ECOLOGICAL CORRELATES OF INCUBATION FEEDING: A COMPARATIVE STUDY OF HIGH ARCTIC FINCHES[1]

BRUCE E. LYON[2] AND ROBERT D. MONTGOMERIE
Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada

Abstract. We compared the ecology of two high arctic finches to determine which ecological factors might influence male parental roles during incubation. Male Snow Buntings (*Plectrophenax nivalis*) feed their mates at the nest throughout the incubation period, while male Lapland Longspurs (*Calcarius lapponicus*) usually do not. We identified and tested seven ecological factors that could potentially explain the difference between these two species; (1) risk of nest predation, (2) nesting synchrony, (3) potential for polygyny, (4) timing of breeding, (5) diet, (6) distance between nest and foraging areas, and (7) nest microclimate. Of these, only predation rate and nest microclimate differed significantly between longspurs and buntings.

Buntings nest in rock cavities and suffer lower overall nest predation than longspurs (28 vs. 51%, respectively), suggesting that this factor could influence the occurrence of incubation feeding. However, since male longspurs could feed their mates away from the nest, risk of nest predation can only explain why incubation feeding at the nest does not occur, not why incubation feeding per se is rare in longspurs.

Due to differences in nest microclimate on sunny days, eggs cool more rapidly in bunting nests, suggesting that female longspurs can take advantage of solar radiation to warm their eggs and can consequently spend a higher proportion of their time foraging than female buntings. A comparison of female incubation schedules supports this idea; female longspurs spent more total time off their eggs ($\bar{X} = 25.9$ min/h) than female buntings ($\bar{X} = 15.9$ min/h). We conclude that, of the factors we investigated, the colder nest microclimate associated with hole nesting has been the most important ecological factor influencing the occurrence and high frequency of incubation feeding in Snow Buntings. We discuss the possibility that hole nesting favors incubation feeding in passerine birds in general.

Key words: arctic; Snow Bunting; Calcarius lapponicus; *comparative method; ecological correlates; incubation feeding; Lapland Longspur; nest microclimate; nest predation; parental care;* Plectrophenax nivalis.

INTRODUCTION

In birds there is considerable variation in male parental roles during the incubation period. In some species males share incubation duties with females, whereas in others the male either is the sole incubator, feeds the incubating female, or does nothing at all (Kendeigh 1952). Recently, Silver et al. (1985) made a broad-scale comparison (at the subfamily level) of parental behavior in birds, but there is still little information available on the ecological factors that could explain differences in male behavior between closely related species during the incubation period.

In some species of passerine birds, for example, males feed their mates during incubation, while in closely related species females incubate their eggs without male assistance. A comparative study was unable to identify broad ecological correlates of incubation feeding (Ricklefs 1974), and the taxonomic distribution of incubation feeding indicates that it has arisen independently

in several taxa (e.g., hornbills (Coraciiformes), diurnal raptors (Falconiformes), and songbirds (Passeriformes) (Kendeigh 1952). Thus, this broad-scale comparative approach may have failed to identify ecological correlates of incubation feeding because this trait is favored for different reasons among different taxa of birds. A small-scale comparison of closely related species living in the same habitat would avoid the problem of confounding factors that complicate the detection of ecological correlates (Jarman 1982), and is therefore a useful tool for understanding specific examples of variation in behavior (e.g., Post and Greenlaw 1983).

In this study, we compare the ecology of two arctic finches, Snow Buntings (*Plectrophenax nivalis*) and Lapland Longspurs (*Calcarius lapponicus*), to explore the ecological correlates of incubation feeding that might help to explain why male Snow Buntings feed their mates throughout incubation (Hussell 1972, Lyon and Montgomerie 1985), but incubation feeding does not normally occur in longspurs (Williamson 1968, Hussell 1972). These species are excellent subjects for a comparative study because their life history tactics are so similar and have been thoroughly examined (see Stearns 1976). Their breeding ranges overlap almost entirely,

[2] Present address: Department of Biology, Princeton University, Princeton, New Jersey 08544 USA.
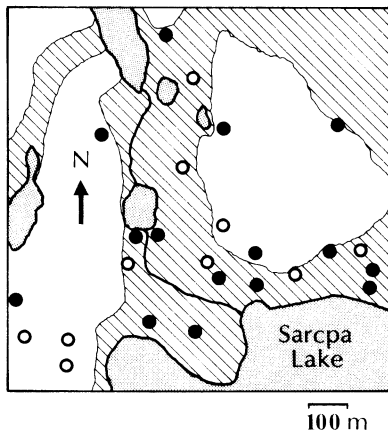
FIG. 1. Distribution of ○ Snow Bunting and ● Lapland Longspur nests on a 1-km² section of tundra in 1983. Habitats shown are □ lakes and ponds, ▨ well-vegetated, and □ dry, rocky tundra.

and both species use similar habitats in winter (Godfrey 1966). At some sites, buntings have slightly larger clutches (Hussell 1972, but see below), but the growth rates of their chicks are identical to those of longspurs (Maher 1964). In summer, both species feed in similar habitats and their diets appear to be almost identical (Custer and Pitelka 1975). The most notable habitat difference on the breeding grounds is their nest site; longspurs nest in open cups, often tucked into the sides of hummocks, while buntings nest in rock crevices or under boulders and their nests are well hidden (Hussell 1972).

Elsewhere we have shown that incubation feeding in buntings sometimes enhances their immediate reproductive success (Lyon and Montgomerie 1985). In this study we ask why the incidence of incubation feeding in these two species differs and whether the difference has an adaptive basis. We address these questions by examining a number of ecological and behavioral factors that might differ between the species and could logically account for the difference in incubation feeding by males.

STUDY AREA AND SPECIES

Our study area was 13 km² of upland high arctic tundra on the north shore of Sarcpa Lake, Melville Peninsula, Northwest Territories, Canada (68°33′ N, 83°19′ W). Within this area we have identified six major habitat types (see also Montgomerie et al. 1983): ponds and small lakes (5% of total area), wet sedge meadows (10%), solifluction zones (30%), dry ridges vegetated with lichens and mat-forming shrubs like *Dryas integrifolia* M. Vahl (20%), boulder fields and exposed rock (25%), and disturbed areas (10%). Most of our work was done in two 2-km² sites, one at the eastern and one at the western end of our main study area.

Longspurs and buntings are the most common

breeding birds at this site (Montgomerie et al. 1983), with breeding densities as high as 25 and 12 pairs/km², respectively. Although their specific nest site requirements differ markedly, the distribution of suitable nest habitats is fine grained enough that these species usually nest close to each other over much of the study area (Fig. 1). Both species return to the study area in late May, begin nesting in mid-June, and leave the area in late July and early August (Montgomerie et al. 1983). The clutch sizes of buntings ($\bar{X}$ = 5.18, n = 81) and longspurs ($\bar{X}$ = 5.08, n = 105) did not differ significantly at our site during the period 1981–1985; t = 0.92, P = .36).

Because of the short breeding season we worked on different problems in different years from 1981 to 1985. As a result, some of the comparisons between species are made for only one or two breeding seasons during this 5-yr period.

POSSIBLE ECOLOGICAL CORRELATES

During the course of our study we identified the following seven ecological and behavioral factors that could potentially explain the presence of incubation feeding in Snow Buntings and its virtual absence in longspurs. For convenience, we group these seven factors into three major categories of explanation, as follows:

Nest predation

1. *Risk of nest predation.* — Incubation feeding may be absent in longspurs because the predation risks of male attendance at the nest during incubation outweigh the benefits of incubation feeding. Although males of both species are relatively conspicuous (compared to females), longspurs may be more susceptible to nest predation than buntings because they nest on the open tundra. Certainly all longspur nests that we have seen (n > 200) would be accessible to predators. In contrast, bunting nests are never visible from above and, even when they can be seen down a rock crevice or under boulders, they are often inaccessible to most predators (B. E. Lyon and R. D. Montgomerie, *personal observations*). Aerial nest predators (jaegers, gulls, and owls) would not be able to prey on most bunting nests even if they could find them, and large mammalian predators (fox, wolf) would find them equally inaccessible. Although males of both species would attract predators to the nest site, incubation feeding by male longspurs at the nest would incur a higher cost because their nests are more accessible.

Sexual selection

Interspecific differences in male parental care may result from differences in the intensity of sexual selection (Trivers 1972). Thus, incubation feeding might enhance the immediate reproductive success of the female in both species, but be absent in longspurs because males gain more by additional matings (e.g., cuckoldry

or polygyny) than they gain by feeding their mates. If this is true, then incubation feeding in buntings would occur because male buntings have a much lower probability than male longspurs of obtaining additional matings. The following two factors could explain why male longspurs might have a higher potential for additional matings than buntings.

2. *Nesting synchrony and cuckoldry.* — Male longspurs attempt to cuckold other males after their own female's clutch has been laid (R. D. Montgomerie and R. L. McLaughlin, *personal observation*). Thus the potential for additional matings through cuckoldry may be a function of nesting synchrony in the population, as has been suggested in a general treatment of sexual selection (Knowlton 1979). If buntings nested more synchronously than longspurs, there would be little opportunity for additional matings by male buntings.

3. *Potential for polygyny.* — There would be more potential for polygyny in longspurs if their operational sex ratio were more female biased. If the potential for polygyny were high enough, male longspurs that tried to acquire an additional mate might gain an advantage over those who fed their single mate.

Female self-sufficiency

Female longspurs may be able to carry out an optimal incubation schedule unaided by the male, while female buntings require male assistance to maintain optimal conditions for egg development. We assume here that the eggs of longspurs and buntings have similar thermal requirements for optimal development (e.g., high hatch success and maximum development rate; White and Kinney 1974), and therefore that the differences in incubation tactics between these two species result in the same thermal conditions for their eggs. Based on this assumption we suggest the following four ecological factors that could influence a female bunting's incubation schedule or foraging behavior, and therefore limit her self-sufficiency during incubation.

4. *Timing of breeding.* — The availability of insect food on the tundra increases rapidly after snow melt and peaks in mid-July (Holmes 1966, McLaughlin and Montgomerie 1987). Thus if buntings nested earlier than longspurs, fewer insects would be available to them during incubation and an unaided female bunting would require more foraging time to meet its daily energy demands. Thus, incubation feeding would be necessary to permit females to achieve optimal incubation conditions.

5. *Diet differences.* — If the food eaten by buntings were less abundant or more difficult to gather (i.e., longer search or handling times) than that eaten by longspurs, then an unaided female bunting would have to spend more time away from her nest to meet her daily energy demands than would a female longspur.

6. *Distance to foraging areas.* — Both longspurs and buntings forage in wet sedge meadows or on well-vegetated dry tundra at Sarcpa Lake (B. E. Lyon and R.
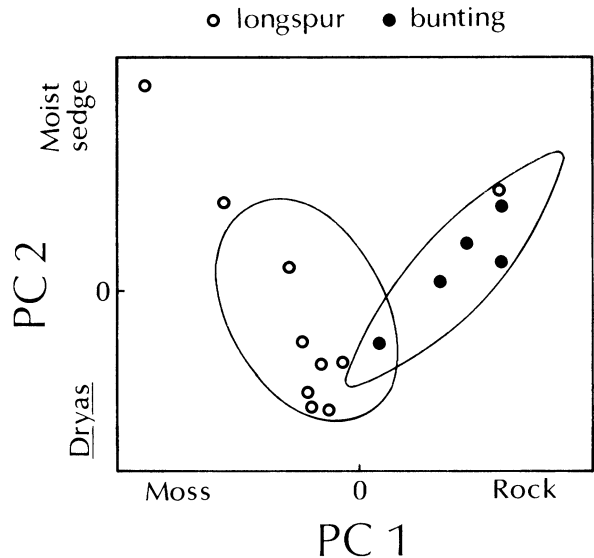

FIG. 2. Principal component analysis of habitat around 10 Lapland Longspur and 5 Snow Bunting nests. For each nest we took 300 point samples within 50 m of the nest and classified these according to nine microhabitat types: stone, rock, peat, moist sedge, wet sedge, dry sedge, *Dryas*, dry mud, and water. First and second principal components are plotted; PC1 is a moss-to-rock axis and PC2 is a *Dryas*-to-moist-sedge axis. Longspur and bunting nests separate significantly on PC1; (two-tailed t test, $t = -3.47$, $P < .005$). The 95% confidence ellipses of the samples are shown.

D. Montgomerie, *personal observations*) but their nesting habitats are distinctly different (Fig. 2). Longspurs nest on well-vegetated tundra similar to that on which they forage, whereas buntings nest in rocky areas. If the special nest habitat requirements of buntings result in their nesting at considerable distances from foraging sites, foraging females may incur high travel costs and a longer absence from the eggs during foraging bouts.

7. *Nest microclimate.* — Buntings nest in rock cavities and, at most nests, eggs are always in the shade. At a few nests, eggs may be in the sun for up to 1 h per day, depending on the nest orientation. In contrast, longspurs nest in the open and could readily take advantage of solar radiation. Thus, when the incubating female is away foraging, eggs in bunting nests may cool more rapidly and to lower equilibrium temperatures. If bunting nest sites have a colder microclimate during most days during the incubation period, female buntings may be forced to spend less time away from the eggs than female longspurs to maintain optimal thermal conditions for the eggs. Incubation feeding by male buntings would therefore permit females to spend less time away from their nests and still meet their own energy demands.

METHODS AND RESULTS

Incidence of incubation feeding

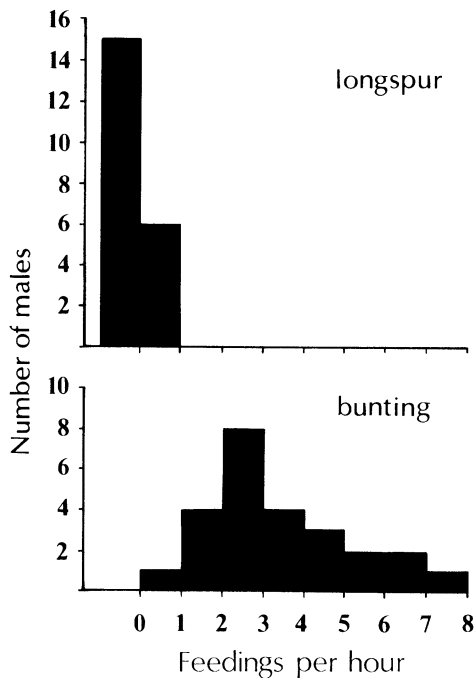We observed buntings and longspurs during the incubation period to document the occurrence and fre-

FIG. 3. Mean rates of incubation feeding for 21 male Lapland Longspurs and 25 male Snow Buntings (see Methods for monitoring of nests).

TABLE 1. Nest predation rates for Snow Buntings and Lapland Longspurs at Sarcpa Lake. Rates are proportions of all nests found that were preyed on before fledging. Sample sizes are given in parentheses.

	Nest predation rate		G test*	
Year	Longspur	Bunting	G	P
1981	0.47 (17)	0 (7)	6.97	<.01
1982	0.48 (21)	0.27 (15)	1.58	>.2
1983	0.18 (17)	0.31 (32)	1.06	>.3
1984	0.85 (20)	0.43 (7)	3.99	<.05
All years	0.51 (75)	0.28 (61)	7.31	<.01

* G tests compared predation rates within years.

In contrast, incubation feeding was observed only once during direct observations of male longspurs, and this feeding took place at the nest. However, a low frequency of incubation feeding was observed at five of the six nests monitored by movie cameras in 1984 (Fig. 3), but at neither of the nests monitored in 1983. Since these nests were monitored by cameras set at 1-min intervals, the actual frequency of incubation feeding at these five nests is difficult to assess. To calculate an approximate rate of feeding, we assumed that each feeding visit lasted 10 s and therefore that our cameras recorded only $\frac{1}{6}$ of the visits. Our observations at bunting nests indicate that the males are present at the nest a minimum of 10 s, so that our estimates of feeding rates in longspurs may be somewhat inflated.

Ecological factors: data collection and tests

In this section we examine each of the seven ecological and behavioral factors that might have an influence on incubation feeding. One-tailed statistical tests were used whenever a specific directional difference between buntings and longspurs was expected from theory.

1. Risk of nest predation. — To determine conclusively whether the risk of nest predation has influenced incubation feeding in longspurs, we would have to compare the reproductive success of pairs with and without this male behavior. Since such a comparison is impossible because longspur males so rarely feed their mates, we performed an indirect test of this prediction by comparing nest predation rates between the two species. In making such a comparison we assume that both species are susceptible to the same nest predators and that parental nest defence in both species would have the same effect on nest predation rates. Thus we also assume that any difference in nest predation rates reflects differences in the accessibility of nests between the two species.

To determine predation rates on nests, we visited nests of both species regularly during the incubation period. In 1985 we did not monitor a sufficient number of bunting nests closely enough to determine predation rates, so we compare predation rates for only 4 yr of the study (Table 1). Nest locations of both species were

quency of incubation feeding. Most bunting nests were observed for 1-h periods between 0800 and 1800 on at least four different days to record the number of times the male brought food to the female at the nest. Eight nests were watched during incubation in 1982 and 17 in 1983.

To determine whether male longspurs ever fed their mates during incubation, we followed 13 males for 30-min periods during incubation, 6 males in 1981 and 7 males in 1985. Each male was observed for a total of at least 90 min, resulting in a grand total of 55 h of observation. By following males rather than observing nests, we could monitor the occurrence of incubation feeding both at and away from the nest (since, in some species, incubation feeding takes place primarily away from the nest; East 1981).

As part of another study, we also monitored the nests of eight longspurs during the incubation period (two in 1983, six in 1984) using Minolta XL-401 movie cameras. These cameras have built-in intervalometers and photos were taken automatically every minute of the 24-h day. From these films we used data only from 0800–1800 to correspond to the time of day when buntings were observed. Because buntings nest in dark cavities, it was not possible to use these cameras to monitor their nests as well.

All male Snow Buntings watched during the incubation period fed their mates (Fig. 3). Although there was much variation in the frequency of incubation feeding among males, all males fed their females throughout the incubation period.

cryptically marked, and we have no evidence that our activities caused differential predation rates on the nests of one species. During the course of our study we observed nest predation by weasels and arctic foxes *(Alopex lagopus)* and we expect that most nest predation was due to these two species.

The predation rates reported here are the proportions of nests lost to predators during the entire nesting period. Since almost all nests were found before incubation began (e.g., 37 of 38 bunting and 36 of 42 longspur nests), there was no need to apply a correction factor to determine predation rates (e.g., Mayfield 1975).

Longspurs lost a significantly higher proportion of their nests to predators in 2 of the 4 yr, and overall had a significantly higher rate of nest predation (Table 1). We interpret these results as demonstrating that longspur nests are more accessible to predators. Thus, risk of nest predation may be an important factor in influencing the occurrence of incubation feeding.

2. *Nesting synchrony and cuckoldry.* — To compare the breeding synchrony of these two species, we used the date of clutch completion for each nest. Most nests were found during laying so the date on which the last egg was laid in each nest was observed directly. Egg-laying dates for the few nests (one bunting and six longspur nests) that were found after egg-laying was complete were determined by extrapolation from egg-hatching dates (assuming 12-d incubation periods for both species; Hussell 1972). A sufficient number of nests of both species (i.e., at least 10) to permit a comparison was found only in 1982 and 1983, so our analysis is limited to these 2 yr.

Nest initiation was relatively asynchronous in both species in 1982 and 1983 (Fig. 4), but there was no significant difference between the species in the distribution of nest initiations for either year (Kolmogorov-Smirnov two-sample test; for 1982 $D = 0.14$, $n_1 = 13$, $n_2 = 23$, $P > .1$; for 1983 $D = 0.04$, $n_1 = 25$, $n_2 = 19$, $P > .1$). We conclude that there was no difference in the degree of synchrony that could contribute to differences in the level of cuckoldry.

3. *Potential for polygyny.* — For both species, the mating status (i.e., number of mates) of territorial males was determined by daily observation of known individuals. Individuals of both sexes were readily identifiable by colored leg bands and/or distinctive plumage; males and females of both species have considerable interindividual variation in plumage (B. E. Lyon and R. D. Montgomerie, *personal observation*). We also watched carefully for unmated females, who were conspicuous because of the attention they received from territorial males. Whether or not males had mates was obvious, since the members of mated pairs were almost never more than a few metres apart when the females were fertilizable. Any males that did not have mates were conspicuous by their high song rates.

Polygyny is rare in these species at our study site, with one known case and an additional suspected case
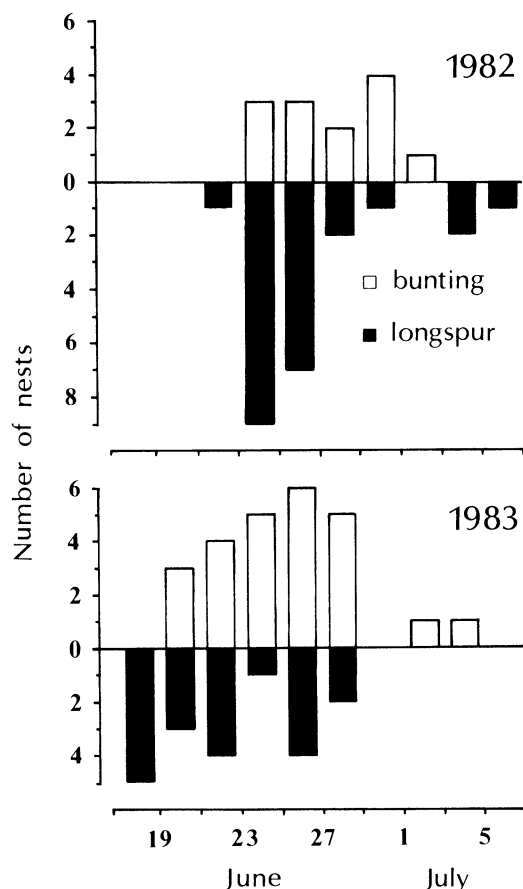

FIG. 4. Date of clutch completion for Snow Buntings and Lapland Longspurs in 1982 and 1983.

in each species in 1982 ($n = 20$ male buntings, 18 male longspurs), but no known cases in the other 4 yr of the study. In both 1982 and 1983, when buntings were observed most intensively, there appeared to be a slight excess of female buntings, as small flocks of unmated females were noted up to the end of the 3rd wk in June, when all males in the population had mates. These females visited paired males but were chased off by resident females. We have never observed unmated female longspurs.

In 1982, two territorial male longspurs did not obtain mates, though they defended territories well past the latest date of clutch initiation. No unmated male buntings have ever been observed in the study area after the normal period of clutch initiation.

The occasional presence of unmated *male* longspurs and unmated *female* buntings indicates that male buntings should have more potential than male longspurs to obtain additional mates. Thus, a difference in the intensity of sexual selection between longspurs and buntings does not appear to be an important factor affecting the availability of males to feed their incubating females.

4. *Timing of breeding.* — The relative timing of
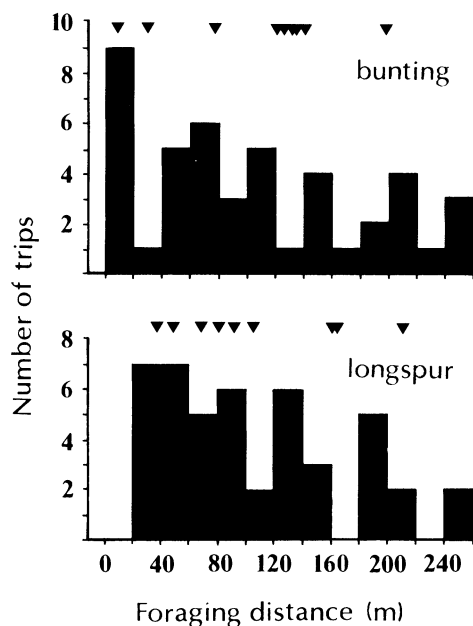
BRUCE E. LYON AND ROBERT D. MONTGOMERIE

FIG. 5. Distribution of distances (5 per female) flown to foraging areas during incubation by 9 female Lapland Longspurs and 9 female Snow Buntings in 1985. Triangles above histograms are means for each individual female.

breeding of the two species is shown in Fig. 4. The median clutch-completion date in both years was actually slightly later for buntings than longspurs, but these differences were not significant in either year (Median test, 1982: $\chi^2 = 1.93$, $P > .1$; 1983: $\chi^2 = 2.45$, $P > .1$). Thus, earlier breeding by buntings can be ruled out as an explanation for the occurrence of incubation feeding.

5. *Diet differences.*—We did not collect data on the diets of these species at Sarcpa Lake, but extensive data are available from the nestling period on Devon Island, Northwest Territories (Hussell 1972). To compare diets we calculated a simple percent overlap index (based on numerical representation) for the 12 classes of prey identified by Hussell (1972), following the method described by Holmes and Pitelka (1968).

Nestling diet overlap between these species on Devon Island was 96.9%; the species do not differ significantly in the relative abundance of each prey class in the total diet ($G = 6.34$, 7 df, $P > .1$; prey classes were collapsed to eight types to avoid cells with small frequencies).

6. *Distance to foraging area.*—Data on the distances flown from the nest to foraging sites were collected during the incubation period in 1985. We recorded distances on five trips for each of nine females of each species. Distances were measured by following the female from her nest and dropping a marker at the farthest foraging site visited on each trip.

Female buntings did not fly farther to forage during the incubation period than longspurs (Fig. 5). Individual females flew a wide range of distances, but there

was no significant difference between the species (comparing means for each female; Mann-Whitney $U = 42$, $P > .05$, one-tailed test).

7. *Nest microclimate.*—We determined the effect of nest microclimate on the cooling rates of eggs by using a dummy egg made of Silastic, a substance with cooling properties similar to avian eggs (Calder 1971). Internal dummy egg temperature was measured with a thermistor probe attached to a telethermometer. Before each trial, the dummy egg was brought to 40°C in a water bath. It was then quickly dried and the trial started as the egg was placed in the nest. We recorded egg temperature every 15 s for 10 min, or until an equilibrium temperature was reached. Cooling trials were run in several nests of each species in late July 1983, after young had fledged from the nests. Paired cooling runs (one longspur, one bunting) were done in random order by species within 30 min of each other to minimize differences due to changing weather conditions.

Under warm, sunny conditions, eggs cooled more rapidly in bunting nests (Fig. 6A) and to a lower equilibrium temperature. In the example shown in Fig. 6A, the dummy egg in the longspur nest took 8 min to cool to the same temperature reached by the egg in the bunting nest in 1 min.

To test whether solar radiation and not some property of the nest itself was responsible for these differences, trials were also run on cool, overcast days (e.g., Fig. 6B). The rate of cooling under these conditions was nearly identical in the nests of the two species.

A summary of all trials is illustrated in Fig. 6C. Here we have plotted the difference in egg temperature between the longspur and bunting nest at each minute of the paired runs. Whenever the longspur nest was in the sun (three trials), the egg cooled much more rapidly in the bunting nest and to a much lower equilibrium temperature, while under cloudy conditions (two trials) there was virtually no difference in the cooling rates of the egg in the two nest types.

DISCUSSION

This study has identified two correlates that might have influenced the occurrence of incubation feeding in Snow Buntings: a lower risk of nest predation, and a colder nest microclimate. Two further considerations are important before we can conclude that these correlates are indeed factors that are responsible for the interspecific differences in the role of the male during incubation. First, we must consider whether the difference between buntings and longspurs is actually an adaptive difference. If it is not, then a search for causal factors is unwarranted. Second, since these correlations may not represent causal relationships, it is important to consider whether they have actually influenced the evolution of incubation feeding. We address each of these two considerations below, followed by a discussion of more general factors that may have influenced the evolution of incubation feeding.
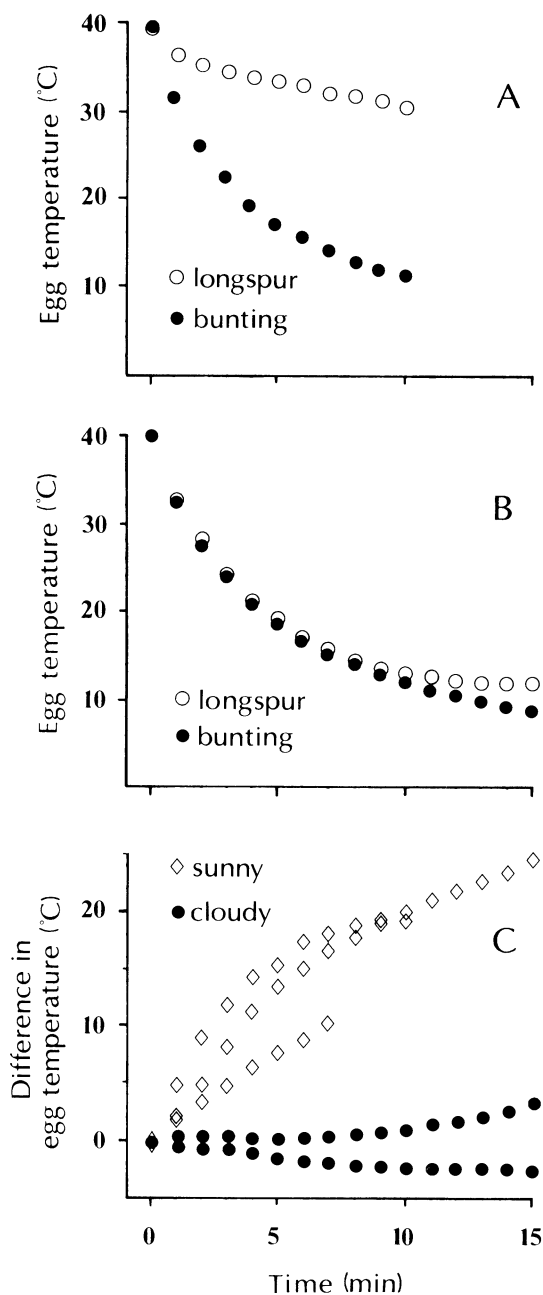
FIG. 6. Cooling rate of a Silastic egg in nests of Snow Buntings and Lapland Longspurs: (A) example of a trial run on a sunny day, (B) example of a trial run on a cloudy day, and (C) results of all five paired trials (three on sunny days, two on cloudy days) plotted as the difference in egg temperature between the longspur and bunting nest at each minute of the trial. A rapid increase in the temperature difference (e.g., top three curves in [C]) indicates a much more rapid cooling of the egg in the bunting nest.

Is the difference between these species adaptive?

Interspecific comparisons are useful tools for unravelling the various biological factors that underlie patterns in animal behavior and social organization. Our

use of the comparative method here assumes that the traits of interest are indeed adaptations, and not simply developmental or historical constraints. We have used the comparative approach to identify two ecological correlates of incubation feeding in Snow Buntings and Lapland Longspurs, but it is important to consider the possibility that a difference between the two species may not be an adaptive difference, but the result of nonadaptive constraints on the evolution of behavior (e.g., Jarman 1982).

Two lines of evidence indicate that the difference in incubation feeding between these two species is, in fact, adaptive. First, incubation feeding does affect correlates of fitness in Snow Buntings. We have previously shown that when female Snow Buntings are experimentally deprived of incubation feeding, they increase the amount of time spent off the eggs, and have a reduction in hatch success and a longer incubation period (Lyon and Montgomerie 1985). Both of these fitness consequences are known to result from exposure of eggs to cold temperature (Lundy 1969, Romanoff and Romanoff 1972), adding further support to our finding that nest microclimate is important. Second, incubation feeding is not absent in longspurs due to nonadaptive constraints on the evolution of this behavior. The fact that in 1984 we observed incubation feeding by 5 of the 6 males observed indicates that incubation feeding is part of the behavioral repertoire of most male longspurs. Thus, the expression of this behavior could increase in the longspur population if it had a positive effect on male fitness.

We can now ask whether incubation feeding may also be an adaptive behavior in longspurs, even though it is rare. We observed regularly occuring incubation feeding in only one (1984) of the 5 yr of observations on longspurs. That year appeared to have the lowest food availability during laying and incubation, demonstrated by significantly smaller longspur clutch sizes in 1984 than in any other year (Table 2). Thus, it appears that the potential for incubation feeding is part of each male longspur's behavioral repertoire, but that the behavior appears only under extreme conditions that render it useful to both parents. Such a close match between the occurrence and the apparent usefulness of incubation feeding can easily be understood if the rate

TABLE 2. Lapland Longspur clutch size distributions. Mean clutch sizes for each year are compared (two-tailed t test) to 1984, the year in which most incubation feeding by longspurs was observed.

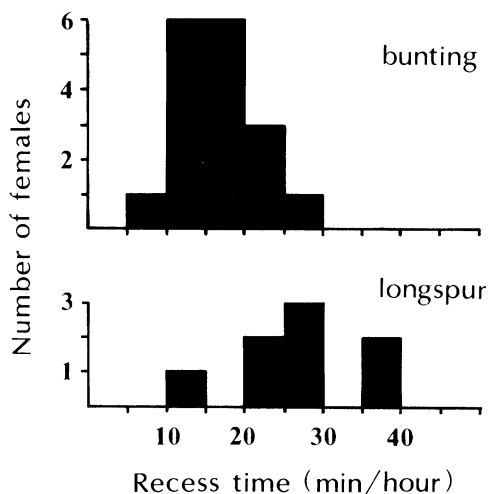| Year	Clutch size						Comparison with 1984	
	3	4	5	6	7	Mean	t	P
1981	0	1	12	2	0	5.07	−3.22	.003
1982	0	5	16	3	1	5.00	−2.95	.005
1983	1	5	15	3	0	4.83	−2.13	.037
1984	2	11	9	1	0	4.39	···	···
1985	0	0	2	12	4	5.11	−3.44	.001

FIG. 7. Amount of time spent off eggs per hour by 17 female Snow Buntings fed by their mates and 8 female Lapland Longspurs. The mean hourly absence is plotted for each female based on at least four 1-h observation periods.

of incubation feeding is correlated with the rate of begging by females (e.g., East 1981). Thus, female longspurs may only beg for food when feeding conditions are extremely poor.

Correlates of incubation feeding: are they causes?

Nest predation was significantly lower at bunting nests in 2 of the 4 yr examined, as was the overall average risk of predation. Thus, even without male visits to the nest during incubation, longspurs are more vulnerable to nest predation than buntings. This relatively high susceptibility to nest predation might be magnified if males visited the nest more frequently during incubation, and the added risk might outweigh the modest advantages of incubation feeding (Lyon and Montgomerie 1985).

Risk of predation, however, can explain only why incubation feeding *at the nest* does not occur, and not why incubation feeding in general is lacking. In some passerine species, incubation feeding occurs commonly but almost always away from the nest (e.g., East 1981). Given that this option would be available to Lapland Longspurs, it seems unlikely that the high risk of nest predation for this species has played an important role in influencing the frequency of incubation feeding per se.

A cold nest microclimate is also associated with incubation feeding in buntings. We suggest that female longspurs can take advantage of solar radiation and can therefore afford to spend more time away from their eggs than female buntings, without subjecting the eggs to dangerously cold temperatures. This increased foraging time permits female longspurs to meet their energy demands. In contrast, female buntings require food from the male to meet their demands.

To conclude that nest microclimate could be an important influence on the occurrence of incubation feeding, we need to demonstrate that the effects of nest microclimate are important enough to influence female incubation behavior, and therefore indirectly affect fitness. Thus, if nest microclimate is important, we predict that incubation feeding should permit female buntings to spend less time away from their eggs than female longspurs. We can test this prediction by comparing incubation schedules.

In 1983, we watched 17 Snow Bunting nests for at least four 1-h observation periods each and recorded the total number of minutes per hour spent off the nest. Female buntings at all 17 nests were fed by their mates. For longspurs, we analyzed the films made by automatic camera records at 8 longspur nests as described earlier. For both species, observations were made between 0800 and 1800.

Female buntings spent significantly less time away from their eggs ($\bar{X} = 15.9$ min/h, $n = 17$) than female longspurs ($\bar{X} = 25.9$ min/h, $n = 8$; Mann-Whitney $U =$
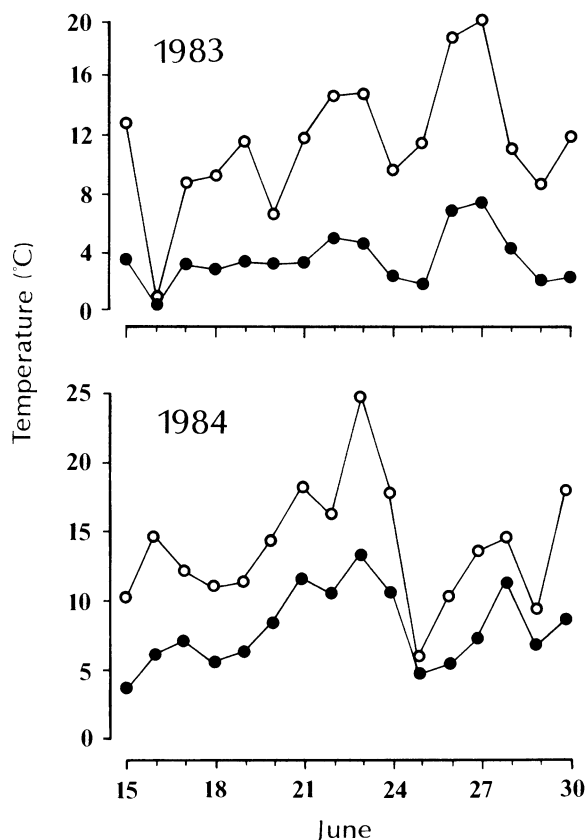

FIG. 8. Daily mean temperature of ○ a Silastic egg on the ground, exposed to solar radiation and ● a thermal probe measuring air temperature in the shade. Shown are the daily means for the 2-wk period when almost all Lapland Longspurs are incubating. Each daily mean is calculated from temperatures taken every minute between 0600 and 1800, to correspond to the time of day when longspurs could potentially take advantage of solar radiation.

18, $P < .005$, one-tailed test; Fig. 7). Thus, the importance of nest microclimate as a factor influencing incubation feeding is supported both by direct and indirect tests: (1) eggs cooled more rapidly under sunny conditions in bunting nests than in longspur nests, and (2) female buntings that were fed by their mates spent less time away from their nests than female longspurs.

Although the open nests of female longspurs permit them to take advantage of solar radiation, this advantage could be slight if it is usually heavily overcast during their incubation period. We can evaluate this possibility using weather data collected as part of our ongoing studies of tundra birds. We use a CR21 micrologger (Campbell Scientific, Incorporated) to record several weather parameters automatically every minute of the 24-h day (see Cartar and Montgomerie 1985 for details).

In 1983 and 1984 we measured the temperatures (1) of a Silastic egg placed in a shallow nest cup on the ground and exposed to both wind and solar radiation, and (2) of a thermal probe in a Stevenson screen to measure air temperature out of the wind and in the shade. The difference between these two temperatures indicates the influence of both solar radiation and wind on egg temperature and accurately represents the influence of bunting and longspur nest microclimates on egg temperatures.

In both 1983 and 1984, there was a substantial difference in temperature between the egg in the open and the probe in the shade on virtually every day of the period when birds are incubating (Fig. 8). For most days the difference in temperature ranged between 5° and 10°, but on some days the difference was as high as 13°. Clearly, female longspurs can take advantage of solar radiation on most days of incubation.

The evolution of incubation feeding

White and Kinney (1974) pointed out that some assistance from the male may be favored when bird species with uniparental female incubation (e.g., most passerines) invade a region with a colder, harsher environment. We suggest that the evolution of hole nesting in Snow Buntings represents such an invasion into a colder nest microclimate. When male assistance during incubation is favored, the evolution of male assistance can proceed in either of two directions: incubation feeding or male incubation (White and Kinney 1974). For many species, including Snow Buntings, incubation feeding may be the easier evolutionary solution. Males already have the necessary behavioral repertoire for incubation feeding since they feed their offspring, whereas incubation itself involves both a change in physiology and anatomy with the development of a brood patch (Jones 1971).

Recent studies have demonstrated that nest microclimate can have important reproductive consequences. For example, individuals of some species choose nest sites that minimize cold stress, heat stress, or both (Calder 1971, Walsberg 1981, Zerba and Morton 1983). In addition, birds can vary nest orientation to minimize thermal stress (Walsberg and King 1978, Verbeek 1981). In extreme climates, nest orientation can even influence reproductive success (Austin 1974). However, hole-nesting birds like Snow Buntings are much less flexible in their ability to choose sites that minimize thermal stress, although species that excavate their own cavities can often choose a beneficial orientation (Inouye 1976, Inouye et al. 1981). In a recent cost-benefit analysis of the evolution of hole nesting, Alerstam and Hogstedt (1981) identify competition for the limited number of suitable sites as the major cost of adopting a hole-nesting strategy. One cost they did not consider is the microclimatic consequences of nesting in holes; nesting in holes or cavities may entail a reduction in the quality of thermal conditions for unattended eggs. This problem appears to have been an important one in the evolution of hole nesting by Snow Buntings, but it has been ameliorated by incubation feeding by the male.

Available data on the occurrence of incubation feeding in other passerine birds suggest that the correlation between hole nesting and incubation feeding may be more general. Lack's (1940) early review of the instances of courtship and incubation feeding in birds still stands as the most complete review, and many of the passerine species listed by Lack as exhibiting incubation feeding are hole-nesting birds: e.g., members of the families Paridae, Sittidae, and Certhiidae. Further, within the family Muscicapidae, incubation feeding occurs in some of the hole- and cavity-nesting genera (e.g., *Sialia, Muscicapa*), but not in the open-nesting genera (e.g., *Turdus, Saxicola*). Thus, it is tempting to speculate that the nest microclimate of these hole-nesting birds has favored male assistance during incubation. On the other hand, Alerstam and Hogstedt (1981) suggested that competition for holes should select for early arrival on the breeding grounds, and they found that hole-nesting birds are most often year-round residents or early-returning migrants. If these hole-nesting species also breed earlier than open-nesting taxa, the lower food availability during incubation would also favor male assistance like incubation feeding. Although we demonstrated that timing of breeding (and therefore food availability) would not explain the difference between longspurs and buntings, it would be profitable to test this idea in an interspecific comparison of other species.

logistic support for our studies at Sarcpa Lake. Linda Hamilton helped collect data and provided excellent assistance in the field for all phases of this project. M. A. Domarchuk, R. L. McLaughlin, J. K. Morgan, and M. F. Willson helped collect data in 1985. This work has benefitted from discussions with R. V. Cartar, F. Cooke, R. L. McLaughlin, G. C. Williams, and R. Stewart. J. C. Davies and D. B. Lank read and provided critical comments on the manuscript.

LITERATURE CITED

Alerstam, T., and G. Hogstedt. 1981. Evolution of hole-nesting in birds. Ornis Scandinavica 12:188–193.

Austin, G. T. 1974. Nesting success of the Cactus Wren in relation to nest orientation. Condor 76:216–217.

Calder, W. A. 1971. Temperature relationships and nesting of the Calliope Hummingbird. Condor 73:314–321.

Cartar, R. V., and R. D. Montgomerie. 1985. The influence of weather on incubation scheduling of the white-rumped sandpiper *(Calidris fuscicollis)*: a uniparental incubator in a cold environment. Behaviour 95:261–289.

Custer, T. W., and F. A. Pitelka. 1975. Correction factors for digestion rates for prey taken by Snow Buntings *(Plectrophenax nivalis)*. Condor 77:210–212.

East, M. 1981. Aspects of courtship and parental care in the European robin *Erithacus rubecula*. Ornis Scandinavica 12: 230–239.

Godfrey, W. E. 1966. The birds of Canada. Bryant, Toronto, Ontario, Canada.

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

Holmes, R. T., and F. A. Pitelka. 1968. Food overlap among co-existing sandpipers on northern Alaskan tundra. Systematic Zoology 17:305–318.

Hussell, D. J. T. 1972. Factors affecting clutch size in arctic passerines. Ecological Monographs 42:317–364.

Inouye, D. W. 1976. Non-random orientation of entrance holes to woodpecker nests in aspen trees. Condor 78:101–102.

Inouye, R. S., N. J. Huntly, and D. W. Inouye. 1981. Non-random orientation of Gila Woodpecker nest entrances in saguaro cacti. Condor 83:88–89.

Jarman, P. J. 1982. Prospects for interspecific comparisons in sociobiology. Pages 323–324 *in* King's College Sociobiology Group, editor. Current problems in sociobiology. Cambridge University Press, Cambridge, England.

Jones, R. E. 1971. The incubation patch in birds. Biological Reviews 46:315–339.

Kendeigh, S. C. 1952. Parental care and its evolution in birds. Illinois Biological Monograph 22:1–357.

Knowlton, N. 1979. Reproductive synchrony, parental investment and the evolutionary dynamics of sexual selection. Animal Behaviour 27:1022–1033.

Lack, D. 1940. Courtship feeding in birds. Auk 57:169–178.

Lundy, H. 1969. A review of the effects of temperature, humidity, turning and gaseous environment in the incu-bator on the hatchability of the hen's egg. Pages 143–176 *in* T. C. Carter and B. M. Freeman, editors. The fertility and hatchability of the hen's egg. Oliver and Boyd, Edinburgh, Scotland.

Lyon, B., and R. D. Montgomerie. 1985. Incubation feeding in snow buntings: female manipulation or indirect male parental care? Behavioral Ecology and Sociobiology 17:279–284.

Maher, W. J. 1964. Growth rate and development of endothermy in the Snow Bunting *(Plectrophenax nivalis)* and Lapland Longspur *(Calcarius lapponicus)* at Barrow, Alaska. Ecology 45:520–528.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

McLaughlin, R. L., and R. D. Montgomerie. 1987. Central place foraging by Lapland longspurs: response to offspring requirements. Canadian Journal of Zoology, *in press*.

Montgomerie, R. D., R. V. Cartar, R. L. McLaughlin, and B. Lyon. 1983. Birds of Sarcpa Lake, Melville Peninsula, Northwest Territories: breeding phenologies, densities and biogeography. Arctic 36:65–75.

Post, W., and J. S. Greenlaw. 1983. Comparative costs of promiscuity and monogamy: a test of reproductive effort theory. Behavioral Ecology and Sociobiology 10:101–107.

Ricklefs, R. E. 1974. Energetics of reproduction in birds. Pages 152–292 *in* R. A. Paynter Jr., editor. Avian energetics. Publications of the Nuttall Ornithological Club 15.

Romanoff, A. L., and A. J. Romanoff. 1972. Pathogenesis of the avian embryo. Wiley, New York, New York, USA.

Silver, R., H. Andrews, and G. F. Ball. 1985. Parental care in an ecological perspective: a quantitative analysis of avian subfamilies. American Zoologist 25:823–840.

Stearns, S. C. 1976. Life history tactics: a review of the ideas. Quarterly Review of Biology 51:3–47.

Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136–179 *in* B. Campbell, editor. Sexual selection and the descent of man; 1871-1971. Aldine, Chicago, Illinois, USA.

Verbeek, N. A. M. 1981. Nesting success and orientation of water pipit *Anthus spinoletta* nests. Ornis Scandinavica 12:37–39.

Walsberg, G. E. 1981. Nest-site selection and the radiative environment of the Warbling Vireo. Condor 83:86–88.

Walsberg, G. E., and J. R. King. 1978. The heat budget of incubating Mountain White-crowned Sparrows *(Zonotrichia leucophrys oriantha)* in Oregon. Physiological Zoology 51:92–103.

White, F. N., and J. L. Kinney. 1974. Avian incubation. Science 189:107–115.

Williamson, F. S. L. 1968. Common Lapland Longspur. Pages 1597–1608 *in* O. L. Austin, editor. Life histories of North American cardinals, buntings, towhees, finches, sparrows and allies. United States National Museum Bulletin 237, Part 3.

Zerba, E., and M. L. Morton. 1983. Dynamics of incubation in Mountain White-crowned Sparrows. Condor 85:1–11.