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BROOD DIVISION BY LAPLAND LONGSPURS

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ABSTRACT.—We recorded parent-offspring feeding interactions for 47 offspring from 16 broods of Lapland Longspurs (*Calcarius lapponicus*) after nest departure. Longspur parents divided their families into single-parent brood units within a day of leaving the nest, and these brood units remained stable until offspring became independent. There were no differences in either the food load sizes or the feeding visit rates of male and female parents, but by the last week of parental care, female-tended offspring had moved an average of 626 m from their nest, almost 4 times farther than those tended by males. We outline the potential costs and benefits of brood division and suggest that this behavior may be common among birds with biparental care because it helps to reduce predation of entire broods and to improve the foraging economics of parents. Received 25 September 1984, accepted 8 April 1985.

In many bird species engaging in biparental care, the parents appear to divide the brood after the young leave the nest (Snow 1958, Tuck 1972, Skutch 1976, Nolan 1978, Smith 1978, Horsfall 1984, Moreno 1984). Despite numerous reports of brood division, the phenomenon remains poorly documented (but see Smith and Merkt 1980, Moreno 1984), and there has been some skepticism over whether it occurs at all (Hailman 1978, Reed 1981). Like other aspects of postnesting parental care, brood division has been particularly difficult to document because adults and mobile young are usually hard to follow. Although it is clear that some parents associate with particular individual offspring for at least short periods, only Tuck (1972) and Moreno (1984) provide clear evidence for stable brood units, each tended by a single parent after the offspring leave the nest.

We describe here stable brood division by Lapland Longspurs (*Calcarius lapponicus*) breeding in the Canadian high Arctic. We addressed the following questions: (1) When does brood division occur? (2) How is the brood divided? (3) How stable are the single-parent brood units? and (4) Do male and female parents treat their brood units differently? To provide a fo-

cus for further study, we also summarize the potential costs and benefits of dividing a brood into separate units, and we provide a digest of reports of brood division in the literature.

METHODS

We collected data during July and early August 1981–1984 at Sarcpa Lake, Melville Peninsula, N.W.T., Canada. At this site, longspurs began breeding during late June in all 4 years, and most young hatched in the first half of July. Young remained in their nest for 8–9 days after hatch and were fed by their parents for an additional 15 days away from the nest prior to independence.

Nestlings were banded 6–8 days after hatching with unique color-band combinations so individuals could be recognized after they left the nest. In 1981, 1982, and 1984, we recorded either body mass or the length of primary 7 (protruding from its sheath) for each offspring at the time of banding. Because body mass and the exposed length of primary 7 follow similar growth curves in longspurs (Hussell 1972), we used one or the other of these measures to rank offspring size within each brood.

We collected data on parental feeding patterns by focusing either on a parent, and following its movements from offspring to offspring, or on an individual offspring, and waiting for an adult to arrive and

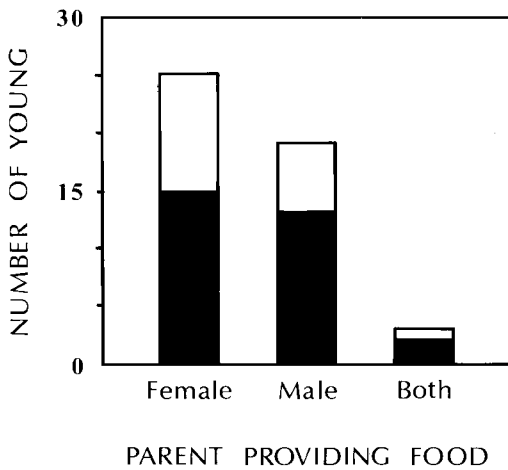


Fig. 1. Numbers of offspring (from 16 broods) fed by a female only, a male only, or by both parents. Each offspring was observed being fed at least twice. Shading indicates offspring observed for more than 5 feeding visits.

feed it. The first method allowed us to determine which offspring were fed by the focal parent during an observation period. However, because offspring from the same brood unit were often far apart ($\bar{x} = 89.4$ m, $SE = 12.3$, $n = 32$), we could not be sure whether an offspring was fed by its other parent after we and the focal parent moved on. Therefore, for approximately half the observation periods, we focused on individual offspring to ensure that we observed all parental visits. Observation periods lasted from 10 min to 3 h ($\bar{x} = 53.1$ min, $n = 71$), which generally was long enough to ensure that we observed more than one visit to an individual offspring whether we focused on parents or on young during each session. All observations were made from distances of 50 m or less. Since broods out of the nest were often difficult to find, our sampling was done opportunistically. Nevertheless, parent-offspring interactions were easy to observe and were rarely hidden by rocks or vegetation. In all, we recorded parental feeding visits by 26 parents to 47 different offspring from 16 broods following nest departure.

Timing of brood division.—To determine whether brood division occurred while offspring were still in the nest, we observed pair 14 for 1 h 2 days before nest departure and identified the offspring that each parent fed. The young were color-marked individually to facilitate observations, and the nest was watched from about 5 m away. Neither parent appeared to be disturbed by our presence.

Using a wire-mesh enclosure (1 m diameter, 15 cm high), we prevented the offspring of pair 10 from leaving their nest area for about 36 h after nest de-

parture and we recorded how parents allocated their feeding for 3 h. This allowed us to determine whether the brood was divided after nest departure even though the young were close together.

Comparison of parental behavior.—To compare the food delivery rates of male and female parents, we estimated load sizes and visit rates to the young whenever possible. Food load sizes were classified into three categories: small (more than $\frac{1}{3}$ of the bird's bill visible), medium—($\frac{1}{3}$ – $\frac{2}{3}$ of the bill visible), and large (more than $\frac{2}{3}$ of the bill hidden by food). One overall feeding visit rate was calculated for each parent using the total number of feeding visits and the total time observed. Only focal offspring data were used in this analysis to ensure that no feeding visits were missed, and only one rate was calculated for each parent to minimize any lack of independence in the data.

To compare the movements of matriarchal and patriarchal brood units, we recorded the location of each young when it was fed by a parent. The distance from the offspring to its nest was estimated using colored territory markers (see McLaughlin and Montgomerie 1985) or detailed maps and aerial photographs (scale 1 cm to 100 m).

RESULTS

Of the 47 offspring observed, 44 were consistently fed by only one parent (Fig. 1). Only 3 young out of the nest were fed by both parents, but in each case this occurred only on their first day away from the nest. Thereafter, each of these young was fed exclusively by one parent.

Because average brood size over the 4 years of this study was 4.3 young and parents tended to divide broods equally, most brood units consisted of 2 or 3 offspring. For the 10 pairs in which we observed at least 75% of the brood, neither parent consistently took a greater proportion of the family (males: $\bar{x} = 1.7$, females: $\bar{x} = 2.3$; Wilcoxon matched-pairs signed-ranks test, $T = 21.5$, $P > 0.05$). This analysis includes one exceptional case where a female raised her brood of 4 alone because her mate disappeared just before the young left the nest. Parental allocation of feeding within broods and the stability of brood units were most clearly demonstrated by 3 broods in which every offspring was observed at least once after nest departure (Table 1). In each case, male and female parents divided broods as equally as possible and stayed with their respective brood units until the young became independent. Only 1 of the 16 offspring in these 3 broods was fed by both

TABLE 1. Number of feeding visits by parent longspurs to their offspring after nest departure.

| Brood | Off-spring | Attending parent | | Sampling | |
|-------|------------|------------------|--------|------------------|------------|
| | | Male | Female | Days after hatch | Total days |
| 1 | A | 22 | 0 | 14-21 | 5 |
| | B | 0 | 4 | 9 | 1 |
| | C | 46 | 0 | 15-23 | 6 |
| | D | 17 | 4 | 9-23 | 7 |
| | E | 0 | 6 | 9-22 | 2 |
| | F | 0 | 1 | 9 | 1 |
| 9 | A | 14 | 0 | 8-22 | 6 |
| | B | 0 | 10 | 9-22 | 5 |
| | C | 0 | 13 | 8-12 | 4 |
| | D | 0 | 23 | 8-21 | 7 |
| | E | 18 | 0 | 9-14 | 3 |
| 10 | A | 0 | 12 | 13-18 | 3 |
| | B | 0 | 34 | 10-19 | 5 |
| | C | 5 | 0 | 10-17 | 2 |
| | D | 12 | 0 | 10-17 | 4 |
| | E | 2 | 0 | 18 | 1 |

parents, and that occurred only on the day after nest departure (age 9 days).

Both the male and female of pair 14 fed each nestling 2 days before nest departure, but once offspring left the nest the brood was clearly divided (Table 2). Similarly, all but 1 offspring of pair 10 were fed by both parents when confined to the nest area by our enclosure, but brood division occurred as soon as the offspring dispersed (Table 2). Although these two experiments were not replicated, the results seem clear and are similar to those reported for Song Sparrows (*Melospiza melodia*; Smith and Merkt 1980, Reed 1981). We conclude that longspur parents did not divide their broods until their offspring left the vicinity of the nest.

A size hierarchy develops within longspur broods, due mainly to asynchronous hatching (Hussell 1972). However, we found no evidence that parents divided broods along this hierarchy (Table 3). There was also no evidence that the last young to leave the nest were the responsibility of the female parent; in 2 of 5 cases, males took the last offspring that left the nest. In 2 other broods, the last 2 offspring left simultaneously and each parent took 1.

There was no significant difference in the distribution of food load sizes brought to the young by male and female parents ($G = 2.9$, $P > 0.20$, $df = 2$; Table 4). Nor was there a significant difference between parents in feed-

TABLE 2. Parental allocation of feedings when offspring were in the nest (brood 14) and in an enclosure (brood 10) compared with feedings after departure from the nest area.

| Brood | Location | Attending parent | Offspring | | | | |
|-------|-----------|------------------|-----------|----|----|----|---|
| | | | A | B | C | D | E |
| 14 | Nest | Male | 3 | 2 | 2 | | |
| | | Female | 2 | 4 | 1 | | |
| | Dispersed | Male | 17 | 0 | 22 | | |
| | | Female | 0 | 17 | 0 | | |
| 10 | Enclosure | Male | 1 | 1 | 4 | 3 | 4 |
| | | Female | 1 | 0 | 1 | 2 | 2 |
| | Dispersed | Male | 0 | 0 | 5 | 12 | 2 |
| | | Female | 12 | 34 | 0 | 0 | 0 |

ing trip rates (Mann-Whitney U -test, $U = 28.5$, $P = 0.68$; Table 4). Thus, male and female parents appeared to deliver food to their offspring at similar rates, although a larger sample is needed to confirm this result.

Young longspurs remained on their parents' territory for the first few days out of the nest, but often moved onto neighboring territories as soon as they began to fly (13-15 days after hatch; unpubl. data). To compare dispersal distances of brood units tended by male and female parents, we calculated the mean distance from the nest for each offspring observed during the last week of parental care (ages 17-23 days). Female-tended offspring moved, on average, almost 4 times as far from their nest as those tended by males (Table 5), and this difference was significant (Mann-Whitney U -test, $U = 6.5$, $P < 0.01$).

DISCUSSION

All Lapland Longspur pairs that we studied divided their offspring into stable single-parent brood units similar to those documented for Common Snipe (*Gallinago gallinago*; Tuck 1972), Prairie Warblers (*Dendroica discolor*; Nolan 1978), Song Sparrows (Smith and Merkt 1980), and Northern Wheatears (*Oenanthe oenanthe*; Moreno 1984). As in those species, longspurs split their broods within a day or two of nest departure. This pattern seems to be typical among terrestrial birds (see also Marler 1956), although in Great Crested Grebes (*Podiceps cristatus*) brood division does not occur until the young are about half grown (Simmons 1974), and in both Red-knobbed Coots (*Fulica cristata*;

TABLE 3. Number of chicks attended by male (M) and female (F) parents (U = unknown) in relation to offspring rank for 4 broods in 1981, 2 broods in 1982, and 2 broods in 1984.

| Offspring rank ^a | Brood size | | | | | | | | | | | |
|-----------------------------|------------|---|---|---|---|---|---|---|---|---|---|---|
| | 3 | | | 4 | | | 5 | | | 6 | | |
| | M | F | U | M | F | U | M | F | U | M | F | U |
| 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 3 | 0 | 1 | 0 |
| 2 | 1 | 0 | 0 | 1 | 0 | 0 | 3 | 2 | 0 | 0 | 1 | 0 |
| 3 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 3 | 2 | 1 | 0 | 0 |
| 4 | | | | 0 | 0 | 1 | 1 | 4 | 0 | 1 | 0 | 0 |
| 5 | | | | | | | 3 | 2 | 0 | 0 | 1 | 0 |
| 6 | | | | | | | | | | 1 | 0 | 0 |

^a Offspring were ranked from largest (1) to smallest (6) within each brood based on nestling weight or the exposed length of primary 7.

Dean 1980) and Horned Grebes (*Podiceps auritus*; Ferguson and Sealy 1983) some pairs never divide their brood, although many do. More studies are needed to determine whether this apparent terrestrial-aquatic difference is a general pattern, but such a difference is expected if aquatic offspring are less susceptible to whole-brood predation (see below).

Sutton and Parmelee (1955) reported that male longspurs regularly took charge of the oldest members of the brood, but the authors provided no quantitative evidence to support their statement. We found no consistent pattern in the division of longspur broods based on offspring age. Male Common Snipe, however, clearly took the first two offspring that left the nest (Tuck 1972). Age-related partitioning may be expected in species where the female does most of the incubating or brooding and where nest departure is highly asynchronous; the male can then take the first offspring out of the nest, while the female feeds or broods the remaining young until they are ready to leave.

Once stable brood units became established the food-gathering behavior of male and female longspur parents was similar, but females took their brood units farther from the nest site. As a result, female-tended brood units usually were well outside their natal territory by the time of independence, whereas male-tended offspring remained much closer to their nest (see also Tuck 1972, Nolan 1978). It is unclear why females move farther away, but differential family unit movements may be related to the tendency for adult male longspurs (Custer 1974), and male birds in general

(Greenwood 1980), to be more philopatric than females.

Costs of brood division.—Brood division could reduce parental reproductive success because brood division requires both parents, and one parent therefore must forego other activities (e.g. early migration, molt, territory defense, or reneating) that could enhance its fitness. For example, male longspurs tending chicks started their postnuptial molt later than males that lost their brood (pers. obs.; see also Custer and Pitelka 1977). Such a delay in molt could be costly in the short arctic summer due to waning food supply. Because female birds often do most of the incubating and brooding, males should have more opportunities to desert their mates and engage in these other activities (Trivers 1972). Thus, the cost of remaining to feed half the brood may be most commonly borne by males. Secondly, because brood units seem to remain discrete until the young are independent (Tuck 1972, Nolan 1978, this study), there is some danger that half the brood will be lost if the attending parent dies or is injured. In undivided broods one parent might be able to compensate for this loss (Snow 1958). Although the death of the attending parent could be a serious loss, particularly if the offspring are young, parental mortality during this period of parental care may be so low that it would not diminish the advantages of splitting the brood. In addition, there is some evidence that brood division may be reversible (Smith and Merkt 1980).

Benefits of brood division.—There are five ways that brood division could benefit parents and offspring.

TABLE 4. Load sizes and feeding visit rates to offspring in male and female brood units. Sample sizes (n) are the numbers of male and female parents observed.

| | Attending parent | |
|---|------------------|--------|
| | Male | Female |
| Load size | | |
| n | 5 | 4 |
| Small | 13 | 15 |
| Medium | 23 | 13 |
| Large | 20 | 10 |
| Feeding rate (trips \cdot young ⁻¹ \cdot h ⁻¹) | | |
| \bar{x} | 5.5 | 4.8 |
| SE | 1.0 | 0.6 |
| n | 8 | 8 |

(1) Minimize effects of predation. The division of broods can prevent predation of whole families because matriarchal and patriarchal brood units are often widely separated (Table 5; see also Tuck 1972, Moreno 1984). Thus, a predator following one parent for clues to the location of offspring could, at best, find only half of the family. Similarly, separated brood units increase the average interoffspring distances within the entire brood without necessarily increasing the actual distances among offspring visited by each parent (Moreno 1984).

Parents with divided broods also should be more efficient at warning offspring about approaching predators because each parent has fewer young to warn and a smaller area to scan. Brood division may occur in precocial birds for this reason (Smith 1978). Furthermore, Safriel (1975) and Walters (1982) suggested that losses to predators might increase as average parent-offspring distance becomes larger. Because brood division can reduce the average distance between young being fed by each parent (Moreno 1984), parents should be better able to detect danger from a predator.

(2) Increased foraging efficiency. Birds forming single-parent brood units should be more efficient at caring for their offspring (Smith 1978, Moreno 1984). A single parent with half the brood has fewer offspring locations to remember, and this should reduce the chances of misplacing a brood member. In species where adults feed their young, caring for fewer offspring also should simplify the foraging route adults use and reduce travel time. For example,

TABLE 5. Dispersal distances of male- and female-tended offspring from their nests measured during the final week of parental care.

| Attending parent | Dispersal distance (m) | | | Offspring age* (days) | |
|------------------|------------------------|-----|-----|-----------------------|-------|
| | \bar{x} | SE | n | \bar{x} | Range |
| Male | 171 | 20 | 9 | 20.6 | 17-23 |
| Female | 626 | 127 | 9 | 20.9 | 17-22 |

* Ages of chicks when dispersal distances were measured.

Moreno (1984) argued that parent wheatears can reduce their travel costs if brood units are spatially separated and parents restrict their activities to the vicinity of the offspring. Brood division also may allow parents to allocate food more efficiently among the young within their brood unit. While young wheatears appear to control the rates at which they are fed by begging and chasing their parents (Moreno 1984), other species distribute food unevenly to ensure maximal growth rates of preferred chicks (Simmons 1974, Horsfall 1984).

(3) Learning to forage. Brood division also may enhance intersexual differences in food preference or foraging behavior since these are learned or reinforced early in life (Immelmann 1975). For example, both brood division (Kilham 1968) and intersexual differences in foraging behavior (Kilham 1965, 1968) have been reported in Hairy Woodpeckers (*Picoides villosus*). We do not know whether Hairy Woodpeckers divide their broods by offspring sex, but this would be especially profitable if different skills were learned from each parent.

(4) Differential dispersal of the sexes. Female birds generally breed farther from their birth site than males (Greenwood 1980). Because grown offspring of some species return to breed near the area where they became independent (Catchpole 1972, Immelmann 1975, Baker and Mewaldt 1979), parents could influence natal philopatry by the movement of brood units. Where data for the movements of brood units have been reported, females moved their offspring farther away from the nest site than males (Tuck 1972, Nolan 1978, this study). Such sex-biased dispersal can be important as a means of avoiding high levels of inbreeding (Greenwood 1980).

(5) Sexual imprinting and mate choice. Bate-

TABLE 6. Reports of brood division in birds.

| Species | Source | Evidence ^a |
|--|--------------------------|-----------------------|
| Eared Grebe (<i>Podiceps nigricollis</i>) | Harrison 1978 | D |
| Great Crested Grebe (<i>P. cristatus</i>) | Simmons 1974 | C |
| Horned Grebe (<i>P. auritus</i>) | Ferguson and Sealy 1983 | D |
| Little Grebe (<i>Tachybaptus ruficollis</i>) | Cramp and Simmons 1977 | D |
| Common Crane (<i>Grus grus</i>) | Cramp and Simmons 1980 | D |
| Common Moorhen (<i>Gallinula chloropus</i>) | Wood 1974 | D |
| American Coot (<i>Fulica americana</i>) | Harrison 1978 | D |
| Red-knobbed Coot (<i>F. cristata</i>) | Dean 1980 | B |
| Eurasian Coot (<i>F. atra</i>) | Horsfall 1984 | A |
| Greater Golden-Plover (<i>Pluvialis apricaria</i>) | Williamson 1948 | D |
| Bar-tailed Godwit (<i>Limosa lapponica</i>) | Harrison 1978 | D |
| Hudsonian Godwit (<i>L. haemastica</i>) | Harrison 1978 | D |
| Marbled Godwit (<i>L. fedoa</i>) | Harrison 1978 | D |
| Whimbrel (<i>Numenius phaeopus</i>) | Williamson 1946 | D |
| Common Snipe (<i>Gallinago gallinago</i>) | Tuck 1972 | A |
| Red-bellied Woodpecker (<i>Melanerpes carolinus</i>) | Kilham 1961 | C |
| Hairy Woodpecker (<i>Picoides villosus</i>) | Kilham 1968 | D |
| Bicolored Antbird (<i>Gymnophithys leucaspis</i>) | Willis 1967 | C |
| Spotted Antbird (<i>Hylophylax naevioides</i>) | Willis 1972 | C |
| Horned Lark (<i>Eremophila alpestris</i>) | Boyd 1976 | C |
| Great Tit (<i>Parus major</i>) | Bengtsson and Ryden 1981 | D |
| Northern Wheatear (<i>Oenanthe oenanthe</i>) | Moreno 1984 | A |
| Wood Thrush (<i>Hylocichla mustelina</i>) | Harrison 1978 | D |
| Eurasian Blackbird (<i>Turdus merula</i>) | Snow 1958 | C |
| | Edwards 1985 | A |
| Ovenbird (<i>Seiurus aurocapillus</i>) | Hann 1937 | D |
| Prairie Warbler (<i>Dendroica discolor</i>) | Nolan 1978 | C |
| American Redstart (<i>Setophaga ruticilla</i>) | Boxall 1983 | C |
| Large Ground-Finch (<i>Geospiza magnirostris</i>) | Grant and Grant 1980 | D |
| Medium Ground-Finch (<i>G. conirostris</i>) | Grant and Grant 1980 | D |
| Sharp-beaked Ground-Finch (<i>G. difficilis</i>) | Grant and Grant 1980 | D |
| Common Chaffinch (<i>Fringilla coelebs</i>) | Marler 1956 | D |
| Song Sparrow (<i>Melospiza melodia</i>) | Smith 1978 | A |
| | Smith and Merkt 1980 | A |
| Five-striped Sparrow (<i>Amphispiza quinquestrata</i>) | Mills et al. 1980 | D |
| Smith's Longspur (<i>Calcarius pictus</i>) | Jehl 1968 | D |
| Lapland Longspur (<i>C. lapponicus</i>) | Sutton and Parmelee 1955 | D |
| | Tryon and MacLean 1980 | D |
| | This study | A |
| Snow Bunting (<i>Plectrophenax nivalis</i>) | Tinbergen 1939 | D |

^a Quantitative evidence for brood division is based on data collected (A) over more than 1 day or (B) for 1 day only; qualitative evidence is either (C) a specific description of different young being fed by different parents or (D) a vague reference to parents splitting up the brood.

son (1978) suggested that sexual imprinting allows individuals to recognize close kin so that they can optimally balance the effects of inbreeding and outbreeding through their choice of a mate. Because sexual imprinting occurs early in life (Immelmann 1975), young birds may develop mating preferences during the time spent in a brood unit. Thus, broods may be divided by sex such that female offspring imprint on their father and male offspring imprint on their mother. There is, however, little evidence of brood division by sex (but see Snow 1958). Snow Buntings (*Plectrophenax nivalis*) also

divide their broods (Tinbergen 1939), but at our study site they do not divide broods on the basis of offspring sex (B. Lyon pers. comm.) even though young buntings can be readily sexed by plumage.

Of the five possibilities outlined above, "learning to forage" and "differential dispersal of the sexes" probably are not important to Lapland Longspurs. There apparently is no sexual difference in the foraging behavior of adult longspurs (Table 4, unpubl. data), so offspring would not learn different skills from male and female parents. Adult female long-

spurs did move their brood units farther from the nest than males, but since none of the 129 chicks that we banded during 1981–1983 has been seen on our study area in subsequent years (see also Custer and Pitelka 1977), it is unlikely that these movements have any effect on natal philopatry.

The remaining three benefits of brood division could all apply to longspurs. First, we recorded high nest predation during this study (37% of nests, range 12–81%/yr), suggesting that there was considerable danger that an entire brood might be lost to predators. The early fledging of longspur chicks at 8–9 days after hatch is probably the result of high predation pressure (Maher 1964). Second, parent longspurs systematically feed each offspring by gathering food near the chick (mean distance = 14.0 m, SE = 2.5, $n = 75$) and feeding it to satiation with 1–8 ($\bar{x} = 2.4$, $n = 59$) short feeding bouts. They then fly the relatively long distance ($\bar{x} = 89$ m) to the next chick and repeat this procedure. Such systematic foraging behavior can easily be accomplished without losing track of the 2 or 3 chicks in a brood unit. Further observations and experiments are needed, however, to critically test whether brood division is the most efficient way to care for young out of the nest. Finally, there may be an advantage to sexual imprinting in longspurs since we have found evidence of positive assortative mating by plumage color in this species (unpubl. data). To date, however, we have no data on the sex of offspring within brood units that would allow us to evaluate this possibility.

Brood division in other birds.—Despite the difficulty of observing young birds after they leave the nest, brood division has been reported for a wide variety of species, although rarely documented quantitatively (Table 6). The separation of families into separate brood units has been reported so often that there is little reason to doubt that it is common among birds with biparental care. This initial survey of the literature suggests that brood division occurs most often in relatively large species with precocial young (Table 6). The majority of these species also nest on or close to the ground, and this may make them particularly vulnerable to predators (Lack 1954). Such apparent trends should be accepted with caution, however, because species nesting on the ground in open habitats may simply be the easiest to observe,

especially if the period of postnesting parental care is long.

To date there have been few detailed studies of the behavior of parent birds tending chicks after they leave the nest, partly because young birds are difficult to follow away from the nest and partly because there has been little theory to focus attention on this aspect of parental care. Although some of the hypotheses to explain brood division will be difficult to test, some progress can be made by determining (1) whether parents divide their broods by age, size, or sex of the offspring, (2) whether parents that divide broods are able to feed their offspring more efficiently, and (3) whether predation risk is lower for divided broods. These questions may be most easily answered by studying species with facultative brood division (e.g. Red-knobbed Coots, Dean 1980) or by manipulating the size of brood units. Although some species with biparental care keep their offspring close together after nest departure (e.g. Boxall 1983), we could find no clear examples of species in which parents did not divide their broods. If brood division is as advantageous as we suggest, then species that do not divide their broods may actually be the exceptions that can help us to understand the apparently more common pattern that broods are divided.

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