USE OF SPACE BY LAPLAND LONGSPURS
BREEDING IN ARCTIC ALASKA

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ABSTRACT.—Use of space for foraging was compared with the defended area for three pairs of Lapland Longspurs breeding on arctic tundra near Barrow, Alaska. The activity space for foraging over the entire season was larger than the defended area and was considerably larger for males than for females. Throughout the season, greatest use was made of the area about the nest. This was more pronounced during the nestling and fledgling periods, when adults make frequent visits to feed the young. Greatest use was made of the defended area in the prenesting period, with a decline in use later in the season as territorial defense waned. Overlap occurred in the use of space by adjacent pairs. During the prenesting and incubation periods, this overlap compensated for the decline in use with distance from the nest, so that the combined use of space by adjacent birds was relatively even. Use of space is influenced by the time and energy requirements of breeding activities and by the availability of prey. *Received 17 July 1979, accepted 14 December 1979.*

THE evolutionary basis of territoriality (defense of space) by birds has been debated for many decades (Nice 1941, Hinde 1956, Verner 1977, MacLean and Seastedt 1979). While the aggressive behavior of territorial birds first called attention to the phenomenon, its ecological significance lies in the exclusive use of space that it allows (Pitelka 1959). In this study we consider the functional basis of territoriality by examining the spatial distribution of foraging during different periods of the breeding season and by comparing this with the behaviorally defined territory (the defended area).

We chose a population of Lapland Longspurs (*Calcarius lapponicus*) at Barrow, Alaska (71°18'N, 156°40'W) for this study because the constant light during the breeding season, level topography, and low vegetation of the arctic tundra allow uninterrupted observation. Longspurs are the predominant passerine of arctic Alaska (Pitelka 1974) and are the most important carnivores in the detritus-based food chain at Barrow (MacLean 1980). The breeding biology of longspurs at Barrow was investigated by Custer and Pitelka (1977, 1978; Custer 1974). In a study simultaneous to that reported here, Seastedt and MacLean (1979) examined the relationship of longspur territory size to abundance of arthropod prey in component habitats.

Longspur breeding activities begin early in the summer, around 1 June, and are highly synchronous; this allows the chicks to reach independence during the peak of insect emergence (Custer and Pitelka 1977, Seastedt and MacLean 1979). The males establish breeding territories while the ground is almost completely covered with snow. Territories are defined by song given in flight or from song-posts on elevated sections of tundra. Pairs are formed soon after the females arrive, usually several days after the males. Some males obtain a second mate after the first mate begins incubation, although the incidence of polygyny at Barrow is low (Custer and Pitelka 1977, Seastedt and MacLean 1979). Unless a clutch is lost early in the season, only one clutch is attempted by each female during a summer.

METHODS

Three pairs of Lapland Longspurs were studied intensively throughout the 1975 breeding season. Two other males associated with one of the pairs were also watched. All but one of these birds and many of

the surrounding ones were marked with unique sets of colored bands. The area surrounding each nest was gridded with stakes placed at 10-m intervals forming squares of 100 m². The snow cover of each square was estimated five times during the period of melt, and the vegetation was described at six points within each square.

Each bird was watched for a period of time (usually 1 h), and a record was made at 1-min intervals of: (1) the bird's activity, (2) the square in which it occurred, (3) the presence of other birds, (4) whether or not chicks had been fed in the last minute, and (5) the number of display flights that occurred in the last minute. Fifteen different activities were recorded and later were lumped for analysis. A total of 185 h of observations were scattered haphazardly throughout the time that longspurs were active (0400–2300). Additional periods at night confirmed this schedule. Data collected for each bird were entered into a data file that was sorted to create maps of all occurrences of a given activity in a given period of time. Activity spaces for foraging were defined as the smallest convex polygon incorporating 95% of the observations of foraging. The outermost 5% of the observations were discarded, eliminating the infrequent observations that contribute inordinately to the size of the activity space (Jennrich and Turner 1969). Activity spaces for defense (the traditional definition of the territory as a defended area) were defined as the smallest convex polygon incorporating all observations of singing and display flights.

We analyzed the use of the area for foraging by comparing the frequency of foraging observed in each of the 10 × 10-m squares within the activity space. The null hypothesis, which states that each square within the defended area or activity space for foraging has an equal probability of use and that foraging is distributed randomly within the area, was tested against several alternative hypotheses that predicted unequal distribution of foraging. In the latter case, the activity space was divided into discrete classes, for example, all squares of a particular vegetation type or terrain feature or all falling within a particular distance from the nest or geometric center of foraging. The density of foraging (observations per 10 × 10-m square) in each of these classes was divided by the average density of foraging over the entire territory to produce a selection coefficient. This selection coefficient takes a value of 0 when a class is not used at all and 1 when a class is used in the same proportion that it occurs in the area as a whole, that is, when no selection is evident. When all of the activity occurs in a particular class, the selection coefficient is the inverse of the proportionate representation of that class in the total area; selectivity is greatest when the favored class makes up a small proportion of the total area.

RESULTS

The breeding season was divided into four periods. The prenesting period began with the arrival of birds (4–6 June). At this time, the male established and defended a territory and attracted a mate. The female then built a nest. The incubation period lasted 12–13 days. Although the female incubated the eggs almost continuously, she moved freely about the territory when foraging. The male frequently followed the female but also flew about, both on and off the territory, apparently seeking to mate with other females. The nestling period started with the hatching of eggs (26–30 June) and continued until the chicks left the nest (5–10 July). Both parents made frequent trips to the nest to feed the chicks. The fledgling period extended from this period until the chicks became independent after 20 July. The chicks were attended exclusively by one or the other adult, either within or outside of the original territory.

All three pairs were located in an area of relatively high longspur nesting density (30 pair/km²) (Seastedt and MacLean 1979). Figure 1 shows territories found on the study area and the surrounding vicinity. The areas not included in any territory were wet habitat, unsuitable for longspurs. Individual behavior patterns of the three pairs were highly variable. Breeding activities of pairs I and III were separated by only 1 day throughout the season. Male I spent more time with his mate than did male III; he often frequented the nest during the incubation period and began to make feeding trips to the nest before the eggs hatched. From hatching until the chicks were independent, both parents made frequent feeding trips. Male III spent less time about the nest or his mate. During the first two periods, we usually lost sight of him on a long flight after only 5–10 min of observation, consequently biasing
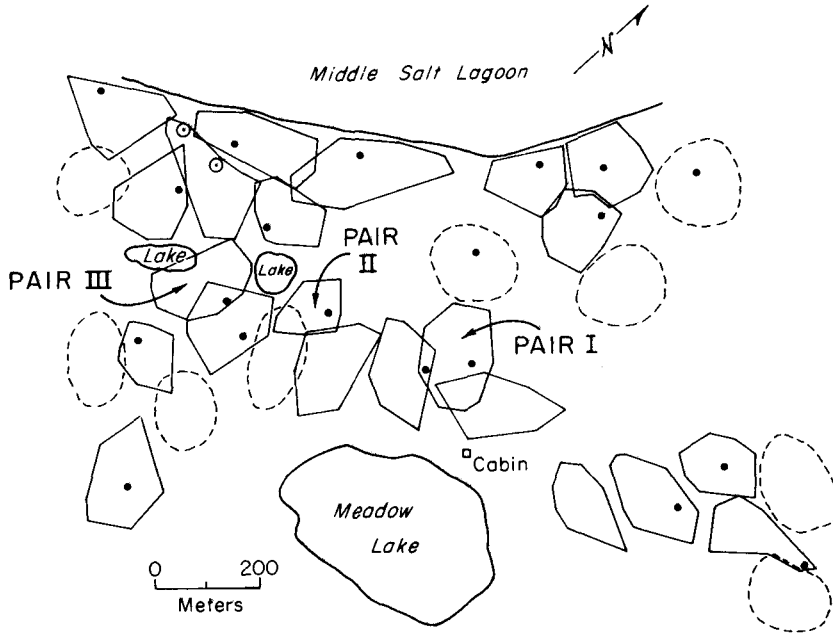
Fig. 1. The size and location of the defended areas of longspurs in the study area. Dotted lines indicate approximate boundaries.

observations in favor of those in the territory. Male III did not begin to make regular feeding trips to the nest until several days after the eggs hatched. When the chicks left the nest, the male moved with 1 or 2 of the chicks 250 m away from the territory. Only two observations of male III were made in this new area. Subjectively, female III did not differ from female I.

Male IIA established a territory at the same time as other males but was one of the last to acquire a mate. Before his mate built a nest, an unpaired male (IIB) drove both birds from the territory onto an adjacent meadow. There, copulation occurred between male IIA and female II and a nest was built. After 3 days of displaying on the original territory without attracting a mate, male IIB drove male IIA away from female II and took over the new territory that male IIA had begun to defend. Copulation was observed between male IIB and female II. During the nesting period, male IIB was seen with decreasing frequency and eventually disappeared altogether. Male IIA did not frequent this territory, but was observed a number of times in the general study area throughout the season. Neither male IIA nor IIB was ever observed bringing food to the chicks, although both apparently contributed their genes to the offspring. Female II did not make as many foraging trips as other females. Male IIC, who had a neighboring territory but no mate, began feeding the young during the nestling period. While we did not observe any copulations between him and female II, he was involved in the battle over her second territory, and it is possible that he was able to mate successfully. Male IIC fed three chicks during the fledgling period. The female was not found after the third day of the fledgling period; she may have left the territory with two chicks and raised them to independence.
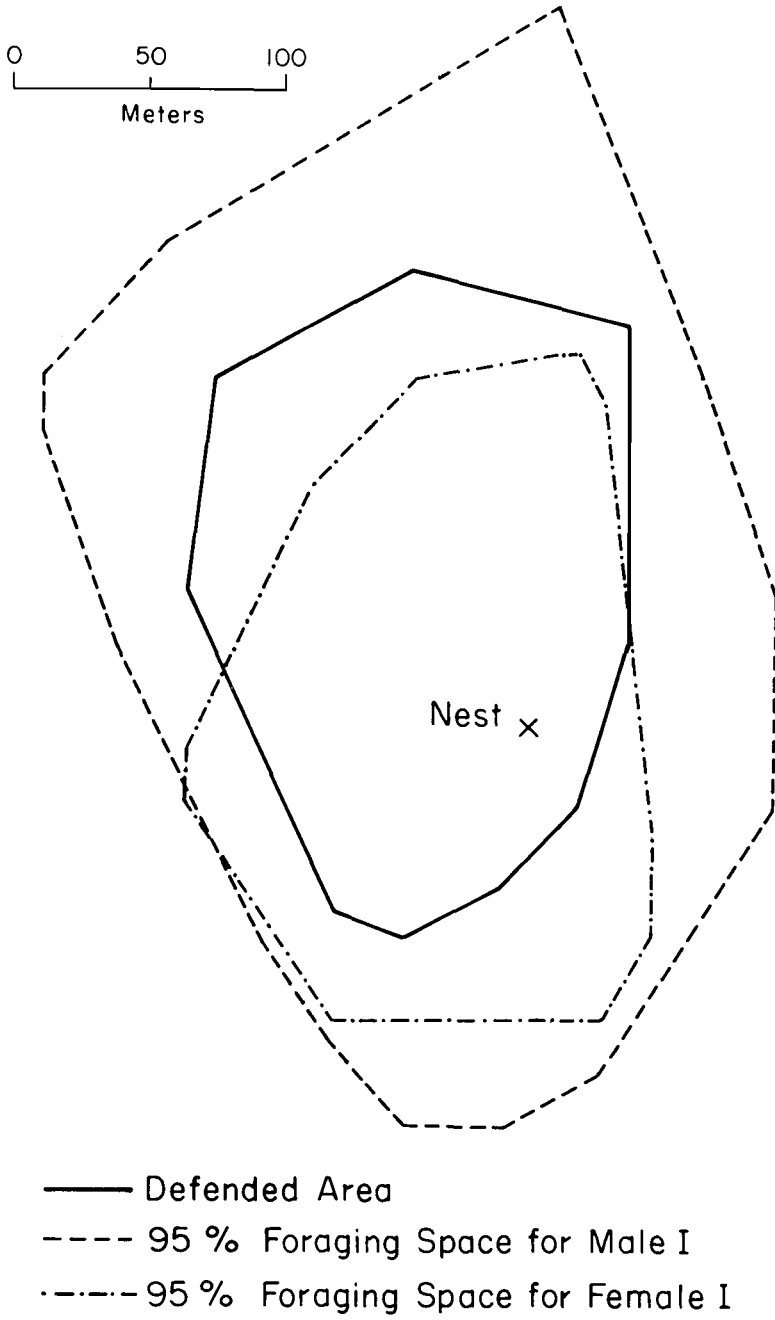
Fig. 2. Activity space for foraging (8.21 ha) and defended area (3.38 ha) for male I and foraging (3.74 ha) for female I.
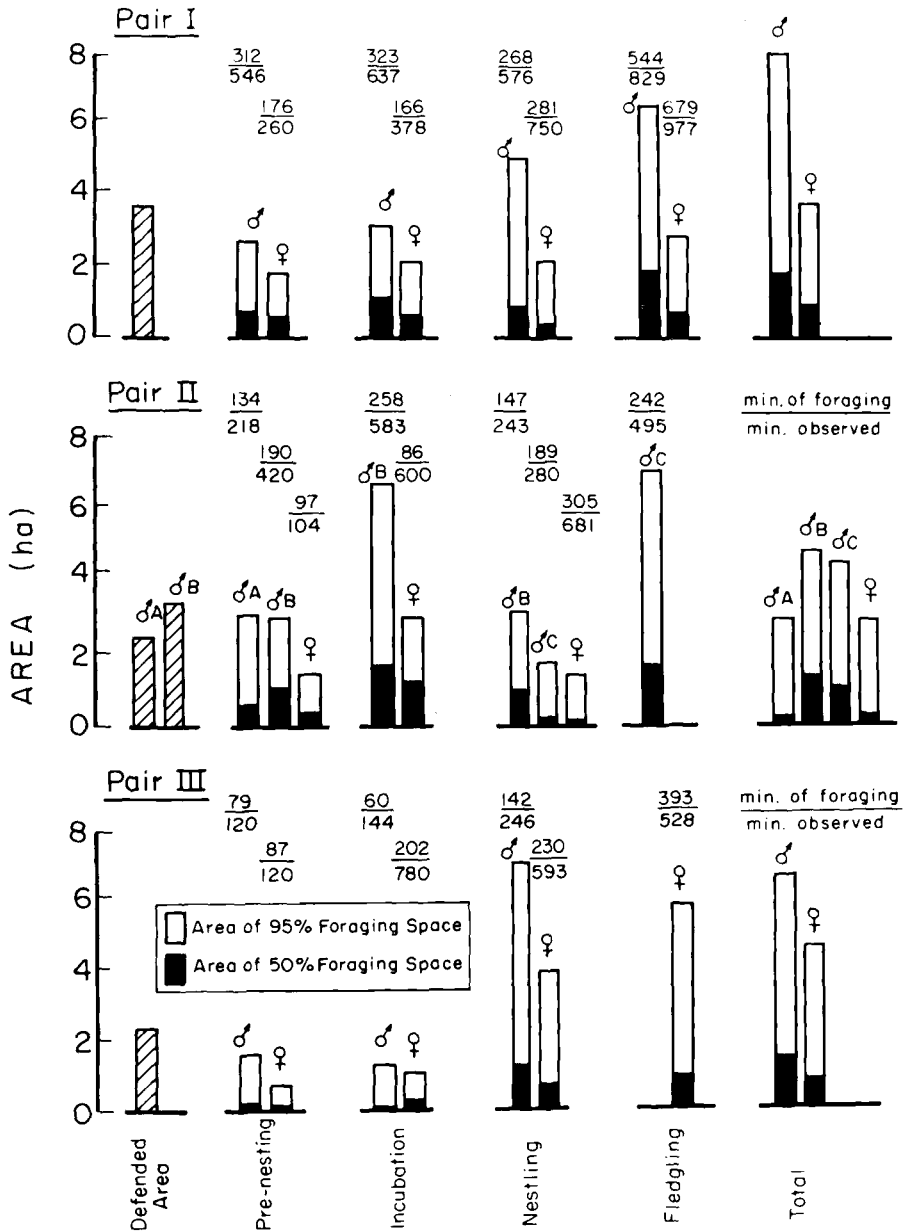
Fig. 3.   Areas of 50% and 95% activity spaces for foraging and territories for all birds during each period and total number of observations and number of observations of foraging for each bird in each period.

Activity spaces.—The distribution and concentration of foraging activity for each bird of pair I for the entire season are shown in Fig. 2. The polygons indicate the area defended by the male and the 95% activity space for foraging. Sixty-five percent of foraging by the male and 83% of foraging by the female occurred within the defended area. Fifty-two observations were made of male I foraging near the nest of an adjacent pair, which male I frequented regularly during the incubation period.

TABLE 1. Percent of foraging within the defended area and within a round area of the same size centered on the nest.

Bird		Prenesting	Incubation	Nestling	Fledgling
Male I	D[a]	91.7	74.3	64.2	43.4
	R	76.3	52.0	70.5	43.6
	S	15.3	22.3	−6.3	−0.2
Female I	D	96.6	92.2	88.6	74.2
	R	81.2	79.5	90.4	78.3
	S	15.4	12.7	−1.8	−4.1
Male IIA	D	41.6	—	—	—
	R	57.7	—	—	—
	S	−16.0	—	—	—
Male IIB	D	92.6	53.9	55.1	—
	R	57.9	44.2	64.0	—
	S	34.7	9.7	−8.9	—
Male IIC	D	—	—	72.5	38.0
	R	—	—	97.9	45.9
	S	—	—	−25.4	−7.9
Female II	D	68.0	15.1	75.4	35.1
	R	78.3	39.5	96.4	86.0
	S	−10.3	−24.4	−21.0	−50.9
Male III	D	57.0	86.7	8.4	0
	R	43.0	48.3	35.2	0
	S	13.9	38.3	−26.8	—
Female III	D	72.4	65.3	50.4	45.5
	R	86.2	70.3	53.0	47.1
	S	−13.8	−5.0	−2.6	−1.6

[a] D = percent of foraging within defended area; R = percent of foraging within round area; S = Difference between the two.

The activity space is not a static area throughout the breeding season. Changes in the behavior of the birds and in the distribution and abundance of prey may lead to changes in the distribution of activities. Figure 3 shows the area of the foraging space for each bird and period. The 50% foraging space is shown as a measure of concentration of activity within the 95% foraging space.

Both birds of pair I showed an increase in the size of the 95% foraging space from the prenesting period to the fledgling period; the area enclosing 50% of the observations of foraging was least, however, in the prenesting and nestling periods. Thus, the relative concentration of foraging within the territory was greatest in the nestling period, when food was brought to the nest. By either the 95% or the 50% measure, the activity space of the male was much greater than that of the female.

Activity spaces for pair II were much like those of pair I, in spite of the turmoil in their home life; both 95% and 50% activity spaces for foraging were much smaller in the nestling period, however, than in the incubation period. This can not be attributed entirely to the need to feed young in the nest, because the reduction was also seen in male IIB, who did not participate in care of the young. Foraging was remarkably concentrated in male IIC and female II, the birds that did feed the young, in the nestling period.

A different pattern appeared for pair III. Both of the birds were recorded within very restricted areas in the first two periods but enlarged their foraging areas in the nestling and fledgling periods. As explained earlier, we feel that the areas recorded for male III during the first two periods are probably underestimates because of the difficulty in following this bird; female III showed a similar pattern, however.
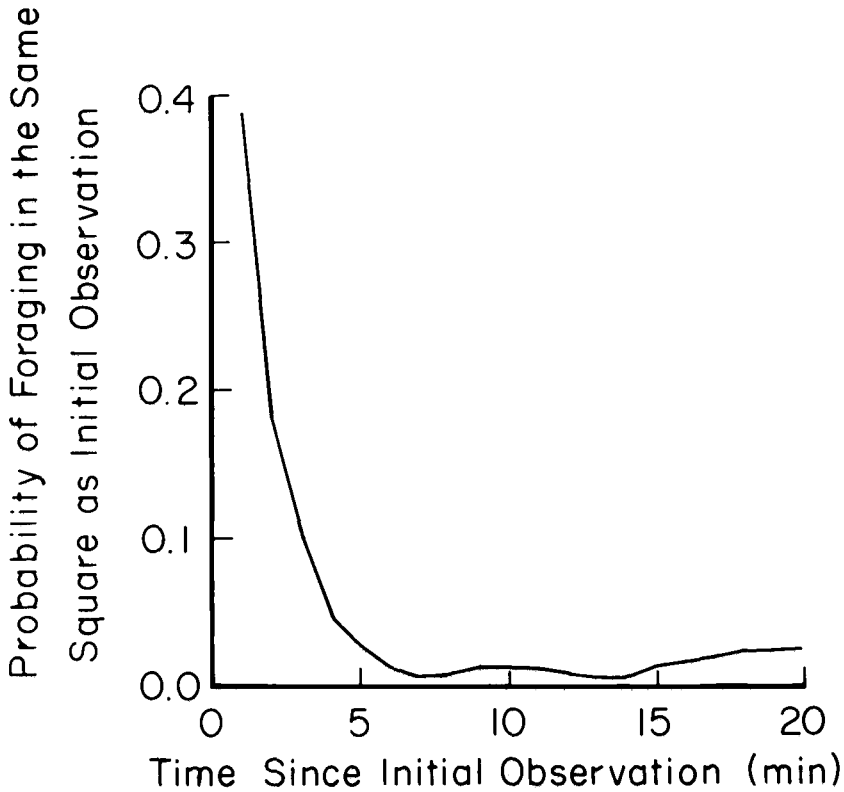
Fig. 4. Representative curve of serial correlation between observations of foraging.

Use of the behaviorally defined defended area was compared with the same area centered on the nest (Table 1). Seastedt and MacLean (1980) have shown that there is no tendency for the female to locate the nest near the center of the male's display territory at Barrow, although such a tendency was found in longspurs breeding in subarctic tundra. One would expect that a round area centered on the nest would better predict the birds' activities if the defended area lost its significance after the nest was established. The predominant pattern, shown especially by pair I, is a change from the defended area to the round area between the incubation and the

TABLE 2. Chi-square values comparing the observed distribution of the number of observations of foraging with an hypothesized random distribution, a typical pair of distributions.

Typical distribution			Chi-square values (df = 3)		
Number of observations per square	Observed number of squares	Expected number of squares	Replicate	Male I	Female I
0	226	208.1	1	14.33	36.75
1	92	110.5	2	23.60	39.38
2	23	29.4	3	13.38	20.88
3 or more	13	6.0	4	9.63[a]	18.13
$\chi^2 = 14.33$, df = 3			5	12.69	27.14

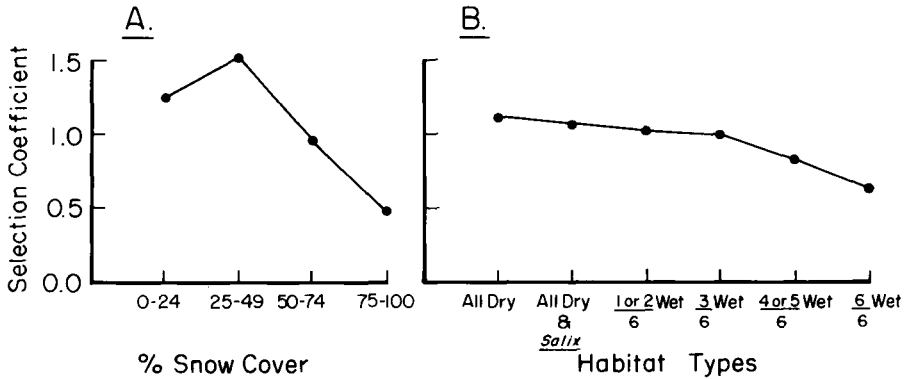[a] Significant at $P < 0.05$; all others $P < 0.01$.

Fig. 5. Selection coefficients for foraging versus snow cover and vegetation, a weighted average for all birds.

nestling periods. This suggests that the defended area has a special significance during the first two periods but that this disappears during the last two periods when active defense of the territory ceases.

Patterns of use of space.—The simplest pattern of use of space would occur if each bird foraged at random throughout the foraging area. In that case, the distribution of observations per 10 × 10-m square is predicted by the Poisson distribution. A test of this hypothesis requires a set of independent observations of foraging sites. Unfortunately, our data, like most behavioral observations, are not independent observations. The location of a bird at any time, t, is related to its location in the recent past, $t - 1$, $t - 2$, ... An examole of the serial correlation of observations of foraging is shown in Fig. 4. The probability that a bird would be observed foraging in the same square in successive observations separated by 1 min was high; this effect decayed rapidly, however, and was essentially lost after 5 min. To test the hypothesis that the foraging occurred at random, we used a Chi-square test to compare the distribution of the number of observations per square with a similar distribution generated by the Poisson distribution. We used observations separated by 5 min to minimize the effect of serial correlation. This allows five replicate distributions throughout the breeding season (t = 1, 6, 11, . . . ; t = 2, 7, 12, . . . ; etc.). Because the replicates are not independent of each other, they are tested separately against the null hypothesis (Poisson distribution). A typical pair of distributions is included in Table 2. All replicates for male I and female I were significantly different (P = 0.05) and all but one were highly significantly different (P = 0.01) (Table 2). In all cases the observed distributions were more clumped than the random foraging distribution model. This clumped pattern of use might result from either the characteristics of the habitat found in each square, which would influence productivity of prey, or from the location of the square within the defended area. We considered both of these possibilities.

Snow cover and vegetation type are habitat characteristics that might influence frequency of use of an area of foraging. During the prenesting and incubation periods, when a large part of the area was covered by snow, we found a disproportionate use of squares with partial (0–24% and 25–49%) snow cover, compared with squares that were nearly or fully (50–74% or 75–100%) covered (Fig. 5A). The birds
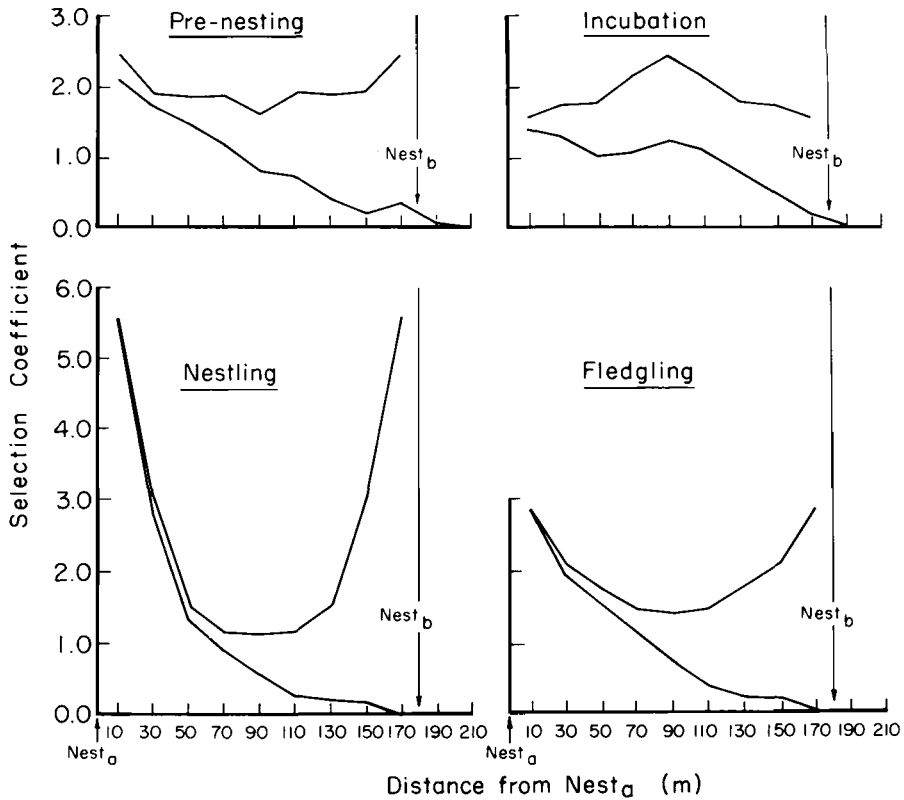
Fig. 6.   Selection coefficients for foraging versus distance from nest, a weighted average for all birds. The lower curve is a measure of foraging for one pair versus the distance from its nest. The upper curve is the sum of foraging of 2 pairs along the line between their nests if they were placed 180 m apart (the mean distance of the 3 closest nests).

spent a large amount of time feeding along the retreating margin of snow fields; as these areas move from day to day, however, this behavior should not seriously bias the use of the total area over the entire period or season.

The pattern of microtopographic features and vegetation of the coastal plain tundra forms a fine-grained mosaic relative to the feeding behavior of the birds; thus, many of our 10 × 10-m squares contained more than one topographic and vegetation unit. As a result, the response of the birds to these features may be obscured in our data. Seastedt and MacLean (1979) used substrate moisture (dry, mesic, and wet) to indicate vegetation type and prey productivity. Lumping our data for the six sample points in each square in the same way (Fig. 5B), we find a modest selection for areas of dry and mesic habitat and a strong selection against squares dominated by wet habitat. This is consistent with gross habitat selection by longspurs; nesting density is highest on raised ridges and other areas of well-drained tundra, while continuous areas of wet meadow are not used at all.

We next considered the effect of location of a square upon its frequency of use. Distances were measured to the nest in the first three periods, but, as the nest was not used as a focal point in the fledgling period, the center of activity was used in that period. It is defined as the geometrical average of all observations of foraging

in the fledgling period. The lower curves of Fig. 6 show the relationship between amount of foraging and distance from the nest, expressed as a weighted average for all birds and graphed for each period. A decrease in use is shown with distance from the nest or center of activity. This relationship is weakest in the incubation period and strongest in the nestling period, when both adults make recurrent visits to the nest to feed the young.

The overall use of tundra resources can be estimated by considering the overlapping use (because foraging spaces are larger than defended areas) by neighboring birds. The mean distance from each of the three nests observed to the three closest nests was 180 m. If we assume that neighboring birds used the surrounding areas in a manner similar to the birds that we observed, the use of any area along the line between two nests should approximate:

use(pair A) at x m from nest + use(pair B) at $(180 - x)$ m from nest.

Use of the area by adjacent pairs is shown in the upper curves of Fig. 6. These show that use of tundra resources was rather even during the first two periods of the season, actually reaching a peak between the two nests in the incubation period. Use then became concentrated about the nest in the nestling period and the center of activity in the fledgling period; the use of intervening areas was low in the nestling period. We cannot make the same claim for the fledgling period, because, once the young leave the nest and territoriality wanes, the 180-m mean distance between nests loses its significance. A comparable concentration of activity in the center of the activity space was reported by Weeden (1965) for Tree Sparrows (*Spizella arborea*); the overlap in use by longspurs, however, appears to be greater than that of tree sparrows.

DISCUSSION

Odum and Kuenzler (1955) examined changes in the area used by three passerine bird species throughout the breeding season and found that utilized space was smallest during the period of feeding the nestlings. They argued that because the defended area was much larger than the area used to feed the chicks during the period of highest energy demand, defense of space must provide some benefit other than the food supply contained therein. They argued further that if this were shown to be a general pattern, it would provide evidence against the hypothesis that the function of the defended area (territory) is to protect an adequate food resource. Other studies by Young (1951), Weeden (1965), Willson (1966), Stefanski (1967), Root (1969), and Yarrow (1970) have shown a similar decline in the area used during the period of feeding the nestlings. The present study on Lapland Longspurs shows an increased concentration of use about the nest at this time, although the total area used does not decrease. In contrast, Stenger and Falls (1959) found that the area used by foraging Ovenbirds (*Seiurus aurocapillus*) increased while feeding nestlings.

Interpretation of the area of foraging spaces is hampered by the serial correlation of observations. The measure of serial correlation that we used (Fig. 4) is conservative in that it did not consider use of adjacent squares in successive time periods. Odum and Kuenzler (1955) suggested that 25–90 serial observations at 5-min intervals or 2–8 h of field observation were required to define territory size adequately. We suspect (as Odum and Kuenzler's figures indicate) that this is a minimum estimate. In our study, area gains curves leveled off after approximately 8 h of observation.

Certainly, the sample sizes reported by Stefanski (1967) (observation periods of 1 h) and Yarrow (1970) (20 observations chosen at random) are too small to characterize the total area of use although they might indicate the relative concentration of use during the period of observation.

In order to test the hypothesis that the function of territoriality is related to the food that it provides, the pattern of use of the territory must be considered in conjunction with changes in the time and energy requirements of reproductive activities and in the availability of food.

The energy demands of the adult Lapland Longspurs increase steadily until just before the chicks are independent (Custer 1974). If the availability of food resources were constant, the decrease in area used while feeding the chicks would contradict the food hypothesis. Although the absolute food requirements are highest while feeding the chicks, the abundance of food may be great enough to lessen the demands on the adults. Nesting is apparently timed so that the fledging of the chicks corresponds with the emergence of adult craneflies (Diptera, Tipulidae). Pupae are the primary food brought to the nestlings (Seastedt and MacLean 1979). Craneflies pupate in the surface moss layer of the tundra, and pupae are easily found by foraging longspurs.

During the prenesting and incubation periods adult activities are dispersed over the available area. The distribution of male activities is influenced by the location of the territory boundaries to be defended, the location of the female, and of other potential mates. Although a female's activities become centered upon the nest, she can most efficiently use the food resources by long foraging trips, limited only by the time that eggs can be left unattended.

The uniform use of an area by neighboring pairs during the prenesting and incubation periods supports the position that territoriality serves to disperse breeding pairs in order to distribute their foraging activity evenly over the available resources. Once all nests have been established, this objective has been served, and active defense of the territory can wane without placing the birds in direct competition for the resources. During the nestling period, foraging activities of the adult are focused upon the nest. Concentration of foraging around the nest minimizes the time and energy that must be spent in flight to and from the nest and young. At this time the intermediate areas that were heavily used in the incubation period receive very little use. This concentration of use is made possible by the increased availability of foraging area due to the completion of snow melt and by the increased availability of prey resulting from pupation of craneflies.

Food is maximally available during the fledgling period, when the tundra surface is often aswarm with adult Diptera. The concentration of foraging declines because of the movement of the young within or even away from the territory as territorial boundaries lose their meaning. It is hard to believe that competition for food is significant at this time. Food availability may decline drastically due to periods of inclement weather, but this would not be influenced by the presence of other birds with overlapping foraging spaces.

Thus, we believe that territorial behavior serves to space out the birds and minimize (but not prevent) direct competition for food in the first half of the breeding cycle, when both time and space available for foraging are limited and food availability is less than maximum. This behavior also contributes to the spacing of nests, which provides exclusive use of the resources immediately around the nest during

the nestling period when concentration of foraging is important. This is achieved without the need for active defense of the resources at this important time, so that time and effort may be devoted entirely to feeding the young. Thus, territorial behavior and the use of space are both adaptive with respect to use of the food resource.

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