TERRITORY SIZE AND COMPOSITION IN RELATION TO RESOURCE ABUNDANCE IN LAPLAND LONGSPURS BREEDING IN ARCTIC ALASKA

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ABSTRACT.—The relationship of size and composition of breeding territories to productivity of arthropod prey in the component habitats was studied in a population of Lapland Longspurs (*Calcarius lapponicus*) nesting on arctic tundra near Barrow, Alaska. Territories are established quite synchronously around the time of snow melt in early June, before their resource value can be assessed directly. Twenty territories averaged 1.76 ± 0.46 (SD) ha in area. Large territories contained nearly equal amounts of wet, mesic, and dry habitat. Small territories contained less wet and dry habitat, but a much larger proportion of mesic habitat. Territory size was positively correlated with prey density in the year of measurement, due to an unusual abundance of prey in the relatively unpreferred wet habitat. Territory size was inversely correlated with indices of resource density based upon 3 and 7 years of data on prey productivity in the various habitats. These indices show average or expected prey density. The inverse correlation is increased when prey biomass data are weighted for prey selectivity by longspurs. No relationship between territory size and reproductive success was seen. *Received 25 April 1978, accepted 1 November 1978.*

THE relationship of territory size to resource abundance in solitary nesting species has been the subject of numerous reports and reviews (e.g. Stenger 1958, Brown 1964, Schoener 1968, Orians 1969, Holmes 1970, Cody and Cody 1972, Wiens 1973, Gill and Wolf 1975, Verner 1977, MacLean and Seastedt 1979). The contention that territory size is related to food resources is now well founded in theory, although far from universally accepted. Lack (1954, 1966) observed that year to year variation in territory size is frequently not correlated with fluctuations of food availability; he took this to indicate that territory size has probably not evolved to assure an adequate food supply for reproduction of the territory holder. Hildén (1965) suggested that birds may respond to proximate factors related to food abundance. If so, territory size should conform to expected food availability, but not necessarily to that found in any given year. Unfortunately, the long term data on food abundance required to test Hildén's hypothesis are rarely collected.

The present study concerns intra-population variation in the size of territories of Lapland Longspurs (*Calcarius lapponicus*) breeding on arctic tundra. We compare the size and composition of territories with habitat productivity measured in the same season (1975), and over a sequence of seasons taken to indicate average conditions.

STUDY AREA

The study site near Barrow, Alaska (71°18′N, 156°40′W), was about 2 km SE of the Naval Arctic Research Laboratory and encompassed an area of several km^2 centered on "The Beach Ridge." Extensive data exist on the breeding ecology of Lapland Longspurs (Custer and Pitelka 1977) and other insectivorous birds (Pitelka, 1959, 1974; Holmes, 1966a, b, 1970; Holmes and Pitelka, 1968; Pitelka et al., 1974; Safriel,

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1975) near Barrow. The insect prey of terrestrial birds have been identified, and the distribution and abundance of terrestrial arthropods in various habitats have been documented (MacLean and Pitelka 1971, MacLean 1973, Clement 1975, MacLean et al. 1977).

A description of the Barrow tundra ecosystem was given by Bunnell et al. (1975). The vegetation has been described by Britton (1957) and Webber (in press). Lowland sites are strongly dominated by the grass *Dupontia fischeri* and the sedges *Carex aquatilis* and *Eriophorum angustifolium.* Better drained sites support prostrate willows (*Salix rotundifolia, S. pulchra, S. phlebophylla*) and various forbs (e.g. *Saxifraga* spp., *Potentilla hyparctica*) mixed with grasses and sedges. The area shows little large scale topographic relief; microtopographic features are a complex of drained and undrained meadows, old beach ridges, and a variety of polygonal forms.

The Barrow area supports a variety of wader species, but longspurs are virtually the only passerine species breeding on the tundra (Pitelka 1974). Longspurs arrive at Barrow during the last week of May when the tundra is almost completely snowcovered. Melt-off takes approximately 3 weeks, and daily mean temperatures do not go above freezing until about 11 June. The snow is gone by 20 June; however, fresh snow can fall at any time during summer.

METHODS

Territory delineation.—Territorial males were live-trapped and marked with U.S.F.W.S. leg bands and 1–3 colored plastic bands. Most males on the study area were banded and individually recognizable. Unbanded males were identified by flight behavior, site specificity, and territorial song.

Display activities were used to delineate territories. Longspur displays consist of circular flights interspersed with glides accompanied by song. Display flights usually end at an elevated or snow-free spot on the tundra. These landing sites were marked with color-coded flags and distances between markers were later measured with a surveyor's transit. All undisputed landing sites and areas between outer display points were considered the exclusive area of a territorial male. Sites where two or more males were observed displaying were included in each of the territories. The largest possible polygon created by connecting straight lines to the outermost display points was usually considered to be the final territory size; however, if an area between two points was claimed by a neighboring male and was not defended by the bird whose territory was being measured, then the non-defended area was excluded from the territory. Thus, territory as used in this paper refers to the area within which male display activities were confined.

Twenty territories were delineated. A minimum of 30 min was spent each day between 2 and 22 June observing male activities on each territory. It was usually possible to watch activities on two or more territories simultaneously. Plots of apparent territory size vs. duration of observation revealed that 10 h of observation was sufficient to define the display areas of the birds, while fewer than 5–6 h led to underestimates of the size of the display area.

Microhabitat classification.—Following territory delineation, a 7.1-m grid was marked out on each territory. This grid provided one intersection point for every 50 m^2, giving between 218 and 566 points per territory. Each intersection point was visited and the site was classified into one of 17 categories based upon soil moisture and dominant plant species. These were later lumped for subsequent analyses into dry, mesic, or wet (saturated) habitats. The amounts of these habitat categories were tabulated for each territory.

Prey abundance.—The abundance of arthropod prey was assessed each season between 1966 and 1972, and in 1975, through the use of "sticky boards" covered with a resin. These are exposed on the tundra surface to capture arthropods that walk onto or land upon the board. MacLean and Pitelka (1971) reported results obtained between 1966 and 1969. Here we report further data. Sixteen sticky boards, each 1 m × 0.1 m, were placed in 11 vegetation types in 1975, when territories were recorded. Six of the boards were placed on the exact sites used in the earlier studies. Results of sticky board captures of adult crane flies have been compared with the numbers emerging into emergence traps and counted on transects across a variety of habitat types at the same time (Clement 1975). We believe that the sticky boards accurately reflect the relative abundance and habitat distribution of adult arthropod prey of Longspurs. The total amount of biomass captured on sticky boards is influenced by abundance, activity, and physical characteristics of the arthropods. Activity is influenced by temperature during the emergence period. Thus, comparisons between years and between disparate taxa must be made with caution. Sticky board data are used here primarily to compare the relative abundance of prey in the various habitat types.

Methods of counting and classifying the captured arthropods followed those of MacLean and Pitelka (1971). Only the crane flies (Diptera, Tipulidae) were identified to species. Others were grouped into large

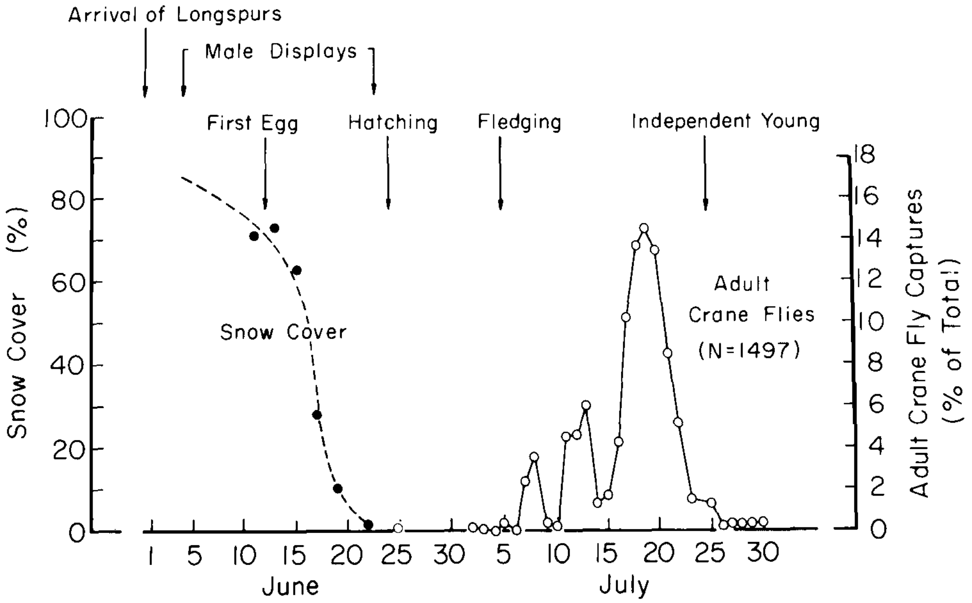

Fig. 1. Phenology of longspur breeding at Barrow, Alaska in 1975, in relation to snow melt and activity of adult crane flies on the tundra.

taxonomic categories (Table 3). Insects smaller than 2 mm (micro-Nematocera of MacLean and Pitelka 1971) were excluded from the counts, as they are not taken by longspurs.

Prey items fed to nestling longspurs were obtained by placing pipe-cleaner ligatures on the throats of nestlings (Hussell 1972). Nestlings older than 7 days were kept in the nest area by a wire mesh enclosure. Prey items were placed in 70% alcohol for later identification. Stomachs of nestlings found dead were also preserved. Classification of prey items followed that used for arthropod collections.

Weights of prey items were obtained from freeze-dried samples and from published reports (Table 3). Weights reported here are those of newly-emerged adults, while weights of crane fly larvae are those of the fourth (final) instar, which make up almost all of the larvae taken by foraging longspurs.

RESULTS

Territory size and variation.—Territorial display began in the first days of June, when the tundra was almost entirely snow covered (Fig. 1). Small patches of exposed ground served as foci of territorial activity. Only males that obtained territories within an 8-day period (4–12 June) were successful in attracting mates, although pair formation was observed as late as 16 June. Six of 28 males that established territories on the study area before 12 June and all three males that established territories after 12 June failed to attract males. One male (number 087, Fig. 2) attracted two females in succession, and mated bigamously. The total sex ratio (31 males, 23 females) indicates that females were in short supply in this population.

Territories of 20 male longspurs (Fig. 2) varied from 1.09 to 2.83 ha ($\bar{x}$ = 1.76, SD = 0.46). The birds did not occupy all of the study area, so that territories were not entirely contiguous. The overall density in the study area was about one pair per 3 ha, a value well below the maximum but above the minimum reported by Custer and Pitelka (1977) on an adjacent study plot for the period 1967–1973. This

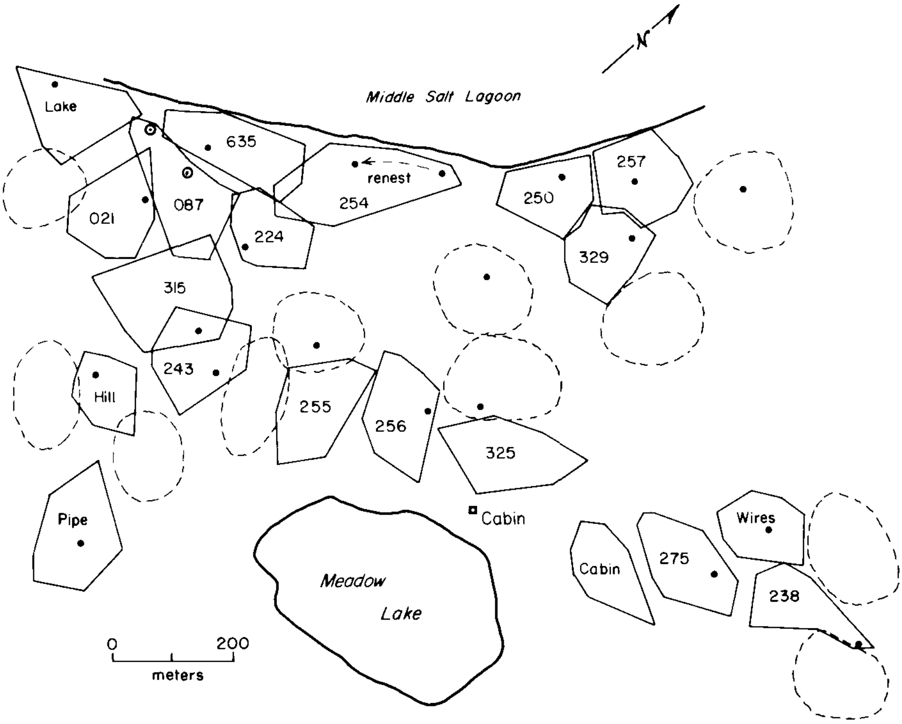

Fig. 2. The size and location of longspur territories in the study area. Dotted lines indicate territories present but not plotted. Nest locations are indicated by dots. The circled dots indicate the two nests of bigamous male 087.

supports their suggestion that the population was recovering from a low point reached in 1972.

Female behavior influenced territory size directly by selection of the nest site, and indirectly by date of pair bond formation. In three instances (territories 315, 254, and 238; Fig. 2), females placed their nests outside of the exclusive area of the males. The males then increased the areas covered by their display activities to include the nest sites. Two of these territories (315 and 254) were considerably larger than any others, and at least part of the large size was due to the female's choice of nest site.

Males continued to display after their females began to incubate eggs, and often flew from their own territories to pursue unattached females or neighboring females with incomplete clutches. Two males (territories 087 and Hill) that acquired mates later than other males were forced to spend much of their time driving off intruders. Thus, time spent in normal display activities was curtailed. Territory size delineation was dependent upon these displays, and in such cases competition for the female rather than the area may have reduced the size of the exclusive areas.

We divided the total sample into subsamples consisting of the largest and smallest 10 territories in order to compare the habitat composition of large and small territories (Table 1). Large territories contained nearly equal amounts of wet, mesic, and dry habitats. Small territories contained significantly less dry and, especially, wet habitats, but a much larger proportion of mesic habitats (Mann Whitney U-test,

TABLE 1. Habitat composition of the ten largest and ten smallest territories.

	Large territories (n = 10)		Small territories (n = 10)	
Habitat type:	%	Area (ha)	%	Area (ha)
Wet	32.8	0.69	17.0	0.24
Mesic	31.2	0.65	53.2	0.76
Dry	35.6	0.75	29.8	0.42
Total		2.10		1.42

$.05 > P > .02$). In fact, the actual amount of mesic habitat was, on the average, greater in the smaller territories.

Dry habitats consisted primarily of raised polygon centers, where *Luzula confusa, Poa arctica,* and a sparce lichen cover formed the dominant vegetation. Wet habitats in longspur territories consisted mainly of polygon troughs, where the grass *Dupontia fischeri,* the sedges *Carex aquatilis* and *Eriophorum vaginatum,* and the moss *Oncophorus wahlenbergii* were dominant. Continuous expanses of such habitat, forming wet meadows, were not occupied by territorial longspurs. The main mesic habitats were gently sloping meadows of *Carex aquatilis, Poa arctica* and *Salix* spp.

Eighteen nests in delineated territories were undisturbed by the research protocol; these produced 5.22 eggs and 3.72 fledglings per nest, for a mean fledging success of 71%. These values are slightly higher than those observed for the population as a whole (5.03 eggs and 3.03 fledglings per nest, based upon 34 nests). Five of the 34 nests were preyed upon during the nestling stage, one by a Snowy Owl (*Nyctea scandiaca*) and the others by Pomarine or Parasitic jaegers (*Stercorarius pomarinus, S. parasiticus*) or, in one case, perhaps by a least weasel (*Mustela nivalis*). Nineteen nestlings starved or died from a combination of starvation and exposure. Thus, of 53 nestling deaths, 64% were caused by predation and 36% resulted from starvation. No correlation existed between territory size and either clutch size or number of young fledged (Fig. 3A, 3B). Thus, the data show no reproductive advantage associated with territory size in 1975.

Arthropod abundance.—Table 2 summarizes the biomass of arthropod prey captured on sticky boards in wet, mesic, and dry habitats on the study area in seven different seasons, including 1975. The major component of biomass consists of adult craneflies: *Tipula carinifrons* in dry and mesic habitats, *Prionocera gracilistyla* and *Pedicia hannai* in mesic and wet habitats. This was particularly the case in 1975, when crane flies made up 63% of all biomass, compared with the 7-yr average of 48%. Much of the difference between 1975 and earlier years can be attributed to an unusual abundance of *P. gracilistyla.* In each of the prior seasons the number of *T. carinifrons* captured exceeded the number of *P. gracilistyla.* Dry habitats produced more biomass than wet habitats in five of these six seasons, and the average prey productivity of dry and mesic habitats was greater than that of wet habitats. In 1975, with the large abundance of *P. gracilistyla,* wet habitats were most productive. Overall, the biomass of adult arthropods captured on sticky boards in 1975 was well below the 7-yr average for this site. The peak of emergence in 1975 (Fig. 1) was slightly delayed compared to other seasons (MacLean and Pitelka 1971) due to a period of cold weather, with daily maximum temperatures below 4°C, that lasted for 3 days in mid-July and suppressed the emergence of adult Diptera.

Food of nestling longspurs.—Prey fed to nestlings consisted almost entirely of insects and spiders (Table 3). Crane flies are by far the most important component of the biomass of the nestling diet; over 60% of the biomass fed to nestlings in 1975 consisted of the crane fly species *Tipula carinifrons*. Hatching of longspurs preceded the peak crane fly emergence (Fig. 1), and pupae were more numerous than adults and larvae in the prey fed to nestlings. *Tipula carinifrons* and sawflies (Tenthredinidae), both larval and adult, occurred in the nestling diet in greater proportion than their capture on sticky boards (Table 3). *Prionocera gracilistyla* were not heavily used by longspurs, despite their great abundance in wet habitats.

Territory size in relation to prey abundance.—The prey capture data for wet, mesic and dry habitats (Table 2) were used to estimate the prey value of each of the 1975 territories. Since over 98% of the nestling diet consisted of the three crane fly species, sawflies, spiders, small Nematocera, and muscoid flies, only these seven groups were used in constructing the index. A biomass density index was calculated for each territory from the formula:

$$\text{Biomass Density Index} = \frac{\sum_{i=1}^{3}\sum_{j=1}^{7} a_i b_{ij}}{\sum_{i=1}^{3} a_i} \qquad (1)$$

where a_i is the area of moisture class i (wet, mesic, or dry) in a particular territory and b_{ij} is the biomass of insect j captured per sticky board placed in moisture class i. The values generated by this procedure express the relative prey availability of different territories.

Estimates of prey availability were compared with territory size using the Spearman Rank Correlation (Snedecor and Cochran 1967). There is a significant positive correlation between territory size and relative prey density in 1975 (Table 4). We believe that this is due to the unusual abundance of *Prionocera gracilistyla* in wet habitats in 1975.

MacLean and Pitelka (1971) reported densities of arthropods captured in 1967–1969 in wet, mesic, and dry habitats that included the sites sampled in 1975. Territory size in 1975 shows a strong negative correlation with expected prey density, calculated from the 3-yr average arthropod abundance data for wet, mesic, and dry habitats (b_{ij} of equation 1) (Table 4). The 7-yr prey-capture data for the Beach Ridge site used in this study (Table 2) include more temporal but less spatial variation than the 3-yr data used above. When the 7-yr averages are used to indicate prey abundance in the three habitat categories, a significant negative correlation between territory size in 1975 and expected prey density is again found (Table 4).

These correlations weight all prey in the seven major categories equally, without considering selectivity by foraging longspurs. Comparison of prey items obtained from nestling longspurs with sticky board captures (Table 3) shows considerable selection in favor of *T. carinifrons* and sawflies and against other prey categories. The ratio of biomass fed to nestlings to biomass captured on sticky boards (Table 3) was used as an index of selectivity to weight the importance of the various prey categories. This weighting factor emphasizes the nestling period, when food abundance is likely to be of particular importance. We assume that the habitat distribution of larval and pupal flies and sawflies follows that of adults captured on sticky boards (MacLean 1973, Clement 1975). Since only fourth (final) instar crane fly

TABLE 2. Biomass (mg) of arthropods captured on two sticky boards in wet, mesic, and dry habitats on the Old Beach Ridge study site, 1967–1972 and 1975. Biomass calculated from numbers of arthropods captured and mean biomass values given in Table 3.

		Tipula carinifrons	*Prionocera gracilistyla*	*Pedicia hannai*	Small Nematocera	Muscoid flies	Tenthredinidae	Araneida	Total
1967	Wet	1,614	282	211	1,365	247	58	77	3,854
	Mesic	1,640	339	68	1,252	379	16	31	3,725
	Dry	3,050	85	63	1,241	576	14	45	5,074
1968	Wet	318	113	416	3,128	707	110	94	4,886
	Mesic	712	367	236	3,416	1,000	52	15	5,798
	Dry	1,284	85	94	3,123	1,065	32	25	5,708
1969	Wet	229	141	191	740	1,669	167	482	3,619
	Mesic	318	56	83	730	1,196	74	98	2,555
	Dry	534	42	27	716	1,065	27	64	2,475
1970	Wet	458	42	126	1,551	710	61	372	3,320
	Mesic	521	28	72	1,453	912	32	200	3,218
	Dry	470	28	20	1,507	1,418	18	139	3,600
1971	Wet	902	691	252	887	1,067	88	560	4,447
	Mesic	1,322	409	189	764	2,159	63	174	5,023
	Dry	1,538	56	43	866	2,697	40	101	5,341
1972	Wet	2,669	3,640	656	289	866	124	—	8,564[a]
	Mesic	5,669	2,667	504	493	1,480	171	—	11,112[a]
	Dry	4,944	1,947	189	540	1,619	63	—	9,384[a]
1975	Wet	414	1,746	198	357	397	40	337	3,489
	Mesic	686	858	198	402	237	38	249	2,668
	Dry	850	270	14	609	189	43	119	2,094
Mean	Wet	943	951	293	1,188	808	93	320	4,597
	Mesic	1,552	675	193	1,216	1,052	64	128	4,871
	Dry	1,810	359	64	1,229	1,233	34	82	4,811

[a] 1972 spider data are missing. Total biomass estimated using habitat-specific means for the other 6 yr.

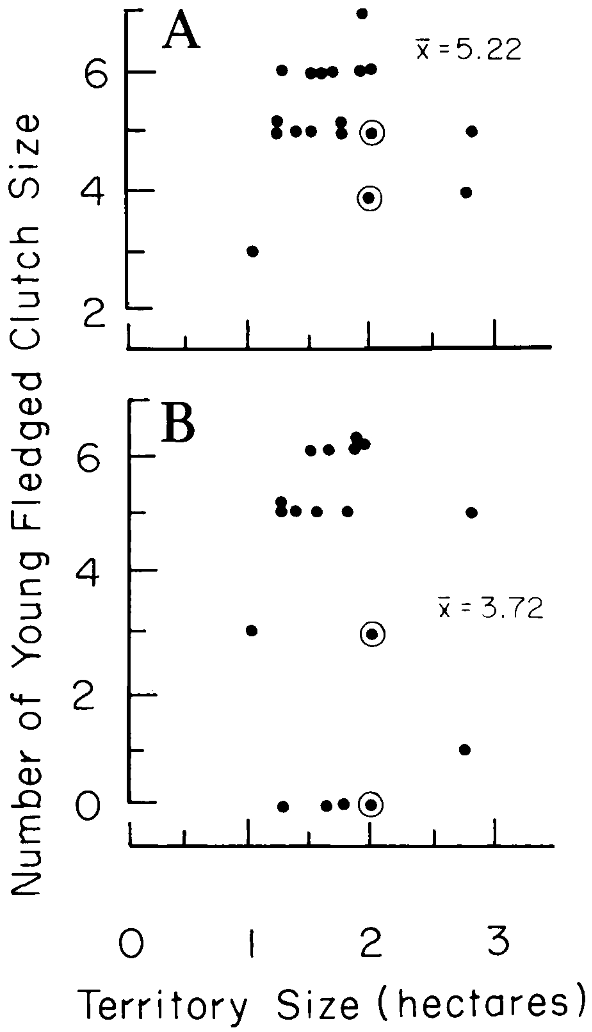

Fig. 3A. Relationship between territory size and clutch size at Barrow. B. Relationship between territory size and number of young fledged at Barrow. Values of bigamous male are circled.

larvae are taken in significant numbers by foraging birds, the larvae and pupae are taken from the same cohort represented by adults captured on the sticky boards.

Adjusted biomass density indices were calculated for each 1975 territory according to the formula:

$$\text{Adjusted Biomass Density Index} = \frac{\sum_{i=1}^{3}\sum_{j=1}^{7} a_i b_{ij} s_j}{\sum_{i=1}^{3} a_i} \qquad (2)$$

where s_j is the prey selectivity index for prey category j. Other terms are the same as in equation 1. If territory size is related to expected prey productivity, use of the adjusted biomass density index, which weights prey categories according to their importance in the diet, should emphasize the relationship. This is the case for all

TABLE 3. Major invertebrates obtained from esophageal ligature and stomach samples of nestling longspurs, and from 16 sticky-boards on the tundra surface in 1975.

		A. Obtained from nestlings		B. Sticky-board captures		
Prey item	Weight (mg)	Number	% of biomass	Number	% of biomass	A/B
Tipula carinifrons						
larvae	25.0	12	6.2			
pupae—male	21.8	95	36.9			
pupae—female	27.7					
adult—male	10.0	48	15.6	156	18.9	
adult—female	26.0			15	4.7	2.5
Prionocera gracilistyla						
larvae	30.0	—	—			
pupae—male	14.0	—	—			
pupae—female	32.0					
adult—male	12.0	17	6.9	177	25.7	
adult—female	30.0			25	9.1	0.2
Pedicia hannai						
larvae	5.0	5	0.5			
adult	1.8	66	2.4	228	5.0	0.6
Small Nematocera						
larvae	0.2	75	0.3			
pupae	0.4	23	0.2			
adults	0.3	880	4.3	4,561	16.6	0.3
Muscoid flies						
larvae	0.7	7	0.1			
pupae	0.9	57	1.0			
adult	0.9	221	4.2	914	9.9	0.5
Tenthredinidae						
larvae	6.0	81	10.2			
adults	1.8	140	4.7	67	1.5	9.9
Araneida	1.4	122	4.7	504	8.6	0.5
Other		33	1.8			

three sources of prey density data: 1975, 1967–1969, (MacLean and Pitelka 1971), and 1967–1972 plus 1975 (Table 4). Using the adjusted prey biomass density index, territory size in 1975 was inversely correlated with quality. The adjustment for prey selectivity removes the effect of the unusual abundance of *Prionocera gracilistyla* in 1975, since this abundance was not reflected in the prey fed to nestling longspurs.

DISCUSSION

The results of this study indicate that the size of breeding territories of Lapland Longspurs in arctic Alaska is related to the "expected" food density of the habitats comprising the territory. Territories that contain a large proportion of the most favored feeding habitats are, on the average, smaller than territories that contain a large proportion of wet habitats. The fact that this relationship applies most strongly to average or expected food density indicates that the birds respond to the habitat composition of the area rather than assessing food density directly. Similar patterns have been found in Ovenbirds, *Seiurus aurocapillus* (Stenger 1958), and in Sparrowhawks, *Accipiter nisus* (Newton et al. 1977).

Longspurs at Barrow begin territorial behavior when the tundra is mostly snow covered. This is necessary in order that the young will fledge while the easily-captured adult crane flies are abundant on the tundra (Fig. 1). The pattern of snow melt provides some information regarding the habitats occurring in a particular

TABLE 4. Spearman rank correlation coefficients of territory size in 1975 with estimates of prey biomass density, unweighted and weighted for prey selectivity by longspurs.

	Nature of data	
Year(s)	Sticky-board captures, not adjusted	Adjusted for prey selection by longspurs
1975 prey data (6 boards)	+0.54**	−0.40*
1967–1969 (12 boards) (MacLean & Pitelka)	−0.60**	−0.63**
1967–1972 & 1975 (6 boards)	−0.43*	−0.52**

* $P < 0.05$; ** $P < 0.01$.

area, but details of habitat composition and year-to-year variations in their productivity cannot be assessed. The information available to direct habitat selection increases as the season progresses (Wittenberger 1976), and adjustments to territory boundaries occur. Still more information is available by the time of egg-laying, and females may select nest sites close to productive feeding habitat. In three cases, two of them involving territories established quite early in the season, this took the female off the original territory of the male altogether. Thus, two levels of choice are available to the female: selection of a male (in part based upon the characteristics of the territory that he possesses), and selection of a site on (or near) the territory to place the nest.

It should be stressed that territory, as used here, refers to the area encompassing male displays. This is the usual operational definition of territory. The relationship of display area to foraging areas of the male and female was considered in a companion study on this same population (Tryon 1978, Tryon and MacLean MS). In the normal case, over 90% of the foraging of both male and female occurred on the territory early in the season, when territories were most actively defended. This value declined later in the season. The nest site became a strong focus for foraging activities, with less regard for territorial boundaries, when nestlings were being fed. Thus, the location of the territory and placement of the nest (in most cases) within the territory strongly influence access of the birds to potential feeding sites, particularly when feeding nestlings.

A large and high quality territory is beneficial to a male in attracting a female (or multiple females), and in assuring the success of the nest or nests. These are obviously related, since a female should not mate with a male whose territory is inadequate to allow successful reproduction. The observed inverse correlation between territory size and food density might result if (1) males recognize the resource value of their territories, and do not attempt to defend more resources than are required for successful reproduction, or (2) competition is most severe for areas of high quality (high food density) habitat, leading to a greater cost of defense per unit area of territory. The first of these alternatives is the "sufficient resource" hypothesis of Verner (1977). MacLean and Seastedt (1979) showed that this is unlikely, and that this hypothesis can be rejected without negating the central hypothesis that the basic function (cause for the evolution) of territoriality is the securing of adequate resources for reproduction. The high level of agression observed between territorial males, and the fact that areas temporarily vacated when a territorial male was trapped for banding were almost immediately occupied by neighboring or intruding males, argues that territory size is limited by competition for suitable habitat, or by the cost of defense of the area.

While competition for favorable habitat provides a mechanism of territory size determination, the fact that 36% of nestling deaths resulted from a combination of starvation and exposure indicates that the food value of the territory is important to the reproductive success of the occupants. We believe that it is food density in productive habitats, rather than total quantity of food, that is important to the birds. A large area of low productivity habitat is not the equivalent of a smaller area of highly productive habitat, in which food can rapidly be gathered for delivery to nestlings or fledglings. Further, it would be misleading to compare the total food requirements for reproduction with the total productivity of the territory. Each day the adults must supply the requirements of the growing young. Calculating from energetic and time budget estimates presented by Custer (1974), we estimate that each adult must gather one *Tipula* larva or pupa or two *Tipula* adults per min of foraging time to satisfy their own requirements plus the needs of five nestlings. The daily emergence of adult prey varies widely, depending upon both time of season and weather conditions. On favorable days the daily emergence far exceeds the requirements of the birds, but on unfavorable days the birds may be hard-pressed to collect sufficient food. On such days access to adequate areas of highly productive habitat without competition from conspecifics may be critical to successful reproduction.

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LITERATURE CITED

BRITTON, M. E. 1957. Vegetation of the arctic tundra. Pp. 26–61 *in* Arctic Biology (H. P. Hansen, Ed.) Corvallis, Oregon State Univ. Press.

BUNNELL, F., S. F. MACLEAN, JR., & J. BROWN. 1975. Barrow, Alaska, U.S.A. Pp. 73–124 *in* Structure and Function in Tundra Ecosystems (T. Rosswall and O. W. Heal, Eds.) Ecol. Bull. (Stockholm), Vol. 20.

BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76: 160–169.

CLEMENT, L. E. 1975. The ecology of *Tipula carinifrons* Holm (Diptera, Tipulidae) in the arctic coastal tundra of northern Alaska. Unpublished M.S. thesis, Fairbanks, Univ. of Alaska.

CODY, M. L., & C. B. J. CODY. 1972. Territory size, clutch size and food in populations of wrens. Condor 74: 473–477.

CUSTER, T. W. 1974. Population ecology and bioenergetics of the Lapland Longspur (*Calcarius lapponicus*) near Barrow, Alaska. Unpublished Ph.D. dissertation, Berkeley, Univ. of California.

———, & F. A. PITELKA. 1977. Demographic features of a Lapland Longspur population near Barrow, Alaska. Auk 94: 505–526.

GILL, F. B., & L. L. WOLF. 1975. Economics of feeding territoriality in the golden-winged sunbird. Ecology 56: 333–345.

HILDÉN, O. 1965. Habitat selection in birds. A review. Ann. Zool. Fennica 2: 53–74.

HOLMES, R. T. 1966a. Feeding ecology of the red-backed sandpiper (*Calidris alpina*) in arctic Alaska. Ecology 47: 32–45.

———. 1966b. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper (*Calidris alpina*) in northern Alaska. Condor 68: 3–46.

———. 1970. Differences in population density, territoriality and food supply of dunlin on arctic and subarctic tundra. Pp. 303–320 *in* Animal Populations in Relation to Food Resources (A. Watson, Ed.) Brit. Ecol. Soc. Symp. 10. Oxford, Blackwell Scientific Publ.

———, & F. A. PITELKA. 1968. Food overlap among coexisting sandpipers on northern Alaskan tundra. Syst. Zool. 17: 305–318.

HUSSELL, D. J. T. 1972. Factors affecting clutch size in arctic passerines. Ecol. Monogr. 42: 317–364.

LACK, D. 1954. The natural regulation of animal numbers. London, Oxford Univ. Press.

———. 1966. Population studies of birds. Oxford, Clarendon Press.

MACLEAN, S. F., JR. 1973. The life cycle and growth energetics of ***Pedicia hannai*** Alex. (Diptera: Tipulidae), an arctic crane fly. Oikos 24: 436–443.

———, & F. A. PITELKA. 1971. Seasonal patterns of abundance of tundra arthropods near Barrow. Arctic 24: 19–40.

———, G. K. DOUCE, E. A. MORGAN, & M. A. SKEEL. 1977. Community organization in the soil invertebrates of Alaskan arctic tundra. *In* Soil Organisms as Components of Ecosystems (U. Lohm and T. Persson, Eds.). Ecol. Bull. (Stockholm), Vol. 25.

———, & T. R. SEASTEDT. 1979. Avian territoriality: sufficient resources or interference competition. Amer. Natur. 113: (in press).

NEWTON, I., M. MARQUISS, D. N. WEIR, & D. MOSS. 1977. Spacing of sparrowhawk nesting territories. J. Anim. Ecol. 46: 425–441.

ORIANS, G. H. 1969. On the evolution of mating systems in birds and mammals. Amer. Natur. 103: 589–603.

PITELKA, F. A. 1959. Numbers, breeding schedule, and territoriality in Pectoral Sandpipers of northern Alaska. Condor 61: 233–264.

———. 1974. An avifaunal review for the Barrow region and north slope of arctic Alaska. Arctic Alpine Res. 6: 161–184.

———, R. T. HOLMES, & S. F. MACLEAN, JR. 1974. Ecology and evolution of social organization in arctic sandpipers. Amer. Zool. 14: 185–204.

SAFRIEL, U. N. 1975. On the significance of clutch size in nidifugous birds. Ecology 56: 703–708.

SCHOENER, T. W. 1968. Sizes of feeding territories among birds. Ecology 49: 123–141.

SNEDECOR, G. W., & W. G. COCHRAN. 1967. Statistical methods, 6th ed. Ames, Iowa State Univ. Press.

STENGER, J. 1958. Food habits and available food of ovenbirds in relation to territory size. Auk 75: 335–346.

TRYON, P. R. 1978. Use of space by breeding Lapland Longspurs (*Calcarius lapponicus*) in arctic Alaska. Unpublished M.S. thesis, Fairbanks, Univ. of Alaska.

VERNER, J. 1977. On the adaptive significance of territoriality. Amer. Natur. 111: 769–775.

WEBBER, P. J. In press. Spatial and temporal variation of the vegetation and its productivity, Barrow, Alaska. *In* Plant ecology of the Alaskan arctic tundra (L. L. Tieszen, Ed.) New York, Springer-Verlag.

WIENS, J. A. 1973. Interterritorial habitat variation in grasshopper and savannah sparrows. Ecology 54: 877–884.

WITTENBERGER, J. F. 1976. The ecological factors selecting for polygyny in altricial birds. Amer. Natur. 110: 779–799.