The Auk 109(3):563-575, 1992

COPULATION PATTERNS AND SPERM COMPETITION IN THE POLYGYNANDROUS SMITH'S LONGSPUR

JAMES V. BRISKIE[1]
Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada

ABSTRACT.—In a color-marked population of Smith's Longspurs (*Calcarius pictus*) near Churchill, Manitoba, I recorded the timing and frequency of copulatory and mate-guarding behavior in relation to breeding season and time of day. Longspurs formed mating associations best described as female-defense polygynandry. Females copulated with two (rarely three) males (designated alpha, beta and gamma according to mating order), and each male with one to three females for an estimated average of 365 (range 214-629) copulations per clutch. This is one of the highest copulation rates reported in birds. More than 99% of all copulations were preceded by female solicitation but only about one-third of all solicitations were followed by mounting. Copulations began three to five days before clutch initiation and ceased just before or shortly after the penultimate egg was laid. Female copulations with alpha males peaked at clutch initiation at a rate of 5.3 copulations per hour. The copulation rate of beta and gamma males peaked two days after laying was initiated at 2.6 copulations per hour. All copulations probably occurred within the female's fertilization period and, thus, potentially could have resulted in fertilization of eggs. Copulations were most frequent during morning and late evening; they were rare during the afternoon. This diurnal pattern also corresponds to the period when inseminations were most likely to fertilize eggs. During the copulation period, males guarded their mates by closely following females and chasing away intruding males. Guarding and chasing by alpha males were most intense just before the first egg was laid, while guarding by beta and gamma males peaked on the day the third egg was laid. As with copulations, mate guarding and chasing were most intense in the morning and evening. The occurrence of multiple mating by females and the lack of territorial behavior in males suggests that frequent copulations in this species evolved as an adaptation to sperm competition. *Received 24 April 1991, accepted 13 January 1992.*

THE RECOGNITION that in many species a female may mate with more than one male led Parker (1970) to develop the idea of sperm competition (i.e. competition between the ejaculates of two or more males to fertilize the eggs of a single female). Sperm from more than one male can co-occur within the reproductive tract of a female during the span of one breeding attempt either as a result of mate replacements, extrapair matings or the formation of polyandrous associations (Birkhead 1988). Cuckoldry or extrapair paternity can be the proximate result of sperm competition, but over evolutionary time the advantages of avoiding sperm competition by males are thought to have favored a variety of elaborate anticuckoldry tactics such as mate guarding (e.g. Montgomerie 1988), copulatory plugs (e.g. Devine 1975), sperm removal (e.g. Davies 1983) and high copulation frequency (Birkhead et al. 1987). For example, guarding by males can reduce the number of extrapair copulations or copulation attempts made on their mate (Møller 1987a), whereas high copulation rates may function to dilute or displace any other male's sperm already present (Birkhead et al. 1987). Moreover, by timing mate-guarding behavior, copulations and other anticuckoldry tactics to coincide with periods of peak female fertility, it may be possible for males to maximize their confidence of paternity while minimizing costs in terms of energy or lost mating opportunities. How successfully males avoid cuckoldry will in turn depend upon female willingness to accept and even seek out extrapair matings.

In birds, female fertility varies both with the time of day and over the season. A diurnal pattern of fertility arises because eggs must be fertilized within 30 min of ovulation; otherwise, the deposition of albumin effectively prevents sperm from reaching the egg (Howarth 1974). In most passerine birds, eggs are ovulated and fertilized in the early morning, approximately 24 h before they are laid, and it is during this

---

[1] Present address: Department of Animal and Plant Sciences, P.O. Box 601, The University of Sheffield, Sheffield S10 2UQ, United Kingdom.

"fertilization window" that copulations should be most successful in fertilizing eggs (Cheng et al. 1983). The benefit of timing copulations to coincide with the morning increase in female fertility should hold for nonmate males as well; thus, both extrapair copulation attempts directed toward females and mate guarding by males to thwart such attempts are also expected to peak at this time.

On the other hand, a seasonal pattern of fertilizability arises because eggs are ovulated only during a brief period of the breeding cycle. However, as most female birds can store sperm in specialized tubules located at the junction of the uterus and vagina (Hatch 1983, Shugart 1988, Birkhead and Hunter 1990), copulations that occur several days or even weeks before ovulation can potentially fertilize eggs. The period over which sperm remain viable in storage is known for only a few species but varies from only six days in the Ringed Turtle-Dove (*Streptopelia risoria;* Zenone et al. 1979) up to a maximum of 72 days in the domestic turkey (*Meleagris gallopavo;* Lorenz 1950). The only passerine for which the duration of sperm storage has been determined is the Zebra Finch (*Taeniopygia guttata;* Birkhead et al. 1989). Using captive birds, Birkhead et al. (1989) found that female finches were able to store sperm for up to 13 days but that after 10 days only 50% of eggs laid were fertile.

In most birds with multi-egg clutches, eggs are laid one a day for several days. Since eggs are fertilized 24 h before they are laid, all inseminations that occur up to a day before the last egg is laid could lead to successful fertilization. Thus, the total period over which sperm introduced into a female bird's reproductive tract has the potential to fertilize at least one egg comprises about 24 h less than the egg-laying period plus the duration of sperm storage before the first egg is laid. This time interval is termed the "fertilization period" (Birkhead 1988). For example, a female Zebra Finch capable of storing sperm for 10 days and laying an egg every 24 h until the clutch of four eggs is complete would have a fertilization period that is the sum of these two periods less 24 h (i.e. about 13 days). Copulations before this period would have little chance of fertilizing eggs and are expected to be selected against, because, for males, they entail costs in wasted mate-searching, courtship and ejaculates without any possible benefit via increased paternity. For males attempting to avoid cuckoldry, it is also advantageous both to time copulations to coincide with this fertilization period and at the same time to prevent other males from copulating with their mates. In the Zebra Finch, all of these expected behaviors have been recorded (Birkhead et al. 1989).

Although sperm competition is thought to play an important role in the evolution of mating behavior in socially monogamous birds like Zebra Finches (Birkhead 1988), it is among polyandrous species that sperm competition is considered most intense (Davies 1983, 1985, Oring 1986, Birkhead et al. 1987). In polyandrous birds, two or more males share the single breeding effort of one female and conflicts may arise over each male's contribution to paternity. How such conflicts are resolved is not clear since presumably it is advantageous for each male to try to father the entire brood. In these circumstances, knowing how the timing and frequency of copulations by each male varies in relation to the fertilizability of the female may be particularly important to our understanding the outcome of this competition.

In 1987, I discovered a high level of polyandry and polygyny in Smith's Longspurs (*Calcarius pictus*), a small bunting of the Canadian subarctic. My observations revealed that most females associated and copulated with two or more males, and males with one to several females, during a single breeding attempt. In the short summers of this region, only one brood can be raised per year. This suggested that competition between males for paternity could be particularly intense as males later provided almost one-half of the food to the nestlings and, because of cuckoldry, might end up devoting effort to the raising of another male's offspring. To determine how copulatory behavior varied in relation to the fertilization period of the female and how these behaviors varied between mates of polyandrous females, I recorded the frequency and timing of mating behavior in a small, color-marked population of Smith's Longspurs during three breeding seasons. My main objective was to test the predictions from sperm-competition theory that the timing of copulations (both pair and extrapair) and other anticuckoldry tactics should coincide with seasonal and diurnal changes in female fertilizability. I also provide the first detailed description of the unusual mating system of this species and speculate on how such a system may have evolved.

STUDY AREA AND METHODS

Smith's Longspurs breed along the northern edge of the tree line in western and central North America. I studied the mating behavior of this species near Churchill, Manitoba in June 1988, 1989 and 1990. In northern Manitoba, longspurs are restricted to a narrow band of tundra that follows the southwestern coast of Hudson Bay. This habitat is dominated by wet sedge (*Carex* spp.) meadows and the terrain is relatively flat. A few scattered clumps of stunted white spruce (*Picea glauca*) dot the area and are used frequently as song perches by male longspurs. The breeding biology of this species in Churchill was investigated previously by Jehl (1968), but he did not report any observations of their mating system or behavior. A general description of the vegetation and climate of the area is provided by Johnson (1987).

Smith's Longspurs arrived in the Churchill area in early June in each year of this study. Breeding densities were relatively low with only six to nine birds of either sex on my 1-by-0.5-km study site. Nests were built in mid-June to late June in a shallow depression on the ground, usually beside a small shrub or tuft of grass. Clutch initiation began shortly thereafter and clutch size ranged from three to six eggs; clutches of four were the most common (66.7% of 21 clutches from 1988–1990). Nesting was highly synchronous on the study area with only six days between the first and last clutch initiation attempts in 1988 ($n = 7$), five days in 1989 ($n = 6$) and eight days in 1990 ($n = 8$). Eggs hatched after 11.5 days incubation (range 11 to 13, $n = 8$ nests) and young fledged after 8.1 days in the nest (range 7 to 9, $n = 27$ nests). By late July, all nestlings had fledged and adults were feeding free-ranging juveniles. Smith's Longspurs are single brooded and renesting was observed only once out of seven nest failures.

To determine whether copulatory behavior coincided with the periods of peak female fertilizability, information on both the length of the fertilization period and the timing of the fertilization window are required. Although numerous sperm-storage tubules occur in the uterovaginal junction of Smith's Longspurs (Briskie 1990), the duration of sperm storage is not known. The closest related species for which the period of sperm storage is known is the Zebra Finch (10 days; Birkhead et al. 1989); therefore, I assumed for the purposes of this study that female longspurs also were capable of storing sperm for at least as long before clutch initiation. As with most other passerines (see Skutch 1952, Schifferli 1979), Smith's Longspurs laid eggs between 0600 and 0900 CDT (pers. observ.) even though the sun rose around 0430 during the egg-laying period. A female longspur collected in late morning (ca. 1100 CDT) contained a recently ovulated egg in the upper magnum of the oviduct and supports the hypothesis that the fertilization window occurs in the morning.

I trapped and color banded most longspurs on the study site shortly after their arrival. In addition to a numbered aluminum band, all birds received three color bands. Six males and seven females were present on the study site in 1988, eight males and seven females in 1989, and nine males and eight females in 1990. All observations reported here involved only banded birds.

I monitored the mating behavior of Smith's Longspurs by making intensive observations on six different females: two in 1988, three in 1989, and one in 1990. I recorded the activities of each bird by closely following individuals as they foraged and interacted with other individuals on the study area. Observations began as soon as birds arrived back in the spring or were first banded but systematic observations were not made daily until six or seven days before egg laying began—earlier than this, females associated only rarely with males and no copulations were seen. I stopped systematic observations after the laying of the last egg, as females devoted themselves entirely to incubation and all mating behavior ceased. I defined the day of clutch initiation as day 0; days prior to this are indicated by minus signs while those following clutch initiation by plus signs. Observation periods lasted for 1 h of data collection, although in absolute time this period may have exceeded an hour by up to 30 min if I temporarily lost track of an individual. The flat and open nature of the tundra environment allowed me to follow birds continuously for extended periods even when they flew several hundred meters. Although I was in full view of the birds at all times, Smith's Longspurs were relatively tame and allowed me to approach to within 10 to 15 m before giving alarm "rattles" (see Jehl 1968). Because birds continued to forage, sing, and copulate without apparent regard for my presence at distances greater than 15 m, I assumed that their mating behavior was not significantly affected by my observations.

I made observations over all daylight hours. At this high latitude, days are very long in June and birds were active from sunrise (about 0430 CDT) to sunset (2300). To determine mating patterns over the day I divided observation bouts into four periods: early morning (0600–0900), late morning (0900–1200), afternoon (1300–1600) and evening (1900–2200). Observations were made daily for each female in the early morning period but females were not observed as regularly during the late morning, afternoon and evening. In total, 73 h of observations were made on focal birds. In 1990, I also made a daily survey of the study area to determine the mating status of all focal and nonfocal birds.

During each observation period, I recorded the following behaviors: (1) number of solicitations and cop-

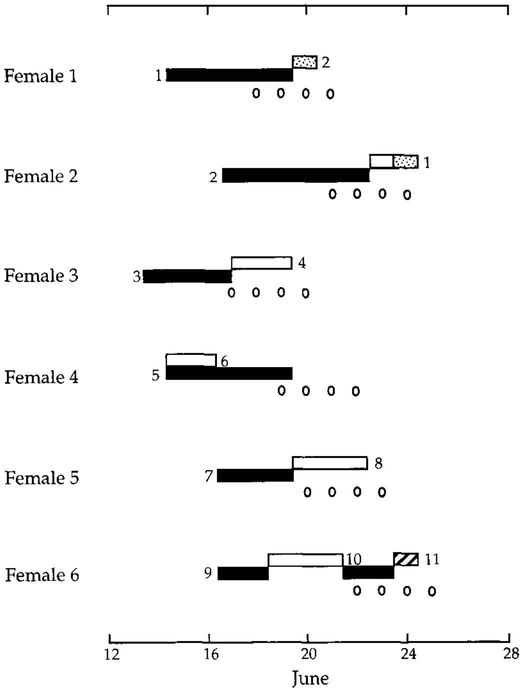

Fig. 1. Copulation patterns in six focal female Smith's Longspurs relative to clutch initiation. (O = day egg laid). Days on which an alpha male (solid bars), beta male (open bars) and gamma male (diagonal bars) were observed copulating with each female are given above her laying schedule. Days on which solicitations but not copulations were observed are indicated by stippled bar. Each male given only one subscript; thus, male 1 was an alpha male with female 1 and a beta male with female 2. Males 3, 6, 7, 8, and 9 were also paired as either alpha or beta males with other nonfocal females on the study site. Beta male 6 was taken by a predator on 17 June. Data for females 1 and 2 from 1988, females 3 to 5 from 1989, female 6 from 1990.

ulations; (2) time spent mate guarding; (3) time spent by each male chasing away intruders; and (4) frequency of leaving and/or following by either sex during mate guarding. I could not distinguish mountings that resulted in cloacal contact from those where contact was not made; thus, I scored all mountings as copulations. Unforced copulations were defined as those copulations actively solicited by the female or those initiated by the male but accepted by the female. Forced copulations were not solicited, and females tried to resist the male's advances. I considered a male to be mate guarding when he was less than 5 m from a female. Although this may seem an arbitrary number, it is unlikely that a male would be able to monitor the activities of a female from the ground at any greater distance because of obscuring vegetation (also see Alatalo et al. 1987). Indeed, when males were not within 5 m of the female, they were at distances of several hundred meters away or completely out of sight (i.e. males were either very close to a female or very far away). Descriptions of observations were tape recorded and later transcribed.

Solicitation and copulation rates were not normally distributed, so I log-transformed data before analyses. Note that the SEs reported for back-transformed means are asymmetrical. I also calculated mean values for individual birds for all analyses of diurnal patterns, rather than use the raw data, to avoid problems with pseudoreplication. Data expressed as percentages were arcsine transformed before analyses (Sokal and Rohlf 1981).

RESULTS

Mating associations.—Smith's Longspurs formed pair bonds or mating associations that resulted in a mating system best described as a form of female-defense polygynandry (Fig. 1). Four of the six females studied were observed copulating repeatedly with two different males before and during the laying of their single clutch of eggs. Another female copulated with three different males over the same period, whereas the final study female copulated with only a single male, although she was later observed soliciting to a second male. During my more general survey in 1990, I observed seven additional females; six were observed copulating with at least two males and one with only a single male (Fig. 2). Thus, of the 13 females whose social mating status was known, 10 (77%) were biandrous, 1 (8%) was triandrous, and 2 (15%) were monogamous.

The extent of polygyny in males was less easily assessed because focal-animal sampling was limited to females. Nonetheless, within a breeding season, 10 males (62.5%) were observed mating with at least two females, two males (12.5%) with three females, and four males (25%) with one female. As some of these males may have had additional mates off the study area (e.g. male 10; Figs. 1 and 2), these observations may underestimate the actual level of polygyny.

I called this mating system polygynandry because females associated and copulated with two or three males for a single nesting attempt during which those same males associated and copulated with one to three females. Polygynandry in Smith's Longspurs differs from that found in other birds (e.g. Dunnocks, *Prunella modularis* [Davies 1985]; Alpine Accentors, *P. collaris* [Nakamura 1990]) in that longspurs did not form

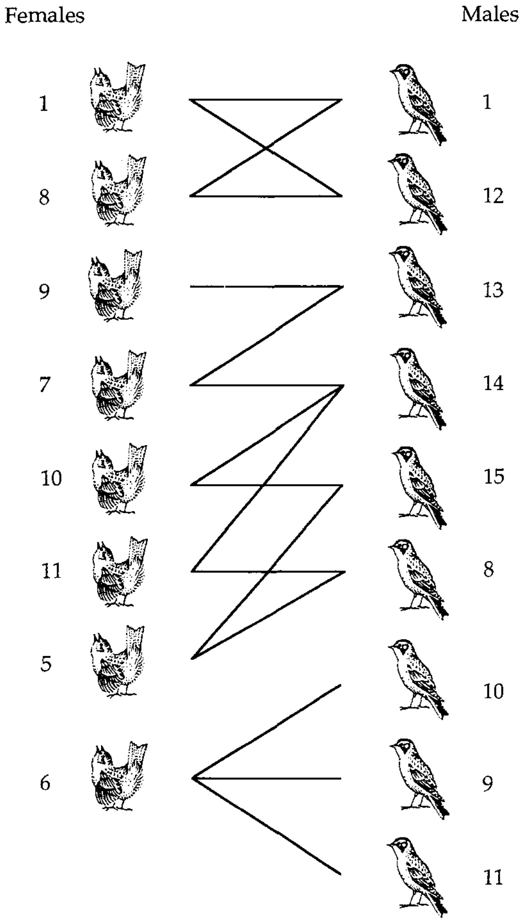

Fig. 2. Mating relationships between all birds present on study site in 1990. Lines connect birds observed copulating on at least one day. All birds were color-marked residents. Numbers identifying individual males and females match those in Figure 1.

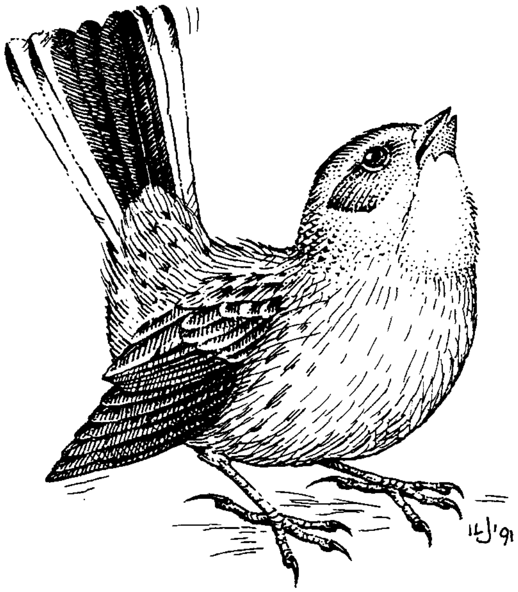

Fig. 3. Solicitation posture of female Smith's Longspur.

discrete mating units in which two or more females shared the same two or more males or males the same two or more females. Thus, although a male longspur might share a female with another male, he also may have had one or more such arrangements with different females and males. Likewise, females typically had two mates for a given clutch but shared at least one of these males with another (usually neighboring) female. Smith's Longspurs also differ from Dunnocks and other polygynandrous birds in that neither sex was territorial in the sense that no individuals or mating units tried to defend particular areas. Only when copulating with a female were males aggressive toward other males. Thus, this behavior is more appropriately considered female defense or mate guarding because it was a female rather than an area that was being defended (see below).

I called the first male to pair and copulate with a female the alpha male, the second was designated as the beta male, and so on. Although this terminology is used to denote the order in which males gained access to a particular female, it was not necessarily indicative of dominance or status in the population as a whole, since an alpha male with one female may have been the beta male of another female (e.g. male 1 in Fig. 1). Due to low natal philopatry, it also is very unlikely that alpha and beta males were members of the same family—I banded 83 offspring from 1987 to 1989 but only one male was recovered breeding in a later year and this individual had dispersed over 3 km from his natal site.

Pair solicitations and copulations.—All unforced copulations that I observed (n = 245) were preceded by female solicitation (n = 692), but only about one-third of all solicitations were followed by mounting. Female Smith's Longspurs solicited by tilting forward, cocking their tail until almost vertical, and throwing their head back toward the male (Fig. 3). The wings also were lowered and vibrated and the bill opened slightly but no vocalizations were audible from 15 m distant. All solicitations by the female were

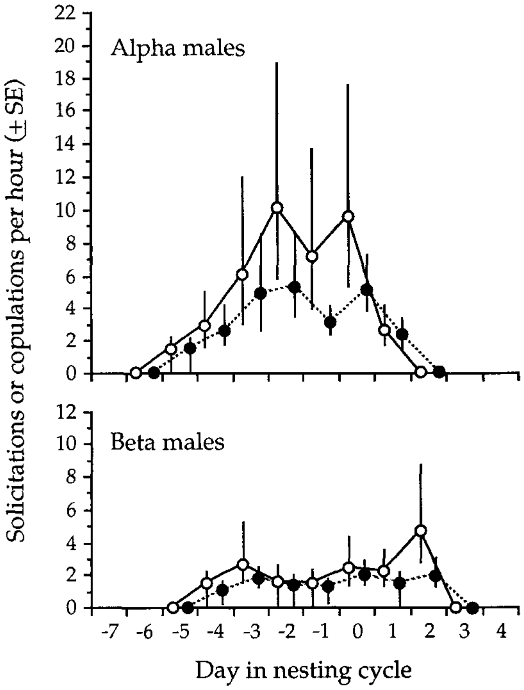

Fig. 4. Timing and rate (±SE) of solicitations (open circles) and copulations (solid circles) by female Smith's Longspurs with alpha and beta males in relation to stage of nesting cycle. Day 0 is day that first egg in clutch was laid. All observations from 0600–0900 CDT. Sample size of six females on each day.

made on the ground and with the cloaca directed toward the nearby male. Males mounted soliciting females from the rear and without any precopulatory displays or courtship feeding. Mounting lasted only 1 to 3 s and males flapped their wings rapidly during mounting, presumably to maintain balance. Copulations appeared to involve only a single cloacal contact. No postcopulatory displays were observed.

Females began soliciting and copulating from three to five days (mean 3.7 days, $n = 6$ females) before the first egg was laid and ceased upon the laying of the first (one female), penultimate (four females) or final egg (one female; mean = day 1.8; see Fig. 1). The total number of days over which copulation occurred ranged from five to eight (mean = 6.5 days, $n = 6$). This period falls well within the 13-day fertilization period assumed for this species.

Because of the diurnal variation in mating behavior (see below), I used only observations from the early morning period to examine seasonal patterns in copulation patterns. I also combined my observations of the single gamma male (female 6, Fig. 1) with those of the beta males since this male was the only gamma male during the study and behaved similarly to the other beta males.

Solicitations to and copulations with the alpha male peaked at 5.3 copulations/h, on the day the first egg was laid and with the beta male at 2.6 copulations/h, two days after the first egg was laid (Fig. 4). This difference in copulation rates was not quite significant ($t = 1.56$, df = 10, $P = 0.07$), although the period of days over which copulations occurred was significantly different between the two males (Mann-Whitney test, $U = 105.5$, $z = 2.32$, $P = 0.01$). Although females typically copulated with only one male on a given day, female 4 copulated with two different males concurrently (see Fig. 1), but the beta male was subsequently killed and this female associated only with the alpha male for the remainder of the breeding attempt.

Despite the difference in the timing of copulations, alpha males copulated at roughly the same rate overall as beta males when only days on which males were associating with females are considered (figures are means [SE in brackets]; alpha male = 5.2 copulations/h [4.0, 6.6], beta male = 3.4 copulations/h [2.5, 4.5], $t = 1.09$, df = 10, $P = 0.30$). This pattern held even when females were actually ovulating (i.e. days −1 to +2; alpha males = 4.0 copulations/h [3.3, 4.9], beta males = 4.0 copulations/h [2.8, 5.9], $t = -0.02$, df = 9, $P = 0.98$). Females also solicited to alpha and beta males at similar rates over both the entire copulation period (alpha males = 14.2 solicitations/h [11.0, 18.3], beta males = 11.6 solictations/h [8.9, 15.1], $t = 0.54$, df = 9, $P = 0.60$) or only when females were ovulating (alpha males = 9.7 solicitations/h [5.7, 16.6], beta males = 11.6 solicitations/h [9.6, 14.0], $t = -0.28$, df = 9, $P = 0.78$).

Copulation frequency might be expected to increase immediately after a switch in mates if males attempt to dilute or displace rival ejaculates. I compared solicitation and copulation rates on the day before and the day after a mate switch took place ($n = 7$). Females solicited more frequently to a new male on the day after a mate switch (13.3 solicitations/h [10.9, 16.3]) than to the previous male on the day before a switch (5.6 solicitations/h [4.0, 7.9]; $t = 2.55$, df = 6, $P = 0.044$). However, copulation rates before a switch (3.2 copulations/h [2.5, 4.1]) did not differ significantly from that after a switch (4.1 copulations/h [3.0, 5.8]; $t = 0.59$, df = 6, P

= 0.58). Thus, males did not increase their copulation rate after obtaining a new mate despite the higher rate of solicitation by females.

I did not have sufficient data to analyze diurnal patterns for alpha and beta males separately, so I combined observations from all males. Solicitation and copulation rates varied significantly over the day (Fig. 5; one-way repeated-measures ANOVA: $F = 12.8$, df = 3 and 13, $P = 0.0003$ and $F = 13.9$, $P = 0.0002$ for solicitations and copulations, respectively). Solicitations and copulations were most frequent over the two morning observation periods and during the evening period; birds normally were not active in the afternoon or foraged solitarily. Copulation and solicitation rates did not differ between the two morning and evening observation periods (Scheffe's multiple-comparison test; $P > 0.20$ for all comparisons) but all were significantly greater than that in the afternoon ($P < 0.02$ for all comparisons). No observations were made at night but it is unlikely that much activity occurs since birds began to roost (sleep) just prior to sunset (pers. observ.).

If males copulate mainly during the expected fertilization window, inseminations are expected to be most successful around ovulation and males should time copulations to coincide with this period. In Smith's Longspurs, the fertilization window encompasses the morning periods from one day before the first egg is laid to the morning the third egg is laid (assuming a clutch of four eggs), since eggs are ovulated and fertilized 24 h before laying. To determine whether copulation rate increased during the fertilization window, I compared copulation rate (by both males combined) during the early morning period (0600–0900) when females were ovulating with that of the pre-ovulatory period. However, copulation rate in the ovulatory period (4.9 copulations/h [4.1, 5.8]) was not higher than that during the pre-ovulatory period (5.6 copulations/h [4.6, 6.8]; $t = 0.53$, df = 9, $P > 0.61$). Likewise, there was no significant difference between solicitation rates during the pre-ovulatory period (12.5 solitations/h [10.3, 15.0]) and during the ovulatory period (15.7 solicitations/h [11.7, 21.0]; $t = -0.63$, df = 9, $P = 0.54$).

Averaged over all time periods, female longspurs solicited 7.0 times/h and males mounted soliciting females 3.1 times/h. Since birds were active for about 18 h/day during the 6.5 day copulation period, this equals approximately 819 solicitations and 365 copulations per female per clutch. On an individual basis, copulation frequency varied from an estimated low of 511 solicitations and 214 copulations per clutch by female 1 to a high of 2,163 solicitations and 629 copulations per clutch by female 3.

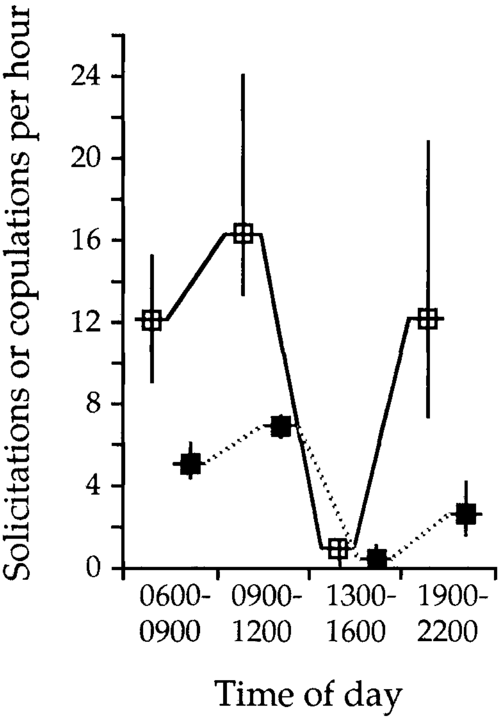

Fig. 5. Rate (±SE) of solicitations (open boxes) and copulations (solid boxes) by female Smith's Longspurs in relation to time of day (CDT). Sample size of six females. Observations in first morning period calculated using mean values for each female to avoid pseudoreplication.

Mate guarding.—Males guarded females by following them closely as they foraged on the ground. Mate guarding by alpha males was greatest on the day before and the day of clutch initiation (76.2 ± 16.0% of their time was spent guarding; Fig. 6A). This corresponds to the period when the first and second eggs were available for fertilization. Guarding by beta males was greatest after the third egg was laid (43.0 ± 19.9% of time spent guarding), a time when the fourth egg could be fertilized (Fig. 6A). This difference in guarding intensity by alpha and beta males was not significant ($t = 1.07$, df = 11, $P = 0.31$).

Averaged over all days on which males were copulating with females, the percent time spent guarding by alpha (72.8 ± 14.5%, $n = 6$) and beta males (61.2 ± 21.3%, $n = 6$) was not sig-

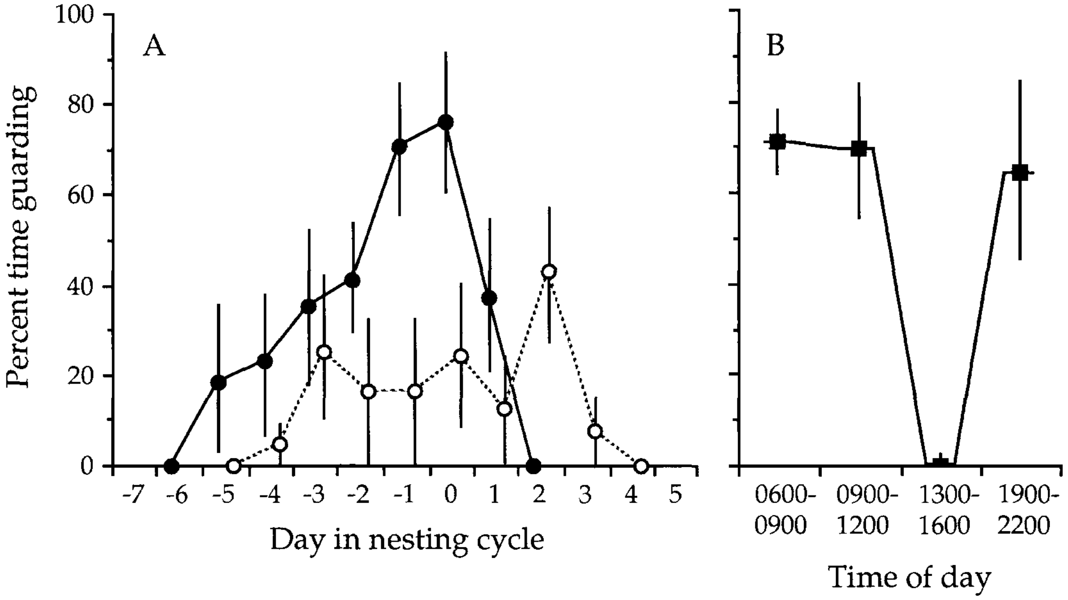

Fig. 6. Percent of time (±SE) spent by alpha (solid circles) and beta males (open circles) mate-guarding females in relation to (A) stage of nesting cycle and (B) time of day (all males combined; CDT). Sample size of six females.

nificantly different ($t = 0.60$, df = 10, $P = 0.56$). Similarly, the time spent guarding during the ovulation period by alpha males (86.8 ± 9.2%, $n = 6$) and beta males (72.7 ± 18.3%, $n = 5$) was not significantly different ($t = 0.85$, df = 9, $P = 0.42$). Time spent guarding was also not significantly different ($t = -1.04$, df = 9, $P = 0.33$) between the pre-ovulation (67.0 ± 22.7%, $n = 5$) and ovulation (83.4 ± 11.4%, $n = 6$) periods when observations from all males were combined.

Mate guarding varied significantly over the day (one-day repeated-measures ANOVA; $F = 8.7$, df = 3 and 13, $P = 0.002$). As with copulation behavior, it was most evident in the two morning and the evening periods, but largely nonexistent during the afternoon (Fig. 6B). Guarding did not differ significantly between the morning and evening observation periods (Scheffe's multiple-comparison test; $P > 0.36$ for all comparisons), but it was significantly greater in all these periods than in the afternoon ($P < 0.003$ in each case).

Females were more likely to fly away from a guarding male (58/87 = 66.7%) than vice versa (29/87 = 33.3%; $G = 19.7$, df = 1, $P < 0.001$) and males were more likely to follow when a female left (55/58 = 94.8%) than females follow when their mate left (5/29 = 17.2%; $G = 57.5$, df = 1, $P < 0.001$). That males were in fact guarding rather than simply following the female to wait for copulations is also evidenced by their efforts to prevent other males from approaching the female. When an intruding male was detected, the guarding male flew up and chased the intruder for up to 100 m.

Intruders were particularly persistent just before the female initiated her clutch (Fig. 7A). At that time, mate-guarding alpha males spent about 4 min out of every hour chasing away intruders. Beta males chased most on the third day after clutch initiation (Fig. 7A). There was a trend for intrusions against guarding males to be most frequent during the early morning observation period (Fig. 7B), but this difference was not significant (one-way repeated-measures ANOVA; $F = 0.6$, df = 3 and 13, $P = 0.66$). All intruders observed were color-banded males resident on the study area.

Forced copulations and copulation attempts.—Forced copulation attempts (FCA) were not preceded by female solicitation. During a FCA, the female gave an alarm call and tried to escape or dislodge the male from her back. FCAs were attempted either by the guarding alpha or beta male (FPCA), or by an extrapair male (FEPCA).

Nine FPCAs were recorded during 73 h of observations of which two were judged as suc-

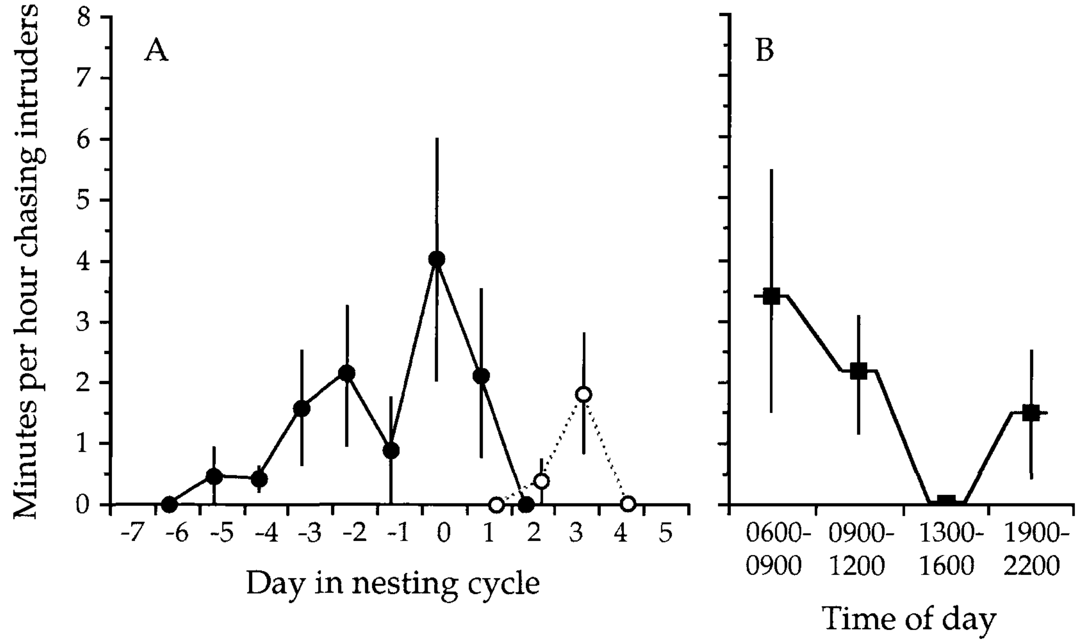

Fig. 7. Time spent per hour (±SE) by alpha (solid circles) and beta males (open circles) chasing intruders from vicinity of female in relation to (A) stage of nesting cycle and (B) time of day (all males combined; CDT). Sample size of six females.

cessful in achieving cloacal contact. Thus, FPCs comprised less than 1% of all within-pair copulations observed. Guarding males may have used FCAs to insure paternity when the risk of EPCs on their mate was greatest. There was a nonsignificant difference ($t = 1.83$, df = 26, $P = 0.08$) for guarding males to have spent more time chasing intruders (i.e. out of sight of their mates) during observation bouts with FPCAs (5.4 ± 2.8 min) than without FPCAs (1.5 ± 0.6 min). The percent of time spent guarding did not differ significantly between bouts where FPCAs occurred (63.7 ± 13.7%) than where no FPCAs were witnessed (74.4 ± 13.5%; $t = -0.67$, df = 26, $P = 0.51$). Five FPCAs (including the two successful FPCs) occurred during the early morning and four in the late morning and from four days before laying until the third egg was laid. Thus, all could have potentially fertilized eggs.

Three FEPCAs were observed, of which two were regarded as successful. All three FEPCAs were by neighboring males, one of which later became a beta male of the female. Females were not being guarded when FEPCAs occurred although in one case the alpha male had been guarding just prior to chasing an intruding male when a second intruding male attempted to copulate with his female. Two FEPCAs took place during the early morning while the third FEPCA occurred during the late morning. All occurred during the female's fertile period (from three days before clutch initiation to the day the second egg was laid) and, thus, could have fertilized eggs. No unforced EPCs were observed.

DISCUSSION

Copulation patterns.—All mating behavior in Smith's Longspurs occurred within a five- to eight-day period which centered on clutch initiation and usually ceased by the laying of the penultimate egg. This period is only about one-half of the 13-day fertilization period assumed for Smith's Longspurs and could arise for several reasons. First, it is possible that longspurs simply cannot store sperm as long as Zebra Finches (i.e. 10 days). Unfortunately, the exact period of sperm storage for Smith's Longspurs is not known and this hypothesis cannot be ruled out at the present time. Second, even if sperm could be stored for up to 10 days, time constraints from the time of arrival to pairing and clutch initiation may select against such an extended copulation period. At this latitude, summers are very short and selection has probably favored rapid nesting rather than a long period of courtship. Smith's Longspurs return to their breeding grounds in Churchill in early June; thus, only about 10 to 12 days are available for pairing and mating before clutch initiation. Although occasional renesting by some longspurs suggests clutches could be initiated later, late clutches in other species are less successful (e.g. Perrins 1965) and it may pay longspurs to breed earlier even if it cuts short the time required for mating. Finally, males may be unwilling to copulate any earlier in the season so that they can allocate ejaculates to those times when they are most likely to fertilize eggs. Because of the frequency of copulations in this species, inseminations more than five days before ovulation are probably highly devalued by the more than 350 copulations that follow, and it may pay to save sperm and energy for inseminations with better odds of fertilization.

Solicitations, copulations and mate guarding were most frequent in the morning as would be expected if inseminations are timed to coincide with the fertilization window. A morning peak in copulations has been found in many species, including Goshawks (*Accipiter gentilis;* Møller 1987b), Ospreys (*Pandion haliaetus;* Birkhead and Lessells 1988) and Zebra Finches (Birkhead et al. 1989; see review in Birkhead et al. 1987), but in none of these birds or Smith's Longspurs did morning copulations increase during the morning on days when eggs were ovulated as would be expected if males take advantage of the fertilization window. Birkhead and Lessells (1988) suggested that copulation frequency did not increase during ovulation because males were unable to tell when their mate would initiate laying; however, this cannot explain the cessation of copulations in species such as Zebra Finches, which stop copulating once laying begins (Birkhead et al. 1989). One possible explanation for the decrease in copulation activity during laying—that females must spend some time incubating eggs already laid—is not applicable because Smith's Longspurs do not begin incubating eggs until the last or penultimate egg is laid. Another possibility is that females already have sufficient sperm stored to fertilize the remainder of their clutch and thus stop soliciting. However, this hypothesis seems unlikely because a single insemination is sufficient to fertilize an entire clutch in other species (Birkhead et al. 1987, 1989), yet Smith's Longspurs continue to copulate until most or all eggs are fertilized. Finally, inseminations also may be less efficient during the egg-laying period because previously fertilized eggs block the oviduct while the deposition of albumin and shell occurs. Thus, copulation frequency may decline over laying simply because the effectiveness of inseminations declines.

Apart from frequent morning copulations, Smith's Longspurs displayed a pronounced increase in mating behavior just prior to sunset. A similar increase was also found in about 25% of the genera surveyed by Birkhead et al. (1987), who suggested that this might be advantageous if ovulation and fertilization occur very early in the morning. Since laying in Smith's Longspurs occurs in the morning, copulations just prior to dark could increase the probability of paternity should ovulation occur shortly before sunrise and before copulations begin in the morning. The absence of an evening peak in copulations in most other species, however, suggests the probability of missing ovulation may be small. On the other hand, the high level of competition between male Smith's Longspurs created by polyandry may favor evening copulations and mate guarding as paternity insurance. Indeed, in one case a female switched mates between the morning and evening of the same day (female 3, Fig. 1). For the beta male of this female, copulations in the evening could have increased the probability that his sperm were present during the next ovulation. Because sperm precedence patterns in birds appear to provide an advantage to the last male to copulate (Birkhead et al. 1988), it may pay a male to copulate in the evening to ensure that his sperm is the last to enter the female even if the probability is high that he will be around to copulate the following morning.

Copulation frequency.—Smith's Longspurs have one of the highest copulation rates in birds reported to date—for a single clutch each female on average copulates about 350 times. In a cross-species comparison, Birkhead et al. (1987) found that copulation frequency ranged from only one copulation per clutch in the Skylark (*Alauda arvensis*) to more than 500 in the Goshawk. They attributed this variation to differences in the probability of extrapair copulations. When the risk of EPCs was high, such as in colonial birds or species in which males cannot guard their mates, copulation frequencies were greater than in solitary, guarding species (Birkhead et al. 1987). Frequent pair copulations are favored because they allow males to displace or devalue sperm of possible competitors. Smith's Longspurs do not defend territories (Jehl 1968), but they guard females during the copulation period. Nevertheless, sperm competition still is expected to be intense because females are regularly polyandrous. Thus, the best strategy for a male may be to mate as often as possible (Birkhead et al. 1987, Ginsberg and Huck 1989). As selection will favor a similar strategy by other males, the net result may be an arms race (Dawkins and Krebs 1979) between males for increasingly higher copulation rates. Indeed, the only two other known polygynandrous passerine species both copulate very frequently (Dunnock, 90 to 200 copulations/clutch, Davies 1985; Alpine Accentor, 123 copulations/clutch, Nakamura 1990).

Frequent copulation may also allow females to assess male quality (Birkhead et al. 1987). When it is costly for males to engage frequently in copulations (e.g. Dewsbury 1982), female choice could lead to the evolution of high copulation frequency in much the same manner as it has led to the development of other male secondary sexual characters such as plumage ornaments or vocalizations (e.g. Andersson 1982). One prediction of the female-choice hypothesis is that females rather than males will solicit most copulations. In Smith's Longspurs, female-solicited copulations comprised more than 99% of all mountings. Such repeated soliciting could be used to test a male's sperm production or sexual endurance as only about 35% of all female solicitations were followed by mounting. This pattern contrasts sharply with that of many other species in which most mating behavior was initiated by the male and few female solicitations were not followed by mounting (Møller 1987b, Birkhead et al. 1987, 1989). It also might be expected that copulations should be greatest during pair formation or that females assess male quality by copulating with several males during the initial stages of pair formation. In fact, copulation did not peak until two to three days after copulation activity first began and no female was observed copulating willingly with more than her two or three mates. Thus, this hypothesis is not supported. Nonetheless, by enticing males to copulate frequently, females effectively force their mates' sperm to co-occur with and compete within the oviduct. If sperm from different males differ in their competitive ability (e.g. success at reaching the sperm storage tubules), then females may use polyandry to ensure their eggs are fertilized by the highest-quality sperm.

Frequent copulations might also function to "disguise" the fertile period and thereby reduce the number of extrapair male intrusions (Birkhead et al. 1987). If copulations do function in such a context, mating behavior would be expected to occur without any systematic pattern that might reveal the true fertility status of the female. In fact, copulation behavior in Smith's Longspurs showed a pronounced increase and peak just as clutch initiation began and females were most fertile. It seems more likely that frequent copulation behavior in this species draws attention to females and to the detriment of guarding males. Frequent copulations might even be a way that females could incite male-male competition and thereby test a male's quality by his ability to prevent extrapair intrusions (e.g. Montgomerie and Thornhill 1989).

Finally, frequent copulations might function as some sort of "pair-bonding" behavior that presumably coordinates and synchronizes the members of a breeding unit. Such a function has been suggested for some species of waterfowl, which often copulate during the winter when their reproductive organs are regressed and insemination is impossible (Birkhead et al. 1987). Although a similar function in Smith's Longspurs cannot be ruled out, it seems improbable because frequent copulations did not occur in the afternoon or after the last egg was fertilized. Instead, both the seasonal and diurnal patterns suggest that high copulation frequency in this species evolved as a consequence of sperm competition.

Evolution of polygynandry.—Despite the apparent correlation between female fertilizability and copulation behavior, the desertion of a female by an alpha male presents a paradox—why should an alpha male desert his mate before laying is complete and eggs can still be fertilized? Instead, a second and even third male may arrive and begin copulating and mate guarding until all eggs are fertilized or laid. Part of the answer may lie in the identity of the beta males. In most cases, beta males were alpha males that had deserted at another neighboring nest. Thus, the former alphas might lose one or two eggs to the beta male at their first female's nest, but they also may gain one or more fertilizations at their second female's nest. Some males even obtained copulations with a third female. Although the benefits of fathering offspring in secondary nests appears to lessen the costs of sharing paternity at a primary nest, that gained at a secondary nest would seem an even trade, and it is difficult to understand how and why such a system could have evolved.

Polygynandry in Dunnocks is thought to result from the inability of males to defend a territory that encompasses the exclusive range of at least a single female (Davies and Lundberg 1985). In this species, various mating combinations from polyandry through to polygyny arise and reflect, to varying degrees, a male's ability to monopolize females. Thus, polyandry results when males cannot defend the home range of a single female and must share her with another neighboring male, while polygyny occurs when males succeed at gaining sole access to several females. The ability of males to defend a female's entire range seems to depend in part on the distribution of food. When food is densely distributed, female ranges were small and males could monopolize one or more females. In contrast, when food was patchy, females' ranges were large and difficult to defend, either alone or with a second male (Davies and Lundberg 1985). Unlike Dunnocks, male Smith's Longspurs did not attempt to defend exclusive areas that encompassed the range(s) of one or more females. Instead, they defended only a small area around the female as she wandered over the study area, and even this was restricted to the few days before and during egg laying. Smith's Longspurs feed mostly on seeds during the early part of the breeding season but the distribution of their food in the environment is not known. It is possible that food availability is low when females arrive and begin egg laying since each female was observed feeding over a large portion of the study area (i.e. overlapping the ranges of several males). If males are unable to defend such large areas economically, then it may pay them to abandon territorial behavior altogether and pursue fertilizations by other mechanisms such as frequent copulations with several different females.

Although the inability of males to monopolize females might provide some insight into the evolution of polygynandry in Smith's Longspurs, it is important to consider female strategies as well. As with males, females also may gain several benefits from mating with several males. For example, if males provide females with some nutrient benefit, either through ejaculates or courtship feedings, then it may pay females to copulate with two males to increase this contribution. Since male longspurs do not courtship feed and it is unlikely that the small ejaculate volumes characteristic of birds (Wolfson 1960) could provide much nutrition, direct material benefits do not appear to provide an incentive for multiple matings. By mating with two or more males, females might increase the genetic diversity of their offspring, although Williams (1975) has argued that the amount of meiosis and recombination involved in a single mating produces considerable genetic diversity and additional matings are unlikely to increase diversity greatly.

Perhaps the greatest potential benefit females might obtain from copulating with several males is the subsequent assistance of those males in caring for the offspring. On my study area, alpha, beta and gamma males were observed feeding nestlings (unpubl. data); thus, females appear successful in recruiting male help through copulating with several partners at least sometimes. Burke et al. (1989) reported that alpha and beta males in polyandrous trios of Dunnocks also contributed parental care but only if they had mating access to the female during the fertile period. Female Dunnocks that had extramale assistance raised more and better fed nestlings than when unassisted or assisted by only a single male (Davies 1985). By providing unlimited copulation opportunities, a female Smith's Longspur may use frequent soliciting and copulations as a mechanism to enlist paternal help from two or more males and thereby reduce her own costs of raising offspring.

ACKNOWLEDGMENTS

This study was funded by Indian and Northern Affairs Canada (Northern Scientific Training Grants Program), the Frank M. Chapman Fund, the Churchill Northern Studies Centre, and the Natural Sciences and Engineering Research Council of Canada through a scholarship to myself and an operating grant to Robert Montgomerie. Special thanks go to Dawn Sutherland, Paul Golding and Sarah Kalff for their patient assistance in the field and for their keen scanning for polar bears! The Churchill Northern Studies Centre provided many essential comforts during this work and I thank them for their continued support. I also thank Ian Jones for drawing the longspurs. This project formed part of my Ph.D. thesis and benefited greatly from the guidance of Robert Montgomerie. T. R. Birkhead, K. Cheng, J. R. Jehl, S. G. Sealy, and an anonymous reviewer provided many useful comments on an earlier draft of this paper.

LITERATURE CITED

ALATALO, R. V., K. GOTTLANDER, AND A. LUNDBERG. 1987. Extra-pair copulations and mate guarding in the polyterritorial Pied Flycatcher, *Ficedula hypoleuca*. Behaviour 101:139-155.

ANDERSSON, M. 1982. Female choice selects for extreme tail length in a widowbird. Nature (Lond.) 299:818-820.

BIRKHEAD, T. R. 1988. Behavioral aspects of sperm competition in birds. Adv. Study Behav. 18:35-72.

BIRKHEAD, T. R., L. ATKIN, AND A. P. MØLLER. 1987. Copulation behaviour in birds. Behaviour 101: 101-138.

BIRKHEAD, T. R., AND F. M. HUNTER. 1990. Numbers of sperm-storage tubules in the Zebra Finch (*Poephila guttata*) and Bengalese Finch (*Lonchura striata*). Auk 107:193-197.

BIRKHEAD, T. R., F. M. HUNTER, AND J. E. PELLATT. 1989. Sperm competition in the Zebra Finch, *Taeniopygia guttata*. Anim. Behav. 38:935-950.

BIRKHEAD, T. R., AND C. M. LESSELLS. 1988. Copulation behaviour of the Osprey *Pandion haliaetus*. Anim. Behav. 36:1672-1682.

BIRKHEAD, T. R., J. PELLATT, AND F. M. HUNTER. 1988. Extra-pair copulation and sperm competition in the Zebra Finch. Nature (Lond.) 334:60-62.

BRISKIE, J. V. 1990. Behavioural and anatomical correlates of sperm competition in birds. Ph.D. thesis, Queen's Univ., Kingston, Canada.

BURKE, T., N. B. DAVIES, M. W. BRUFORD, AND B. J. HATCHWELL. 1989. Parental care and mating behaviour of polyandrous Dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. Nature (Lond.) 338:249-251.

CHENG, K. M., J. T. BURNS, AND F. MCKINNEY. 1983. Forced copulation in captive Mallards. III. Sperm competition. Auk 100:302-310.

DAVIES, N. B. 1983. Polyandry, cloaca-pecking and sperm competition in Dunnocks. Nature (Lond.) 302:334-336.

DAVIES, N. B. 1985. Cooperation and conflict among Dunnocks, *Prunella modularis*, in a variable mating system. Anim. Behav. 33:628-648.

DAVIES, N. B., AND A. LUNDBERG. 1985. The influence of food on time budgets and timing of breeding of the Dunnock, *Prunella modularis*. Ibis 127:100-110.

DAWKINS, R., AND J. R. KREBS. 1979. Arms races between and within species. Proc. R. Soc. Lond. B 205:489-511.

DEVINE, M. C. 1975. Copulatory plugs in snakes: Enforced chastity. Science 187:844-845.

DEWSBURY, D. A. 1982. Ejaculate cost and male choice. Am. Nat. 119:601-610.

GINSBERG, J. R., AND U. W. HUCK. 1989. Sperm competition in mammals. Trends Ecol. & Evol. 4:74-79.

HATCH, S. A. 1983. Mechanism and ecological significance of sperm storage in the Northern Fulmar with reference to its occurrence in other birds. Auk 100:593-600.

HOWARTH, B., JR. 1974. Sperm storage: As a function of the female reproductive tract. Pages 237-270 *in* The oviduct and its functions (A. D. Johnson and C. W. Foley, Eds.). Academic Press, New York.

JEHL, J. R., JR. 1968. The breeding biology of Smith's Longspur. Wilson Bull. 80:123-149.

JOHNSON, K. L. 1987. Wildflowers of Churchill and the Hudson Bay Region. Manitoba Mus. Man and Nature, Winnipeg.

LORENZ, F. W. 1950. Onset and duration of fertility in Turkeys. Poult. Sci. 29:20-26.

MØLLER, A. P. 1987a. Mate guarding in the Swallow *Hirundo rustica*. Behav. Ecol. Sociobiol. 21:119-123.

MØLLER, A. P. 1987b. Copulation behaviour in the Goshawk, *Accipiter gentilis*. Anim. Behav. 35:755-763.

MONTGOMERIE, R. D. 1988. Seasonal patterns of mate guarding in Lapland Longspurs. Pages 447-453 *in* Acta XIX Congressus Internationalis Ornithologici (H. Ouellet, Ed.). Ottawa, Ontario, 1986. Univ. Ottawa Press, Ottawa.

MONTGOMERIE, R. D., AND R. THORNHILL. 1989. Fertility advertisement in birds: A means of inciting male-male competition? Ethology 81:209-220.

NAKAMURA, M. 1990. Cloacal protuberance and copulatory behavior of the Alpine Accentor (*Prunella collaris*). Auk 107:284-295.

ORING, L. W. 1986. Avian polyandry. Curr. Ornithol. 3:309-351.

PARKER, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. Biol. Rev. 45:525-567.

PERRINS, C. M. 1965. Population fluctuations and clutch size in the Great Tit, *Parus major* L. J. Anim. Ecol. 34:601-647.

SCHIFFERLI, L. 1979. Why do passerines lay their eggs early in the morning? Ornithol. Beob. 76:33-36.

SHUGART, G. W. 1988. Uterovaginal sperm-storage glands in sixteen species with comments on morphological differences. Auk 105:379-384.

SKUTCH, A. F. 1952. On the hour of laying and hatching of birds' eggs. Ibis 94:49-61.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, 2nd ed. W. H. Freeman and Co., San Francisco.

WILLIAMS, G. C. 1975. Sex and evolution. Princeton Univ. Press, Princeton.

WOLFSON, A. 1960. The ejaculate and the nature of coition in some passerine birds. Ibis 102:124-125.

ZENONE, P. G., M. E. SIMS, AND C. J. ERICKSON. 1979. Male Ring Dove behavior and the defense of genetic paternity. Am. Nat. 114:615-626.