledging. Of those dying, most (79%) disappeared

Figure 4. The Percentage of Eggs Laid by Snowy Owls During Weekly Periods in 1969 and 1971. All clutches were found during laying so that the exact laying date of one or more eggs was known, allowing laying dates for the remaining eggs to be calculated, assuming each egg was laid 48 hours apart. Data given in columns are not cumulative.

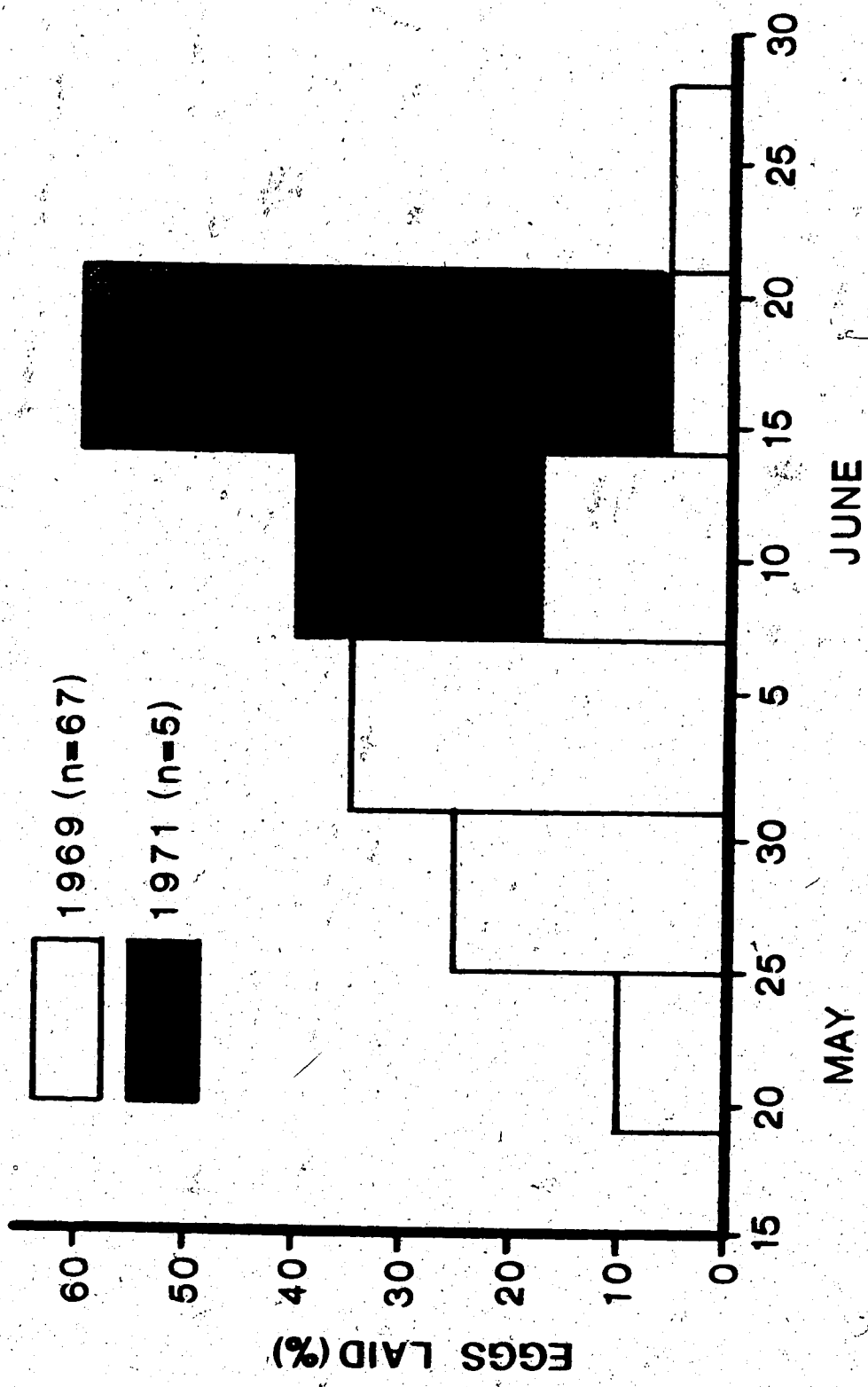


Table 8. The Total Number and Fate of Eggs Laid by Snowy Owls Nesting on the Study Area from 1968 to 1971.

Year	Number of Clutches	Number of Eggs Laid	EGGS				CHICKS				Last Seen Alive
			Fate Unknown	Eaten or Disappeared	Failed to Hatch or Abandoned	Hatched	Disappeared	Found Dead	Collected		
1968	0	0	0	0	0	0	0	0	0	0	0
1969	15	83	7(8) ^a	11(13)	11(13)	54(65)	23(27)	6(7)	5(6)	20(24)	
1970	0	0	0	0	0	0	0	0	0	0	0
1971	1	5	0	5(100) ^b	0	0	0	0	0	0	0

^a Figures in parentheses are percentages of the number of eggs laid,

^b Destroyed by long-tailed jaeger as result of human disturbance.

Table 9. Frequency of Size of Completed Clutches for Snowy Owls Found Nesting on the Study Area in 1969 and 1971.

Year	Number of Clutches	Clutch Size							Total Number of Eggs	Mean Clutch Size
		3	4	5	6	7	8	9		
1969 ^a	13	1	2	3	3	2	1	1	75	5.8
1971 ^b	1	0	0	1	0	0	0	0	5	5

^aTwo additional clutches initiated, each containing four eggs, before being abandoned,

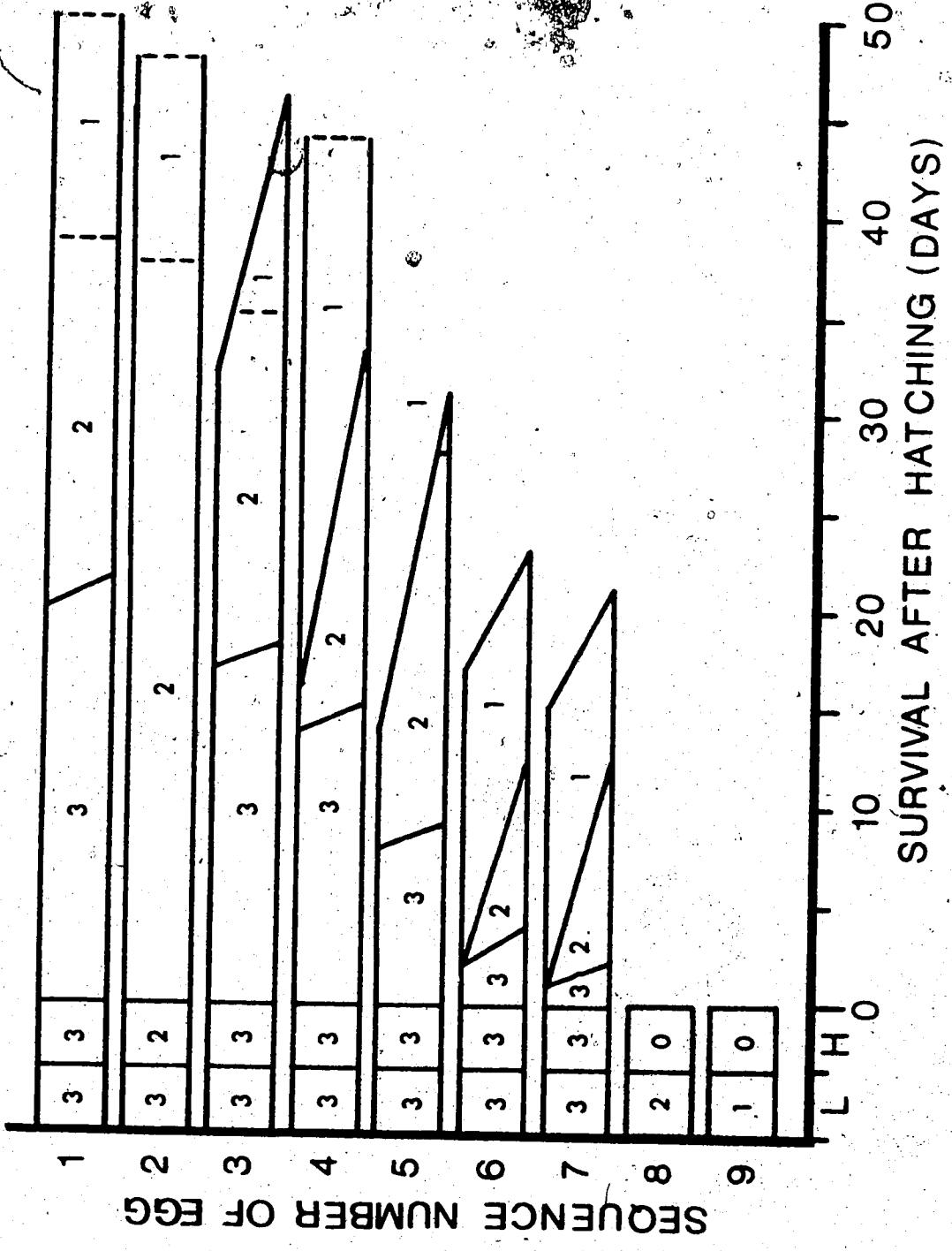
^bTwo nests were located outside the study area in 1971. One had a clutch of eight eggs (S. D. MacDonald, pers. comm. 1971). No one visited the second.

from the nest. Observations of nesting pairs and visits to nests suggest that chilling of owlets in the nest as the result of irregular brooding by females late in incubation, combined with cool, wet weather, was an important cause of these deaths. I suspect cannibalism contributed to this mortality and it may account for most chick disappearance. Predation on snowy owl nests was low (less than 13% of the eggs laid) in 1969. Human disturbance of the only nest in 1971 kept the female owl off her eggs, allowing long-tailed jaegers to destroy the eggs.

Snowy owl eggs hatch asynchronously because incubation begins with the first egg, facilitating differential mortality within broods. In order to evaluate the effect of differential mortality within owl broods produced in 1969, I individually marked the young from three nests, and recorded the length of their survival (Figure 5). Most of the mortality observed in these chicks involved the younger and presumably weaker individuals. The eighth, and ninth eggs of two clutches failed to hatch, some having embryos. The only owlets reaching fledging age were from eggs 1, 2, 3, or 4.

I estimated the immediate post-fledging mortality among 20 owlets. All 20 birds had bands, and seven of these bore individual color markings from color dyes. The remains of two color marked and two unmarked owls were discovered on the

Figure 5. Number of Eggs Hatching and the Survival of Owlets in Days, from Three Nests Containing 7, 8, and 9 Eggs. Eggs numbered according to the sequence in which they were laid. Number laid (L) and number hatched (H) appear in respective boxes. Dashed lines show a bird likely survived beyond this date. Slanted solid lines show range of time over which death for an individual owlet could have occurred.



study area during subsequent summers. No bands were among the remains, thus the two color marked owlets are the only birds of known origin and therefore, I feel they give the best measure of owlet mortality immediately after fledging, in 1969.

$$\begin{aligned} \text{Estimated mortality} &= \frac{\text{Number color marked owlets recovered}}{\text{Total number color marked owlets}} \times \text{Total number banded owlets} \\ &= \frac{2}{7} \times 20 = 5.7 \end{aligned}$$

A total of six young owls out of the 20, last seen alive, probably died before leaving the study area. Thus, each pair of snowy owls on the study area in 1969 successfully raised an average of 1.1 owlets.

Most pairs of owls which left first nests, probably did not renest. One nest still containing eggs on 18 July, and a clutch laid late in June, was possibly a result of renesting. I did not find the 1971 pair renesting.

C. Fidelity to territories.

1. Long-tailed jaegers.

In order to assess the faithfulness of long-tailed jaegers to their territories from year to year and throughout each summer, I individually marked with colored and aluminum leg bands seven territorial adults, each from a separate pair, in 1970. Six returned to the study area in

1971 and each occupied the same territory as in 1970 or the tundra immediately adjacent. The seventh bird, a female, nested 3.5 km west of its 1970 nest just outside of the study area. In 1970, it was this bird which had the only single-egg clutch known and she was a member of the least territorial pair of long-tailed jaegers on the study area.

The distribution of most nests and the behavior of specific territorial birds in 1969 was very similar to the 1970 and 1971 population, suggesting that many of the same birds were present in 1969. I saw the first territorial birds each summer in the second week of June. Both sexes appeared to arrive together. These jaegers could usually be found on their territories from mid-June to mid-August, regardless of the fate of the nest. In 1970, a bird banded on 18 June was defending its territory on 18 August. Another banded bird was defending its territory on 26 August, 1971. Presumably, pairs of long-tailed jaegers did all hunting and feeding within their territories. These jaegers did not leave their territories as often as parasitic jaegers appeared to. Nevertheless, on 16 July, 1970, I saw two marked long-tailed jaegers 0.5 and 2 km from their respective territories. Large numbers of non-territorial birds were in the vicinity at the time. In 1968, one nest was abandoned, perhaps because one adult appeared to have been lost since two were never

seen on the territory. Pairs of long-tailed jaegers appeared to be very faithful to their territories during the season, perhaps more so than any of the other jaegers or snowy owls.

I observed non-territorial jaegers throughout the study area, both on and off established jaeger territories. However, territorial jaegers kept most non-territorial individuals off their territories much of the time.

2. Parasitic jaegers.

Parasitic jaegers showed great territorial fidelity from year to year but seemingly less throughout each season than did long-tailed jaegers. A melanistic male and an intermediate female occupied the same territory each year. In 1968, I collected the female on 5 August and by June of 1969 the dark male had another mate. The jaegers established each new nest within approximately 100 m of the nests from earlier years. I saw parasitic jaegers on their territories from four to nine days after noticing the first arrivals. They did not remain within their territory boundaries all summer and were occasionally absent for periods of a few hours; I once observed the distinguishable male flying 5 km from the nesting area. These wanderings were most common late in summer. In 1968, I did not see the male on the territory after collecting the female. On 26 August, 1971, I observed

the female and dark male chasing an intruding pair of parasitic jaegers from the territory, despite the female having lost one leg in a fox trap on 21 July, 1971. Parasitic jaegers could usually be found on their territories well into August.

This strong attachment to the territory was also true of pairs outside the study area, which resulted in a fairly stable parasitic jaeger population.

3. Pomarine jaegers.

Territorial pomarine jaegers were on the study area for a comparatively short time, and they showed less territory fidelity than the other jaegers. They established territories rather quickly, and I found peak numbers of pairs by late June of 1969 and by 21-22 June of 1971. Some pairs deserted territories without attempting to nest. One pair in 1971 stayed only two days. Birds that lost nests usually remained in the area for a few days before departing. I found no evidence for the renesting of pomarine jaegers.

That pomarine jaegers do not return to regular breeding territories on Bathurst Island is suggested by differences in density of the territorial pairs, and location and color of individual pairs in the study area from year to year.

4. Snowy owls.

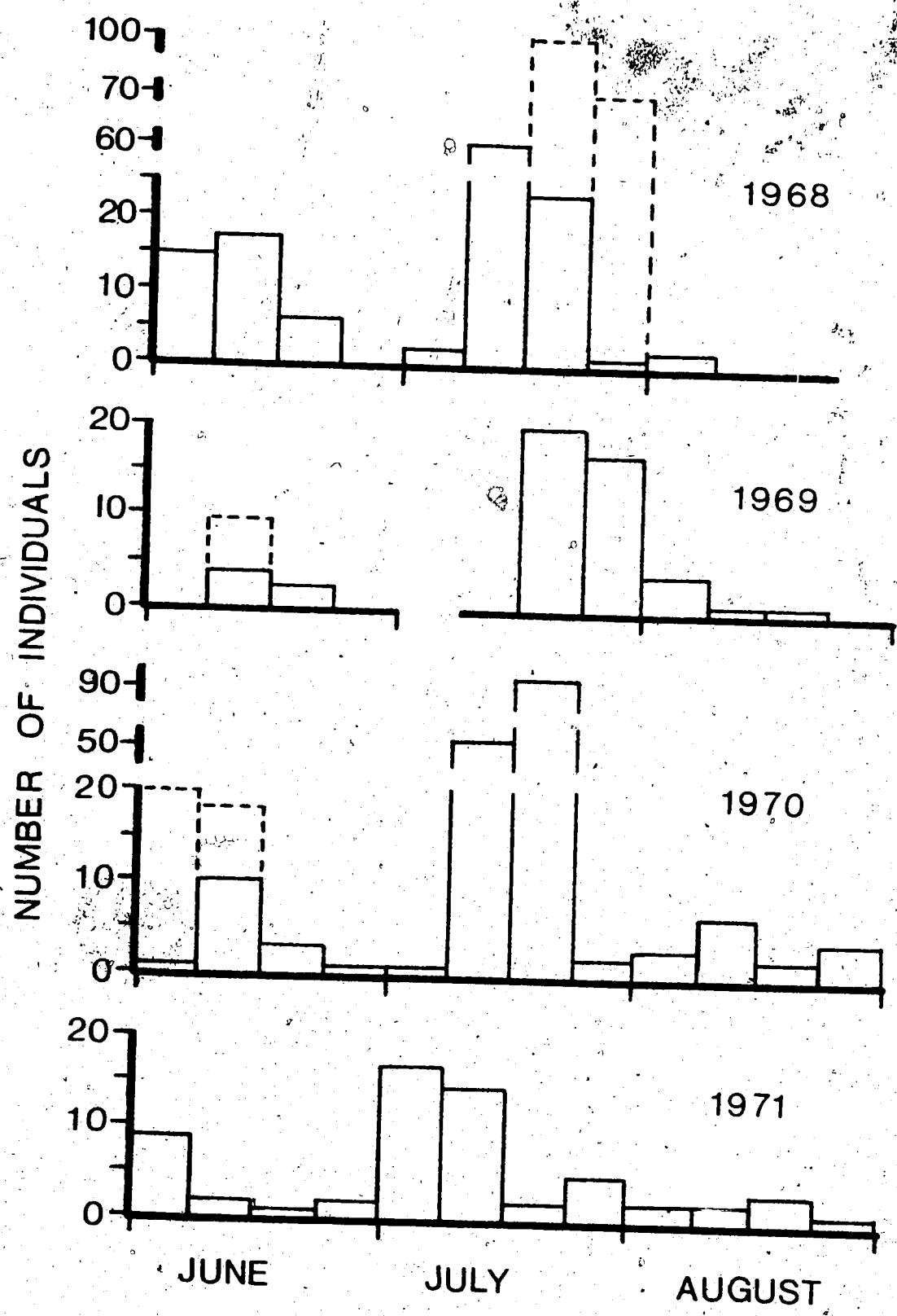
The number of territorial pairs of snowy owls present on the study area declined as the summer progressed in 1969, and 1971. In 1969, fourteen pairs of owls were territorial from early May until mid-July, then the number slowly dropped to nine pairs by mid-August, while in 1971, one pair was territorial until the first week in July. Once they abandoned the nest or the eggs or young disappeared, the territorial bond apparently diminished. Adult owls could not be found regularly in the area thereafter. Once away from their territories, these adults were indistinguishable from the non-territorial owls in the study area.

D. Numbers of non-territorial birds.

1. Long-tailed jaegers.

The numbers of non-territorial long-tailed jaegers fluctuated markedly within the study area each summer following a fairly regular pattern (Figure 6). The earliest long-tailed jaegers arrived the first or second week of June, often in small flocks of four to eight birds, never more than 20. In 1968 and 1970 they arrived in larger flocks than in 1969 and 1971. Frequently, I saw them first in the early melt areas near the study area where they remained for a few days before leaving or dispersing to territories on other

Figure 6. Maximum Number of Non-territorial Long-tailed Jaegers Counted on the 8.75 km² Census Area in Each Quarter of the Months of June, July, and August. In 1970 and 1971, observations continued after August, but no long-tailed jaegers were seen. Numbers shown with dashed lines are of flocks outside the study area but within Polar Bear Pass and are presented for comparison.



areas. In late June and early July, non-territorial birds became less common, and they flew through the study area, usually singly, rarely stopping. Between 18 July, 1969 and 8 July, 1971, the first of a large mid-summer population of non-territorial long-tailed jaegers arrived on the study area. This increased the local density as much as nine times. They reached peak numbers within one or two days, and I observed flocks in the study area for up to eight days (1971). They remained in the valley in loose flocks of up to 74 individuals while feeding and resting. These concentrations occurred in the sedge marsh tundra around ponds and lake edges in the main valley away from most of the territories of resident jaegers. The influx seemed to coincide with the major hatch of large chironomids. Two adult jaegers collected from a flock of non-territorial birds on 16 July, 1970 were eating chironomids exclusively (Appendix IV). A trend to earlier influxes from 1968 to 1971 is evident. I do not know if this is significant or not. Movements of flocks and the sighting of about 100 birds 9 km east of the study area four days after numbers diminished in the study area suggests that these birds moved eastward. Again, in late July and August, only small groups passed quickly through, seldom stopping. Most flew east. Perhaps the frequency with which this occurred increased in early August. I saw long-tailed

jaegers as late as 31 August.

The majority of non-territorial long-tailed jaegers had complete adult plumage. Occasionally, I saw a bird with a few barred feathers from the juvenile plumage (usually under-tail coverts). I do not know whether these non-territorial jaegers attempted to breed or not.

2. Parasitic jaegers.

Non-territorial parasitic jaegers occurred regularly on the study area but in small numbers (Figure 7). The first birds arrived between 10 and 13 June. Non-territorial individuals did not remain in the study area and this prevented any build-up in their numbers over the summer. I saw these jaegers either as singles or in small flocks of less than four birds. Often they intruded into an occupied jaeger territory. The occasional bird had a few juvenile feathers but most were in adult plumage. Some parasitic jaegers classified here as non-territorial may have been territorial birds which wandered outside their own territories. I saw parasitic jaegers as late as the fourth week of August.

3. Pomarine jaegers.

The first spring sightings of non-territorial pomarine jaegers reveal a trend to earlier arrival dates and larger flocks from 1968 through to 1971 (Figure 8). From

Figure 7. Maximum Number of Non-territorial Parasitic Jaegers Counted on the 8.75 km² Census Area in Each Quarter of the Months of June, July, and August of 1968 to 1971. In 1970 and 1971, observations continued after August, but no jaegers were seen. Numbers shown with dashed lines are flocks outside the study area but within Polar Bear Pass and are presented for comparison.

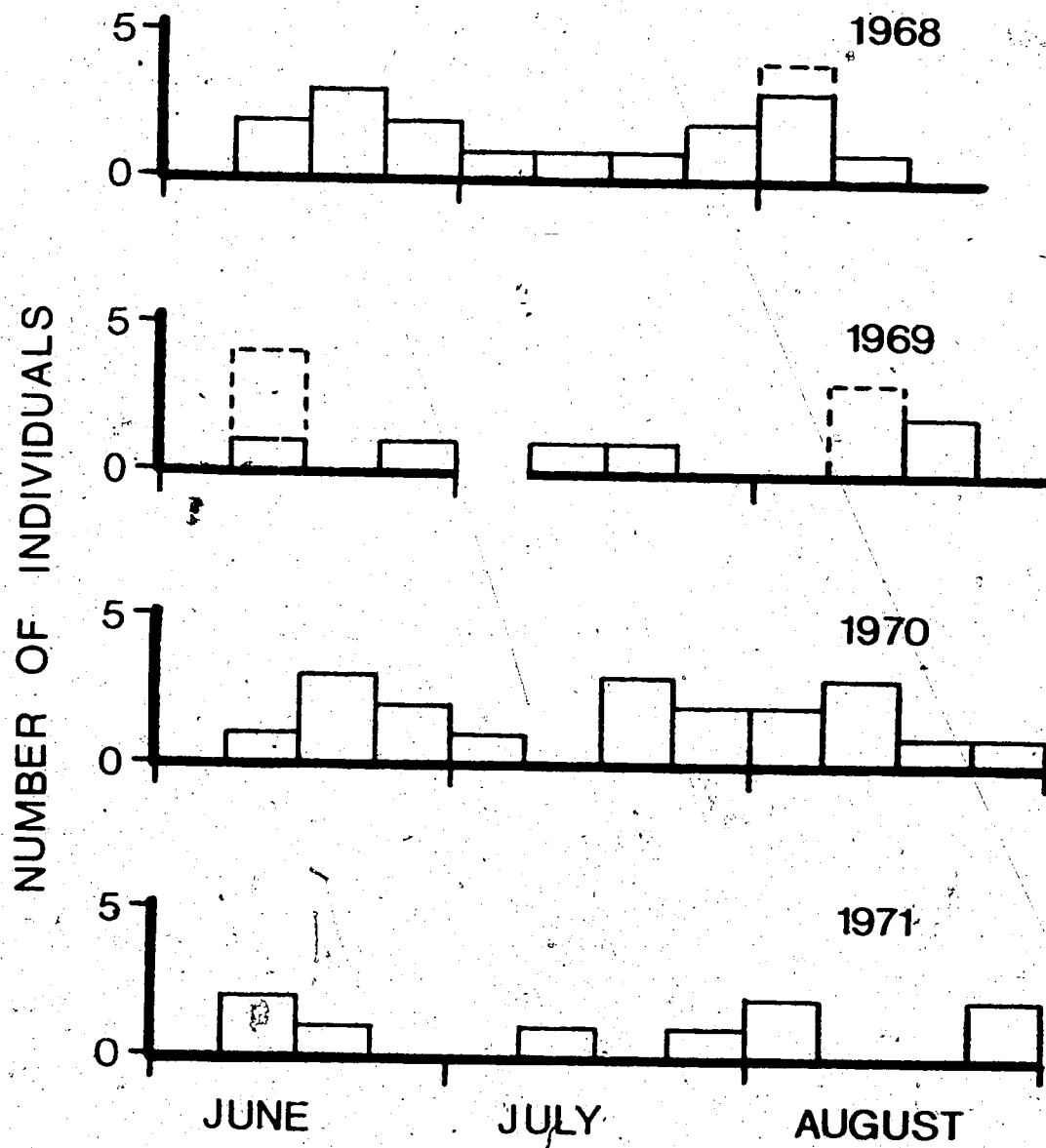
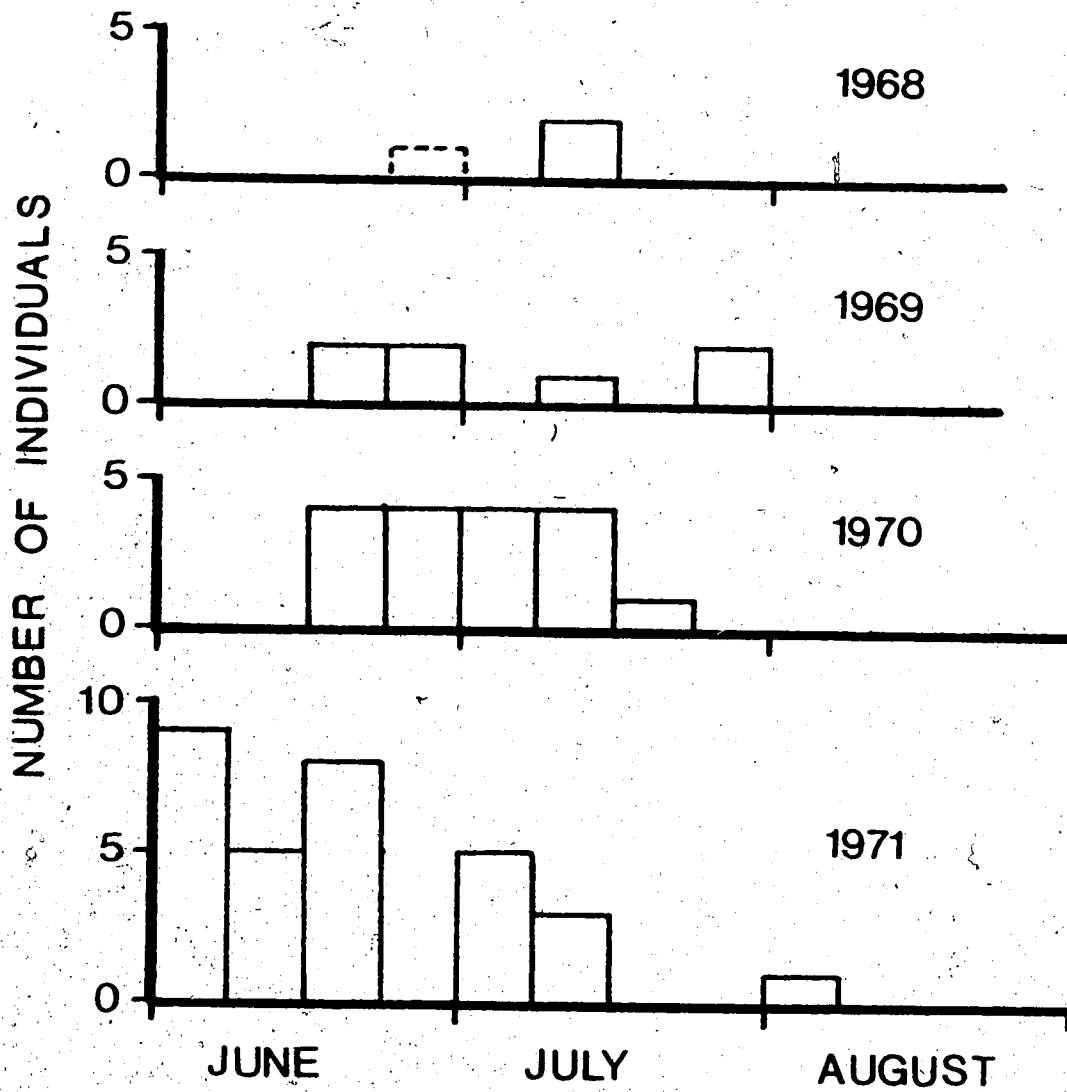


Figure 8. Maximum Number of Non-territorial Pomarine Jaegers Counted on the 8.75 km² Census Area in Each Quarter of the Months of June, July, and August of 1968 to 1971. In 1970 and 1971, counts continued after August, but no pomarine jaegers were seen. Numbers shown with dashed lines are flocks outside the study area but within Polar Bear Pass and are presented for comparison.



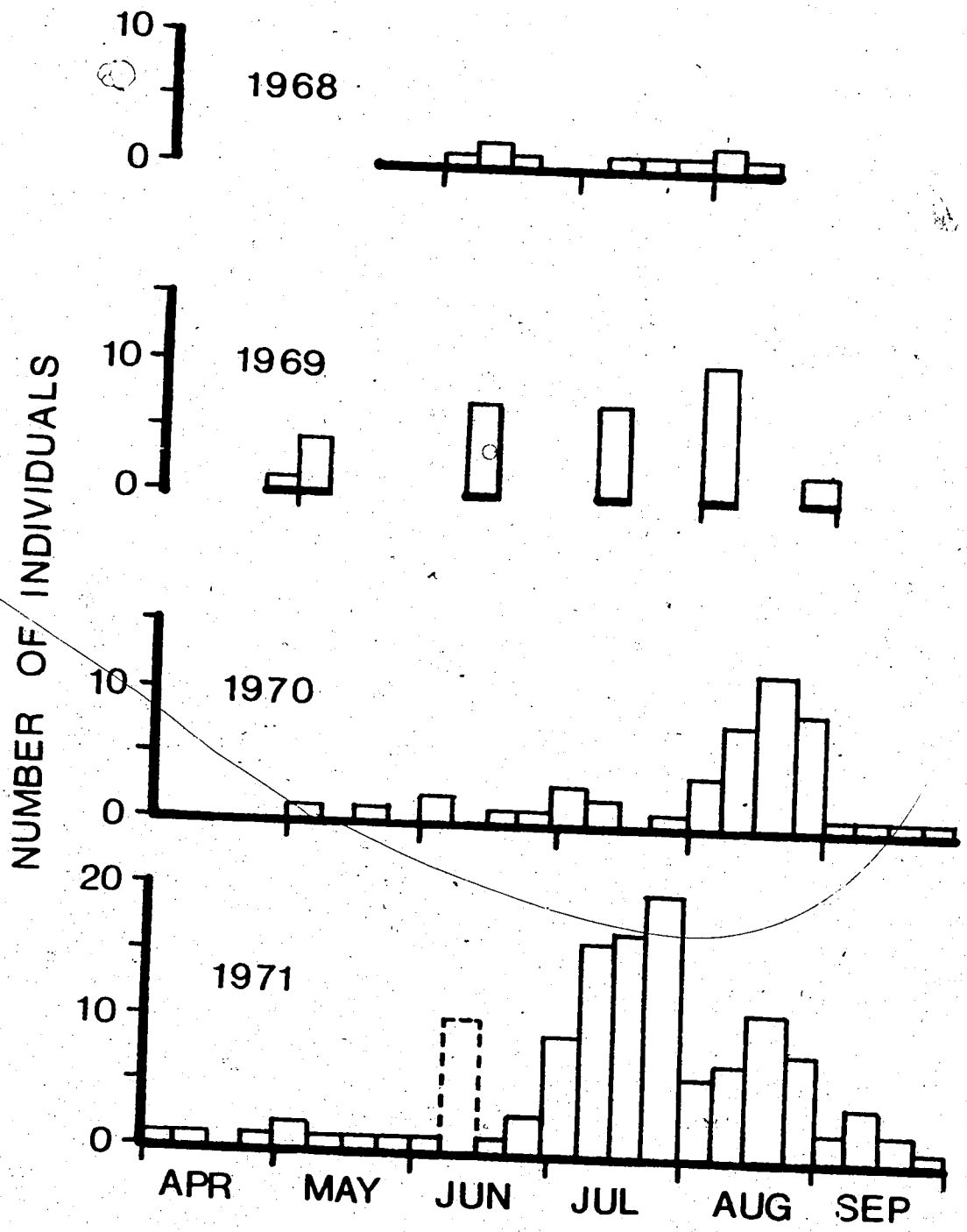
1968 to 1970 they arrived at least a week after the parasitic and long-tailed jaegers, while in 1971 they arrived with the long-tailed jaegers, but slightly earlier than the parasitics. Singles or small groups of less than four birds were most common, particularly later in the summer, though I saw a flock of nine in the spring of 1971. Many non-territorial pomarine jaegers flew directly through the study area and most of those that stopped did not seem to remain longer than a day or two. It was unusual to see a pomarine jaeger on the study area later than the third week of July.

All the pomarines appeared to be adults. A few individuals had short central rectrices and one such bird bred in 1969.

4. Snowy owls.

The number of non-territorial owls within the census area fluctuated yearly in a more regular way than the numbers of territorial owls (Figure 9). Single owls were recorded as early as 27 February (1971) and as late as 12 October (1971). Despite individual non-territorial owls seldom being found in one location for more than three or four days, fairly uniform but low numbers remained in the census area for extended periods of time. This was the case throughout 1968 and much of the summers of 1969, 1970, and 1971.

Figure 9. Maximum Number of Non-territorial Snowy Owls Counted on the 53.5 km² Census Area in Each Quarter of the Months of April to September. Breaks in the abscissa indicate no censuses taken. Single owls were seen in the census area in 1971 on each of 27 February, 8 March, 1, 4, and 12 October. Numbers shown with dashed lines are birds outside the study area but within Polar Bear Pass and are presented for comparison.



Immaculate white males (presumed to be adults) outnumbered dark birds (presumed to be females) by two to three times during these periods.

The large increase in numbers of owls late in the summers of 1970 and 1971 resulted from a gradual movement of non-territorial owls onto the area. I presumed most of these birds to be adult males because they were in immaculate white plumage. At these times, the owl density approximated the breeding density of 1969. In the last week of July, 1971, the density of non-territorial snowy owls was 25% higher than the peak breeding density of 1969. In 1971, large numbers of non-territorial owls appeared a full month earlier than in 1970. The few accurate censuses taken in 1969 plus observations of the movements of single owls suggest that a similar increase in the number of non-territorial owls occurred in July and August of that year. However, the precise magnitude of this increase is not known.

Non-territorial owls were usually solitary, seldom approaching one another within 100 m. However, on 16 June, 1971, I saw a concentration of ten owls, as many as seven being perched within 7 m of each other at one time: all were quite dark in color, so they could have been sub-adults. They hunted arctic hares at the time.

II. Food habits of long-tailed jaegers.

Time budgets based on 4970 and 4865 minutes of observations of males and females respectively, enabled me to determine the proportion of time long-tailed jaegers spent at the following activities: resting, incubating, alert, displaying or defending the territory, bathing, ingesting, hunting for lemmings, hunting for arthropods, and not visible (Table 10). I compared the duration of these activities from two sampling periods (data gathered between 1500 and 1800 hours, and data gathered between 1200 and 2400 hours) using chi-square contingency tables to determine how representative the central three-hour period was. The differences between the two samples were not statistically significant, however the variability within the 1500 to 1800 hour period was less, and therefore provides the best comparison of results between nesting periods. However, observations made between 1200 and 2400 hours were probably more representative of the total daily activity pattern of the birds. I present data from both sampling periods when the two are somewhat different, or occasionally, even statistically different from each other. I do not detail the statistical differences since they may reflect my sampling technique rather than true circadian patterns of the birds. In the pre-, first, and post-nesting periods when sample times were generally largest, the patterns

Table 10. Duration of Observations of Territorial Male and Female Long-tailed Jaegers. Includes only times when activity of birds known. Observations began on 16 June and ended on 13 August, 1971.

Period in Nesting Cycle	Observation Dates Corresponding to Period	Duration of Observations in Minutes			
		Males	Females	Males	Females
		1200 and 2400	Between 1500 and 1800 hours		
Pre-nest	16 to 18 June	501	501	501	501
First nest	19 June to 4 July	2359	2261	1085	1017
Inter-nest	5 to 13 July	706	710	544	560
Re-nest	20 to 23 July	483	488	305	306
Post-nest	25 July to 13 August	921	906	582	572
Total	16 June to 13 August	4970	4865	3017	2956

of jaeger activity observed from 1500 to 1800 hours corresponded more closely to the 1200 to 2400 hour observations than in the inter- and re-nesting periods.

A description of hunting behavior and details of the time spent foraging for lemmings and invertebrates, habitat utilization and hunting success for male and female long-tailed jaegers follow. Details of the other activities are included elsewhere (Appendix III).

A. Hunting for lemmings.

1. Behavior.

Territorial long-tailed jaegers hunted mainly in their territories. I saw none hunting outside its territory in 1971, but I saw single marked males feeding on arthropods up to 1.2 km from their respective territories on 16 July, 1970.

Long-tailed jaegers hunted for lemmings in three main ways. The first method was by hovering above the tundra at a height of 1 to 10 m (usually about 4 m) in various locations throughout the territory. Most often, after hovering in one spot, the bird flew low over the terrain to a new location, either near or far. Here it suddenly soared up to a desired height and began hovering. This type of hunting often occurred when there was a breeze or light wind which allowed

the jaegers to reduce, or stop altogether their wing beats and thus probably conserve energy. This was commonly done over hillsides, where the jaegers could presumably make use of updraughts. The second method involved low, rapid, and often long flights of more than 50 m to new observation posts, usually frost mounds. They landed either on top, or more often, low down on the side of the mound from whence they walked to a vantage point. Here they remained for a number of minutes, still and alert, before flying to the next perch. Males often used this method of hunting after an extended period of rest or low activity, and one male flew a circuit of paths throughout his territory, which took a little less than 60 minutes to complete. The third hunting method involved standing and waiting near lemming burrows -- usually frost mounds and mats of monocotyledenous plants which held a concentration of complex burrow-systems. This became most common in late July and early August when young lemmings first emerged from their burrows. One male jaeger caught two young lemmings in 23 minutes at the same burrow system on 27 July. This is similar to a hunting method used by pomarine jaegers (Andersson 1973).

Jaegers killed lemmings with a series of hard pecks or by dropping them to the tundra while flying. The latter possibly happened inadvertently, since jaegers often attempted

to carry the lemming some distance from the site of capture before killing it. The female joined the male at this point and they commenced feeding.

I considered time spent ingesting vertebrate prey separately from hunting and killing the prey. It includes the time spent eating lemmings after the kill or feeding on such things as carrion or the eggs or nestlings of birds. Once killed, small lemmings (weighing less than about 25 g) were eaten whole, while the larger lemmings were torn open, and then eaten. If one bird was present, it pecked and shook the lemmings' ventral skin until it tore. It eviscerated the lemming, then tore it still further consuming all but the stomach and its contents. If both birds were present, each grabbed part of the lemming, pulled the lemming apart, and consumed it comparatively rapidly.

Less than 5% of the ingestion time involved eating eggs in nests. I recorded this only during the first nest period. Though males "spent" twice as much time ingesting as the females did, perhaps because males made all the lemming kills, it still amounted to less than 3% of the total time observed.

2. Seasonal changes in time spent hunting. (Based on data collected between 1500 and 1800 hours and shown in Figures 10 and 11).




Figure 10. Percentage of Time Spent by Territorial Male and Female Long-tailed Jaegers at Different Activities during the 1971 Season. Bars (columns) show data gathered between 1500 and 1800 hours and dots show data gathered between 1200 and 2400 hours. Numbers along abscissa refer to the following activities: (1) Not visible, (2) Resting, (3) Incubating, (4) Perching/hunting, (5) Displaying or Defending Territory, (6) Bathing, (7) Ingesting, (8) Hunting for Lemmings, (9) Hunting for Invertebrates.

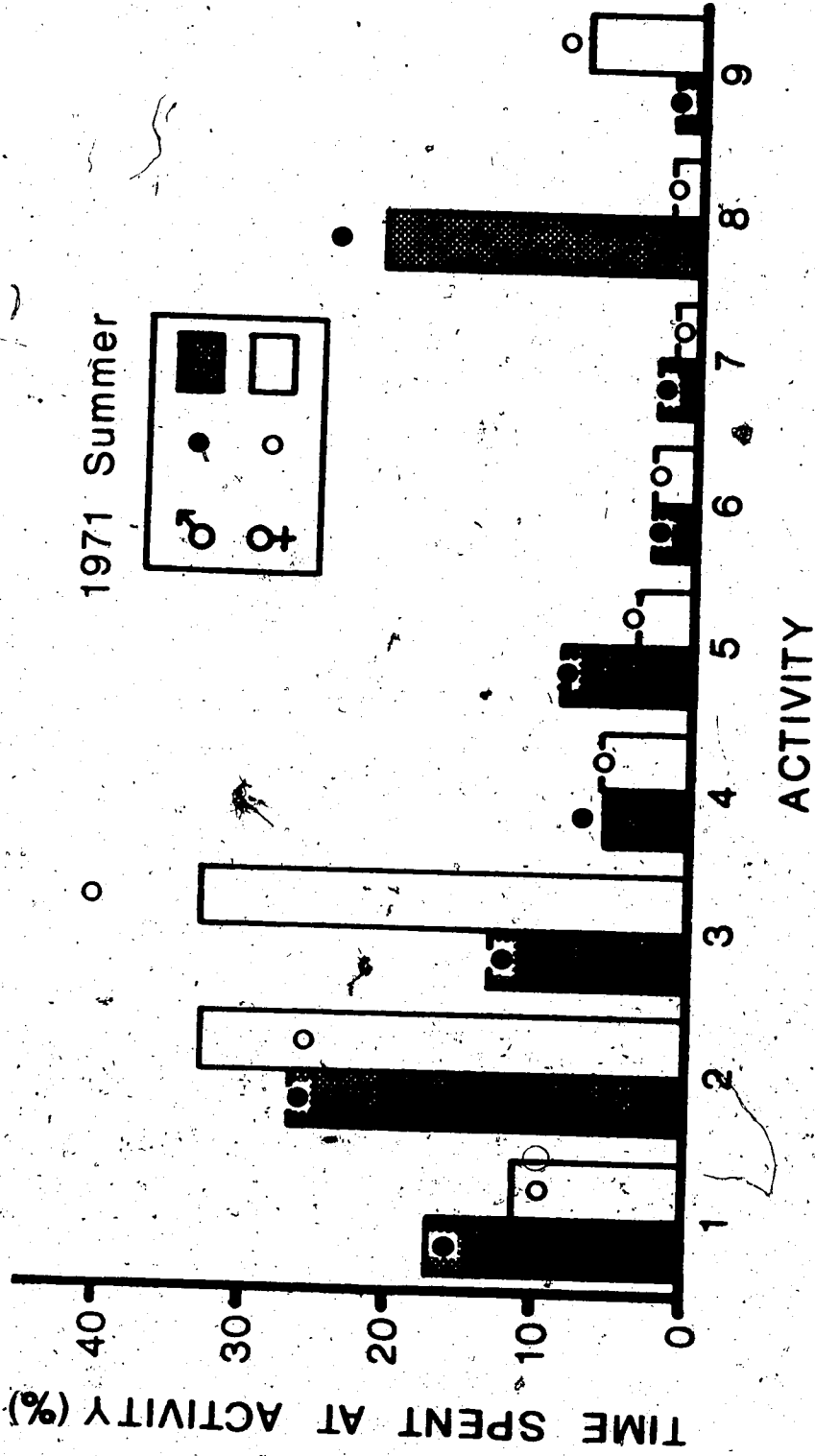
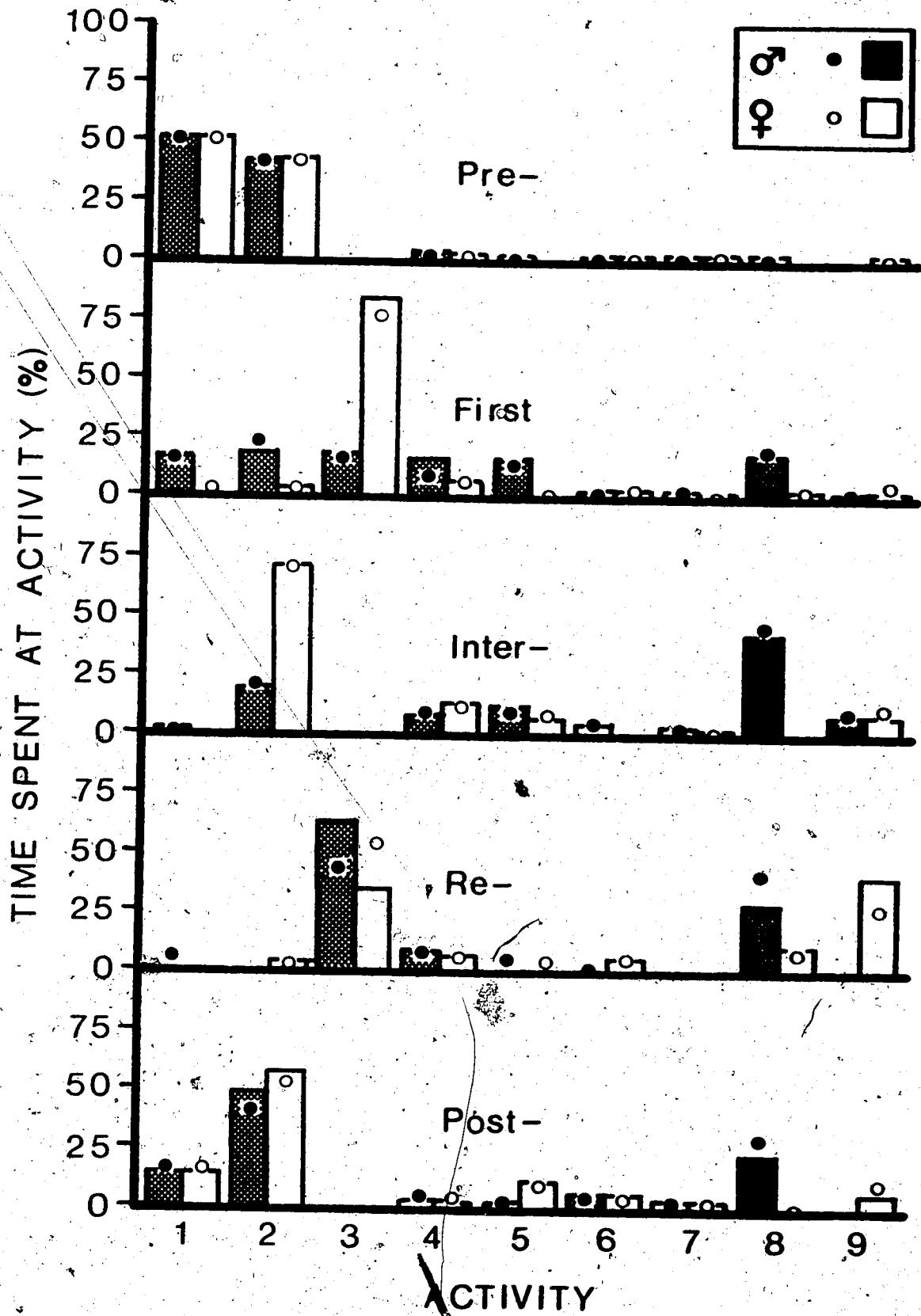


Figure 11. Percentage of Time Spent by Territorial Male and Female Long-tailed Jaegers at Different Activities during the 1971 Nesting Season According to Nesting Periods. Bars (columns) show data gathered between 1500 and 1800 hours and dots show data gathered between 1200 and 2400 hours. A Key to the activities which are numbered along the abscissa is given in Figure 10.



Male long-tailed jaegers did over 92% of all lemming hunting observed, spending at least 21% of their time during the season foraging for lemmings: perhaps closer to 25% as indicated by the data collected between 1200 and 2400 hours. Foraging for lemmings is therefore one of the males' major activities. The sharp increases in time spent hunting for lemmings by the males from the prenesting to the first nesting period and from the first to the internesting period were statistically significant. Male jaegers continued to spend a long time hunting lemmings in the renesting period, and this, along with decreased wandering from territories, suggests more difficulty in killing prey or more prey being required by the birds. Males reduced their foraging time for lemmings in the post-nesting period.

Each male spent an average of six hours' daily foraging for lemmings in the 1971 season (Table 11). During the pre- and first nesting periods, they spent less than six hours foraging for lemmings daily, after which they spent more than six hours daily.

Since female jaegers did less than 8% of the pair's lemming hunting, the equivalent of only 2% of the total time I observed females, I do not consider it an important part of the females' time or energy budget for 1971. That one female did resort to lemming hunting in the renesting period, when

Table 11. Number of Hours Male Long-tailed Jaegers Foraged for Lemmings in a Day during Various Nesting Periods. (Assuming that the birds foraged at equal rates in the first half of the day as in the second half). Data from Figures 10 and 11.

Nesting Period	Daily Hunting Time (Hours)
Pre-	< 0.2
First	4.5
Inter-	10.6
Re-	9.8+
Post-	7.0
Average for Season	6.0

male jaegers were experiencing their poorest success at killing lemmings (discussed below), may indicate a potential for hunting this prey. Instead, females spent considerable amounts of time resting during the prenesting, internesting, and post-nesting periods, or incubating when compared to males.

Throughout the season, pairs of long-tailed jaegers spent more than twice as much time hunting for lemmings as they did for invertebrates (Figure 10).

3. Time spent hunting over various habitats.

(Based on observations between 1500 and 1800 hours and shown in Figures 12 and 13).

Male long-tailed jaegers hunted for lemmings over snow melt areas during the pre- and first nesting periods, spending a total of only 2% of the season's foraging time in these areas. However, it is perhaps significant that all foraging during the prenesting period occurred in snow melt areas where lemmings were vulnerable as they left their wintering areas for drier ground.

Male long-tailed jaegers spent 65% of their total foraging time (71%, based on data for the 1200 to 2400 hour period), hunting for lemmings over the barrens. In the first, inter-, re-, and post-nesting periods, males spent from 60 to 71% of their foraging time hunting for lemmings in this area (66 to

Figure 12. Percentage of Time Spent Foraging for Lemmings and Arthropods by Long-tailed Jaegers in Different Habitat Types. Bars (columns) show data gathered between 1500 and 1800 hours and dots show data gathered between 1200 and 2400 hours. The habitats are: snow melt (S), barrens (B), hummocky tundra (H), and marshy meadows (M).

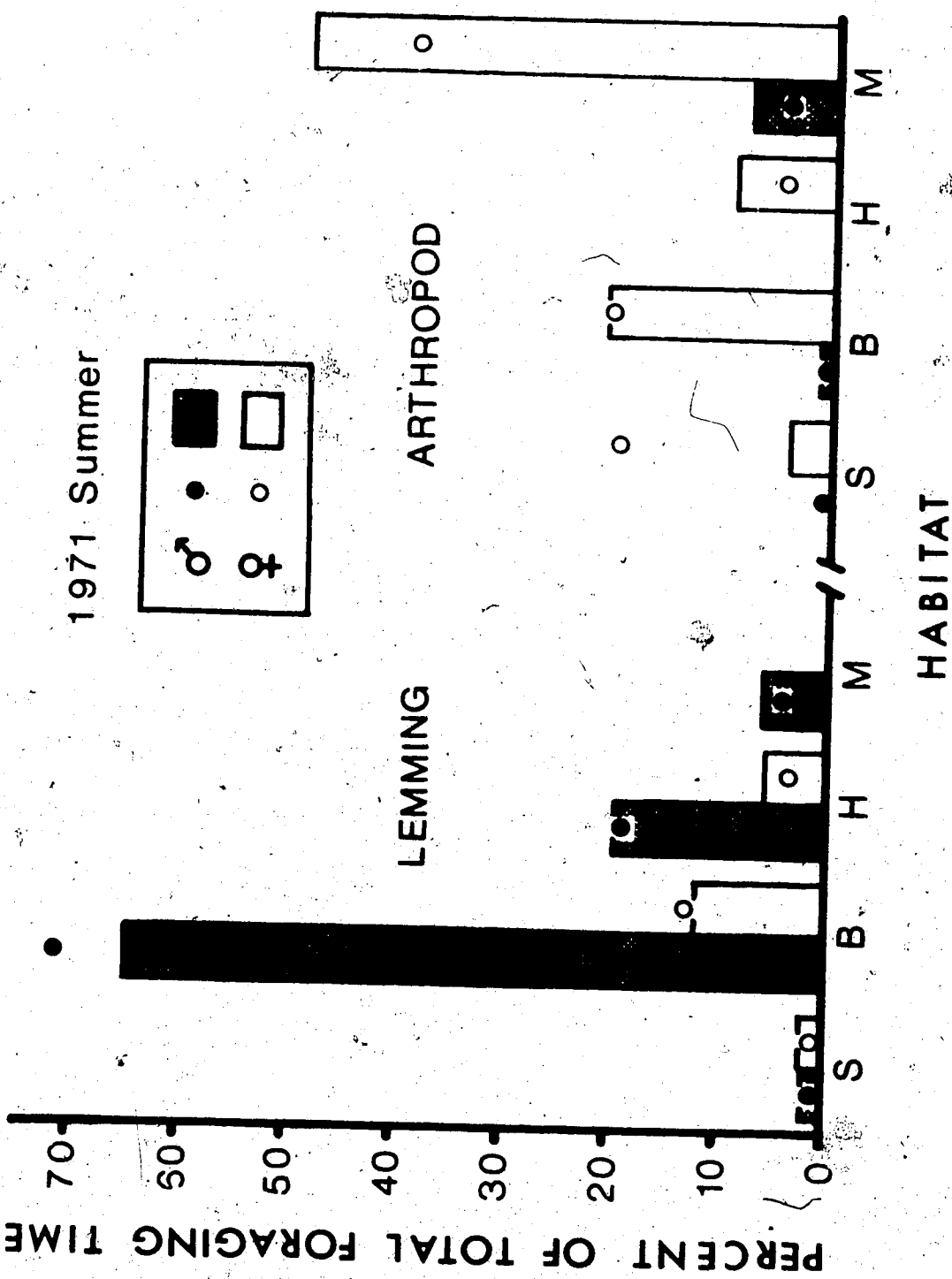
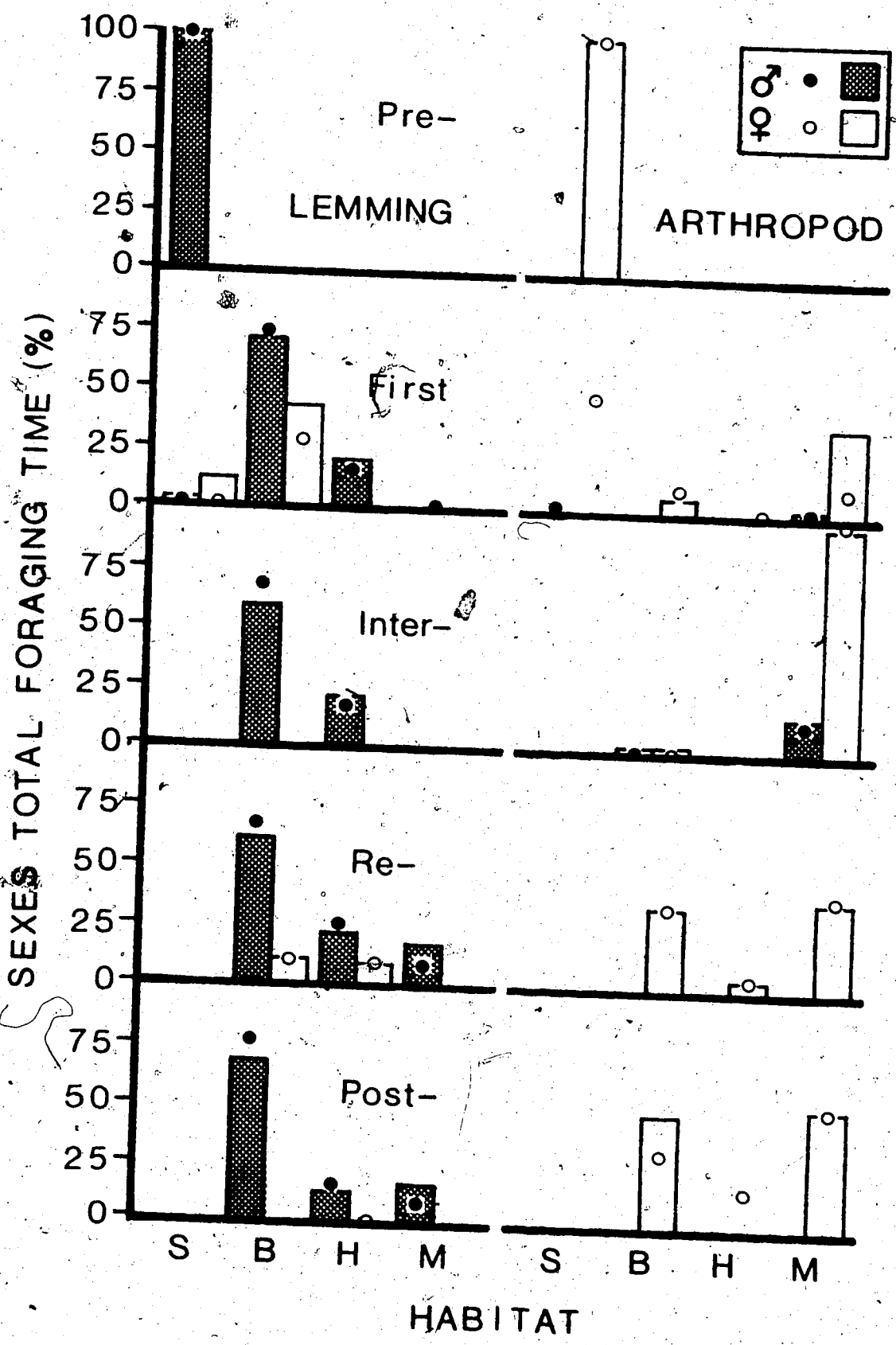


Figure 13. Percentage of Time Spent by Territorial Male and Female Long-tailed Jaegers Foraging for Lemmings and Arthropods in Different Habitats within Their Territories in 1971, According to Nesting Period. Bars (columns) show data gathered between 1500 and 1800 hours and dots show data gathered between 1200 and 2400 hours. The habitats are: snow melt (S), barrens (B), hummocky tundra (H), and marshy meadows (M).



76% using data from 1200 to 2400 hours). While the proportion of time males spent hunting lemmings between nest periods remained similar, males increased the actual minutes spent hunting for lemmings in the barrens significantly from the pre- to the first nesting period and then again from the first to the internesting period ($p < 0.001$) after which slight, but not significant, decreases occurred. Lowest proportions of time spent lemming hunting in the barrens occurred in the inter- and renesting periods when males did more foraging for lemmings in the hummock tundra and more foraging for arthropods.

The second most important habitat hunted was hummock tundra where males spent 14 to 22% of the foraging time in search of lemmings (16 to 26% using 1200 to 2400 hour data). The increase in time spent hunting lemmings in the hummocky tundra was significant ($p < 0.001$) between prenesting and first nesting and between first and internesting periods.

Hunting for lemmings at large grassy lemming burrow complexes constituted a small but important segment of the males foraging time in the re- and post-nesting periods. Males increased the amount of time spent at these sites in the renesting period significantly ($p < 0.001$) and maintained that level into the post-nesting period, when young lemmings left their burrows. During the re- and postnesting periods,

they spent significantly more⁹ time hunting lemmings in meadow sites than during the first nesting period ($p < 0.001$). Only during the first nesting period did I see any lemming hunting in the extensive low-lying marshy meadows.

Lemming hunting by females was primarily over the barrens and hummocky tundra (Figure 13).

4. Hunting success. (Based on observations between 1200 and 2400 hours).

I recorded long-tailed jaegers killing lemmings on 12 occasions. All 12 kills were made by males within their respective territories (unpublished data). From my observations, males spent an average of 102 minutes foraging for every lemming killed (Table 12). If males average 6.0 hours foraging for lemmings per day (Table 11), an average of 3.5 lemmings is taken per day for the pair assuming lemmings are killed at the same rate for the first half of the day. Those lemmings killed by the male jaeger were usually shared with the female, thus providing food to the pair.

a. Success according to nest period.

During the prenest period, when the daily kill rate was 2.9 lemmings per pair of jaegers, male jaegers spent very little time foraging before making a kill (Table 12). The time spent foraging per kill increased sharply in

both the first and interesting periods, and these increases were significant, as discussed above. In the former, the daily kill rate remained near three lemmings. However, in the latter, the daily kill rate diminished to two, suggesting that lemmings became progressively less available, either more difficult to find or more difficult to catch.

During the renesting period I observed no kills, and thus accurate calculations of daily kill rate and minutes of hunting per kill are not possible. However, because the percent of time spent foraging which I observed during both the inter- and renesting periods are not significantly different, I assumed that minutes of hunting per kill and daily kill rates were similar for both periods.

The daily kill rate of lemmings was much higher during the post-nesting period and, as a result, birds spent less time foraging per kill. At least three of the observed lemming kills during this time were of juveniles.

Male jaegers made a successful lemming kill approximately once every four tries. I observed 28 (85%) of the total 33 misses during the inter- and second nesting periods, five in the post-nesting period, and none earlier. Many attempts to catch a lemming, which halted very early in the chase were likely overlooked since the jaeger had to make a definite attempt, usually a stoop, to catch a lemming before I

Table 12. The Hunting Success of Male Long-tailed Jaegers Foraging within Their Territories for Lemmings during Different Parts of the 1971 Season.

Part of Season	Misses	Kills	Kills/Day ^a	Minutes Foraging/Kill	Time Spent Foraging ^b
Prenest	0	1	2.9	3	1
First Nest	0	5	3.1	88	19
Internest	18	1	2.0	319	45
Renest	10	0	(<3.0)	(>196)	41
Post-nest	5	5	7.8	54	29
Total	33	12			
Mean			(3.5)	102	25

^a Assuming that hours spent hunting lemmings per day varied seasonally, and that kill rates measured between 1500 and 1800 hours are representative of rates at other times of day (Table 11).

^b Percentage of total time observed.

identified it as an unsuccessful attack, a miss. This may have been particularly true in the pre- and first nesting periods when lemmings seemed to be more vulnerable than later in the season.

b. Success according to habitat.

Jaegers killed few lemmings in the snow melt areas (Table 13). However, the short time spent foraging per kill and the lack of unsuccessful attacks in this habitat suggests that lemmings were more easily killed in snow melt areas than anywhere else.

The barrens yielded the greatest number of lemming kills to territorial long-tailed jaegers over the season. In this habitat, the number of minutes spent hunting per kill was very close to the average rate of 102 minutes per kill and the proportion of successful capture attempts in the barrens (27%) was the same as that for the seasonal total.

The jaegers did not make a large number of lemming kills in the hummocky tundra. Ninety percent of the capture attempts failed and the minutes of hunting time per kill was more than double the average rate, suggesting that it was difficult to capture lemmings in this rough, uneven habitat.

The grassy mats were an important source of lemmings for territorial jaegers. The short amount of time spent

Table 13. The Hunting Success of Male Long-tailed Jaegers Foraging within Their Territories for Lemmings in Different Habitats in the 1971 Season.^a

	Snow Melt	Barrens	Hummock Tundra	Marshy Meadows ^b	Total	Mean
Misses	0	22	9	2	33	
Kills	1(8) ^c	8(67)	1(8)	2(17)	12(100)	
Percent Successful	100	26.7	10	50		26.7
Minutes/kill	11.5	116.9	235.5	23		102.3
Percent of Time Foraging in Habitat	1	76	19	4	100	
Percent of total area ^d	<10	45	<10	30		

^aBased on observations between 1200 and 2400 hours.

^bIncludes grassy mats in barrens.

^cPercentage in parentheses.

^dEstimated.

hunting per kill (25% of the average) and the relatively high proportion of successful capture attempts (50%) indicates that lemmings were fairly easy to catch in this habitat.

Female long-tailed jaegers made little consistent effort to hunt lemmings and only once did I see an attempt to catch a lemming -- it failed.

B. Hunting for arthropods.

1. Behavior.

Under arthropod hunting I included the foraging for and eating of arthropods, mainly anachnids and insects, by territorial long-tailed jaegers of both sexes. When hunting arthropods, the jaegers ran or walked over the tundra in an upright posture, stopping either to peck or to momentarily pause before moving on. After spending a number of minutes in one spot, the feeding bird flew to another in the same or different habitat and continued foraging. I observed both long and short feeding periods throughout the season, females often spending 15 to 30 minutes at a time hunting arthropods. By observing feeding jaegers within 5 m distances, I concluded that most pecking was directed at arthropods on either the ground or vegetation and only very occasionally did a jaeger attempt to capture a flying insect.

2. Seasonal changes in time spent hunting (Figures 10 and 11). Female long-tailed jaegers fed on arthropods for a significantly greater proportion, 81%, of their total foraging time than males and for significantly ($p < 0.05$ to 0.001) greater periods of time in all but the internesting period. Females increased the proportion of time they spent insect hunting up to the post-nesting period, when it decreased. In general, this corresponds to an increase and subsequent decrease in the numbers of arthropods (discussed below) and in the effort expended by male jaegers hunting for lemmings described earlier. I only saw males hunt arthropods in the first and the internesting periods, the latter at a level not significantly different from that of the females.

3. Time spent hunting over various habitats. (Figures 12 and 13). Early in the summer, snow melt areas provided an important foraging area for female jaegers hunting arthropods, most notably in the prenesting period.

Foraging for insects on the barrens occurred late in the summer reaching peak levels, significantly higher than other periods ($p < 0.001$) in the second nesting period. Late in the summer, females spent 32 to 35% of their foraging time on the low well-vegetated barrens, specifically in

areas with Dryas tussocks where late blooms held large numbers of dipterans.

Females foraged in hummocky tundra primarily late in the summer, however they spent less than 5% of their total foraging time there.

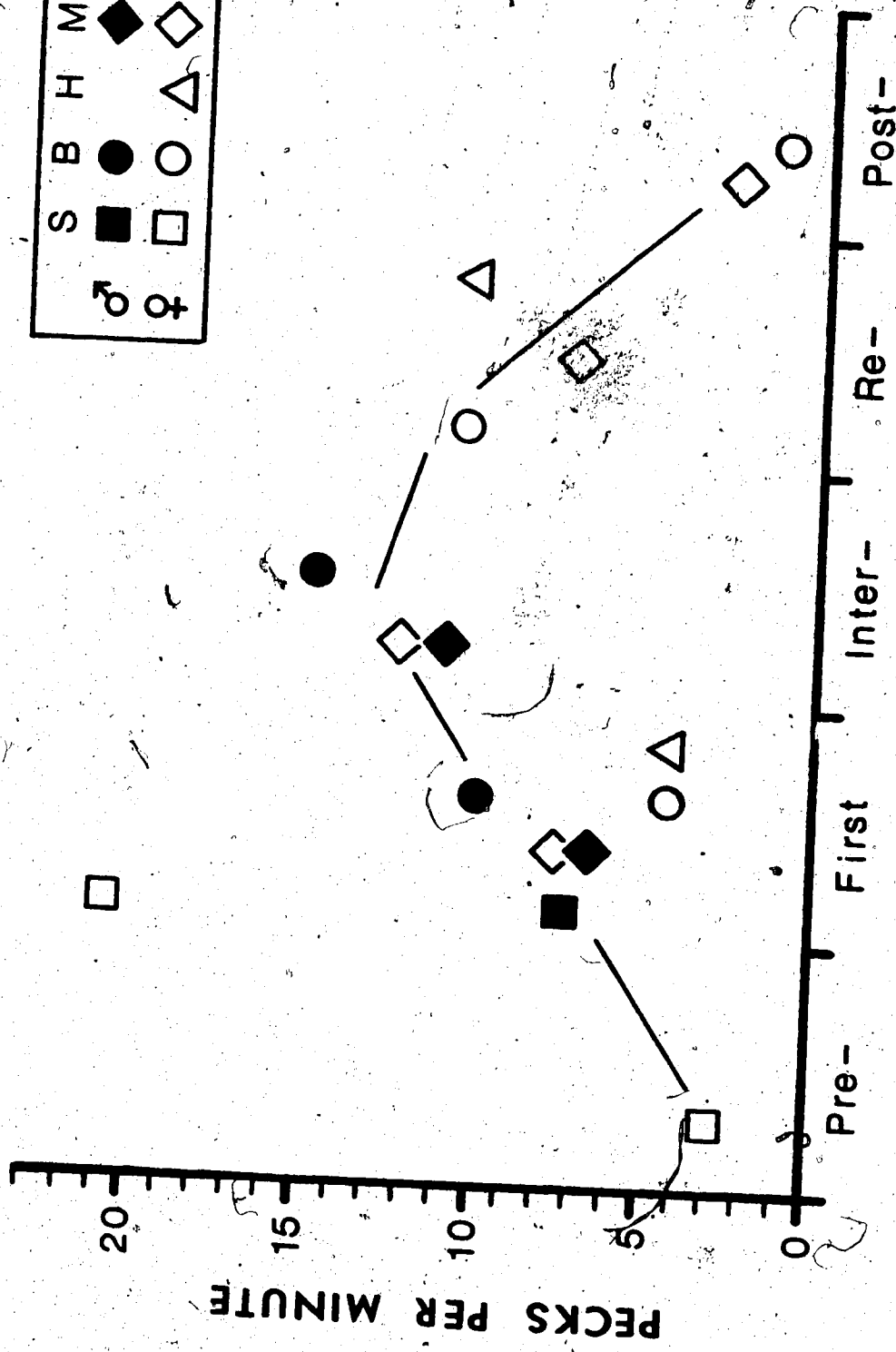
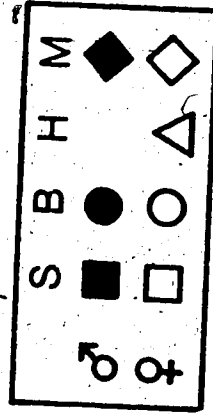
Female long-tailed jaegers spent 38% of their total foraging time in the marshy meadow habitat, most of it being concentrated after 5 July. Time spent foraging in this habitat was significantly greater during the internesting and renesting periods ($p < 0.001$) than earlier or later. In the internesting period, females spent 98% of their foraging time seeking arthropods in the marshy meadows!

I observed male long-tailed jaegers hunting for arthropods during only 8% of their total foraging time (6% using data collected between 1200 and 2400 hours). They foraged in the first and internesting periods, when chironomids were most abundant (discussed below), concentrating their efforts in the marshy meadows.

4. Hunting success. (Based on data collected between 1200 and 2400 hours and shown in Figure 14).

Female long-tailed jaegers, foraging throughout the season when arthropods were scarce as well as abundant, averaged 8 pecks per minute over the season (range 3 to 20

Figure 14. Rate (pecks per minute) at which Male and Female Long-tailed Jaegers Fed on Arthropods in Various Habitats within Their Territories in 1971. Line is drawn by approximation to show general trend. The habitats are: snow melt (S), barrens (B), hummocky tundra (H), and marshy meadows (M).



PHASES OF NESTING CYCLE

pecks per minute). Male jaegers also averaged 8 pecks per minute over the season (range 7 to 15 pecks per minute).

I was unable to determine the percentage of pecks that were successful because the time from prey capture to ingestion was negligible and, in many instances, I was unable to determine whether swallowing occurred because of distance or the angle of view.

a. Success according to nest period.

From the peck rate of 3 per minute in the prenesting period, female jaegers increased their average pecking rates, relatively high average pecking rates being maintained in the inter- (12 per minute) and renesting (7 to 10 per minute) periods, after which average peck rates dropped to less than 3 per minute.

During the different nesting periods throughout the season the jaegers had different success exploiting various habitats as indicated by peck rates.

b. Success according to habitat.

Female long-tailed jaegers averaged their highest peck rate for the season in the snow melt areas (17), their lowest in the barrens (6.2) and very similar medium rates in the hummocky and meadow tundras (8.3 and 8.2 respectively). Males averaged their highest peck rate for the

season in the barrens (14.3) and lower values in the meadow (8.9) and snow melt habitats (7.4).

C. Analysis of pellets, specimens, and droppings.

1. Pellets.

I found the fur and bones of collared lemmings in 1003 of 1005 pellets (99.8%) regurgitated by adult territorial long-tailed jaegers (Table 14), and in 41 of 47 pellets (87%) regurgitated by chicks (Table 15). These percentages are not significantly different. No pellet contained the remains of more than one lemming. The frequency of occurrence of lemming remains in fresh (1971) and old (1970) pellets cast by adult jaegers was the same, 99.7 and 99.9%, respectively. Despite a smaller proportion of the 1971 pellets containing 100% lemming matter (75% versus 83%), over 97% of all adult pellets contained a volume of lemming remains exceeding 95%. Chicks cast fewer pellets which were composed of 100% lemming remains (43%) than the adults and only 61.8% of chick pellets held greater than 95% lemming matter. Results of the pellet analysis suggest that collared lemmings are the major food item of long-tailed jaegers on Bathurst Island.

Remains of invertebrates, the second most common food item in long-tailed jaeger pellets, occurred in 143 pellets

Table 14. Frequency of Occurrence of Food and Non-food Items in 1005 Pellets Cast by Adult Long-tailed Jaegers in 1971 and Earlier on Bathurst Island.

Item	Percent ^a Volume	Number of Pellets Cast in:		Subtotal
		1971	1970 or earlier	
Lemming		335 (99.7) ^b	668 (99.9) ^b	1003
	100	253 (76)	556 (83)	
	95	79 (24)	94 (14)	
	75-94	2 (<1)	12 (2)	
	50-74	1 (<0.5)	4 (<1)	
	25-49	0 (0)	2 (<0.5)	
	tr.-24	0 (0)	0 (0)	
Bird		2 (0.6)	4 (0.6)	6
	100	0 (0)	1 (25)	
	50-99	0 (0)	2 (50)	
	tr.-49	2 (100)	1 (25)	
Arthropods		61 (18.2)	82 (12.3)	143
	75-100	0 (0)	0 (0)	
	50-74	0 (0)	1 (1)	
	25-49	2 (3)	4 (5)	
	tr.-24	59 (97)	77 (94)	
Rock		14 (4.2)	23 (3.4)	37
Vegetation		8 (2.4)	14 (2.1)	22
Total		336 (100)	669 (100)	1005

^aThe percentage volume of each pellet composed of lemming, bird, and arthropod remains estimated on scale given,

^bPercentage of sample in parentheses.

Table 15. Frequency of Occurrence of Food and Non-food Items in 47 Pellets Cast by Long-tailed Jaeger Chicks around Their Nests, in 1970 and 1971, on Bathurst Island.

Item	Percent ^a Volume	Number of Pellets
Lemming		41 (87.2) ^b
	100	20 (49)
	95	9 (22)
	75-94	8 (20)
	50-74	4 (10)
	tr.-49	0 (0)
Bird		7 (14.9)
	100	1 (14)
	75-99	2 (29)
	50-74	2 (29)
	25-49	1 (14)
	5-24	0 (0)
	tr.- 4	1 (14)
Arthropods		21 (44.7)
	75-100	1 (5)
	50-74	0 (0)
	25-49	3 (14)
	5-24	7 (33)
	tr.- 4	10 (48)
Rock		4 (8.5)
Vegetation		9 (19.2)
Total		47 (100)

^a The percentage volume of each pellet composed of lemming, bird, and arthropod remains estimated on scale given,

^b Percentage of sample in parentheses.

(14%) cast by adults and 21 pellets (45%) cast by chicks. Invertebrates were more frequently found in the adult's fresh than old pellets of adults (18% vs. 12%), which may indicate an annual difference in feeding or a more rapid breakdown of pellets containing invertebrates. The volume of invertebrates found in pellets was usually low; only seven pellets (5%) cast by adults and four (19%) by chicks contained more than 25% invertebrates. Young jaegers probably forage for invertebrates on their own to supplement the diet provided by their parents, which would account for the greater numbers of invertebrates found in chick pellets. Diptera are the most common invertebrate found in pellets of adult jaegers and their chicks with lepidopteran larvae and spiders occurring regularly, but much less frequently (Table 16).

By pellet analysis, invertebrates appear to be of less importance in the diet of long-tailed jaegers than the behavioral data would indicate.

I found bird remains, including egg shells, in only six pellets (1%) cast by adult jaegers (no difference between old and fresh pellets) and seven pellets (15%) cast by chicks. That a larger proportion of the chick pellets contained bird material was probably an artifact of the small sample size rather than a real annual difference in feeding or a selection

Table 16. Arthropod Remains Occurring in Fresh Pellets Cast by Adult and Chick Long-tailed Jaegers in 1970 and 1971 on Bathurst Island.

Taxa	Number of Pellets Containing Arthropoda	
	Adult	Chick
ARACHNIDA		
Araneida	4 (3) ^a	5 (24)
INSECTA		
Lepidoptera Geometridae ^b	12 (8)	0
Diptera Chironomidae ^c	112 (78)	12 (57)
Calliphoridae ^d	3 (2)	3 (14)
UNIDENTIFIED	12 (8)	1 (5)
Total Number of Pellets	143 (100)	21 (100)

^a Percentage of total sample in parentheses,

^b Larvae -- probably Psychophora sabini,

^c Probably including some Mycetophilidae, Sciaridae, and Cecidomyidae,

^d Probably including some Muscidae and Piophilidae.

of birds for chicks by adult jaegers. Though birds were not utilized heavily, a variety of species were taken for food (Table 17), including long-tailed jaegers, suggesting that cannibalism took place.

I found small rocks in 37 (4%) and four (9%) pellets cast, respectively, by adult and chick jaegers. Vegetation found in 22 (2%) of adult, and nine (19%) of chick pellets was probably ingested accidentally while swallowing lemming carcasses. However, I believe that one pellet containing several hairy fruit capsules of the arctic poppy (Papaver radicatum) was cast by a marked female long-tailed jaeger which I saw deliberately peck and eat poppy capsules in the same manner jaegers feed on invertebrates. I expect chicks swallow more non-food items than the adults while learning to distinguish edible from non-edible items.

In those pellets cast by adult long-tailed jaegers, containing one or more prey species or items, in addition to lemming remains, arthropods were the most common "second item", with birds being less common than either rocks or vegetation (Table 18).

The prey species, particularly arthropods, recorded in freshly cast pellets of territorial long-tailed jaegers in 1971 changed through the season (Table 19). This seasonal

Table 17. Bird Remains Recorded in Long-tailed Jaeger Pellets.

Contents	Adult: 1970 or Older	Adult: 1971	Chick
Egg Shell:			
King Eider	0	0	1 ^b
Unidentified	1	1	1
Birds			
Black-bellied Plover juvenile	1 (banded)	0	0
Red Knot	0	0	2 ^{a,b}
Sanderling juvenile	0	0	1 ^a
Long-tailed Jaeger juvenile	1 ^b	0	1 ^b
Snow Bunting	1 ^a	0	0
Fringillid sp.	0	0	1
Unidentified	0	1	1 ^b
Total Number of Pellets	4	2	7

^a Comprising 95-100% by volume.

^b Comprising 50-75% by volume.

Table 18. The Occurrence of Other Items in Addition to Lemmings, in Pellets of Long-tailed Jaegers.

Additional Prey Item	Old Pellets	Fresh Pellets
Birds	3 (3) ^a	1 (1) ^a
Arthropods	82 (73)	61 (73)
Rock	23 (21)	14 (17)
Vegetation	14 (13)	8 (10)
Total Number of Pellets	112	82

^a Percentage of total sample in parentheses.

Table 19. Use of Arthropods and Lemmings by Long-tailed Jaegers, as Reflected in Pellet Contents, at Various Times of the 1971 June-August Period.

Pair	Sample Dates	Pellets Containing:		Mean Number of Pellets per Pair per Day
		Arthropods No. (%)	Lemmings No. (%)	
A	13 to 15 June	0 (0)	3 (100)	1.5
	15 June to 26 August	19 (22)	87 (100)	1.2
B	15 June to 15 July	0 (0)	6 (100)	0.2
	15 July to 26 August	6 (25)	23 (100)	0.6
C	21 July to 28 July	0 (0)	9 (100)	1.3
D	13 June to 6 August	8 (11)	75 (100)	1.4
	6 to 26 August	4 (12)	31 (100)	1.6
E	15 July to 25 August	2 (7)	28 (97)	0.7
	25 to 27 August	0 (0)	6 (100)	3.0
F	17 July to 26 August	20 (30)	67 (100)	1.8
Total Pellets			336	1.1 ^a

^a Weighted mean.

change in prey is most evident when the two sampling periods for each of pairs A, B, and E are compared. Pellets gathered from restricted time periods, earliest and latest in the season, did not contain arthropods. These periods correspond to times of least arthropod hunting by adult long-tailed jaegers as determined by the behavioral data (q.v.). Individual pairs of jaegers may utilize arthropods to different extents, for example pair E versus pairs F and B.

The proportion of chick pellets containing arthropods was higher in late July than in early August, always remaining higher than that of adult pellets (Table 20).

In 1971, I collected an average of 0.55 pellets per day per bird (Table 19). Rate of finding pellets varied from 0.1 to 1.5 per day per bird; this variation was not correlated with season. A combination of the screening effect of new vegetation, my collecting technique, and changes in the birds' behavior or food habits were possibly responsible. The rate of pellet production by penned jaeger chicks was higher than that of the adults, averaging 1.7 pellets per day per bird (range 0.5 to 4.0 pellets per day per bird). The chicks' pellet production likely varied with amounts of food given to them by the adults. One chick which survived fourteen days produced an average of one pellet per day during the first three days, 2.7 pellets per day from

Table 20. Use of Arthropods and Lemmings by Long-tailed Jaeger Chicks, as Reflected in Pellet Contents, at Various Times of the 1970 Season (Nests 22 and 23).

Sample Dates	Pellets Containing:		Mean Number of Pellets per Chick Per Day
	Arthropods No. (%)	Lemmings No. (%)	
22 to 29 July	14 (50)	15 (57)	1.8
30 July to 7 August	3 (38)	7 (88)	1.6

the fourth to the eighth day and 1.6 pellets per day until death, suggesting a difference in the rate at which chicks ingested and/or digested food.

I was unable to determine what proportion of the pellets cast by adult jaegers I in fact collected. If adults produced pellets at a similar rate to chicks, I must conclude that I was successful in gathering less than half of the fresh pellets cast by adult long-tailed jaegers.

2. Specimens.

Information on the food habits and condition of nine adult and one chick long-tailed jaeger, collected from Polar Bear Pass, albeit a small sample (Appendix IV), can be compared with the results of the observational data and pellet analyses. Birds collected in June, soon after their arrival, despite having little or nothing in their stomachs, were in excellent condition having large subcutaneous fat deposits. Food found in birds collected in July varied; there were lemmings, birds, and arthropods in most stomachs. Subcutaneous fat deposits on all birds from this period were less than those of June birds. The contents of the stomach of the only juvenile jaeger examined were largely adult chironomids over 5 mm in length. The stomachs of one male and one female non-territorial adult long-tailed

jaegers contained only arthropods. One had approximately 1130 and the other 1380 large chironomids (over 5 mm). Both birds were feeding near tundra ponds in the valley, along with a flock of other long-tailed jaegers, at a time when great numbers of these large chironomids were present.

Long-tailed jaegers appear to select the larger invertebrates when feeding and insects are ingested in large numbers by some birds. In August, lemmings were the most important food item found in jaeger stomachs.

3. Droppings.

Ninety (78%) of 116 droppings collected from long-tailed jaeger territories contained predominantly lemming remains and the other 26 droppings (23%) contained predominantly arthropod remains. I did not collect droppings systematically, therefore, I cannot place much confidence in the quantitative aspects of these data. However, they do indicate that many arthropod exoskeletons pass through the digestive system into the feces, rather than being regurgitated in pellets. Thus without collecting birds, only by examining both the jaeger's pellets and its droppings for arthropod remains, can a true estimate of the jaeger's utilization of arthropods be made.

D. Food used by long-tailed jaegers in 1971.

In estimating the food used by a pair of territorial long-tailed jaegers, I considered only lemmings and arthropods. Vegetation, carrion, birds, and mammals other than lemmings apparently constituted a minor proportion of the jaegers' diet (Tables 14 and 15). Pairs of jaegers were considered to have occupied their territories from 15 June to 15 August, and each territory encompassed approximately 2 km² (0.8 mi²).

I estimated the amount of prey taken daily from daily kill rates and weight of lemmings trapped (Table 21). I calculated the average biomass of prey taken daily by a pair of long-tailed jaegers in 1971 to be 151 to 182 g or 76 to 91 g per bird. This represents 24 to 29% of the pairs' total weight of 618 g, based on four females averaging 325 g and five males averaging 293 g (Appendix IV). Lemmings constituted most of the daily biomass intake, particularly in the pre-, first, and post-nesting periods (Table 14). Changes in the age structure of the lemming population and thus in the average weights of lemmings are taken into account in the adjusted weights of lemmings killed daily. Thus adjusted values are considered more accurate than average weights. Whether the male and female shared each lemming equally is not known. During the inter- and re-nesting

periods, when fewer lemmings were being killed per day by males, it is possible that a smaller proportion was given up to females; especially if the males continued to eat an average of 76 to 91 g of lemmings daily. Thus, alternate food sources, such as arthropods, would be more important to females at these times.

An estimated 260 lemmings were killed by each pair of long-tailed jaegers during the 62-day summer from 15 June to 15 August (which was the length of stay in 1971). The large number of lemmings killed in the post-nesting period is a reflection of the jaegers compensating for the smaller average weight of the lemmings. Using the mean number of lemming kills per day per pair (3.5), to calculate total lemmings killed during the summer, gives a figure of 217 which may be more realistic if more adult lemmings were captured in the post-nesting period than I recorded.

The biomass (estimated) of arthropods ingested daily by the jaegers was smallest early in the summer when the average weight of insects was lowest. Later in the summer, when average insect weights were greater and more insects were present, estimates of biomass ingested reached their greatest levels.

Arthropods were not important in the daily diet of male long-tailed jaegers until the internesting period (Table 22)

Table 21. Estimated Weight and Number of Lemmings Killed per Pair of Long-tailed Jaegers in 1971.

	Nesting Period				
	Pre-	First	Inter-	Re-	Post-Mean
Number of Lemmings Killed/Day	2.9	3.1	2.0	<2.0	7.8 3.5
Weight of Lemmings ^a Killed/Day/Pair (g)	174	186	120	<120	156 ≈ 151
Percent Ingested ^b	99.9	99.9	94.5	90.0	99.5
Number of Lemmings Killed/Period	12	50	18	24	156
Total Lemming Kill					260

^a Values adjusted from the average weight of 50.6 g: using 60 g for all but post-nesting period when a value of 20 g is used (based upon three known kills of 15 g, 15 g, and 30 g).

^b Estimated, using data from Table 15.

Table 22. Estimated Weight in Grams of Arthropods Ingested Daily by Male and Female Long-tailed Jaegers in 1971.

Value	Nest Period				
	Pre-	First	Inter-	Re-	Post-
Minimum^a					
Males	0	0.005	0.21	0	0
Females	0.02	0.05	0.15	6.79	0.40
Maximum^b					
Males	0	0.07	6.57	0	0
Females	0.08	0.60	9.36	18.12	1.73
Probable^c					
Males	0	0.03	3.00	0	0
Females	0.05	0.30	4.00	13.00	1.00
% of total daily biomass	<0.1	<0.1	5.5	10.0	0.5

^a Minimum values were arrived at using the formula: Minutes spent hunting X pecks per minute X 70% success of capture X mean insect weight = value,

^b Maximum values used the formula: Minutes spent hunting X pecks per minute X 100% success of capture X maximum insect weight = value,

^c Probable values assume a 90% success of capture and some selection for larger invertebrate individuals.

and even then they composed probably less than 5% of the biomass ingested daily. For the females, however, arthropods were most important in the inter-, and reneating periods. Arthropods eaten by female jaegers in the reneating period constituted about 10% of the pairs' total daily food biomass, and at least 17.8% of the females' food biomass, perhaps much more if females ate less than half of the lemmings killed, as happened with pomarine jaegers (Andersson 1973).

I defined the limits of arthropod use by long-tailed jaegers in detail for three reasons. First, the behavioral data, pellets, and stomachs from the jaegers did not provide a good idea of the size of prey selected which I needed for very accurate estimates. Secondly, as mentioned before, other workers differ considerably in their opinion of the extent to which long-tailed jaegers depend upon arthropods, usually insects, for food. Thirdly, this is the first estimate of arthropod use by long-tailed jaegers available. The minimum and probable values are based on work by Goss-Custard (1970), the latter "probable values", being the most reasonable for long-tailed jaegers in 1971.

III. Food habits of parasitic and pomarine jaegers and snowy owls.

A. Parasitic jaegers.

I saw parasitic jaegers hunting for or feeding

upon lemmings, birds (eggs of king eider, young of sanders and red phalaropes), arthropods, and carrion. Lemmings were probably the major prey item; nevertheless, parasitic jaegers seemed to hunt for birds more regularly than the other jaegers. Both sexes foraged on foot for arthropods in the marshy meadows in July of 1970 and 1971 but to a lesser extent than the long-tailed jaegers. Parasitic jaegers probably forage over a much wider area than the other jaegers on Bathurst Island, as they nest 3 or more km (1.8 miles) apart.

B. Pomarine jaegers.

The few pomarine jaeger pellets examined contained only lemming remains. They hunted lemmings in similar ways to those of the long-tailed jaeger. I did not observe pomarine jaegers feeding on birds but did occasionally see them unsuccessfully harass gulls in an effort to make them regurgitate. Some fed on carrion. I saw single pomarine jaegers feeding on arthropods only between 4 and 9 July, 1971, near large bodies of water in the valley. Chironomids were abundant there at the time (Table 25).

C. Snowy owls.

I found lemming, arctic hare, short-tailed weasel, snow bunting, and female king eider remains in the pellets

or at the nests of snowy owls on Bathurst Island. I did not examine snowy owl pellets systematically, but of hundreds opened in the field from 1968 to 1971, Dicrostonyx was the commonest prey item, comprising over 90% by volume of most pellets. Single pellets contained the remains of from one to eight (usually two to three) individual lemmings. In June of 1969 and 1971, I saw lemmings which were not immediately eaten, left around the nests and on perches. On 18 and 29 June, 1969, I found nine uneaten lemmings at one nest, and fewer at many others. Snowy owls occasionally hovered while hunting for lemmings, as do rough-legged hawks, but normally they moved from perch to perch throughout their territory. In addition, I saw single snowy owls hunting arctic hares, rock ptarmigan, and red-throated loons.

I watched a flock of ten snowy owls hunting arctic hares on 16 June, 1971. The owls made repeated unsuccessful stoops, one bird after another, at the dodging hares. They stopped hunting and perched near one another periodically, apparently resting before continuing to hunt. All individuals in the flock appeared fairly dark, suggesting that they were non-breeding, sub-adults.

IV. Prey densities.

A. Lemmings.

An average of 0.05 collared lemmings were caught per trap night, using snap traps, in 1970, compared to 0.09 lemmings per trap night in 1971 (Table 23); this suggests that a substantial increase in the lemming population had occurred. These indices of abundance may have underestimated the actual increase in the 1971 lemming population because, in 1971, more traps were set in snow conditions, where trapping success was poorest, than in 1970 (64% versus 50%). I did not trap lemmings in 1968 or 1969, therefore comparable indices of abundance are not available for these summers. However, in 1968, the lemming population was much lower than in the other three years. Indeed, I saw only five lemmings all summer, so that I would estimate that trap success did not exceed 0.01 lemmings per trap night. I would estimate that the 1969 lemming population approximated or slightly exceeded the 1971 level.

Trapping success was poorest before the snow melt began when lemmings were in their winter quarters beneath large snow drifts (Table 23). With the onset of the melt in late June, lemmings moved to summer burrows on more elevated tundra and trap success increased markedly. Fewer lemmings were taken per trap night during July and early August when

Table 23. Results of Trapping for Collared Lemmings in 1970 and 1971 Courtesy of David A. Gill (N.M.N.S.).

Habitat	Date	Trap Nights	Yield	Lemmings/ Trap Night
Snap Trap - 1970				
Snow	3 May - 9 June	582	0	0
Snow	11 - 20 June	158	6	0.04
Snow Melt	21 - 25 June	96	19	0.20
Barrens	26 June - 3 July	204	21	0.10
Lemming mats ^a	24 - 27 July	84	6	0.07
Lemming mats ^a	27 July - 8 August	364	20	0.05
1970: Average number of lemmings/trap night 0.05				
Live Trap - 1970				
Barrens	4 - 10 July	-	9	0.11
Lemming mats	11 - 13 July	41	8	0.20
Snap Trap - 1971				
Snow	20 April - 20 May	372	14	0.04
Snow	27 May - 22 June	312	19	0.06
Barrens	22 June - 1 August	200	33	0.17
Hummocks ^b	8 - 14 August	96	10	0.10
Barrens	15 - 17 August	90	22	0.24
1971: Average number of lemmings/trap night 0.09				

^aOn mounds in marshy meadows,

^bCollected by P. S. Taylor.

summer burrows were occupied. Snap trapping in the barrens was more productive than in other habitats. Lemmings were not found in marshy meadows in the summer. The increase in 1971 trap success after mid-August was attributable to increased captures of young lemmings born in late July.

The average weight of lemmings trapped in 1971 was 50.6 g (D. Gill, pers. comm. 1971).

Results of live trapping in 1970 are not directly comparable to snap trapping data since trapping methods differed considerably for each (D. Gill, pers. comm. 1971). Snap and live trapping results indicate that local areas may have higher densities of lemmings than the barrens.

B. Birds.

Fewer than 35 nests of all species of birds, other than jaegers and owls were found in a 4 km² area around the National Museum's field station each summer, indicating a low density of breeding birds (Table 24) compared to areas to the south (Carbyn 1967).

King eiders were one of the most numerous breeding birds in the study area each summer, and were found nesting in all habitats with sites on the poorly vegetated barrens being favored (Lamothe 1973). Usually, half or more of the nests located each summer were of shorebirds; sanderlings and red

Table 24. Abundance of Potential Avian Prey as Reflected in Nests of Breeding Birds Found Annually from 1968 to 1971 in Four Square Kilometers of Tundra around the N.M.S. Field Station.

Species	Usual Clutch	Number of Nests Located in			
		1968	1969	1970	1971
Red-throated loon	2	2	2	1	1
King eider	4-6	4	5	5	10
Oldsquaw	6	0	0	0	(1) ^a
Black-bellied plover	4	2	1	2	2
Ruddy turnstone	4	(1) ^a	0	0	0
Red knot	4	0	0	0	(1) ^a
Sanderling ^b	4	4	2	3	2
Red phalarope	4	2	4	7	16
Rock ptarmigan	7-10	2-3	1	1	0
Lapland longspur	5-6	0	0	1	1
Snow bunting	5-6	1	0	1	0
Total		18(19)	15	21	32(34)

^aSuspected but not located,

^bTwo clutches per pair (Parmelee 1970).

phalaropes were the most common. The former nested on the barrens and the latter in marshy meadows, often in loose colonies. Rock ptarmigan, most common in 1968, when jaegers and owls were least common, were rather local in distribution. Few nests of passerines were found in the 4 km² area, but sheltered valleys with rocky scree slopes north of the field station held better populations of snow buntings, with pairs spaced every 300 to 400 m.

Probably no more than 10 to 15 birds' nests (excluding jaegers and owls) are initiated per km² of tundra on the study area, assuming we find about half the nests ourselves (Parmelee 1970). Arctic fox predation likely accounts for most nest losses. The very low occurrence of bird remains in long-tailed jaeger pellets (<1%) suggests that long-tailed jaegers may not have destroyed many birds' nests; however, if egg shells were not eaten, the egg contents from destroyed nests would not be detected, and therefore, destruction would be underestimated.

C. Arthropods.

The numbers and biomass of arthropods in the study area varied seasonally. However, peak numbers did not coincide with the greatest biomass (Tables 25 and 26). In June, sweep netting yielded only a few small arthropods, mainly

Table 25. Numbers and Biomass of Arthropods Sampled in 200 Sweeps with an Insect Net at Three Sites in Each of Two Habitats, Meadow and Barrens, during the Summer of 1971.

	15 June	26 June	1 July	10 July	22 July	29 July	8 August	26 August
Mean Number	? ^a	9 ^b	395 ^c	890.3	162.7	46.3	0.3	1.3
Mean Weight (mg) per individual	?	<0.05	0.08	0.12	1.69	2.61	1.7	0.04
Estimated Total Biomass (mg) in 200 Sweeps	?	<0.5	31.68	110.13	275.17	120.8	1.7	0.05
	M E A D O W							
Mean Number	14 ^b	1 ^c	204.5	11.5	44.5	10.5	0	0.5
Mean Weight (mg) per individual	<0.4	0.04	0.05	1.01	3.36	3.17	0	0.04
Estimated Total Biomass (mg) in 200 Sweeps	<3	0.04	5.2	11.64	149.66	33.28	0	0.04
	B A R R E N S							

^aAll sites snow-covered: none sampled,

^bTwo sites snow-covered: one sampled,

^cOne site snow-covered: two sampled,

^dBased on data from James K. Ryan, University of Alberta.

Table 26. Numbers and Biomass of Arthropods Sampled at Other Sites during July of 1970 and 1971.

	Snow Melt		Barrens		Marsh-Meadow				
	1	23	16	23	8	10	16		
	July 1971	July 1971	July 1970	July 1971 ^c	July 1970	July 1971	July 1970		
	24	6	260	52	480	1254	880		
Number	0	24	6	260	52	480	1254	880	57
Mean Weight (mg) of Individual	0	3.76	5	0.23	2.39	0.21	0.09	0.10	1.1
Biomass (mg) in 200 Sweeps	0	90.24	30	60.8	124	98.4	116.36	85.6	63.24

^aRidge top,

^bLow ridge,

^cDryas barrens,

^dBased on data from James K. Ryan, University of Alberta.

chironomids, in both the barrens and meadow habitats. Many spiders were seen, particularly in areas recently exposed by melting snow, but they were not picked up consistently by the sweep nets. Arthropod numbers reached their peak in early July when large numbers of chironomids began hatching in the marshy meadows. Hatches of a small species of chironomid (less than 3 mm in length and weighing approximately 0.04 mg) were first encountered in late June and continued into August. A major hatch of a large species of chironomid (6-10 mm in length and weighing 0.4 mg) occurred annually during the second week of July. Chironomid numbers diminished by late July but the many individuals of muscid flies present (each approximately 5 mg in weight) resulted in a large arthropod biomass. These flies were most common in the flowers of late-blooming plants such as Dryas integrifolia. In August, the numbers and biomass declined to low levels. Chironomids were apparently only locally abundant in late July and August.

Marshy meadows held greater numbers and total biomass of arthropods than the barrens throughout the summer. This was probably because larval forms were present in the marsh and adults, on emergence, were dispersed from this center of abundance into other habitats by the wind.

V. Biomass of aviar predators and prey.

Breeding long-tailed jaegers were responsible for the highest proportion of lemming predation in years of low and moderate lemming densities when pomarine jaegers and snowy owls were less abundant (Figure 15). However, the greater daily food requirements of individual pomarine jaegers and snowy owls makes them important, even if present in fairly low densities (Table 27). Breeding parasitic jaegers maintained the same predatory pressure from year to year.

The loss of pomarine jaegers from the study area and the resultant lowering of prey biomass removed daily in late July would have been more than compensated for in 1969 and 1971 by the energy requirements of the newly-hatched jaegers and owls and the increased number of non-territorial owls. For example, an influx of four adult snowy owls into the 10 km² area (data from last week in July, 1971), would result in an additional 1000 g of food being removed from the area daily, assuming a daily requirement of 250 g of food per owl (Gessaman 1968).

The impact upon prey species, primarily lemmings, would have been greatest and most prolonged in 1969 when chick survival was best for jaegers and owls, partly because of lower fox predation compared with 1971.

Figure 15. Biomass Values of Territorial Jaegers and Owls for Early July on a 10 km² Area and the Estimated Daily Biomass of Food Required by Those Birds. A scale of lemming numbers is given for conversion of prey biomass. Biomass values for each species are presented cumulatively in each column. The four species represented are: long-tailed jaeger (white), parasitic jaeger (black), pomarine jaeger (diagonal), and snowy owl (vertical lines).

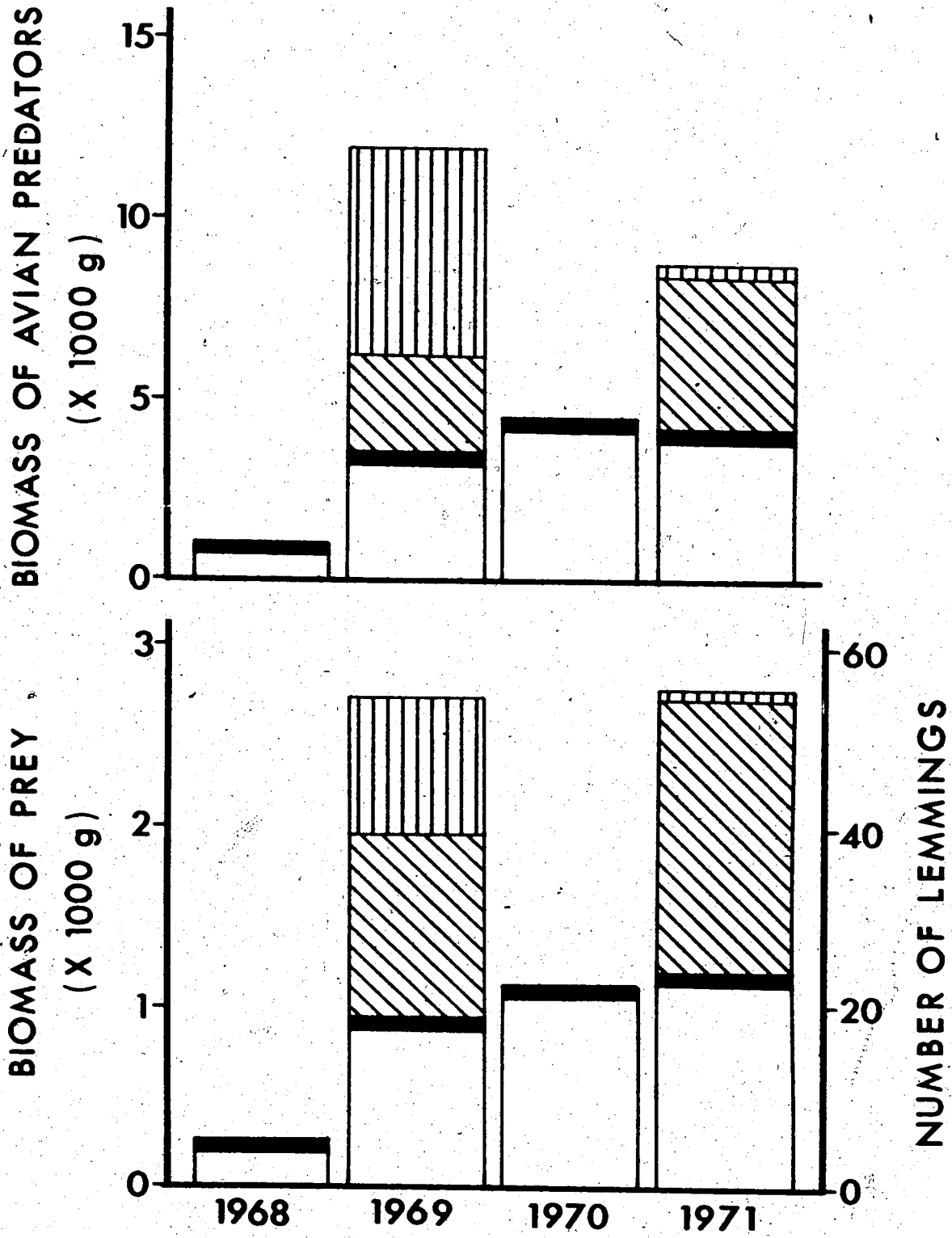


Table 27. Body Weights and Daily Food Requirements (in g) of Long-tailed Jaegers, Parasitic Jaegers, Pomarine Jaegers, and Snowy Owls, Used in Estimating Biomass Values (Figure 15).

	Long-tailed Jaeger	Parasitic Jaeger	Pomarine Jaeger	Snowy Owl
Weight				
Male	293	425	650	1800
Female	325	475	750	2000
Pair	618	900	1400	3800
Daily Food Ingested per Pair (excluding any young)	175	250	500	500
Sources	this study	estimated on basis of weight	Maher (1970)	Watson (1957) Gessaman (1968) Godfrey (pers. comm.)

The daily removal of 2720 g of food per 10 km² by all four species of predatory birds in 1969 and 1971 was the equivalent of 54 lemmings (assuming a mean weight of 50 g per lemming). This is 2.5, and nearly 11 times the respective predation pressure in 1970 and 1968. This predation pressure in 1969 and 1971, if maintained from late June to late August (approximately 60 days), would result in 163,200 g of food being removed per 10 km². This is the equivalent of 3,240 lemmings. Unfortunately, I cannot compare these figures with the indices of lemming abundance, since true lemming densities could not be calculated from those data.

DISCUSSION

I. Relationship of long-tailed jaegers to their prey.

In 1971, the earliness of the season and fairly high lemming population provided excellent breeding conditions for long-tailed jaegers and the data on the jaegers' food habits are, therefore, considered representative of a "good lemming year." Long-tailed jaegers arrive on the breeding grounds before mid-June, thus early food finding must be difficult, particularly if a late blizzard delays the spring melt. At this time, their own fat reserves, and the occasional food item such as hibernating arthropods found beneath stones (Danks 1971), a lemming, or a bit of carrion sustain most birds until the melt. In summers of very low lemming numbers or inclement weather, many long-tailed jaegers do not breed (Løppenthin 1943, Jones 1968, Maher 1970b) and most presumably leave. In such years, some birds may starve (Drury 1960). Long-tailed jaegers utilize a wide variety of foods -- vegetation, berries, arthropods (arachnids, insects, crustaceans, etc.), fish, birds and their eggs, lemmings, carrion and garbage, some of which is most heavily used only in "poor lemming years" (Bent 1921, Løppenthin 1943, Gabrielson and Lincoln 1959). For example, I saw long-tailed jaegers feed regularly on carrion and garbage in 1970, when lemmings were

less numerous, but not in 1971. Though I saw one pair of jaegers hunting young snow buntings in 1971, birds were a less important food than in other areas (Clarke 1940, Maher 1970b).

While euryphagous, long-tailed jaegers are opportunists and when taking advantage of one food source, may specialize in killing it for quite some time, a common characteristic of many predators (Errington 1967, Roseneau 1972). In 1971, territorial long-tailed jaegers changed the amount of time spent foraging, the habitat hunted, and their method of hunting, as changes in the number, location, and vulnerability of their prey (lemmings and arthropods) occurred, apparently to maximize hunting success.

In preying on lemmings, those that are killed are shared between the territorial male and female which, according to Andersson (1971), allows a more efficient use of prey than if the birds ate alone.

In June, in snow melt areas, lemmings were very active and snap trapping success was high. At this time jaegers killed lemmings easily and spent little time foraging. As lemmings became established in summer dens in the barrens, hummocky tundra and grassy mats, the jaegers' hunting success diminished despite great increases in time spent foraging. Snap trapping success also declined. Foraging was

concentrated in the barrens and, to a lesser extent, the hummocky tundra. In late July, hunting success increased as the jaegers changed their hunting method from hovering and perching on observation mounds to waiting at burrows for the young lemmings, which were then emerging. Snap trapping success increased at the same time.

In preying on arthropods, those killed were not shared. During the melt, birds foraging near receding snowbanks had the greatest pecking rate observed during the season. Spiders were particularly active and common at this time (J. Ryan, pers. comm. 1970) and probably were the major arthropod eaten. As chironomids hatched in the marshy meadows, the jaegers began to concentrate their arthropod hunting there, apparently in response to the numbers. While insect numbers increased over 25 fold, as indicated by sweep net samples, peck rates were never higher than 10 times the minimum-season's peck rate. As numbers of insects diminished in the marshy meadows, jaegers hunted more in the hummocky tundra and barrens. Here, large diptera sitting in the blossoms of flowers, particularly Dryas integrifolia, were captured and, though peck rates were low, the average insect size was greater than at any other time of the season.

Compared with long-tailed jaeger pellets collected on Ellesmere Island in 1966 by Maher (1970b), pellets from the

jaegers on Bathurst Island contained fewer arthropods of different families (fresh adults' pellets particularly), fewer bird remains (all pellets), and slightly more lemming material (all pellets) (Table 28). The chicks from the two areas apparently ate arthropods in similar quantities since arthropods appeared in a similar proportion of their pellets. It is conceivable that the lemming population on Ellesmere Island was lower than that of Bathurst Island and, being opportunists, the Ellesmere Island jaegers fed more extensively on birds and different species of arthropods. This apparently happened to an even greater extent in 1955 on Ellesmere Island (Parmelee and MacDonald 1960), in 1930 in East Greenland (Løppenthin 1943), and in 1952 on Banks Island (Manning et al. 1956). The large flocks of non-territorial long-tailed jaegers which move through Polar Bear Pass each summer arrive when the largest species of chironomids are hatching in the marshy meadows. These birds apparently feed almost exclusively on these insects for a number of days at least and, thus, are less dependent upon lemmings than territorial long-tailed jaegers. For what length of time a long-tailed jaeger could exist by feeding on arthropods on Bathurst Island alone, I do not know. The relatively poor arthropod fauna of Bathurst Island suggests that it may be more difficult for jaegers to exist on arthropods here than

Table 28. Frequency of Prey Occurring in 1003 Pellets Collected from Lake Hazen, Ellesmere, Island (E.I.) in 1966 (from Maher 1970b), and 1052 Pellets from Polar Bear Pass, Bathurst Island (B.I.) in 1971.

Prey	Old Pellets: Adult		Fresh Pellets: Adult		Fresh Pellets: Chick	
	-----		-----		-----	
	E.I.	B.I.	E.I.	B.I.	E.I.	B.I.
Lemming	668	668	218	335	39	41
Other Mammals	6	0	1	0	0	0
Birds	51	4	44	2	19	7
Arthropods	?	82	72	61	21	21
Total	710	669	242	336	51	47

elsewhere. My estimates of the jaegers' utilization of arthropods must therefore be considered low and birds in other parts of the arctic probably rely on arthropods to a greater extent.

Estimates of an animals' daily food intake from field observations are difficult to obtain and rather crude at best. Wiens (1969, p. 66) found that continuous activity observations, as opposed to spot observations, gave best estimates of total activity patterns in grassland birds, therefore, my continuous field observations of long-tailed jaeger activity should give the best estimates of food intake possible. Assuming male and female long-tailed jaegers weigh an average of 300 and 325 g, respectively, and each eats approximately 85 g of food daily, they would consume 29 and 26 percent, respectively, of their own body weight in food daily. This compares with estimates of daily food intake for pomarine jaegers, 35.7% (Maher 1970a); snowy owls, 12% (Watson 1957, Gessaman 1968); and chicks of kittiwakes (Rissa tri-dactyla), herring gulls (Larus argentatus), and guillemots (Uria aalge), all requiring 29% (Pearson 1964, cited in Langham 1972). Passerine birds seem to have greater food requirements (Odum 1971). Cade (1967) believed that northern shrikes (Lanius excubitor) required 43% of their total weight in food each day.

I feel that the use of observations from 1200 to 2400 hours is justifiable and fairly represents the jaegers' daily activity because arctic birds, including owls and jaegers, maintain a bimodal circadian rhythm despite the 24 hour light (Armstrong 1954, Shields 1969, Carbyn 1967, Andersson 1971).

Territorial long-tailed jaegers seem to have maximized their efficiency in utilizing the major prey species by having sex specific foraging habits: male jaegers specialized in hunting lemmings, females specialized in hunting arthropods. Separation of foraging and food habits between species (Lack 1947, Selander 1966, Storer 1966, Baldwin 1971, MacArthur 1972) and even between different sexes or ages of the same species (Selander 1966, Storer 1966, Earhart and Johnson 1970, White and Cade 1971, Williamson 1971) is well described for birds and is apparently associated with behavioral and morphological differences (often bill sizes). Behavioral differences, alone causing dichotomy are poorly known but may occur in the mountain bluebird (H. Power pers. comm. 1972), some species of warblers (MacArthur 1958) and probably other species. The bills of male and female long-tailed jaegers are not noticeably different; if anything, the female's bill is a bit larger (Manniche 1910, Manning 1964). An answer as to why the females forage for arthropods

can be given by applying the logic of "economics of consumer choice" (MacArthur 1972, p. 59). This states that with a knowledge of the "structure of the environment, functional morphology of the foraging species, and knowledge of its economic goals, we can draw conclusions" about where an animal should feed to get the most food and what items of food it should pursue. Female long-tailed jaegers spend a considerable amount of their time each summer incubating and were (in 1971) relieved by the males for an average of only 60 minutes at a time. Males spent an average of over 100 minutes foraging for each lemming killed and, therefore, the females would, if they hunted lemmings, conceivably expend considerable amounts of energy without realizing a kill during many periods off of the nest. Arthropods probably provide a more readily available and reliable food source for the females, and it probably requires less energy to forage for them than for lemmings.

The female's weight being greater than the male's is seemingly contradictory to an arthropod foraging habit (see White and Cade 1971 for a discussion), yet the extra weight may allow incubating females to lose more g of body weight than the smaller males (but the same proportion of the total body weight) without ill effects, should lemmings or other food resources become difficult to kill. The ability to

withstand fasting is advantageous to arctic birds (Irving 1960, p. 327; Ryder 1967) and is well known among predatory species (Errington 1967). Resorption of the female's reproductive tract may give her extra nutrients in times of limited food, as happens in arctic geese (Barry 1962). The odd lemming caught in times of limited food is perhaps eaten only by the male (as some 1971 observations indicated) which would maintain his strength and enable him to continue foraging for the pair. Since only males hunted lemmings within the territories, the lemmings may have been disturbed less frequently by hunting birds than if both sexes foraged regularly for lemmings. Provided lemmings are more easily surprised and killed if left undisturbed for longer periods of time (i.e. more vulnerable: Craighead and Craighead 1956, Chapter 7), it is to the pairs' advantage to have only the male foraging for lemmings. Generally, females tend to partake in more low energy expending activities (either resting, and perching, or incubating) than the males and, thus, are apparently adapted to energy conservation, rather than energy expenditure, as are the males.

The efficient use of food resources within the territory by adjusting time and place (habitat) of hunting according to sex, must reduce intraspecific competition. This would seem to be essential in an environment such as the arctic,

where food resources are so variable from season to season.

This strategy of resource utilization is efficient enough that by foraging almost totally within their territories, long-tailed jaegers are able to maintain themselves and breed in years of fairly high lemming numbers (1969, 1971) as well as years of lowered lemming numbers (1970). Efficient use of food resources also enables these jaegers to remain on territory from approximately mid-June to mid-August or later, regardless of nest loss. Some pairs were able to reneest after their first clutches were destroyed by arctic foxes. Relatively small body size and short nesting cycle (Maher 1970b, this study), variable clutch size and differential survival of chicks further facilitate the jaegers breeding at lowered lemming densities. In years of low lemming numbers, such as 1968, only a few pairs bred which seems to be a regular phenomenon in many areas (Løppenthin 1943, Maher 1964 and 1970b). Whether the other pairs were resident on territories for part or all of the season, or departed without breeding as appears to have happened in other areas, I do not know.

Banding indicated that individual long-tailed jaegers were highly faithful to their territories from season to season, which supports Maher's findings (1964 and 1970b). Indeed, the territorial long-tailed jaeger population was

essentially static for at least three years while the lemming population decreased and increased. However, during the same period, territorial pomarine jaegers and snowy owl populations fluctuated greatly. It would appear that long-tailed jaegers are much more tolerant of lower lemming numbers than Maher (1970b) suggests. Long-tailed jaegers can maintain saturated breeding densities when lemming densities are too low to support saturated breeding densities of pomarine jaegers and snowy owls. Thus, long-tailed jaegers are probably adapted to exploit medium rather than high densities of lemmings and to capitalize on all densities greater than this threshold.

Long-tailed jaegers had low breeding success in all years on Bathurst Island, despite differential chick mortality which would apparently lessen food requirements for the pair and their chick. Food was probably less readily available to long-tailed jaegers on Bathurst Island than on Southampton Island (Sutton 1932) and Victoria Island (Parmelee et al. 1967), where two chicks of a number of pairs were raised successfully. What breeding success the Bathurst Island long-tailed jaeger would have had if arctic fox predation had not been so high is not known.

Members of the Family Stercorariidae have a long life expectancy, one male parasitic jaeger was recorded attempting to breed for over 30 summers (Venables and Venables 1955).

Similar to other seabirds having a long life span (Lack 1967), Antarctic skuas (Catharacta maccormicki) do not breed until five or six years of age (Spellerberg 1971), and parasitic jaegers delay breeding for three or more years (Williamson 1959). It is probably safe to assume that long-tailed jaegers have a fairly long life expectancy also. If a pair of long-tailed jaegers attempted to breed for eight or ten seasons before dying, they would need only to successfully raise one chick every four or five years in order to balance their mortality and maintain a stable jaeger population.

The nature of the habitat frequented by long-tailed jaegers in the low and high arctic, having even sparser vegetation and fewer lemmings than the richer, low arctic tundra (Løppenthin 1943, Kessel and Cade 1958, Dunbar 1968, Salomonsen 1972) probably necessitates having these adaptations.

II. Relationship of parasitic and pomarine jaegers and snowy owls to their prey.

Parasitic jaegers differ from long-tailed jaegers in being much less common as territory holders and transients and more inclined to prey upon birds probably because they nest in lower, wetter areas, such as the marshy meadows where many shorebirds nest and forage. The habit of feeding upon birds seems to be consistent throughout most of its range.

(Pleske 1928, Sutton 1932, Clarke 1940, Venables and Venables 1955, Parmelee et al. 1967, Hussell, unpubl. MS) while further south in the low arctic they are more common than long-tailed jaegers (Sutton 1932, Clarke 1940). Parasitic jaegers are similar to long-tailed jaegers in that they regularly forage for arthropods, are faithful to their territory from mid-June to mid-August (this study, T. Barry and M. Martin, pers. comm. 1973) or later, and are faithful to their territory from year to year. Some birds have returned to territories for 31 seasons in Foula, Scotland (Venables and Venables 1955, p. 331). The low breeding density and fairly small body size of the parasitic jaeger may allow it to breed in the low lemming years on Bathurst Island, such as 1968, and elsewhere (Hussell, unpubl. MS). The minimum threshold-density of lemmings required by parasitic jaegers to breed is as low or perhaps lower than that required by long-tailed jaegers on Bathurst Island.

Pomarine jaegers have a much lower tolerance to lowered lemming densities than either long-tailed or parasitic jaegers on Bathurst Island. Pomarine jaegers failed to breed in the low lemming year of 1968, and in 1970, when lemmings were moderately common, good numbers of pomarine jaegers arrived in the spring but failed to breed again. Pitelka et al. (1955a) and Maher (1970a) had similar finding around Point

Barrow, Alaska, where maximum densities of territorial pairs were approximately 20 times those of the 1969 and 1971 Polar Bear Pass populations. As Maher (1970a) states, pomarine jaegers do seem to adjust the fraction of the population which breeds in accordance with lemming numbers. In contrast to the two smaller species of jaegers, pomarines left their territories and the study area soon after their nests were destroyed and, further, showed no fidelity to territory from season to season. Larger size and greater dependence upon lemmings may make it difficult for pomarine jaegers to remain on a territory after a nesting attempt, or to return to that territory in a subsequent season, particularly in the high arctic.

Snowy owls are the largest avian predators found in the study area, yet they have a number of adaptations enabling them to exploit lemmings, their major prey, efficiently. They do however, as Pleske (1928) cautions, feed on a wide variety of other prey: sometimes extensively so. Snowy owls are known to be present longer, and begin nesting earlier than any other predatory bird on the study area. A thick insulating layer of feathers and an ability to conserve energy by lowering their body temperature up to 8.4°C and maintain these depressions for up to 188 minutes at a time (Gessaman 1968) must facilitate such a routine. Snowy owl

clutches found on Bathurst Island were significantly smaller than those found farther south in the Canadian arctic and in the Eurasian tundra, but not those found in Iceland (Table 29). Smaller clutches might be an adjustment to a lower lemming population on Bathurst Island. I have suggested a possible mechanism by which snowy owls can determine whether there are sufficient numbers of lemmings for breeding before the snow melts, and this mechanism might be sensitive enough to trigger clutch size (Taylor 1973). Male snowy owls court with a lemming in their bill and the number of lemmings caught and used in courtship displays may be indicative of the amount of food available in the area. Nevertheless, all evidence to date for individual female snowy owls varying their clutch size, in years of high and low lemming numbers (Irving 1960, p. 318), is indirect so there remains the possibility that different birds are laying clutches of different sizes.

Differential mortality of the young occurs, as it does in long-tailed and parasitic jaegers (this study), Antarctic skuas (Young 1963, Spellerberg 1971), arctic terns (Langham 1972), and other owls and hawks (Craighead and Craighead 1956, p. 240) as a means of minimizing food wastage.

Snowy owls on the study area were apparently as sensitive to low lemming numbers as pomarine jaegers,

Table 29. Number of Snowy Owl Nests and Clutch Size Gathered from Selected References and Representing the Holarctic. See Watson (1957) for another review, where he refers to clutches of from 12 to 15 eggs from Alaska and Lapland.

Reference and Geographic Area	Clutch Size										Total Clutches
	2	3	4	5	6	7	8	9	10	11	
Pleske 1928 Eurasia	0	0	0	0	0	1	9	0	14	0	24
Sutton 1932 Southampton Island	0	0	1?	1?	2	1	1	1	0	0	7
Watson 1957 Baffin Island	0	0	0	0	0	2	2	2	0	0	6
Gudmundsson <u>in</u> Watson 1957 Iceland	0	1	0	2	0	0	0	0	0	0	3
Parmelee <u>et al.</u> 1967 Victoria Island	0	0	0	1	0	0	1	2	5	2	11
This study											
1969	0	2	2	3	4	2	1	1	0	0	15
1971	0	0	0	0	1	0	0	0	0	0	1

since the breeding populations of both species fluctuated similarly in 1968, 1969, and 1970. But, in 1971, when all the jaegers were at as high a level as 1969, snowy owls bred only in very small numbers, though lemming numbers were high. If most snowy owls migrate northward in the early spring, stopping in the first favorable area to breed, the few breeding pairs of owls on Bathurst Island in 1971 might be understood. There might be certain birds which return to a summer nesting territory from season to season, since some banded birds have returned to the same wintering territory in Alberta on more than one winter (A. Oeming, pers. comm. 1970). That such large numbers of non-territorial owls (mostly males) were present on the study area in July and August of 1970 and 1971, when owls did not breed in great numbers, seems contradictory. However, spring lemming densities may have been below the threshold required by snowy owls for successful courtship and breeding (Taylor 1973). This is most likely to have happened in 1970. The build-up of non-territorial owls, seen also on Victoria Island in 1971 (E. Jones, pers. comm. 1972) and in northern Alaska in 1958 (Childs 1969), may be associated with the increased lemming populations (resulting from summer litters of lemmings) at a time when lemming populations can best withstand predation (Maher 1970a). Though snowy owls leave

their territory if their nests are destroyed, as do pomarine jaegers, this would not likely account for the preponderance of males seen in the study area, unless male owls moved north or females south after attempting to breed.

III. Role of avian predators on Bathurst Island.

Jaegers and snowy owls are secondary or tertiary consumers. Lemmings appear to be the major prey utilized by all four species on Bathurst Island.

Long-tailed and parasitic jaegers are able to breed during lower lemming densities than pomarine jaegers or snowy owls. The smaller body size and smaller amount of food required for maintenance by the first two species probably facilitates their being more tolerant of lowered lemming numbers. They also show less dependence upon lemmings as their only food source, feeding extensively on arthropods and birds. Pomarine jaegers and snowy owls are most important as predators in years of highest lemming abundance.

All four species do, however, take full advantage of lemming highs on Bathurst Island. The number of breeding pairs increases, clutch sizes increase in some, and productivity increases, which suggests that they function in a similar way to pomarine jaegers in Alaska (Maher 1970a).

Maher (1970a, p. 155) states that avian predators are

able to "truncate peak (lemming) populations, but they are unable to reduce the lemming population to the low point of the cycle", and suggests "that mammalian predators, especially Mustela rixosa, are responsible for reducing the population completely and delaying recovery of the lemming population until they themselves, decline in numbers," and is supported by Pearson (1966). This is contrary to other workers, who feel cycles are controlled intrinsically (Christian 1950, Chitty 1952), or by food supply (Pitelka 1957). The long-tailed jaegers' ability to maintain saturated breeding densities in seasons of lower lemming numbers may allow them to function much as weasels do in Alaska -- as an important predator during lowered lemming numbers.

IV. Interspecific competition.

The food eaten by all four species was similar enough that the existing differences in prey utilization, for example, long-tailed jaegers fed on arthropods and snowy owls killed female eiders, probably did little to reduce competition.

Salomonsen (1972) states that species of arctic predatory birds have maintained high rates of interspecific aggression while breeding, whereas many other arctic birds have relaxed this, apparently because of the super-abundance of food in

the higher latitudes. Territorial pairs of long-tailed, parasitic, and pomarine jaegers on Bathurst Island showed high interspecific aggression toward other jaegers, snowy owls, ravens, rough-legged hawks, falcons, and gulls. All jaeger territories were more or less mutually exclusive of one another. Snowy owls, however, showed little overt inter-, or intraspecific aggression, contrary to the findings of Keith (1964). In 1969 and 1971, established snowy owls had jaegers arriving and nesting within their territorial limits. The owls were kept out of a sizeable area (0.5 km²) around each jaeger nest by the aggressive jaegers. One such pomarine jaeger nest was destroyed by foxes, whereupon the jaegers left and the male owl once again began hunting in the area. Any advantage the snowy owls have by arriving and establishing a territory early does not seem apparent. The owls' large territory size and low density possibly allowing some compression of territory size, would be advantageous under these circumstances when jaegers establish territories within snowy owl hunting areas.

Jaegers did show habitat preferences for nesting: long-tailed jaegers preferred drier sites, usually in the barrens, and parasitic and pomarine jaegers preferred wetter sites, usually in the marshy meadows. Snowy owls tended to nest in the barren areas, usually on low rolling hills. Some spatial

separation resulted since barrens areas tended to be higher in elevation than marshy meadow areas. However, it may not be as important on Bathurst Island as in the low arctic (Kessell and Cade 1958).

Faithfulness to a territory throughout the season, and from year to year, by long-tailed and parasitic jaegers might facilitate more efficient hunting in the area, thus giving them an advantage over pomarine jaegers on Bathurst Island. Snowy owls and pomarine jaegers, which lose their nests, leave their territories and, in the case of pomarine jaegers, the study area, for the ocean (Frame 1973), further reducing predation pressure.

Temporal differences in the breeding schedules of jaegers and snowy owls may reduce competition slightly. Snowy owls do arrive on the breeding grounds earlier than jaegers, and many owl eggs hatch sooner than jaeger eggs.

Inter- and, indeed, intraspecific competition may be reduced indirectly by having smaller clutch sizes and differential chick mortality followed by cannibalism, as mechanisms of adjustment to changing prey levels.

The actual fluctuation in numbers of breeding predatory birds can be considered as a mechanism which reduces inter- and intraspecific competition.

Where food resources exceed the needs both spatially and

temporally of the breeding predatory birds "resident" in an area, non-territorial individuals are able to move into the area for a brief period of time as the long-tailed jaegers or for a longer time as the snowy owls do in the Polar Bear Pass area of Bathurst Island. The relatively mobile subunits of non-territorial birds are thus able to shift according to food availability and avoid areas with territorial birds dependent upon low prey levels, while also lessening both inter- and intraspecific competition.

The similarity of foods eaten by all four species has probably necessitated the evolution of more or less mutually exclusive territories between pairs of different, as well as the same, species. The net result is populations of different species, functioning as one super species in the arctic ecosystem. Different thresholds of tolerance to varying densities of lemmings allows each species to fluctuate independently of one another over a number of years.

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APPENDIX I. A list of birds and mammals recorded on Bathurst Island from 1968 to 1972 by personnel at the N.M.N.S. Research Station. Breeding (B) and Migrant (M) refer to species of regular occurrence and are separable from Irregular (I) species seen only once or twice. Hypothetical records (H) of two species of birds are included.

<u>Birds</u>		<u>Status</u>
Arctic loon	<i>Gavia arctica</i>	B
Red-throated loon	<i>G. stellata</i>	B
Whistling swan	<i>Olor columbianus</i>	I
Canada goose	<i>Branta canadensis</i>	I
Brant (pale form)	<i>B. bernicla</i>	B,M
Snow goose (white and blue forms)	<i>Chen caerulescens</i>	B
Oldsquaw	<i>Clangula hyemalis</i>	B
Common eider ^a	<i>Somateria mollissima</i>	I,M
King eider	<i>S. spectabilis</i>	B
Rough-legged hawk	<i>Buteo lagopus</i>	B
Peregrine	<i>Falco peregrinus</i>	I
Gyr Falcon	<i>F. rusticolus</i>	I,M
Rock ptarmigan	<i>Lagopus mutus</i>	B
Semipalmated plover	<i>Charadrius semipalmatus</i>	H
Golden plover	<i>Pluvialis dominica</i>	I,M
Black-bellied plover	<i>P. squatarola</i>	B
Ruddy turnstone	<i>Arenaria interpres</i>	B
Red knot	<i>Calidris canutus</i>	B
Purple sandpiper	<i>C. maritima</i>	M (B?)
Pectoral sandpiper	<i>C. melanotos</i>	I
White-rumped sandpiper	<i>C. fuscicollis</i>	(B?)
Baird's sandpiper	<i>C. bairdii</i>	B

<u>Birds</u>		<u>Status</u>
Semipalmated sandpiper	<i>C. pusilla</i>	H
Buff-breasted sandpiper	<i>Tryngites subruficollis</i>	I
Sanderling	<i>Calidris alba</i>	B
Red phalarope	<i>Phalaropus fulicarius</i>	B
Northern phalarope	<i>Lobipes lobatus</i>	I
Pomarine jaeger	<i>Stercorarius pomarinus</i>	B
Parasitic jaeger	<i>S. parasiticus</i>	B
○ Long-tailed jaeger	<i>S. longicaudus</i>	B
Glaucous gull	<i>Larus hyperboreus</i>	B
Thayer's gull	<i>L. thayeri</i>	B
Ivory gull	<i>Pagophila eburnea</i>	I
Sabine's gull	<i>Xema sabini</i>	B
Arctic tern	<i>Sterna paradisaea</i>	B
Snowy owl	<i>Nyctea scandiaca</i>	B
Horned lark	<i>Eremophila alpestris</i>	M
Common raven	<i>Corvus corax</i>	M (B?)
Wheatear	<i>Oenanthe oenanthe</i>	I
Water pipit	<i>Anthus spinoletta</i>	M
Lapland longspur	<i>Calcarius lapponicus</i>	B
Snow bunting	<i>Plectrophenax nivalis</i>	B
<u>Mammals</u>		
Peary's caribou	<i>Rangifer tarandus</i>	B
Muskox	<i>Ovibos moschatus</i>	B

<u>Mammals</u>		<u>Status</u>
Polar bear	<i>Ursus maritimus</i>	M (B?)
Short-tailed weasel	<i>Mustela erminea</i>	B, I
Arctic fox	<i>Alopex lagopus</i>	B
Wolf	<i>Canis lupus</i>	B
Collared lemming	<i>Dicrostonyx groenlandicus</i>	B
Arctic hare	<i>Lepus arcticus</i>	B
Bearded seal ^a	<i>Erignathus barbatus</i>	B
Ringed seal ^a	<i>Phoca hispida</i>	B
Walrus ^a	<i>Odobenus rosmarus</i>	B
Beluga ^a	<i>Delphinapterus leucas</i>	B
Narwal ^a	<i>Monodon monoceros</i>	(I?)

^aCoastal waters only.

APPENDIX II.

Data on the growth and food intake of a captive long-tailed jaeger chick monitored from 29 July, 1971 (at age 2 days), until its death on 15 August (at age 20 days) are given (Part A). The chick taken from nest 42 was the older sibling. I fed it fresh lemmings, caribou, including hair and bones, and flies. The chick did not peck at flies when two days of age, but did when four days of age. It lost its egg tooth when seven days of age.

Data on the growth of six wild but restrained (1970) and six wild unrestrained (1971) long-tailed jaeger chicks are also given (Part B).

I took live weights to the nearest tenth of a g for the captive chick (using a triple beam balance) and to the nearest g for wild chicks (using Pesola 300 and 1500\g spring scales). I measured bill and wing chord to the nearest mm.

The captive chick grew more rapidly after its eighth or ninth day than the single surviving wild chick. Wing chord measurements of the captive and wild chicks were more similar during growth than bill or weight measurements. Neither captive nor wild chicks probably had adequate diets.

PART A

Age (days)	Weight (g)	Bill Length ^a (mm)	Right Wing Chord (mm)	Food Intake (g)	Dry Weight of Droppings (g)	Number of Pellets
2	45.0			26.1		
3				14.0	2.2+	
4	55.7	13	34	30.4	3.1	
5				20.5	3.3	
6	64.5	15	39	19.1	1.9+	
7				37.3	1.0+	
8	85.6	15	49	35.8	2.3+	
9				22.0	3.1	
10	102.3	16	61	32.1	4.3	
11				40.2		
12	118.6	17	75	28.4	5.0	
13				66.1	5.4	
14	127.6	18	95	34.1	7.4	
15				64.4	5.0+	
16	129.1	18	106	55.5	8.2	
17				54.6	6.7	
18	132.3	18	117	28.6	5.9	
19				62.3	4.0+	1
20	151.4			0		

^a Measurement from bill tip to base (upper surface) where feathers begin. This is not a measurement of culmen.

APPENDIX III. Long-tailed jaeger activities not involving any element of hunting (Figures 10 to 13).

Those activities termed 'not visible', 'nesting', 'incubating', and 'territory and displays' are considered to involve no element of hunting or feeding.

Not visible refers to the time period when an individual could not be seen within its territory. It was an important segment of the jaeger's activity before 19 June and after the end of [redacted] both sexes, when I gathered 85% and 89% of the total [redacted] of this category for male and female jaegers, respectively. Males continued to wander from their territories all summer. Wandering off the territories, not poor observability of birds within the territory, constitutes the bulk of these figures. The length of time an individual spent away from its territory per trip varied greatly, usually being less than one hour's duration. One male bird, however, was away at least 210 minutes on 18 June. Males wandered from their territories significantly more than did females.

Resting long-tailed jaegers characteristically sat on the tops of favored perches such as frost hummocks for long periods of time with little movement. Occasionally, they were alert, with necks stretched and head held high, but usually they slept with the bill beneath the scapular feathers or sat with head held low. Resting jaegers faced into or

sideways to the wind and when the wind speed increased, they moved into the lee of the prominence they sat on, while still being able to see over its top. Individual birds often rested for up to 60 minutes at a time, or more, but this was variable. Resting took up a major part of the territorial long-tailed jaeger's time during the summer (>25%). Females may rest significantly more time than the males (1500-1800 hour data) or for a similar amount of time (1200-2400 hour data). Some 97.4% of all resting by females occurred when there were no eggs present, while males rested more consistently throughout the season.

Incubation duties were shared by the pair, the female spent 2.5 (based on data collected between 1500 and 1800 hours) to 3.3 (based on data collected between 1200 and 2400 hours) times as much time on the nest as the male ($p < 0.05$). Males usually incubated for about 60 minutes (seven timed incubation periods averaged 66 minutes) before being relieved by the females. Females spent over 32% of their time incubating (1500 to 1800 hour data; 40% for the 1200 to 2400 hour data), making it as important an activity as resting.

Resting and incubating combined took up 65% of the females' total time and 38% of the males' total time, thus these passive activities were an important part of the

jaegers' time budget, particularly so for the females.

Territory and display activities include intra- and interspecific displays and chases toward birds and mammals, and courtship and nest hunting. Both sexes participated in defense of the territory (Andersson 1971). The males did significantly more territorial defense than the females. However, it did not involve more than 6% of their total time budget.

Alert activities describe jaegers which could not be classified as either hunting or resting. Usually the birds stood, not moving, and showed a fair degree of alertness. I categorized 9% of the male's total time as 'alert', and while it was more than twice that recorded for the females, the two were not significantly different ($p > 0.05$). Over 70% of the males' alert activity occurred before 4 July, while 100% of the females' alert activity occurred after that date. Alert activity may be interrupted lemming hunting, in the case of the male particularly, when the birds' full attention was not hunting at the moment.

Bathing, including preening, is related indirectly to feeding and hunting, since it almost invariably followed each lemming kill. Both sexes will often bathe and preen together, after feeding, even if nesting. Birds often preened soon after leaving the nest following any long period

of incubating. Bathing (bobbing, ruffling, and fluffing the feathers in shallow or deep water pond or river) seldom lasted more than a few minutes, but preening often lasted over ten minutes.

APPENDIX IV. General Remarks on the Food (contents of stomachs and oesophagi), Condition, Status, and Other Pertinent Data of all Long-tailed Jaegers Collected on Bathurst Island from 1968 to 1971.

Date	Age Sex	Breeding Status	Collector	Source	Food	Weight (g)	Remarks
13 June/70	Ad. M	prob. terr.	Taylor	This study	Stomach empty trace veg.	328	very fat good shape
16 June/69	Ad. M	(migrant?)	Sutton	Danks 1971	Stomach almost empty: 7 spiders Arachnida, 2 <u>Pay-</u> <u>chophora gabini</u> moth larvae	?	very fat
16 June/69	Ad. ?	?	Lamothe	This study	?	?	?
4 July/68	Ad. M	breeder	Parmelee	"	one lemming	264	little fat
16 July/68	Ad. M	breeder	"	"	one downy knot	275	mod. fat
16 July/68	Ad. F	breeder	"	"	empty	307	?
16 July/70	Ad. F	non-breeder	Taylor	"	100% arthropods		
16 July/70	Ad. M	non-breeder	"	"	1129 Chironomids	307	little fat
26 July/70	juv ?	chick	"	"	100% arthropods 1379 Chironomids 2 Arachnids	294	little fat
1 Aug./71	Ad. F	breeder	"	"	75-95% Invertebrates Most Chironomids over 5-8 mm	?	?
10 Aug./71	Ad. M	territorial?	"	"	Over 95% lemming(skull) trace insect(caterpillar)	322.5	mod. fat
10 Aug./71	Ad. F	territorial?	"	"	100% lemming	304.5	mod. fat
15 Aug./71	juv ?	captive chick	"	"	100% lemming ?	362.5	mod. fat ?

ac. Hampson collected two birds in 1968 but no data are available.