

ECOLOGICAL CORRELATES OF MONOGAMY IN TUNDRA-BREEDING SAVANNAH SPARROWS

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ABSTRACT.—A tundra population of Savannah Sparrows (*Passerculus sandwichensis*) was studied during the 1976 and 1977 breeding seasons. The mating system was monogamous, although variability in breeding-habitat quality indicated some potential for polygyny. Clutch initiation was highly synchronous, and renesting attempts were limited to early nesters suffering early nest failure. Temporal variations in reproductive success and the reduced success of females rearing young without male assistance suggest that monogamy is maintained as a consequence of the brevity of the tundra breeding season. *Received 19 July 1978, accepted 23 January 1979.*

THE Verner-Orians polygyny model (Verner 1964, Verner and Willson 1966, Orians 1969) explained the evolution of polygynous mating systems on the basis of unevenly distributed resources that could be monopolized by a few males. Inequity in territory quality proved sufficient to explain the occurrence of polygyny in a number of species (Verner 1964, Willson 1966, Price and Bock 1973, Carey and Nolan 1975). Other studies have pointed out the need to include other factors as potentially important. Elliott (1975) has shown that polygyny in yellow-bellied marmots (*Marmota flaviventris*) can be explained in terms of the superior predator defense provided by polygynous groupings. Weatherhead and Robertson (1977a, 1979) have argued the importance of male characteristics as distinct from territory parameters in influencing polygynous matings. This factor would most likely be of greater importance once polygyny had occurred, however, when more intense sexual selection could give it impetus.

Recently Emlen and Oring (1977) have presented a mating-systems model defined in terms of resource monopolization. The fundamental difference between this model and the Verner-Orians model is the inclusion of potential mates as a resource equal in importance to habitat quality. They have argued that if breeding is highly synchronous, there will be no opportunity for polygamy, given the time required for one pair to complete courtship and copulation. It is only when the operational sex ratio ("the average ratio of fertilizable females to sexually active males at any given time") deviates from unity in conjunction with some minimum degree of inequity in territory quality that polygamy will occur.

The importance of territory quality in influencing mating systems is well documented, but there is little evidence of situations in which the temporal limitation of mate availability maintains monogamy in spite of other resources being distributed in a manner that would predict the occurrence of polygamy. The ecological conditions most likely to create such a situation would be a marked seasonality, where breeding is confined to a very short period of time. One would expect that at higher latitudes these prerequisites may be met. The aim of this paper is to examine the mating system of a tundra-breeding passerine in order to assess the relative importance of temporal limitations in shaping the observed mating system.

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STUDY AREA AND METHODS

The species chosen for this study was the Savannah Sparrow (*Passerculus sandwichensis*). Other studies have shown that polygyny does occur in this species (McLaren 1972, Welsh 1975, Stobo and McLaren 1975). The work was carried out at the Queen's University Tundra Biology Station at la Pérouse Bay, Manitoba, 40 km east of Churchill on the coast of Hudson Bay. The habitat along the coast is classified as a tundra biome (Cooke et al. 1975). In the immediate area of the study the dominant vegetation was shrub, including several species of willow (*Salix* spp.), dwarf birch (*Betula glandulosa*), and sweet gale (*Myrica gale*). Within the shrub habitat a distinct height transition from low to high shrubs occurred with increasing distance from the coast. This appeared to be closely correlated with a change in species dominance from *Salix brachycarpa*, a short species usually less than 0.5 m tall, to a mixture of *S. candida* and *S. planifolia*, both of which can grow to heights greater than 3 m, in a transition zone. In approximately 50 m the transition zone then gave way to a region dominated by *S. planifolia* that I will term the tall willow habitat.

Accompanying the vegetation and height transitions were changes in the avifauna. Savannah Sparrows were common in both habitats but coexisted with few passerines other than occasional Horned Larks (*Eremophila alpestris*) and Lapland Longspurs (*Calcarius lapponicus*) in the short willow region. In the transition zone, Tree Sparrows (*Spizella arborea*) became abundant and remained so into the tall willow habitat. Also found in the tall willows, but not in the abundance of either Savannah or Tree Sparrows, were White-crowned Sparrows (*Zonotrichia leucophrys*), Hoary and Common Redpolls (*Carduelis hornemanni* and *C. flammea*), Blackpoll Warblers (*Dendroica striata*), Yellow Warblers (*Dendroica petechia*), and Rusty Blackbirds (*Euphagus carolinus*).

The study was conducted during the summers of 1976 and 1977. Prior to the arrival of the birds in 1976, a 550 × 350-m grid, marked at 50-m intervals, was established in a location that encompassed areas of both tall and short willow habitat. To quantify differences between the habitats, the diagonals of every grid square were used as transects. Each transect was walked and the substrate underfoot classified by vegetation type and height. A free-hand map of the study area was drawn indicating the transition between habitats in order to allow comparison with the transect data.

From the first arrival of the birds and throughout the breeding season, mist nets were used to capture adult birds. In addition to a number of morphological measurements taken for another study, each bird was sexed by the presence or absence of a cloacal protuberance (Wolfson 1952) and individually color-banded. In 1977 acrylic paint applied to the end of the tail was also used to facilitate the recognition of males and females. This met with limited success, as some birds removed the paint by preening.

In order to determine the mating system of the population, it was necessary to search thoroughly a sample of males' territories in order to ascertain the number of active nests per territory and hence the number of females. An attempt was made both years to map as many territories as possible within the grid. Because of the size of the grid, the density of birds, and the time required for mapping, however, only the short willow portion of the grid was accurately mapped. Territories were mapped based on regular observation of areas frequented and defended by particular males. Within the tall willows individuals became extremely difficult to follow because of the vegetation, and accurate territory mapping was not possible in the time available. In 1976 nest searching was concentrated in the short willow habitat, although some nests were found in the tall willow habitat. In 1977 both areas were well searched for nests. As nests were located, their position was mapped and marked. Nests were visited a minimum of once every 2 days and usually daily once the eggs hatched. Nestlings were weighed and their tarsal length measured on each visit. Individual nestlings were distinguished by felt-pen markings on their feet. Nests found outside the study area were treated in the same manner, with the exception of mapping. In order to determine the nesting pattern of Tree Sparrows relative to that of Savannah Sparrows, the locations of all Tree Sparrow nests found were recorded.

In 1977 males were removed from eight territories in order to assess the ability of females to rear young alone. All territories were located in the short willow habitat, and the males were removed within a day of their eggs hatching. In addition to the daily measurements of nestling growth at these nests, feeding observations from a blind were made at five of the nests. An additional five nests in the same habitat with the same distribution of initiation dates and clutch size were observed as controls. These nests were chosen so that at least one member of the pair was individually color marked in order that males could be distinguished from females. Observations were made daily between 0800 and 1800, and the order in which nests were observed was varied regularly. A total of 1,640 min of observation time was evenly split between the control and experimental nests, giving a mean daily observation time of approximately 23 min per nest. Observation time began only after the observer was in the blind and the bird(s) had calmed down from the disturbance created by the observer's arrival.

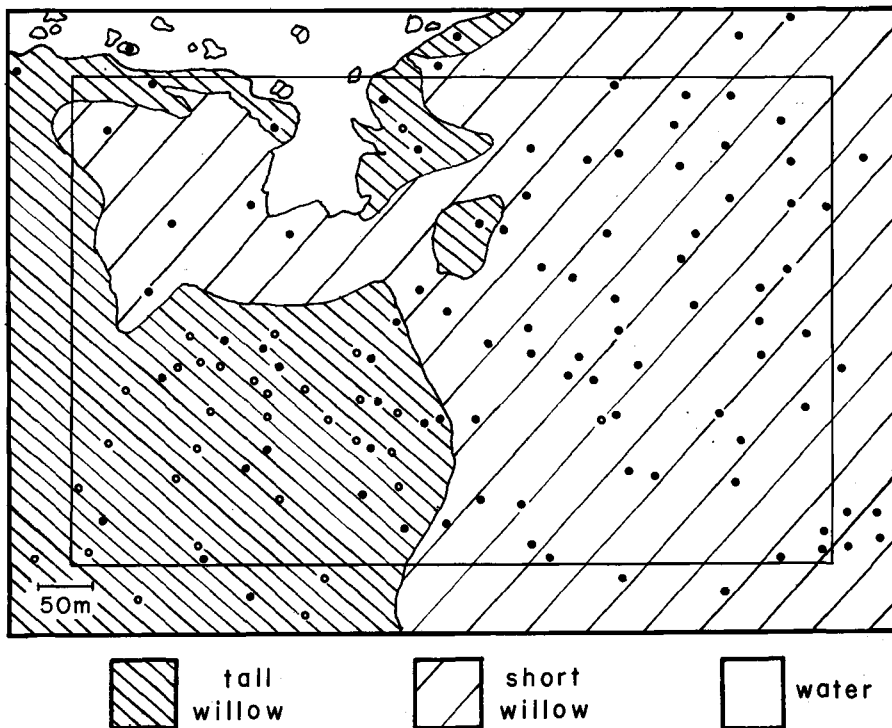


Fig. 1. Map of the study grid (inner rectangle) indicating habitat types and nest locations of Savannah Sparrows (dark circles) and Tree Sparrows (light circles). Included are some nests that were not active during the study but could be attributed to particular species by the nest construction. Several nests used in the study were out of the map area.

The stomachs of males removed for this study and those removed for other studies were saved for analysis to determine if the onset of breeding coincided with a change in diet. The contents of 25 stomachs from birds collected between 24 May and 12 July were examined under a dissecting microscope, and an estimate was made of the percent by volume of seeds and arthropods.

RESULTS

The mating system.—The occurrence of polygynous matings would be signified by the presence of two or more simultaneously active nests in one male's territory. For polygyny to be considered more than accidental, an incidence of more than 5% is the generally accepted level (Verner and Willson 1969). Over two breeding seasons

TABLE 1. Estimated mean percent cover (\pm SD) of different substrates in the short and tall willow habitats.

	Short willow	Tall willow
Number of quadrats sampled	45	17
Willow < 0.5 m	25.5 \pm 10.8	11.0 \pm 14.0
Willow 0.5 m-1.0 m	1.4 \pm 4.2	35.6 \pm 13.5
Willow > 1.0 m	0.0 \pm 0.0	12.3 \pm 14.8
Mud, sedge, and grass	30.2 \pm 13.9	2.5 \pm 4.9
Water	19.7 \pm 8.3	26.2 \pm 7.9

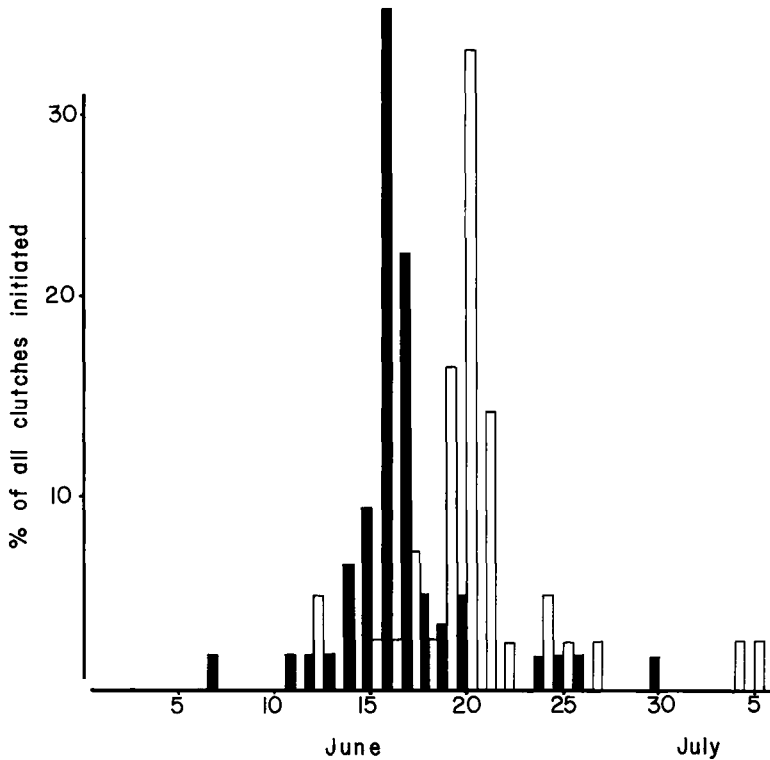


Fig. 2. Distribution of clutch initiation dates for 1976 (open bars) and 1977 (solid bars).

65 territories were both accurately mapped and thoroughly searched regularly for nests. Of these, 59 (90.8%) had 1 nest, 1 (1.5%) had 2 nests and 5 (7.7%) had no nests. In the case involving two nests, it was not possible to confirm that two females were mated to the same male by observing nest defense and feeding behavior, as both nests were unsuccessful before hatching. Even were this a polygynous mating, however, the mating system should be considered monogamous by the criterion given above.

Habitat differences.—From the map (Fig. 1) drawn to indicate the point of transition from short to tall willow habitat, at least 90% of all quadrats chosen fell into one habitat or the other. Both transects in a quadrat were combined to estimate the

TABLE 2. Reproductive success^a in short and tall willow habitats (only nest within 4 days of peak initiation).

	Short willow	Tall willow
Mean clutch size	4.78 ± 0.51 (68)	4.17 ± 0.62 (18)
Percent of nest to hatch	86.1 (72)	94.4 (18)
Percent of nests successful	70.8 (65)	61.1 (18)
Percent of eggs to fledge	63.5 (59)	58.6 (17)
Total young fledged	179 (64)	41 (17)
Young per successful nest	4.07 ± 1.37 (43)	3.73 ± 1.01 (11)
Young per female	2.80 ± 2.18 (64)	2.41 ± 2.00 (17)

^a Values = mean ± SD (sample size); sample size varies due either to incomplete information for some nests or because the use of some nests for experimental purposes allowed only the use of data collected prior to experimentation.

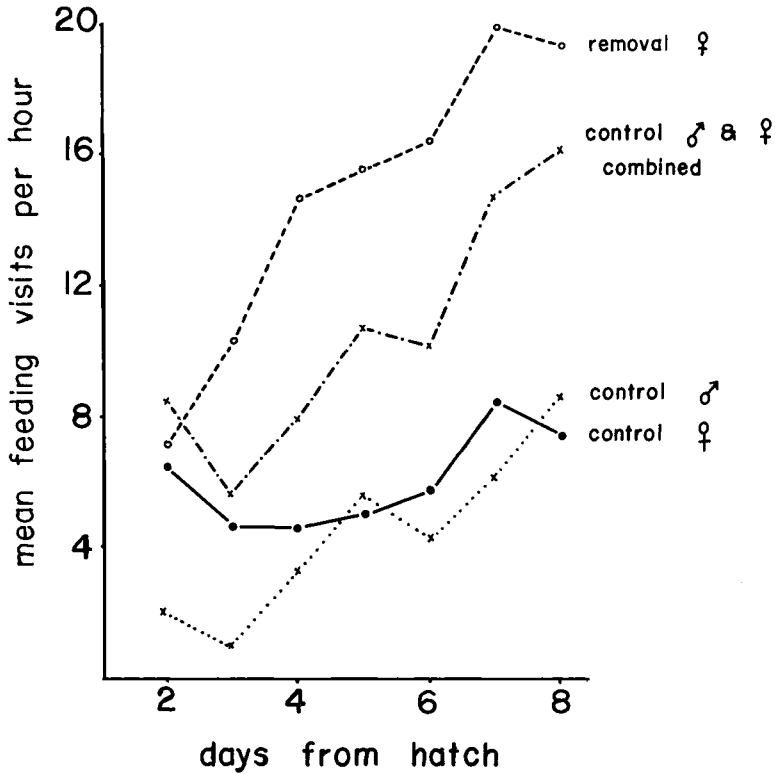


Fig. 3. Feeding rates of experimental and control birds.

percent cover by each substrate category in that quadrat. A comparison of the quadrats from the two habitats (Table 1) verifies the habitat differences. These differences are mirrored by the distribution of Tree Sparrow nests, which were restricted almost exclusively to the tall willow habitat. Savannah Sparrows, however, nested throughout the area.

It seems reasonable to expect Savannah Sparrow reproductive success to be greater in the short willow habitat for two reasons. The habitat is structurally more typical of that in which the species breeds elsewhere (Potter 1972), and, as discussed by Wiens (1973), the vegetational structure in a territory can be of considerable

TABLE 3. Mean nestling weight and tarsus length from hatch date in the short and tall willow habitats (only nests within 4 days of peak initiation).

	Days from hatch							
	1	2	3	4	5	6	7	8
Weight (g)								
Short willow	2.10	3.24	5.02	7.19	9.97	12.19	14.18	15.31
Tall willow	2.00	2.99	4.66	7.03	9.91	12.14	14.42	15.74
Tarsus length (mm)								
Short willow	7.07	8.58	10.83	13.34	15.93	18.25	20.02	21.07
Tall willow	6.98	8.43	10.61	13.10	15.67	18.18	19.96	20.99

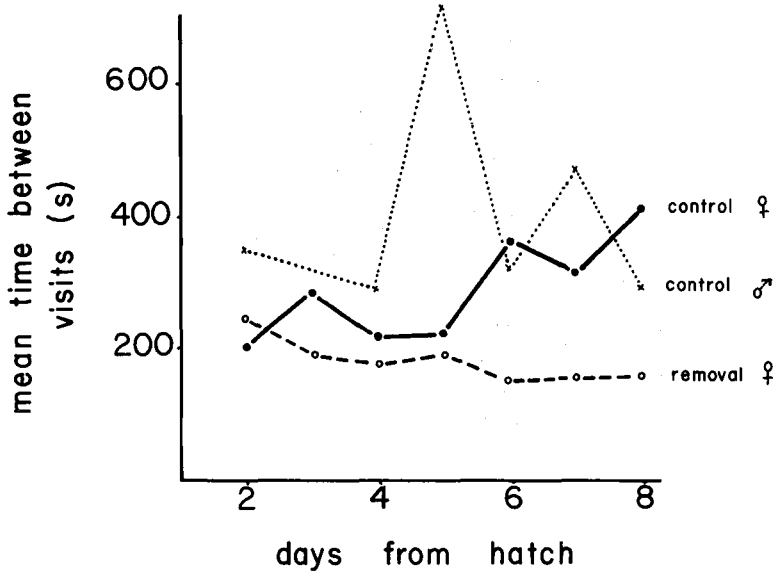


Fig. 4. Time spent away from the nest between visits by experimental and control birds.

ecological importance. Second, the relative paucity of potential interspecific competition in the short willow habitat may improve its suitability for Savannah Sparrows. Clutch size was significantly smaller ($t = 1.99$, $P < 0.05$) in the tall willow habitat, with a modal size of four compared to five in the short willow habitat (Table 2). This suggests that food availability is predictably lower or predation pressure more intense in the tall willow habitat, and clutches are adjusted accordingly. It should be noted that only those nests initiated within 4 days of the peak clutch initiation date were used for this analysis in order to avoid variation in reproductive success due to early or late nesting (discussed below).

A comparison of weight change and tarsus growth of nestlings from both habitats showed no significant difference between the groups on any day (Table 3). The reduced clutch size in the tall willow habitat, therefore, appeared sufficient to compensate for any reduced food availability that may have existed.

Temporal differences.—One of the most striking features of the breeding biology of this Savannah Sparrow population was the high degree of synchrony the females

TABLE 4. Reproductive success^a of nests in different clutch initiation periods (short-willow habitat nests only).

	Time of initiation		
	Pre-peak	Peak	Post-peak
Mean clutch size	4.47 ± 0.74 (15)	4.87 ± 0.44 (52)	4.54 ± 0.52 (13)
Percent of nests to hatch	86.7 (15)	86.0 (57)	92.3 (13)
Percent of nests successful	69.2 (13)	70.0 (50)	69.2 (13)
Percent of eggs to fledge	58.6 (13)	62.9 (46)	47.5 (12)
Total young fledged	34 (13)	141 (49)	28 (13)
Young per successful nest	3.78 ± 1.20 (9)	4.15 ± 1.42 (34)	3.11 ± 1.45 (9)
Young per female	2.62 ± 2.06 (13)	2.88 ± 2.26 (49)	2.15 ± 1.91 (13)

^a Values = mean ± SD (sample size); sample size varies due either to incomplete information for some nests or because the use of some nests for experimental purposes allowed only the use of data collected prior to experimentation.

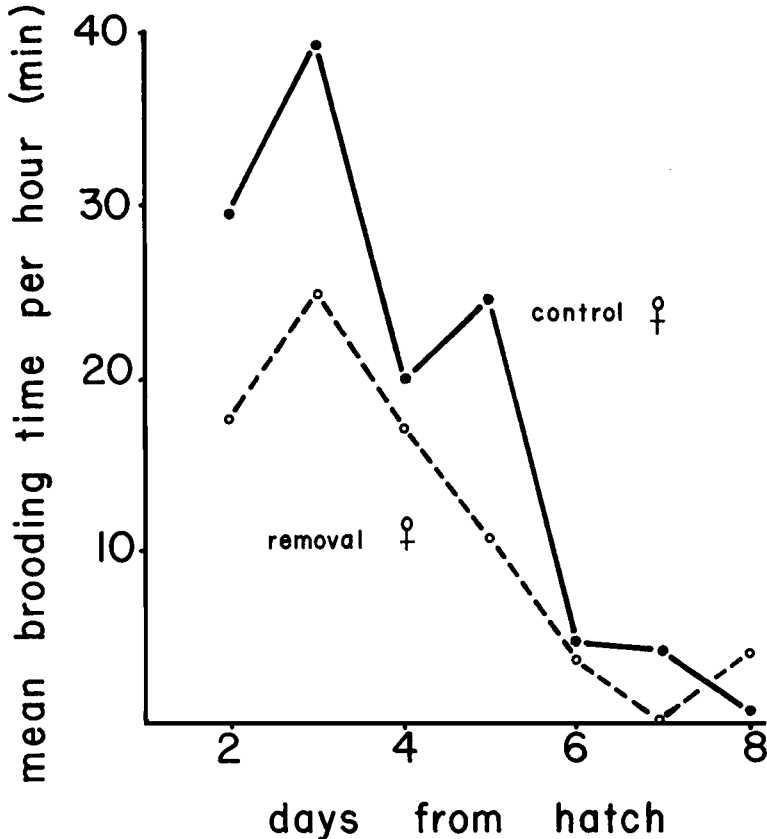


Fig. 5. Time spent brooding by experimental and control females. Brooding was assumed to occur when a visit to a nest lasted longer than 60 s.

achieved in clutch initiation (Fig. 2). Although the first clutch was initiated 4 days earlier in 1977, the total range was 23 days both years. This consistency between years is particularly noteworthy, as 1976 was the latest and 1977 the earliest spring observed in 8 yr of research in this area (Cooke pers. comm.). In both years more than 65% of all clutches found were initiated in a 3-day period. It is this 3-day period that I define as the initiation peak and use to compare temporal differences in reproductive success and growth performance.

The superior quality of the short willow habitat suggests that it was in this region that polygynous matings would have been most likely. Therefore, to determine the importance of temporal factors in limiting the system to monogamy, the analysis of reproductive success relative to initiation date (Table 4) was restricted to nests located in the short willow habitat. Clutch size of peak nests was greater than either pre- or post-peak nests, although the difference was not significant. This initial margin due to clutch size became even greater by the time of fledging, due to greater per-egg success of peak nests. The difference was significant between peak and post-peak nests ($\chi^2 = 8.16$, $P < 0.01$) but not between peak and pre-peak nests.

The growth performance data (Table 5) indicate that pre-peak and peak nestlings differed very little. A comparison of day 8 weights and tarsus lengths of post-peak

TABLE 5. Mean nestling weight and tarsus length from hatch date from nests in different clutch initiation periods (short-willow habitat nests only).

	Days from hatch							
	1	2	3	4	5	6	7	8
Weight (g)								
Pre-peak	1.94	3.22	4.81	7.07	10.00	12.27	14.13	15.42
Peak	2.10	3.19	5.10	7.28	9.97	12.24	14.23	15.15
Post-peak	1.92	2.79	4.44	6.54	8.87	10.64	12.67	13.96
Tarsus length (mm)								
Pre-peak	6.58	8.31	10.06	12.85	15.67	17.93	19.97	20.94
Peak	6.89	8.50	10.69	13.23	15.92	18.27	20.00	21.04
Post-peak	7.00	8.22	10.23	12.79	15.13	17.07	18.73	19.73

nestlings with both other groups, however, indicated that post-peak nestlings were significantly smaller (t -tests, $P < 0.001$). The lighter weight of the nestlings might be expected to reduce further the success of post-peak breeders (Lack 1966).

The importance of male parental care.—The observations at control and experimental nests (Figs. 3, 4, and 5) indicated that males played a substantial role in feeding but not in brooding young. There were two observations of brooding by males, but otherwise brooding was done entirely by females. In the absence of the male, female behavior was radically altered. Experimental females spent less time brooding and made briefer foraging trips, thereby greatly increasing the feeding rate. Comparison of delivery rates each day by Mann-Whitney U -tests indicates that, from day 3 through day 7, experimental females achieved significantly higher rates than those of control males and females combined ($P < 0.01$). A consequence of this change was that foraging by experimental females became concentrated in the immediate area of the nest. These changes are consistent with observations of unassisted female feeding behavior in Bobolinks (*Dolichonyx oryzivorus*) reported by Martin (1974). It may follow that prey selection by experimental females became broader, with a consequent reduction in the quality of food delivered.

The analysis of both reproductive success (Table 6) and nestling growth performance (Table 7) of experimental and control nests indicates that the modification of feeding behavior by the lone female was not sufficient to maintain normal success or growth. From day 2 until fledging, experimental nestlings were significantly lighter than control nestlings (t -tests, $P < 0.01$). The same is true for tarsus length from day 3 to fledging (t -tests, $P < 0.01$). It should be noted that because both experimental and control nests were chosen at the time eggs hatched, neither group was subject to any pre-hatch losses, and consequently their reproductive success appears high relative to other values already reported.

TABLE 6. Reproductive success^a of experimental (male removal) and control (1977, short-willow habitat nests within 3 days of peak initiation) nests.

	Experimental	Control
Mean clutch size	4.88 ± 0.35 (8)	4.96 ± 0.47 (23)
Percent of nests successful	87.5 (8)	95.7 (23)
Percent of eggs to fledge	71.8 (8)	88.3 (23)
Total young fledged	28 (8)	98 (22)
Young per successful nest	4.00 ± 0.58 (7)	4.45 ± 1.26 (22)
Young per female	3.50 ± 1.51 (8)	4.26 ± 1.54 (23)

^a Values = mean ± SD (sample size).

TABLE 7. Mean nestling weight and tarsus length from hatch date in experimental (male removal) and control (1977, short-willow habitat nests within 3 days of peak initiation) nests.

	Days from hatch							
	1	2	3	4	5	6	7	8
Weight (g)								
Experimental	1.88	2.85	4.38	6.04	7.92	10.21	12.20	13.24
Control	2.10	3.33	4.93	6.99	9.68	12.09	14.19	15.40
Tarsus length (mm)								
Experimental	7.00	8.54	10.23	12.51	14.98	17.40	18.79	20.01
Control	7.12	8.64	10.92	13.41	15.98	18.24	20.06	21.16

Diet analysis.—The examination of stomach contents indicated that seeds averaged 45% by volume of identifiable matter for birds collected prior to 11 June and 0% for birds collected after 11 June. This switch from partial granivory to total carnivory coincides closely with clutch initiation, suggesting that breeding may be triggered by the availability of adequate protein resources (Jones and Ward 1976). The diet analysis, however, provided no insight into what factors may be responsible for the abrupt termination of breeding.

DISCUSSION

Studies of avian mating systems have shown that polygyny can be achieved in several ways. In the Red-winged Blackbird (*Agelaius phoeniceus*), the females are able to rear the young alone, and consequently male participation in this aspect of reproduction is very limited (Holm 1973, Weatherhead and Robertson 1977b). The pattern exhibited by Bobolinks is one in which there are primary and secondary females, the former receiving substantial assistance from the male, the latter almost none (Martin 1974). In Savannah Sparrows (Welsh 1975, Stobo and McLaren 1975) and Long-billed Marsh Wrens (*Cistothorus palustris*) (Verner 1964), female recruitment is staggered, thereby allowing males to assist at the nests of all their mates.

If polygyny were to occur in this Savannah Sparrow population, the potential appears greatest in the short willow habitat, where females averaged 1.16 young fledged for every young fledged by tall willow females. Given that this ratio is based on mean reproductive success, the difference between the best and worst territories in the study area would be considerably greater. The fact that females do not chose to mate polygynously would indicate, however, that the expected reproductive success for a secondary female in an optimal territory is less than that for a primary female in a marginal territory (Wittenberger 1976). The reasons for this difference are examined below in the context of the possible options a secondary female would have.

Under the system described for Bobolinks by Martin (1974), females from the tall willow habitat could breed as secondary mates without male assistance in the short willow habitat. This was, in effect, the situation created when males were removed. As all experimental nests were in short willow habitat and were initiated within 3 days of the peak clutch initiation date, the performance of these females was the maximum that could be expected of females rearing young alone. For every young fledged by tall willow females in 1977, experimental females fledged 1.13 young. (The tall willow nests used for this comparison were only those successful to hatch and initiated in the same time period as the experimental nests.) That experimental

females fledged more young would suggest that this form of polygyny should occur. Several factors, however, would be expected to reduce the success of experimental females after fledging. Feeding of fledglings by both males and females was observed in this population at least a week after the young left the nest. As the young tend to disperse during this time, the feeding efficiency of the experimental females would therefore probably be reduced even further relative to control birds. The lighter weight of young fledging from experimental nests would be expected to reduce their post-fledging survival (Lack 1966), and finally, the survival potential of the experimental females might be reduced if their accelerated activity resulted in energetic deficits.

The other alternative for polygyny is to stagger the nest initiation dates of harem females. In both years all clutch initiations spanned only 23 days, with the peak being 8 and 9 days after the first initiation for 1976 and 1977, respectively. Given that the time from hatch to fledging averaged about 9 days, it would be possible for a female to initiate within the peak period and have her clutch hatch at the time another female's young had fledged. This would allow no post-fledging assistance to the first female's young by the male, however. Therefore, the second female recruited must either initiate her clutch after the peak period or accept limited or no male assistance. Both these conditions have been shown to be inferior to nesting in the tall willow habitat with full male assistance. That some females did initiate clutches quite late seems initially at odds with the reasoning presented above. Of these females, however, those that were banded were known to have nested previously and to have been unsuccessful. They were, therefore, not late arrivals that might be expected to accept secondary status as a polygynous mate, but birds that could remain the sole female of their original mate.

The monogamous mating system of this population, therefore, appears to be the consequence of two factors. The male is too important in rearing young for a female to undertake it alone, and there is insufficient time available for the staggered nesting of mates typical of this species when polygynous. These results therefore support the model of Emlen and Oring (1977), in that the limited temporal availability of mates plays an important role in determining the mating system.

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