Polygyny and male parental care in Savannah sparrows: effects on female fitness

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Summary. To determine the effects of male mating status on female fitness, we compared the reproductive success, survival, and future fecundity of female Savannah sparrows (*Passerculus sandwichensis*) mated to monogamous vs. polygynous males in a 5-year study on Kent Island, New Brunswick, Canada. The proportion of males with more than one mate varied from 15 to 43% between years and sites. Polygynous and monogamous males fledged young of equal size in every year of the study. Females who shared paternal care with other females laid as many eggs per clutch and clutches per season as monogamously mated females. In most years polygynously mated females showed no delay in laying a second clutch, and they suffered no reduction in fecundity the following year. Recruitment of a female's offspring into the breeding population was generally independent of her mating status. Fitness costs of being mated to a polygynous male were only apparent in one year of the study, during which females mated to polygynous males had higher over-winter mortality than those mated to monogamous males. That same year, young raised by polygynous males were only one-third as likely to survive to reproductive maturity (as inferred by returns) as those raised by monogamous males. A male's mating status had no effect on his own survivorship. A male's mating status did not necessarily reflect his contributions to raising nestlings, which may partially explain why monogamously and polygynously mated females had equal fitness. At 35 nests the proportion of food deliveries brought by individual males varied from 0 to 75%; on average, males brought fewer than 30% of all food deliveries. Yet parental care by polygynous males was no less than that of monogamous males, at least at the nests of their primary females. Secondary females tended to receive less male assistance during the nestling stage, but their reproductive success was indistinguishable from that of primary females. Females feeding young without male assistance made as many food deliveries/h as did pairs in which males brought at least 30% of all food deliveries. Unassisted females did not suffer diminished fledging success or produce smaller fledglings. The benefits of polygyny for male Savannah sparrows are clear: polygynous males recruit more surviving offspring into the breeding population than monogamous males. The fitness of females, on the other hand, appears to be unaffected by whether their mate was monogamous or polygynous except in occasional years. Polygyny may be maintained in this population by the constraints of a female-biased sex ratio, the inability of females to predict a male's paternal care based on his morphology or behavior, the poor correlation between a male's mating status and his assistance at the nest, and inconsistent natural selection against mating with a polygynous male.

Introduction

It is commonly assumed that polygynous males provide less parental care than monogamous males, and that a female potentially suffers reduced fitness if she chooses to mate with an already mated male, unless she is compensated by his superior genes or resources such as territory quality. What effect does a male's mating status have on female fitness? Are mating status and parental care necessarily correlated? How important is paternal care for successfully raising young? The answers to these questions are central to the understanding of mate choice by females and the evolution of mating systems (Verner and Willson 1966; Orians 1969; Emlen and Oring 1977; Wittenberger and Tilson 1980; Smith et al. 1982; Gowaty 1983; van Rhijn 1984; Alatalo et al. 1986; Lifjeld and Slagsvold 1988; Whittingham 1989).

Two recent reviews of male-removal experiments concluded that male assistance at the nest generally increases female fitness only under stressful environmental conditions (Wolf et al. 1988; Bart and Tornes 1989). In species where males normally provide relatively little help at the nest, their absence tends to have a negligible effect

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on female fitness, at least as measured over the short term. The strength of the studies described in these reviews is their experimental approach; a weakness is that none of them fully measured female fitness. Nestling size, fledgling success and, in some cases, survival of fledglings to several weeks or months of age were used to estimate reproductive success (Bart and Tornes 1989), but a complete picture of how a male's mating status or assistance at the nest influences female fitness should include effects on the survival and future fecundity of his mate, plus the probability that her offspring will survive to reproductive maturity (cf. Nur 1988). Only the study of Wolf et al. (1988) examined the survival of offspring beyond a few weeks, and none considered a female's fecundity the year after being mated to a polygynous male or raising young unaided. Some of the studies only provided data for a single breeding season, another shortcoming in light of Wolf et al. (1988) and Bart and Tornes's (1989) contention that the value of male assistance depends upon temporally variable environmental conditions.

We assessed the importance of male mating status and parental care in Savannah sparrows (*Passerculus sandwichensis*), a species in which the frequency of polygyny and levels of male assistance at the nest vary among individuals, locations, and years (Stobo and McLaren 1975; Welsh 1975; Weatherhead 1979, 1989; Rising 1987a, b, 1989). In a high-latitude population of Savannah sparrows Weatherhead (1979) had earlier demonstrated that females could raise nestlings in the absence of their mates (see also Welsh 1975; Williams 1987). Nonetheless, he hypothesized that polygyny would be selected against because of its negative effect on the survival of females or their young. We tested that proposition by comparing the reproductive success, survival, and future fecundity of female Savannah sparrows mated to monogamous vs. polygynous males in a 5-year study. We also monitored the recruitment of offspring into the breeding population in subsequent years. At 35 nests we determined the proportion of food deliveries brought by males to nestlings, the relationship between a male's mating status and his assistance at the nest, the predictability of male parental care, and the effect of male assistance on female fitness. Given that we found the fitness of females mated to monogamous and polygynous males to be indistinguishable in most years, we discuss some of the constraints female Savannah sparrows face in obtaining high levels of male parental care and speculate on the maintenance of polygyny.

Methods

Study area. Since 1987 we have been studying an isolated population of Savannah sparrows at the Bowdoin Scientific Station, located on Kent Island, an 80-ha island in the Bay of Fundy, New Brunswick, Canada (44°35'N, 66°46'W), about 25 km from the Maine coast. Savannah sparrows nest in a range of open habitats on the island, including areas of low woody vegetation (*Rubus idaeus, Vaccinium* spp.), coastal vegetation (herbs and grasses such as *Elymus arenarius*), marshes, and hay fields abandoned 50 years ago (McCain 1975). Savannah sparrows forage in the fields as well as along the shore, in the intertidal zone, and in the branch-tips of conifers (*Picea rubens, P. glauca, Abies balsamea*).

The study area itself consists of two sites, the "north field" (1.2 ha) and "south field" (5 ha) in the center of the 2.8 km-long island. The sites are isolated from the rest of the island by forest and marsh, and from each other by a 100-m-wide stand of white spruce. A series of parallel trails divides both sites into 50-m² quadrats which provide reference locations for mapping nests, territories, and individuals. About half of Kent Island's Savannah sparrow population breeds in the two study sites (Dixon 1978).

Biology of Savannah sparrows. Savannah sparrows breeding on Kent Island return from their southerly wintering grounds in late April or early May. Males arrive earlier than females on average, quickly establishing territories whose boundaries fluctuate somewhat during the season and overlap neighbors' territories. Females lay 1–2 clutches per year (very rarely 3) in cup nests, well-concealed beneath grass domes on the ground. One egg is laid per day, incubation lasts about 12 days, and nestlings remain in the nest about 10 days, departing several days before they can fly. Fledglings remain with one parent for a median of 15 days (and a maximum of more than 40 days) after leaving the nest (Dixon 1972, 1978; Welsh 1975; Bédard and LaPointe 1984; Wheelwright and Freeman unpubl. data). As in many polygynous species (Hughes and Hughes 1986), Savannah sparrows are sexually dimorphic in body size (Stobo and McLaren 1975; Weatherhead 1980; Rising 1987a, b), even as juveniles (Wheelwright unpubl. data), although the sexes are indistinguishable by plumage.

Females frequently behave aggressively towards other females (Rogers 1988; pers. obs.), an observation that may be explained by intraspecific brood parasitism (of which we have no evidence) or intrasexual competition for male assistance. Males potentially assist females in several ways. Males bring food to nestlings, possibly brood them to some extent, and care for fledglings (see also Dixon 1972, 1978; Weatherhead 1979; Bédard and Meunier 1983). We have never seen males build nests, courtship-feed females, incubate, or deliver food to incubating females. During egg-laying, males accompany females closely and may benefit them by watching for predators. Males give warning calls that alert incubating females to the approach of potential predators (Potter 1974; pers. obs.; cf. Hannon and Martin 1992). Predation by ravens (*Corvus corax*), common crows (*C. brachyrhynchos*), and herring gulls (*Larus argentatus*) claims up to 90% of Savannah sparrow nests in some years and habitats at Kent Island (Dixon 1972, 1978); in 1987–1991 about 20% of nests were destroyed by predators (Wheelwright unpubl. data). The reproductive biology of Savannah sparrows breeding elsewhere is described by Potter (1974), Stobo and McLaren (1975), Welsh (1975), Weatherhead (1979), Ross (1980), Bédard and LaPointe (1985), and Wheelwright and Rising (in press).

The Kent Island population has several advantages for studying the effect on female fitness of polygyny and paternal care of nestlings. Depending upon the year and site, 15–43% of males are polygynous (see below). Dixon's (1972, 1978) and Williams's (1987) earlier research on the same population offers a comparative data base. Sample sizes are ample because of high breeding densities; 15–29 adults bred in the 1.2-ha north field annually between 1987 and 1991. With relatively high rates of adult and nestling philopatry (c. 45% and 11%, respectively), a phenomenon that seems to be associated with Savannah sparrows and other birds on islands (e.g. Stobo and McLaren 1975; Smith et al. 1982), the ages of most individuals in the two study sites are known with certainty (Wheelwright unpubl. data).

Measurements, behavioral observations, determination of mating status, and analyses. We used mist-nets to capture Savannah sparrows. Birds were measured (mass, tarsus, wing) and banded with Canadian Wildlife Service aluminum bands. In addition each adult was given a unique, randomly determined combination of three plastic color-bands; nestlings were marked with a single color-band. In total, 2466 individuals have been banded since 1986, including 305 females banded as adults and 1847 birds banded as nestlings or

fledglings. Since 1987, 100% of the Savannah sparrows breeding in the north field have been banded, which we verified by conducting censuses lasting 2–4 h on alternate days. Every unbanded adult that appeared was captured and banded within a few days of its arrival. The probability of overlooking a breeding individual in the isolated 1.2-ha study site during the 60-day breeding season seems remote. Virtually all birds breeding in the south field were banded, judging from the absence of unbanded adults in daily censuses; by mid-July of 1987 and 1988, fewer than 2% of adults sighted in the south field remained unbanded, and all adults were banded in subsequent years. Every nestling in the north field was banded (judging from the fact that the nests of all north field females could be accounted for and no recently fledged, unbanded juveniles attended by resident birds were sighted there), and approximately 70–90% of south field nestlings were banded (100% in later years of the study).

In 1988 we made quantitative observations of parental feeding rates at 23 north field nests which fledged young over an 8-week period. When the nestlings were 5 days old ("day 6"), the time when parental feeding rates and mass gain are greatest (Dixon 1972; Bédard and Meunier 1983; Meunier and Bédard 1984), we monitored parental feeding behavior at each nest for an average of 2.3 h/nest (SD = 0.4, $n = 23$ nests) and observed an average of 20.9 feedings/nest (± 4.1, range = 16–37). Additional observations in 1990 were made at 12 nests watched for an average of 1.7 h/nest (± 0.5) and 19.6 feedings/nest (± 5.6) (C. Freeman, pers. comm.).

Preliminary observations in 1987, as well as previous studies (Williams 1987; Stobo and McLaren 1975; Welsh 1975 [Table 4]; Smith 1978), established that estimates of male assistance at the nest based on relatively short sampling periods (2–3 h of observation, or 20 feeding trips) on day 6 agreed closely with estimates based on much longer periods, and could reliably be used to distinguish between males that provided little or no assistance from males that provided above-average assistance. For example, at a nest where we conducted an all-day watch on day 6, the male brought 34% of food deliveries during the first 2 h of observation ($n = 29$ deliveries); after 16 h and 216 food deliveries, the male had brought the same percentage of food deliveries. At two nests where males brought no food deliveries during 2 h on day 6, relative male feeding rates remained less than 2% after observations of 52 deliveries on days 6–8. Paszkowski (1973) watched for 1 h/day throughout the nestling period at three nests at the same study site. Her estimates of the proportion of male food deliveries based on 2 h of observation on days 5 and 6 were 27%, 30%, and 38%; the respective proportions for the total nestling period were 29%, 23%, and 37% ($n = 310$ food deliveries). Estimates of relative male feeding rates based on short- and long-term observations at these six nests were positively correlated (Spearman rank: $r_s = 0.93$, $P = 0.038$); short-term determinations of relative male feeding rates were within an average of 2% of the long-term rates.

From a distance of 20–50 m from the nest, a distance sufficient not to disrupt adult feeding behavior (Welsh 1975; pers. obs.; Smith et al. 1982), we used $10 \times$ binoculars or a $15 \times$ telescope trained on a 1-m tall perch placed near each nest to identify adults as they came to the nest to feed young. Observations were made from blinds or from behind tall grass. Arthropod prey delivered to nestlings were identified to order (chiefly Coleoptera, Diptera, Homoptera, and larval and adult Lepidoptera) and their size determined relative to bill length. Unlike Bédard and Meunier (1983), we found that males and females brought the same relative frequency of different prey taxa [index of dietary overlap, C = 0.99, where 1.0 indicates perfect overlap (Horn 1968)] and the same number per load (see also Knapton and Falls 1983; Knapton 1984; Leffelaar and Robertson 1986; Quinney 1986). Therefore, we used the proportion of parental food deliveries made by the male ("relative male feeding rate") as an index of his contribution to feeding nestlings. Each nest was watched at approximately the same time of day. The median time at which observations began was 0845 h; all but two nests were observed before 1200 h.

We did not handle Savannah sparrow nestlings after day 8 to avoid causing premature fledging (Dixon 1972; Potter 1974;

Ross 1980; pers. obs.). When nestlings were 7 days old, their mass was measured with an electronic balance to 0.1 g, their tarsi (proximal end of the tarsometatarsus to the base of the hallux) measured with dial calipers to 0.1 mm, and their flattened wings (proximal end of the carpometacarpus to the distal end of the longest primary feather) measured to 1 mm with a wing ruler. Nestling size just before fledging is commonly considered to be positively correlated with the probability of survival (see references in Wolf et al. 1988; Bart and Tornes 1989; although cf. Krementz et al. 1989). In Savannah sparrows, mass at fledging was greater for individuals that subsequently recruited into the population than for those that never reappeared (Wheelwright unpubl. data). Sample sizes vary because not all measurements were taken on all nestlings, and because certain individuals were excluded from some analyses because they were included in experimental manipulations related to other studies.

Male mating status (number of females with which a male was mated) was determined as follows. If a male conspicuously and closely accompanied a female within his territory and appeared to have exclusive access to her over several days immediately preceding or during egg-laying by the female ("mate-guarding"), and if he was the only male to be closely associated with her, he was considered to be mated to that female. Although extra-pair copulations occur in this population of Savannah sparrows (J. Sevigny, N. Wheelwright, and D. Westneat unpubl. data) as in other species (Birkhead et al. 1987; Westneat 1988), mate-guarding and subsequent nestling feeding are likely to be reasonable predictors of male paternity (Burke et al. 1989). In every case the identity of the mate-guarding male was the same as that of the male feeding nestlings. In the south field, where behavioral observations were less complete and not all nests were found, a male was considered to be mated with a particular female if he was observed feeding nestlings at her nest. If no male was seen feeding her nestlings, the female was considered to be mated to the male seen guarding her or copulating with her, or, in the few cases where no such observations were made, to the male within whose territory she nested. Recognizing the potential differences in accuracy between these methods, we analyzed north field data separately and got qualitatively similar results in all comparisons (see below).

We combined monogamous females and "primary" females (the earliest females to lay eggs with a polygynous mate, or, where it was known, the females with which a polygynous male spent most time) and compared their reproductive success and survival with those of secondary and tertiary females to determine the effects of male mating status. Our results were equivalent to those presented below and are not discussed further.

Although we refer to "survival" in this paper, we actually measured return rates (recaptures and resightings of individually marked birds) one or more years after banding. Our assumption, like that of most workers in the field (references in Breitwisch 1989), is that recapture rates accurately reflect or are at least correlated with actual survival rates, especially for adults, despite the fact that they potentially underestimate survival because some individuals may have dispersed or gone undetected. Given the well-known philopatry of adult Savannah sparrows, birds that breed but subsequently fail to return probably have died rather than dispersed (Potter 1974; Stobo and McLaren 1975; Dixon 1978; Bédard and LaPointe 1984). This must certainly be the case with the "Ipswich" subspecies of the Savannah sparrow (P. sandwichensis princeps), which has diverged evolutionarily from other populations and is not known to breed outside of Sable Island, except for scattered individuals in Halifax Co., Nova Scotia (Stobo and McLaren 1975). High philopatry is well-documented in other island populations of passerine birds (Grant 1968). The same arguments apply to fledglings, although dispersal is much more likely than with adults (Greenwood and Harvey 1982). However, return rates of Savannah sparrows originally banded as nestlings at Kent Island average 8–14%, depending upon the year. If natal dispersal represents more than a trivial fraction of disappearances, Kent Island Savannah sparrows would have to have very high first-year survival rates compared to other similar-sized migratory passerines (Rick-

lefs 1969). Even if a portion of disappearances represents dispersal, one would expect such dispersal to be associated with reduced fitness because dispersing individuals are often restricted to marginal habitats in novel sites or face increased risk of mortality (Greenwood and Harvey 1982). Of more than 4500 adult and juvenile Savannah sparrows banded at Kent Island since 1964, none has ever been recorded breeding elsewhere and we have not discovered banded birds in repeated archipelago-wide censuses at distances greater than 2 km from where they were banded, further indicating that birds that did not return probably had died (see also Dixon 1972).

Statistical analyses included standard nonparametric tests and two-way ANOVA. Continuity corrections were used with χ^2 tests. Analyses were performed with Statview SE+Graphics (Abacus Concepts 1988) on a Macintosh SE computer. Except where noted otherwise, descriptive statistics are given as means ± 1 SD.

Results

Frequency of polygyny

In the population as a whole, the frequency of polygynous males varied from year to year (Table 1; χ^2 test comparing years, both sites combined: $P=0.01$), although it did not differ significantly between study sites (χ^2 test comparing sites: $P>0.10$). In the well-censused north field (see Methods), females consistently outnumbered males (Table 1). The sex ratio (males/females) of all adults banded or observed, whether or not they were known to breed, was equal or female-biased in four of five years (Table 1). In two years of the study there was a single male in the north field who never acquired a mate; in each instance the individual was a yearling who first appeared at the site in mid-July, when he managed to carve out a small peripheral territory. By the time egg-laying began, non-breeding "floater" males were only rarely observed in the south field. Thus, it appeared that most males acquired mates, although a removal experiment would be necessary to document this.

Different females mated to the same male were rarely synchronous in their breeding attempts. Secondary females hatched their young a median of 8 days later than primary females mated with the same male ($\bar{x}=12.5\pm 11.1$ days, $n=23$ females). Because the nestling period in Savannah sparrows is longer than 8 days, however, most polygynous males had the opportunity to provision the offspring of different females simultaneously. Counting the 2–4 week post-fledging period and the occurrence of second clutches, there was a high degree of overlap in the dependent period for the offspring of virtually all females mated with a polygynous male.

It was apparent from numerous behavioral observations that polygyny arose in at least three distinct situations, each of which differed in the degree to which females actually expressed a choice among males. First, younger females often returned from spring migration several days later than older females and mated with a male that was previously mated; such cases arguably still reflected mate choice by females (Searcy and Yasukawa 1989), although the female-biased sex ratio effectively restricted a female's options. Second, territorial males sometimes vanished in the middle of the breeding season, either having fallen victim to predators such as sharp-shinned hawks (*Accipiter striatus*) or merlins (*Falco columbarius*), or having left their territories to care for fledglings from their first brood. In such cases, neighboring males expanded their territories and mated with the resident female (as well as the male's previous mate) if she laid a second clutch. Third, unbanded females occasionally appeared at the study sites as much as 6 weeks after the first clutches in the population were laid. Some of these birds accompanied fledglings from a previous brood raised outside the study area. These new arrivals were quickly and ostentatiously mate-guarded by territorial males (who were previously mated) and remained to lay a second clutch after the young from their first brood became independent.

There was no evidence that females chose mates on the basis of territory quality, for several reasons. Insect density and vegetation composition and structure varied spatially and temporally, but they bore no obvious relationship to male mating status (Wheelwright unpubl. data). In any event, food abundance within a male's territory appeared to be relatively unimportant, because Savannah sparrows feeding nestlings spent at least half of their time foraging off their territories in undefended areas such as the forest margin or intertidal zone (Wheelwright unpubl. data; cf. Welsh 1975; LaPointe and Bédard 1984; Greenlaw and Post 1985). Moreover, the location of the territories of polygynous males changed from year to year. For example, each year in the north field there were 2–3 polygynous males, but between years the territories of the different polygynous males were located in different corners of the field.

Male feeding rate

Female Savannah sparrows fed their nestlings at 2.7 times the rate of males (8.0 ± 3.5 deliveries/h vs. 3.0 ± 2.7 deliveries/h, $n=35$ broods; Wilcoxon Signed-Rank test: $P<0.001$) and tended to be less variable in their feeding rates (coefficient of variation of food deliveries/h for females vs. males $=44.3\%$ vs. 89.5%). On average the proportion of all parental food deliveries that were made by the male (relative male feeding rate) was 28% ($\pm$ 22%). The rate at which a female fed her nestlings was
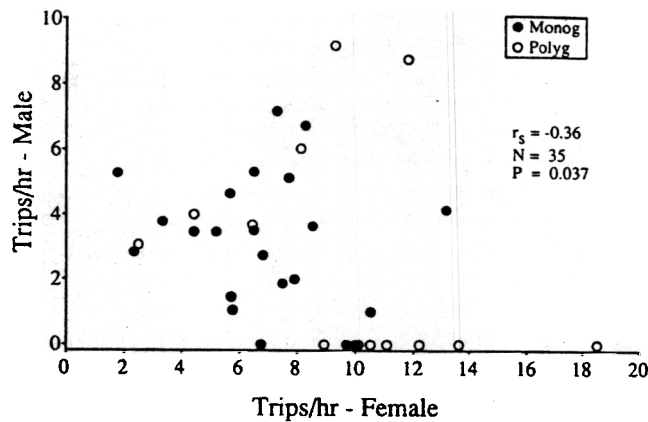
Table 1. Frequency of polygyny and adult sex ratios in a population of Savannah sparrows over a 5-year period at two study sites on Kent Island, New Brunswick

Year	% of Males with >1 mate		Adult sex ratio (n)	
	North Field	South Field	North Field	All birds banded
1987	33	39	0.67 (15)	1.00 (144)
1988	15	16	0.81 (29)	0.79 (195)
1989	18	24	0.79 (25)	0.87 (187)
1990	20	15	0.91 (21)	1.27 (152)
1991	43	17	0.78 (16)	0.90 (171)

Fig. 1. Rate of food delivery (feeding trips/h) by females and males feeding nestlings at the same nest. *Open circles:* polygynous males; *closed circles:* monogamous males. $r_s = -0.36$, $n = 35$, $P = 0.037$
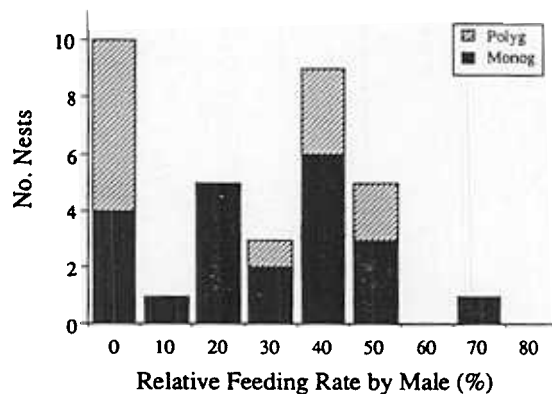

Fig. 2. Frequency distribution of relative feeding rates (proportion of total food deliveries to a nest) by males. *Hatched bars:* polygynous males; *solid bars:* monogamous males

negatively correlated with her mate's feeding rate, indicating that females accelerated their rate of food delivery when male help was sparse (or, conceivably, that males relaxed their efforts when their mate fed at a high rate) (Fig. 1). We distinguished two extreme patterns of male assistance, one in which males hardly helped at the nest versus situations where males brought food at above-average rates (Fig. 2). Females provisioning young with little or no male assistance fed their young at the same rate as did pairs in which males provided at least 30% of all food deliveries (Mann Whitney U-test: $P = 0.84$, $n = 11$ and 18 broods, respectively). Neither absolute male feeding rate ($r_s = -0.12$, $P = 0.50$) nor relative male feeding rate was related to brood size, although biparental feeding rate and female feeding rate increased with brood size (Table 1; $r_s = 0.46$, $P < 0.01$, $n = 24$ broods).

The proportion of food deliveries brought by polygynous males averaged less than that of monogamous males, but differences were far from significant because of small sample sizes and high variability between individuals (polygynous males: 23% ± 24%, $n = 12$ broods; monogamous males: 31% ± 20%, $n = 22$; Mann-Whitney U-test: $P = 0.34$; a comparison between primary and secondary females yielded a similar result; see Methods).

Table 2. Spearman Rank correlations (r_s) between parental feeding rate and reproductive parameters

	Biparental feeding rate (deliveries/h)	Relative male feeding rate (%)
Nestling mass	0.22	0.24
Nestling tarsus	0.57	0.01
Nestling wing	0.24	−0.08
No. fledglings	0.55 **	−0.06
Fledging success (fledglings/egg)	0.55 **	−0.04

Nestling measurements are means of broods on day 8 ($n = 34$ broods). Relative male feeding rate = number of food deliveries by male/total number of food deliveries by both parents. $P > 0.15$ for all correlations except where indicated otherwise. Male assistance at the nest was a poor predictor of factors presumed to be important to female fitness
** $P < 0.01$

Some polygynous males had high relative feeding rates (Fig. 2), and we noticed no difference in vigilance as a function of mating status. Thus, a male's mating status was not necessarily a reliable indicator of his assistance at the nest. Although we did not quantify paternal energetic investment (e.g., Williams 1987), it was our impression that polygynous males expended more time and effort than monogamous males in caring for their collective offspring (nestlings plus fledglings from different broods).

Effect of male feeding rate on nestling size

Unexpectedly, high biparental feeding rates were not correlated with the production of large offspring; variation in relative male feeding rate had even less effect on nestling size (Table 2). Even when we compared males differing distinctly in their relative feeding contributions [those responsible for bringing more than 30% of all food deliveries to a nest (i.e., above-average males, $n = 18$ broods) vs. those bringing almost none (0–5%, $n = 11$)], relative male feeding rates had no effect on brood mean mass, tarsus length or wing length (Mann-Whitney U-test: $P > 0.20$).

Effect of polygyny on nestling size

In all five years of the study, the young from nests associated with polygynous males were as big on day 8 as those of monogamous males in terms of brood mean mass, tarsus length, and wing length (Table 3). Two-way ANOVAs, with year and paternal mating status as factors, and nestling size, brood size, and fledging success (fledglings/egg) as dependent variables, showed significant between-year differences in tarsus length [$P < 0.001$ (a result of employing slightly different methods to mea-

Table 3. Nestling size on day 8, number of fledglings, and overall fledging success as a function of mating status of the presumed father

Year	Mating status of father		
	Monogamous	Polygynous	P
Nestling mass (g)			
1987	15.1 (0.8), 4	14.8 (1.3), 12	0.60
1988	14.4 (1.9), 43	14.4 (1.8), 23	0.98
1989	14.8 (1.8), 54	14.9 (1.5), 25	0.65
1990	14.8 (1.5), 47	14.3 (1.2), 21	0.16
1991	14.9 (1.5), 48	15.5 (1.8), 21	0.18
Nestling tarsus (mm)			
1987	18.1 (0.2), 4	18.0 (1.2), 12	0.90
1988	19.9 (1.1), 46	19.9 (1.1), 24	0.78
1989	18.7 (1.0), 55	19.1 (1.1), 25	0.14
1990	17.4 (0.8), 46	17.5 (1.1), 19	0.54
1991	20.6 (0.9), 47	20.6 (1.0), 20	0.77
Nestling wing (mm)			
1988	28.6 (5.9), 47	29.5 (4.4), 24	0.80
1989	29.8 (4.1), 54	31.0 (4.0), 25	0.30
1990	28.3 (3.6), 45	28.6 (4.0), 19	0.77
1991	28.7 (3.1), 48	29.2 (4.0), 21	0.89
No. fledglings			
1987	3.8 (0.7), 27	3.4 (1.1), 36	0.14
1988	3.5 (0.8), 50	3.8 (0.9), 26	0.19
1989	3.1 (1.8), 69	2.8 (1.5), 30	0.12
1990	3.6 (0.6), 51	3.8 (0.7), 20	0.48
1991	3.6 (0.8), 55	3.1 (1.0), 23	0.06
Fledging success (fledglings/egg)			
1987	0.91 (0.17), 26	0.84 (0.27), 35	0.30
1988	0.72 (0.39), 59	0.83 (0.35), 28	0.23
1989	0.71 (0.40), 56	0.71 (0.34), 23	0.18
1990	0.91 (0.16), 51	0.93 (0.12), 20	0.57
1991	0.87 (0.18), 55	0.76 (0.23), 23	0.03

In 1987 only a subsample of broods was measured on day 8, and wing length was not measured. Methods of measuring tarsi differed slightly between years. Number of fledglings was calculated for nests that fledged at least one young. Fledging success was determined for nests in which the original clutch size was known. Values are means (± 1 SD) of brood means, followed by sample sizes (number of broods). P values refer to results of Mann-Whitney U-tests. (See Results for discussion of two-way ANOVAs)

sure tarsi in different years)], brood size ($P = 0.03$), and fledging success ($P = 0.01$). However, there were no differences due to paternal mating status ($P > 0.05$). Because we did not quantify male feeding behavior in the larger sample of nests or in all years of the study, we do not know whether these results were due to the weak correlation between male mating status and his assistance at the nest, or to the lack of an effect of male assistance on nestling size, both of which were suggested by data presented above.

Effect of male feeding rate on nestling survival

Neither fledging success (fledglings/egg laid) nor the number of nestlings fledged was correlated with relative
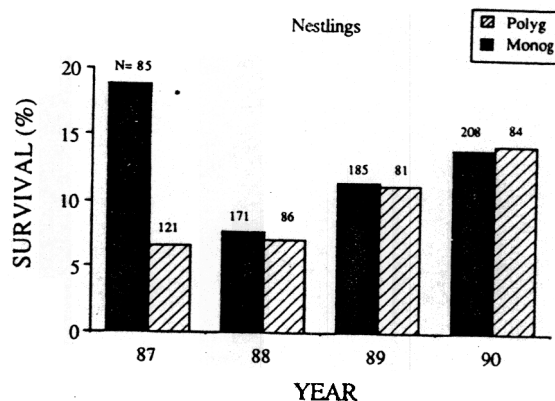

Fig. 3. Survival of nestlings to age 1 year (as inferred from returns) as a function of mating status of the presumed father. *Numbers above bars* refer to number of nestlings. *Hatched bars:* polygynous fathers; *solid bars:* monogamous fathers. * $P \leq 0.05$

male feeding rates (Table 2). Fledging success was no greater for males whose relative feeding rates exceeded 30% of all deliveries to the nest than for males whose rates were less than 5% (fledglings/egg: 0.84 ± 0.17, $n = 18$ broods, vs. 0.88 ± 0.21, $n = 11$; Mann-Whitney U-test: $P > 0.20$). Offspring that returned in 1989 had received no greater relative male feeding rates, on average, than those that did not return ($36\% \pm 15\%$, $n = 6$ nestlings, vs. $26\% \pm 22\%$, $n = 74$; $P = 0.20$).

Effect of polygyny on nestling survival

The nests of monogamous males were no less likely to be preyed upon (χ^2 tests: $P > 0.50$) and had no better fledging success than those of polygynous males (Table 3). For nestlings that successfully fledged in 1987, however, the probability of surviving until the next year (as inferred from returns) and recruiting into the breeding population was nearly 3 times greater for those with monogamous fathers than those with polygynous fathers (18.8% vs. 6.6%; Fig. 3). In other years of the study (1988–1989, 1989–1990, and 1990–1991) a nestling's probability of survival until the following year was unrelated to paternal mating status the previous year. The sex of survivors to 1 year of age was random with respect to paternal mating status (χ^2 tests: $P > 0.30$).

Effect of male feeding rate on survival and future fecundity of their mates

Females that laid a second clutch in the north field in 1988 were not mated to males with significantly higher average feeding rates during the first brood than females that did not lay a second clutch (Mann-Whitney U-test: $P = 0.34$), although the data suggested that larger sample sizes might have demonstrated an effect of relative male feeding rates on future fecundity of their mates. Of 8 females whose mates had delivered more than 30% of all food deliveries during the first clutch 6 produced a second clutch, compared to only 1/5 whose mates de-

Table 4. Female fecundity as a function of male mating status

Variable	Year	Monogamous mate	Polygynous mate	
Interval between 1st and 2nd clutch (days)	1987	37.0 (7.4), 4	36.5 (6.7), 6	0.52
	1988	36.8 (6.0), 18	37.1 (5.5), 8	0.96
	1989	34.9 (7.4), 7	37.7 (4.9), 3	0.49
	1990	30.5 (3.5), 25	35.8 (8.0), 6	0.02
	1991	28.1 (4.0), 14	29.4 (6.2), 7	0.65
No. eggs in 2nd clutch	1987	4.0 (0), 6	3.7 (0.9), 13	0.36
	1988	3.9 (0.5), 28	3.6 (0.5), 11	0.10
	1989	3.9 (0.9), 13	3.8 (0.5), 5	0.59
	1990	4.0 (0.8), 18	4.0 (0.8), 4	1.00
	1991	4.0 (0.4), 12	3.5 (0.5), 10	0.03
No. successful clutches/season	1987	1.3 (0.5), 19	1.2 (0.4), 27	0.53
	1988	1.3 (0.5), 39	1.4 (0.5), 18	0.75
	1989	1.2 (0.4), 40	1.1 (0.5), 18	0.63
	1990	1.5 (0.5), 50	1.3 (0.5), 21	0.33
	1991	1.2 (0.5), 49	1.2 (0.6), 20	0.78

Values are means (± 1 SD) of brood means, followed by sample sizes (number of females whose full reproductive history was known). Interclutch interval (time between hatching of first and second clutches within the same season) and number of eggs in the second clutch were determined only for females who successfully fledged young from the first clutch. P values refer to results of Mann-Whitney U-tests. There was no difference in fecundity between females mated to monogamous vs. polygynous males

livered less than 5% during the first clutch (Fisher's exact test: $P = 0.17$). Possibly, males who helped out during the nestling stage also assumed a large share of parental care after fledging, thereby freeing females to produce a second clutch (C. Freeman, unpubl. data). Nonetheless, relative male feeding rate during the first clutch was unrelated to the time it took for a female to lay a second clutch after young from the first brood fledged, or to female mass or male mass late in the season (after mid-June) (Spearman rank: $P > 0.27$). Females that survived until 1989 had received no more male help at the nest in 1988 than those who did not survive ($n = 9$ and 7 females, respectively; Mann-Whitney U-test: $P = 0.56$).

Effect of polygyny on survival and future fecundity of their mates

One might predict that the mates of polygynous males would take longer than the mates of monogamous males to lay a second clutch after fledging their first broods, especially if females alone had to care for fledglings until they reached independence. Moreover, polygynously mated females might be expected to lay fewer eggs in the second clutch and/or produce fewer successful clutches per season than monogamously mated females because the cost of the first reproductive effort would have been borne with relatively little male assistance. The direction of differences between monogamously and polygynously paired females was in accord with these predictions in 11/13 comparisons, but in only one case were differences statistically significant (Table 4).

Females mated to polygynous males in 1987 were less likely to survive until 1988 than those mated to monogamous males. There was no such relationship between male mating status and female survivorship in 1988–1989, 1989–1990, or 1990–1991 (Fig. 4). A male's survi-
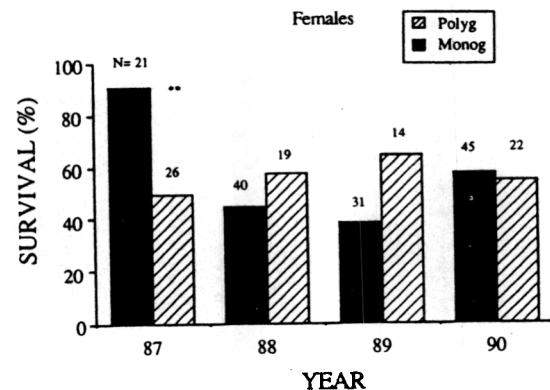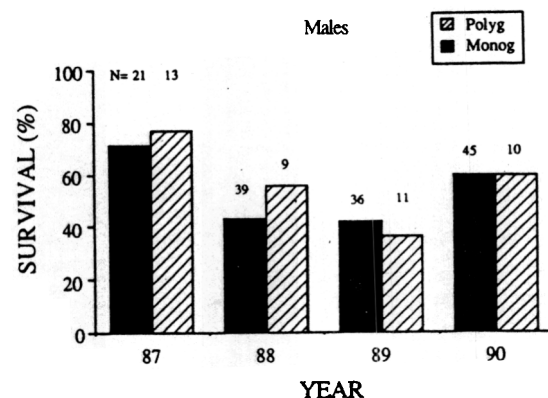
Fig. 4. Survival of females to the following year (as inferred from returns) as a function of mating status during the previous year. *Numbers above bars* refer to number of females. *Hatched bars:* previously polygynously mated; *solid bars:* previously monogamously mated. ** $P \leq 0.01$

Fig. 5. Survival of males to the following year (as inferred from returns) as a function of mating status during the previous year. *Numbers above bars* refer to number of males. *Hatched bars:* previously polygynously mated; *solid bars:* previously monogamously mated

vorship appeared not to be influenced by the number of mates he had had the previous year (Fig. 5).

The mating status of a female's mate in one year had no effect on her fecundity the next year. The size of the first clutch in 1988 for females who had mated with monogamous males in 1987 was 4.2 eggs (± 0.5, $n = 8$) vs. 4.8 eggs (± 0.4, $n = 5$) for females previously mated with polygynous males (Mann-Whitney U-test: $P = 0.06$). In 1989 the equivalent figures were 4.4 eggs (± 0.5, $n = 12$) vs. 4.4 eggs (± 0.5, $n = 7$) ($P = 0.96$). Females mated to polygynous males in a given year showed no delay in initiating their first clutch the next year (Mann-Whitney U-test: 1988: $P = 0.51$; 1989: $P = 0.93$).

Predictability of feeding rates between clutches

Ten females in the north field in 1988 laid two clutches, and six females successfully raised two broods with the same mates, so their behavior and that of their mates could be compared between broods. On average feeding behavior and fledging success were similar for first and second broods collectively (Wilcoxon Signed-Rank test: $P > 0.17$). However, when we compared subsequent clutches within pairs there was no significant correlation between the first and second clutches in biparental feeding rates, absolute feeding rates, or relative male feeding rates, or nestling size (Spearman Rank: absolute $r_s < 0.50$, $P > 0.27$). The one exception was brood mean mass: parents that produced relatively heavy nestlings in the first brood did the same the second brood ($r_s = 0.90$, $P = 0.04$).

Characteristics of polygynous males and their mates

Like other species in which males provide relatively little parental care (Hughes and Hughes 1986), Savannah sparrows on Kent Island are sexually dimorphic in wing length and mass (Mann-Whitney U-test: $P < 0.01$) (Wheelwright unpubl. data). Storer's index of sexual dimorphism (difference between male average and female average for a variable, divided by the overall average, and then multiplied by 100: Rising 1987b) for bill length, bill depth, wing length and tarsus length of Kent Island Savannah sparrows is 1.63, 2.47, 6.23, and 1.90. The degree of sexual dimorphism in the Kent Island population appears typical of that of other polygynous populations of Savannah sparrows. Monogamous and polygynous males did not differ significantly in size or age in any year of the study. Females mated to monogamous males were also no different in size or age than those mated to polygynous males (Mann-Whitney U-test: $P > 0.10$).

Discussion

Field studies have documented that males of a number of polygynous bird species contribute relatively little paternal care (e.g., Patterson 1991), and theoretical models dealing with mating systems often explicitly assume that the degree of paternal care is a function of mating status. Moreover, they assume that a female's fitness is depressed to the degree that she is forced to share a polygynous male's parental care with other females, unless she is compensated by some aspect of "breeding situation quality" (Verner and Willson 1966; Searcy and Yasukawa 1989). However, the results of this study of an island population of Savannah sparrows suggest that there may be little correlation between a male's mating status and his care of nestlings, and that in most years polygynously and monogamously mated females may show little or no difference in fitness.

We found that high rates of food deliveries by males and females combined were associated with improved reproductive success. Such an observation might lead one to predict that females should choose mates on the basis of their mating status, were it not for several considerations: (1) the relatively low proportion of food deliveries by males and the negligible effect of male (vs. biparental) feeding rate or mating status on reproductive success, (2) the difficulty for a female of predicting the level of a male's future parental care based on his morphology, behavior or mating status, and (3) constraints on females in gaining access to suitable nesting habitats or finding unmated mates.

The contribution of male Savannah sparrows to the provisioning of nestlings was less than half that of females, a pattern typical for the species (Dixon 1972; Stobo and McLaren 1975; Welsh 1975; Williams 1987; although see Bédard and Meunier 1983). More importantly, the rate of food deliveries by males and male mating status had no demonstrable effect on nestling size, fledging success, or recruitment of offspring into the breeding population. Females who received little male assistance were apparently able to compensate by increasing their own feeding rates (cf. Weatherhead 1979; Knapton and Falls 1983; however, see Patterson 1991). Some females raised young with no male assistance, as in other Savannah sparrow populations (Welsh 1975; Weatherhead 1979; cf. Post and Greenlaw 1982; Greenlaw and Post 1985; but see Burton 1988). Thus, two of Wittenberger and Tilson's (1980) conditions for the maintenance of monogamy – the necessity or even the advantage of male parental care – were not obviously met. The fact that we found no difference in age or size of females mated to polygynous vs. monogamous males argues against the hypothesis that female Savannah sparrows raising young unaided suffered no loss in reproductive success because they represented a biased (and superior) sample of females in the population. A stronger test of the importance of male parental care would have been to have removed males at a random sample of nests. Nonetheless, our findings lend support to Bart and Tornes's (1989) thesis that in populations in which most males provide relatively little parental care, their absence makes little difference for nestling quality or fledging success.

Male parental care may be most important for the survival of offspring after the brood leaves the nest and disperses, at which point it may not be possible for un-

aided females to attend to all of her offspring (Wheelwright and Freeman unpubl. data). The post-fledging period is probably the period of highest energy demand, highest parental feeding rates, and greatest mortality (Sullivan 1989), and therefore a time when paternal care may be most valuable. Parents often spend more than twice as many days with their offspring after they have left the nest than when they are nestlings (Wheelwright and Freeman unpubl. data; Smith 1978). Studies that examine reproductive success only until the time of fledging may overlook critical events that influence fitness. For example, we found that mating with a polygynous male did not immediately reduce a female's fitness (e.g., the quantity or quality of her fledglings), but negative consequences appeared over the long term in one year of the study. In that year the prospects of joining the breeding population were substantially less for the offspring of females mated to polygynous males than for those of females mated to monogamous males. Females mated to polygynous males in 1987, like their offspring, suffered higher annual mortality than monogamously mated females. Williams (1987) has shown that female Savannah sparrows feeding nestlings alone must pay elevated metabolic costs, and it may be that the burden of raising young unassisted may leave females in poor physical condition and more susceptible to predators or pathogens in years of stressful environmental conditions. There were no obvious abnormalities in insect abundance or weather on the breeding grounds in 1987 to account for the differential mortality. Perhaps at some point during migration or on the wintering ground stressful environmental conditions exposed the vulnerability of polygynously mated females and their offspring. Male feeding rate or mating status had little or no effect on a female's future fecundity (probability of laying two clutches per season, time between successive clutches, size of the second clutch within the same season, or clutch size or clutch initiation date the following year).

If females mated with polygynous males sometimes risk higher annual mortality rates for themselves and their offspring, what clues might a female use to predict a male's contribution to the care of her nestlings? The quality of a male's territory appeared to be unrelated to the number of mates he attracted, judging from the shift between years in the location of different polygynous males' territories, and the lack of differences in predation rates or consistent patterns of invertebrate density between territories. Neither did territory size appear to be related to the likelihood of polygyny in this unusually dense population (cf. Reid and Weatherhead 1990). In any event, much of the foraging by Savannah sparrows is done off-territory in undefended areas (pers. obs., Welsh 1975; Reid 1987). Apparently, female Savannah sparrows at Kent Island are not trading off reduced male parental care in exchange for a superior habitat, as predicted by the polygyny threshold model (Verner and Willson 1966; Orians 1969). Morphology, another possible indicator of male quality, did not differ between monogamous and polygynous males, nor was mating status related to age. Even the relative feeding contribu-

tions made by a male to a female's first brood were a poor indicator of his contributions to her next brood. Conceivably, the intensity of male courtship, frequency of singing, or degree of brood overlap with other females nesting in a male's territory may predict his assistance at the nest (e.g. Nisbet 1973; Greig-Smith 1982; Eckert and Weatherhead 1987; Reid 1987). Still, one is left with the impression that it is extremely difficult for a female Savannah sparrow to distinguish among males on the basis of their likely paternal care.

Determining a male's mating status is not a problem for female Savannah sparrows. Males do not appear to be deceptively polygynous, unlike in some other species (Alatalo et al. 1982; Catchpole et al. 1985). When a male has several mates, it is obvious to human investigators and presumably even more so to their mates. To illustrate with an anecdote, one male we observed divided his morning feeding nestlings at one nest and fledglings from a different female's brood; a third female with whom he had earlier copulated sat on eggs within his territory. His bill full of insects destined for the nestlings, he chased and tried to mount a fourth female who had entered his territory in an apparent attempt at an extra-pair copulation (Westneat 1988). It was our impression that the intensity of courtship, mate-guarding, and territorial defense by males was a major predictor of whether or not they attracted multiple mates, but mating status was often independent of the amount of paternal care provided. Welsh's data (1975, Table 5) provide additional support for the notion that mating status was a poor predictor of nestling care: polygynous and monogamous males had the same relative feeding rates (36.8%, $n=6$ vs. 36.9%, $n=7$; ANOVA: $P=0.99$) (see also Stobo and McLaren 1975).

Despite the occasional long-term fitness costs for females of being mated with a polygynous male and the difficulty for males of disguising their mating status, polygyny in Savannah sparrows may be relatively common at Kent Island because of a combination of factors. The nest initiation period at our study site extends for about two months, more than twice as long as that of the high-latitude population studied by Weatherhead (1979). In the latter population polygyny was uncommon, Weatherhead (1979) proposed, because male parental care was particularly important for reproductive success, and the high degree of synchrony in the nest initiation period (23 days) did not allow males to care sequentially for the young of broods by different females. Male Savannah sparrows at Kent Island, in contrast, can mate with two or more females over the course of a breeding season because reproduction is not strongly synchronous. More importantly, male parental care is not crucial for raising young (see Dunn and Hannon 1992). In any event, females may not discriminate against previously-mated males because of the potential independence of a male's assistance at the nest and his mating status.

It may also be difficult for females, especially late arrivers, to find unmated males in suitable habitats. Whether due to differential mortality of the sexes or territoriality, the operational sex ratio at Kent Island

is female-biased in most years and habitats. The physical structure of the fields in which the birds breed, surrounded by white spruces which males use as perches, may facilitate detection and exclusion of other males and further skew the operational sex ratio (cf. Reid and Weatherhead 1988). Although the chief proximate cause of polygyny in the Kent Island population could be the female-biased sex ratio (e.g., Smith et al. 1982), the existence of sexual dimorphism, even among recently fledged juveniles (Wheelwright unpubl. data) suggests that polygyny is a regular feature of the Savannah sparrow breeding system (although see Rising 1987b).

It is clear why male Savannah sparrows are motivated to mate with more than one female: they fledge more offspring (Stobo and McLaren 1975; Maynard-Smith 1977; Wheelwright unpubl. data) and the survival of their offspring in most years is equivalent to that of the offspring of monogamous males. Why do female Savannah sparrows mate polygynously? We suspect that many polygynous matings arise because females are extremely site faithful (Wheelwright unpubl. data) and often find themselves returning to or remaining on territories defended by males that are already mated. The advantages of philopatry (familiarity with neighbors, feeding areas, or refuges from predators, etc.) presumably outweigh any disadvantages of polygyny (cf. Eliason 1986). Selection on females to discriminate against polygynous males may be relatively weak or at least inconsistent because females can raise young with little or no male assistance and because only in certain years are there fitness costs for females mated to polygynous males. Selection against polygyny is likely to be extreme in more stressful habitats or years, or when females have larger brood sizes (Weatherhead 1979; Quinney 1986; Dhondt 1987; Lyon et al. 1987; Wolf et al. 1988; Bart and Tornes 1989). Even under those conditions, however, the constraints of a female-biased sex-ratio and the unreliability of cues that could be used to predict the level of male assistance at the nest may force females to share male parental care with other females.

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