

POLYGYNY, MALE PARENTAL CARE, AND SEX RATIO IN SONG SPARROWS: AN EXPERIMENTAL STUDY

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ABSTRACT.—Species that are typically monogamous, but occasionally show polygyny, allow tests of several hypotheses about mating systems. We describe seven cases of natural polygyny observed during a 5-yr study of the Song Sparrow (*Melospiza melodia*). We also report on an experiment designed to test whether or not altering sex ratios causes polygyny and to measure some costs associated with polygyny in the Song Sparrow. Natural polygyny occurred in two circumstances: when males died during the breeding season and when the breeding population contained an excess of females. Most bigamous male Song Sparrows fed only the young of their primary females, but unaided secondary females were able to raise some young to independence. In 1979, we removed nine male Song Sparrows soon after their first-brood young hatched. Four of the nine widowed females subsequently formed polygynous associations with already mated males, compared to a natural polygyny rate of 3%. In one case, a male paired with three females. Only one of the widowed females received aid from her new male in feeding the young in her first brood. Young of unaided females grew more slowly and died more often in the nest than young of control females, and only half as many of them survived to independence. Unaided females fed their young twice as often as did control females. Removed males were replaced either by neighbors or by nonterritorial males. The latter group were also removed until all replacements were neighbors. When females remated with these replacements, 8 of their 9 previous mates were released, and 2 of them regained their previous territories. Neither was known to have fed the second-brood young of its regained mate. Foster fathers showed little "altruistic" behavior.

Our results demonstrate that biased sex ratios are a proximate cause of polygyny in the Song Sparrow. We suggest that Song Sparrows are usually monogamous because males with high quality territories outnumber females at the onset of the breeding season. When females are not in short supply, polygyny occurs. Received 24 August 1981, accepted 16 December 1981.

Most passerine birds are monogamous (Lack 1968, Verner and Willson 1969), but polygyny occasionally occurs in normally monogamous species (Nice 1937, Blanchard 1941, Armstrong 1955, Snow 1958, Mayfield 1960, Verner and Willson 1969, Woolfenden 1976, Petrinovich and Patterson 1977, Logan and Rulli 1981). Wittenberger and Tilson (1980) have proposed five general hypotheses to explain the evolution of monogamy: (1) male parental care is indispensable to reproductive success; (2) a female always benefits by pairing with an unmated male, rather than an already mated male, because differences in territory quality among males are insufficient to compensate for loss of male parental care (note that hypothesis 1 is a special case of hypothesis 2); (3) males defend exclusive access to a single

female; (4) aggression by mated females prevents males from acquiring additional mates; and (5) males reject second mates, because polygyny lowers male reproductive success. Wittenberger and Tilson favor hypothesis 2 for most monogamous altricial birds but find the existing data inadequate to discriminate among the other hypotheses clearly.

In a general review of mating systems, Emlen and Oring (1977) have stressed the importance of "operational sex ratio" (the local ratio of fertilizable females to sexually active males). If this ratio (OSR) exceeds unity, polygyny may occur; if it is near unity, monogamy is favored; and polyandry can occur if the OSR falls below unity. This formulation is valuable because it suggests specific experiments. For example, if the OSR is increased by removal of males or

addition of females, the incidence of polygyny should increase.

Monogamous species that show occasional polygyny allow tests of some of the above predictions. The main problem in such studies is ensuring adequate samples of polygynous birds to compare with monogamous controls. A simple experiment that directly tests hypotheses 1 and 5 of Wittenberger and Tilson (1980) and the usefulness of the operational sex ratio concept is to remove males when the young hatch. This allows a measurement of the breeding success of females with and without male aid. Removal of males should increase the OSR and hence increase the incidence of polygyny.

Weatherhead (1979) performed such an experiment in a tundra population of the Savannah Sparrow (*Passerculus sandwichensis*). He found that male parental care was important but not essential for the rearing of most nestlings, but he studied only survival of young in the nest. Polygyny did not occur after male removals, but the breeding season was too short to allow many females to breed again.

The Song Sparrow (*Melospiza melodia*) is occasionally bigamous (Nice 1937, Zach and Smith 1980). Its congener, the Swamp Sparrow (*M. georgiana*), may be regularly polygynous (Willson 1966). In this study, we describe several cases of polygyny in a resident population of Song Sparrows inhabiting Mandarte Island, British Columbia, Canada. We also report the results of a male removal experiment similar to that of Weatherhead (1979). Our procedure differed from Weatherhead's in that males were held in captivity for later release and in that the longer breeding season in our study area allowed a test of the operational sex ratio hypothesis. The aims of the experiment were to: (1) test if increasing the local ratio of females per male increases the incidence of polygyny; (2) measure the contribution of male parental care to female reproductive success and, hence, to test Wittenberger and Tilson's hypotheses 1 and 5; and (3) test whether male Song Sparrows behave "altruistically" by providing parental care to unrelated nestlings and fledglings (Power 1981).

METHODS

The Song Sparrow population and the habitat on Mandarte Island are described in detail by Tompa

(1964) and more briefly by Smith (1981a). The habitat is relatively uniform, and the Song Sparrow is the only abundant small passerine. All breeding adults were individually color-marked from 1975 to 1979. Nests were found by following females to the nest after foraging bouts. Almost all young were color-banded in the nest at about 6 days of age, and most recruits to the population were banded as nestlings. The age structure of the population was therefore known by 1979. The experimental part of the study was conducted in 1979, when 66 females bred on the 6.3-ha island.

The nests of some polygynous females in 1976 and 1977 were watched from 3-m-tall stepladders placed 10–20 m from the nest, and the numbers of feeding visits by males and females were noted. The ladder was positioned so that the birds were not disturbed by the observers. (If the ladder was too close, some birds would perch near the nest with food loads instead of delivering them to the nest.)

In 1979, nine males were removed, either on the day that the young in the first brood hatched (day 0) or the following day (day 1), by attracting them into mist nets with recorded song. Four of the males were mated to females more than 1 yr old, and the remainder to yearlings. Trapped males were housed on the island in a large outdoor aviary and fed millet seed, chopped boiled egg, wheat germ, crushed dog meal, and vitamin supplements. Birds maintained weight well on this diet. Males were removed from the northwestern half of the island (Fig. 1), and we attempted to remove nearby males so that local sex ratios would be altered. Nonterritorial males that settled were also removed and held in captivity. Removals took place from 2 to 22 May; 17 nests from which young hatched during this period were designated as controls (Fig. 1). These were selected from the same part of the island as the experimental nests, and most were active when males were removed. Breeding within the population was asynchronous because of an experiment on the southeastern half of the island reported elsewhere (Smith et al. 1980). One control male died naturally while his mate was incubating her first clutch. This increased the experimental sample to 10 females.

We marked young in all broods on day 1 by clipping the tips from one or more toenails and weighed them at the same time each day from day 1 to day 6 or day 7. Young were not weighed beyond day 8, because handling them at this time can cause premature departure from the nest (Nice 1937). Between day 4 and day 8, we observed feeding rates at nests and the brooding behavior of the female. (Male Song Sparrows seldom brood young.) Nests were observed for 1-h periods from step ladders placed as in 1976–1977. Seventy-two hours of nest observations were made, mostly between 1000 and 1400 and between 1600 and 2000, with about two-thirds of the observation time being devoted to nests of experi-

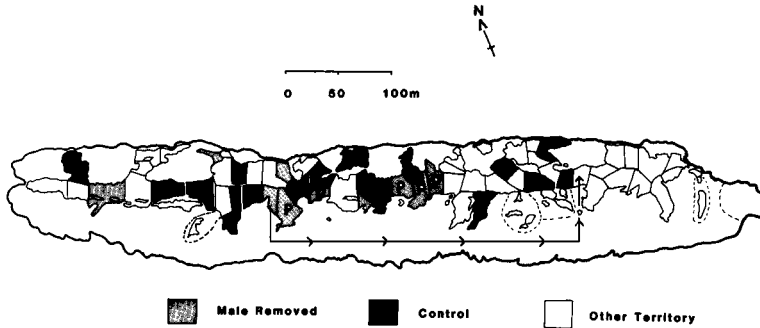


Fig. 1. Map of Mandarte Island showing the locations of Song Sparrow territories (stippled areas) where nine males were removed and a 10th male died naturally ("D"). Black, filled areas indicate territories of control pairs and unfilled areas, other territories. The arrow indicates a change of territory by an experimental female. "P" indicates territories where polygyny occurred.

mental broods. All data on growth and feeding rates were normalized by $\log(x + 1)$ transformations to allow use of parametric statistical tests.

When each experimental female had completed a second clutch with a new mate, we released the original male on the territory during the night. The course of the subsequent breeding attempts of experimental and control birds was followed. We estimated survival of young beyond leaving the nest from sightings of marked individuals of known origin. Most of these sightings were made in flocks of newly independent young. The study ended in late July 1979, too early for an adequate estimate of the later survival of young from second broods of experimental and control females.

Nests of three experimental and three control females were parasitized by Brown-headed Cowbirds (*Molothrus ater*). Parasitism did not influence survival of Song Sparrow nest mates (Smith 1981a). Parasitism was therefore ignored, except that cowbird eggs and young were omitted from the growth data and survival calculations.

RESULTS

NATURAL POLYGyny

Seven cases of natural polygyny were observed, 2 in 1976, 4 in 1977, and 1 in 1979. This constituted 3% of the 213 pairings not involved in the 1979 experiment. All cases were trios of one male and two females. In four of the seven cases, polygyny followed the death of a neighboring territorial male during the breeding season. In the remaining three cases, all in 1977, 2 females were paired with a single male from the start of the breeding season. This was the only spring when the number of breeding females exceeded the number of territory-hold-

ing males. (We never found a nonbreeding female, and females that died during the breeding season were not replaced.) Territories of males with two females were larger than average, as they were often an amalgam of two of the territories defended at the start of breeding. Females within trios overlapped little in their foraging areas, but it was not clear that they defended separate territories, as little overt aggression between them was seen. Females were, however, occasionally aggressive towards nonterritorial females in March and early April, just before the onset of breeding.

We observed the allocation of food by males to nestlings and fledglings in the four trios in 1977. In all, these trios raised six overlapping sets of broods. In four cases in which the clutches hatched asynchronously, the male fed only the older brood of young (Table 1). One of these males, however, seldom fed either brood. In the remaining two cases, the young of both broods hatched on the same day. Despite this hatching synchrony, the males fed both broods unequally, although one male did bring food to both nests. Thus, females accepting polygynous status often had to feed young with little or no help from the male. If hatching was asynchronous, the male fed only the first brood to hatch.

The survival of young from broods of polygynous and monogamous females is shown in Table 2. Five groups of broods are separated: (a) the five broods of "secondary" females (after Martin 1974) that received little or no food from the male in 1977; (b) the five broods of "primary" females in 1977 that received normal

TABLE 1. Allocation of male feedings to nestlings and fledglings of sets of overlapping polygynous broods in 1977.

Trio number	Hatching interval (days) between broods	Observation time (min)	Feedings to first brood to hatch	Feedings to second brood to hatch
1	9	270	57	0
1	5	285	24	0
2	4	150	16	0
3	0	305	1 ^a	23 ^a
4	0	105	16 ^a	0 ^a
4	11	175	1	0

^a First/second broods hatched on the same day.

male parental feeding; (c) all broods of naturally polygynous females in 1976 and 1977; (d) broods of experimentally widowed females in 1979; and (e) contemporaneous control nests of monogamous pairs for each of the 3 yr. Survival to banding age (about day 6) was good in nests of polygynous females in all groups and was, if anything, better than survival in nests of monogamous females. Survival of young to independence (about day 30) from groups (a), (b), and (c) was the same as that for all controls, but survival of controls was poor in 1979. If we consider only 1977, when most cases of polygyny occurred, group (b) females, which were helped by their mates, were as successful as controls. Group (a) females that received little or no help were, however, less than half as successful as controls in raising

young to independence. Three of these females, however, did produce independent young. The losses in these broods mostly occurred between banding and independence, in some instances through starvation of old young in the nest. Although our samples are small, these results suggest two main conclusions: first, feeding assistance by males is not necessary for some Song Sparrow females to raise young to independence; and second, polygyny is only disadvantageous to females if the male does not feed their young.

EXPERIMENTALLY INDUCED POLYGyny

Consequences of male removal.—In three of the nine cases in which the male was removed soon after the young hatched, the male was replaced the same day by a nonterritorial bird. In the remaining cases, replacement was not immediate, and in four of these cases the neighboring male took over the territory before a nonterritorial bird settled. Nine nonterritorial settlers were removed, and, in all nine territories, neighboring males eventually took over the defended shrub. One female disappeared soon after her first brood left the nest, and a second deserted her territory soon after her nest was robbed on day 5. She moved within 4 days to pair with an unmated male on the far end of the island, 16 territories (270 m) to the east (Fig. 1). A third paired monogamously with a neighboring male whose female had just died, a fourth paired with a neigh-

TABLE 2. Survival of young from nests of polygynous and monogamous female Song Sparrows. The asterisked group is a subset of the 1979 total. It describes breeding attempts of control females for experimental group (d).

Group	Number of breeding attempts	Total eggs laid	Proportion of eggs hatching	Proportion of eggs producing banded young	Proportion of eggs producing independent young
(a) Unaided secondary females in 1977	5	17	0.94	0.94	0.24
(b) Aided primary females in 1977	5	18	0.94	0.89	0.61
(c) All naturally polygynous females in 1976 and 1977	18	59	0.85	0.80	0.42
(d) Experimentally widowed females in 1979	10	32	0.88	0.50	0.22
(e) Monogamous females: 1976	40	119	0.71	0.59	0.53
1977	56	195	0.84	0.79	0.52
1979	33	100	0.70	0.57	0.23
1979*	16	53	0.75	0.62	0.40
All years	129	414	0.76	0.68	0.43

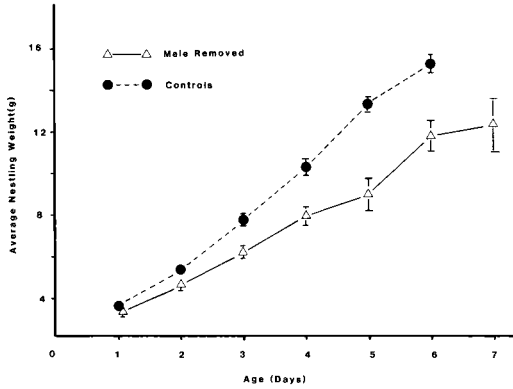


Fig. 2. Average growth of individual Song Sparrows in 10 experimental and 16 control broods. The vertical bars represent ± 1 SE.

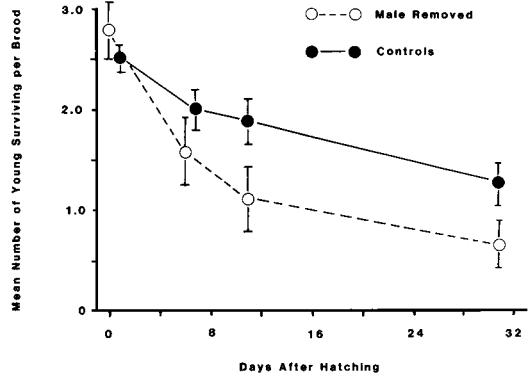


Fig. 3. Survival of young in control and experimental broods. Vertical bars represent ± 1 SE.

boring male that had been deserted by its previous mate, and a fifth did not breed again. The remaining four females formed polygynous associations with mated males, in one case with a male that already had two mates through the death of a male in the control group. Thus, four of our nine (44%) experimental females mated polygynously, compared to a natural polygyny rate of 3%. Our experiment also caused the first case known to us of a Song Sparrow male gaining three mates.

Reproductive success of experimental and control broods.—We predicted slower growth of young in broods of widowed females. This was indeed the case (Fig. 2); 8 young starved in the nests of the 10 unaided females, while only 2 control young starved. By day 3 the young in control broods were significantly heavier ($t = 3.12$, $df = 58$, $P < 0.01$) than experimental young (Fig. 2), and by day 6 the difference was more pronounced ($t = 4.33$, $df = 47$, $P < 0.001$). Individual weight gains from day 3 to day 6 were also significantly greater ($t = 4.19$, $df = 44$, $P < 0.001$) in control young. Weight gained from day 3 to day 6 was significantly heterogeneous among experimental families ($F = 5.45$; $df = 8, 8$; $P < 0.05$, one-way ANOVA). This shows that some widowed females were able to raise their young significantly better than others. Weight gains from day 3 to day 6 did not differ significantly among control broods, ($P > 0.10$, one-way ANOVA). The survivorship of young in broods of pairs and of unaided females is shown in Fig. 3. Fatherless young survived less

well in the nest and to independence. Neither difference, however, was significant ($P > 0.05$, t -tests), as survival in some experimental broods was good. Five of the 10 widowed females raised at least one young to independence. Variation in growth or survival of young among experimental families was not related to age of the female parent, to brood size at hatching, or to territory size before removal of the male.

Parental attentiveness in broods with and without males.—In only one of the 10 broods did the incoming male finally feed his foster young. This was the control brood where the father died during incubation. The incoming male did not visit the nest during 1 h of observation on both day 4 and day 6, when the female brought food 23 times in all, but did provide food 7 times in 2 h of observation on day 7, while the female brought food 26 times.

The rates at which food was brought to experimental and control nests are shown in Fig. 4. Feeding trips of unaided females were approximately twice as frequent as those of paired females each day from day 4 to day 8, and the difference was significant ($t = 3.46$, $df = 18$, $P < 0.01$) on day 7. Feeding rates of unaided females did not differ significantly from those of control pairs on any day from 4 to 7 ($P > 0.10$, t -tests). There were insufficient data from day 8 to allow statistical testing. Unaided females spent more time brooding their young than did control females during observation periods (Fig. 5). Nestlings were brooded much more on days 5–7 by unaided females.

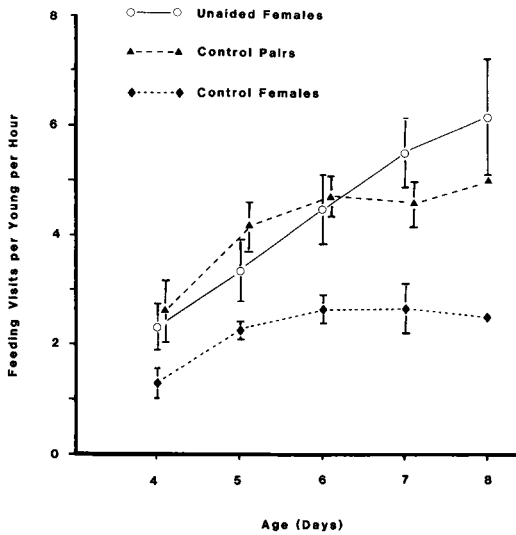


Fig. 4. Rates of bringing food to nests of control pairs, nests of control females, and nests of females whose males had been removed. Vertical lines represent ± 1 SE.

Control young required little brooding after day 4, when they were already significantly larger than experimental young (Fig. 2). This pattern differs from that found by Weatherhead (1979), in which young of unaided females received slightly less brooding from days 4–6. Both samples are small, and further data are needed, especially in the first few days after hatching.

Subsequent performance of experimental males and females.—One of the 9 territorial males that were removed died in captivity. The remaining 8 were released on their previous territories after being held for an average of 26 days. Two of the eight males immediately regained most of their previous territories; both their females had mated polygynously. Two other males were subsequently seen skulking on their previous territories. The other four were not seen again. We saw neither of the two males that regained his territory help his original mate feed the young in her second brood. One of these nests was in a location that was hard to observe, and we cannot say with confidence that the returning male did not bring food to this nest. The presumed father of this brood fed the young of his other female. The other returning male did not regain the portion of his territory containing the second-brood nest of his former mate.

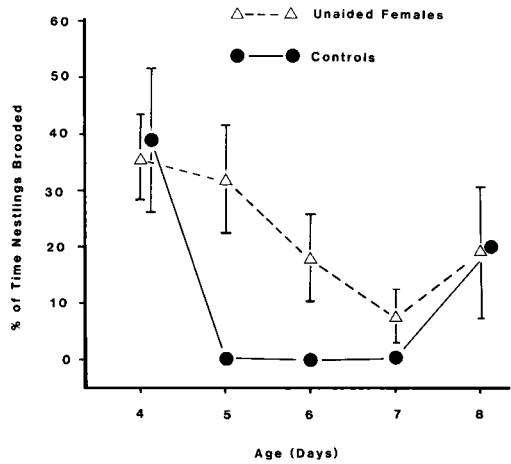


Fig. 5. Mean percentage brooding time of control and experimental females. Vertical lines represent ± 1 SE.

In the other cases of polygyny, two of the males fed young in nests of both primary and secondary females. In the first case, the male first fed the young of his primary female. He was first seen to bring food to the nest of his secondary female on day 9, when the two young of the primary female had reached day 23. This was the male that also obtained a third mate. He did not feed at this third nest, and the young starved by day 6. In the second case, the young of the primary and secondary females hatched 2 days apart, and the male fed both broods equally. Both these broods were small, containing only two young. Wittenberger (1980: Table 4) found that male Bobolinks (*Dolichonyx oryzivorus*) fed their secondary nestlings at a higher rate when the primary brood was small. In the final case of polygyny, the male fed the young in the second brood of the widowed female. His primary female failed to raise a second brood.

The eight widowed females that bred again began to lay their next clutch 20.3 ± 3.0 (SE) days later, while the 10 control females that bred again did so 18.0 ± 1.6 days later. Loss of the original mate did not therefore influence the timing of later breeding attempts. We also tested whether or not widowed females survived less well as a consequence of the loss of male aid. Adult survival was very poor in the 1979–1980 winter, and only three control females and one widowed female survived to breed in 1980.

DISCUSSION

Our experiment shows that the frequency of polygyny can be increased in a normally monogamous species by altering the operational sex ratio. We created local shortages of males by removing territory owners and colonizing floaters. Most females chose to mate with neighbors, rather than delaying breeding until an unmated male was available locally or deserting their territory to look for an unpaired territorial male. One female did, however, follow the last course, and more might have done so if more unmated males with territories had been available. There were only three such males in 1979, less than in most other years (Smith et al. 1980: Table 5). Natural polygyny occurred at the onset of the breeding season only in 1977, which was the only year when the number of females at the onset of breeding (44) exceeded the number of territorial males (41). Other cases of natural polygyny were facultative responses to local shortages of males, as in our removal experiment. Male removals also induced polygyny in a study of Willow Ptarmigan (*Lagopus lagopus*; Watson and Jenkins 1968).

We have shown that local imbalances in the sex ratio during the breeding season are a proximate cause of polygyny and that the mating system of the Song Sparrow is somewhat flexible. Variation in sex ratio, however, is probably not an important evolutionary cause of polygyny (Orians 1969; Wittenberger 1976, 1981), except in that sex ratio is influenced by ecological factors such as the spatial distribution of food (Verner 1964), preferred nesting habitat (Selander 1972), or predators (Picman 1980a, b).

We now consider why Song Sparrows are usually monogamous. We can reject hypothesis 1 of Wittenberger and Tilson (1980). Male feeding assistance is important but clearly not necessary for females to raise some young to independence (Table 2, Fig. 3). Females, however, do incur a cost if they mate with an already mated male, if he does not help them to feed their young. Young of such females grew slowly on average in our experiment and survived less well in the nest than did controls, as also found by Weatherhead (1979) and Martin (1974). We found, however, that several unaided females raised broods that were barely under weight, and young from five of these

broods survived to independence. Differences in female "quality" (Smith 1981b) may explain why only some females can raise young without male aid.

Survival is rarely studied beyond the time that young birds leave the nest. We were able to do so, and we found that young of unaided females in 1977 survived poorly from banding to independence, despite good early survival in the nest (Table 2). In our experiment, young of widowed females survived poorly in the nest compared to controls but did not survive worse thereafter (Fig. 3). Young of unaided females survived equally well from egg to independence in 1977 and 1979 (Table 2). Reproductive success of monogamous pairs was lower on average in 1979 than in 1977 (Table 2), and one might therefore have expected unaided females to raise proportionately fewer young to independence in 1979. We suggest that this did not happen because greater reduction of brood size in the nest in 1979 (Table 2) resulted in improved survival among fledglings and old nestlings. Young of widowed females grew poorly, although widows made as many feeding trips to the nest as did pairs (Fig. 4). Unaided females may bring fewer prey items per trip (Martin 1974) and perhaps smaller prey. J. F. Wittenberger (pers. comm.) has found that male Bobolinks bring larger loads and/or prey to the nest than females. Sexual dimorphism in size is about twice as great in Bobolinks as in Song Sparrows, and load size is presumably related to body size.

We also reject Wittenberger and Tilson's (1980) hypothesis number 5. Males clearly benefit from polygyny, because the females that they help within trios are as successful as controls. Any young raised by a second female then become a bonus, and there is no reason for a male to enforce monogamy by driving off additional females. Males, in fact, show some sexual behaviors toward neighboring territorial females (Nice 1937). Petrinovich and Patterson (1977) obtained similar evidence, contrary to both Wittenberger and Tilson's hypotheses 1 and 5, from the White-crowned Sparrow (*Zonotrichia leucophrys*).

Hypothesis 3 of Wittenberger and Tilson probably does not apply to Song Sparrows, as males defend territories rather than mates. It is rare for a male to leave his territory, even if his mate dies. Males in our experiment were certainly responsive to the presence of wid-

owed females on adjacent territories and eventually accepted them as mates, but no territorial male deserted his original territory to pair with such a female.

We now consider hypothesis 2. According to this hypothesis, the benefits of parental care provided by a male on a poor territory outweigh the gains to a female from pairing with an already mated male on a high-quality territory. We found that the cost of loss of male care was considerable. Unaided females raised about half as many independent young as controls (Table 2, Fig. 3). Territory quality can be estimated by the reproductive success of individuals that use the area. We found no striking variations in reproductive success in different parts of the island. Territory size can therefore be used as an indicator of territory quality. All territories containing above 100 m² of shrub were about equally successful, but territories of less than 100 m² produced less than half as many independent young, because many of these males failed to obtain mates (J.N.M.S. unpubl. data). This suggests that variation in territory quality is small on Mandarte and that females should therefore choose an unmated male over a mated one, unless the territory of the former is very small. Most females in our experiment did not desert their territory when widowed, presumably because the potential costs of relocation were high, and because the chance was good that a floater male would settle to replace the original mate. Our data are thus consistent with hypothesis 2.

Finally, we consider hypothesis 4. Do Song Sparrow females enforce monogamy on their mates by defending them against other females? We are unable to test this hypothesis and can only give some general observations. Song Sparrow males are extremely sedentary (Nice 1937, this study), and defense of a territory by a female is therefore equivalent to defense of a male. Females removed in early spring are rapidly replaced (Knapton and Krebs 1974). Female removals also result in replacement in grouse (Watson and Jenkins 1968, Bendell et al. 1972, Zwickel 1972, Hannon and Zwickel 1979). We saw one fierce fight between a territorial female and a young female intruder in late March and observed other less intense agonistic interactions between females at this time. Such aggression may force some females to leave the population and others to pair with males on small marginal territories. Once

breeding begins, however, females spend much of their time incubating and can no longer prevent unmated females from settling to share their territories (Orians 1980: 87). Three cases of polygyny occurred at the onset of the 1977 breeding season, but did not in other years, because there were always more males with suitable territories than available females. Female spacing behavior may, however, be of limited importance, because females are usually in short supply, as they are less successful than males in competition for food outside the breeding season (Yom-Tov and Ollason 1976, Smith et al. 1980, Boag and Grant 1981). We conclude that our data are most consistent with hypothesis 2.

Several experiments are suggested by these results. Food could be added to some territories to increase the polygyny threshold. We did a separate feeding experiment on Mandarte in 1979 (Smith et al. 1980), but this experiment was not definitive, as we did not continue feeding into the general breeding period. Territories may be more important for their nest sites than for the food they contain, as much of the food is gathered outside the defended area (Tompa 1964, J.N.M.S. unpubl. data). Female removal and addition experiments could be tried in early and late spring, and combining female removals with food additions or habitat manipulation (Pleszczynska 1978) might be instructive. We suggest that Song Sparrows are usually monogamous because males with high-quality territories outnumber females at the onset of breeding.

Finally, we discuss the question of "altruism" by male Song Sparrows (Power 1981). Power (1975) and Weatherhead and Robertson (1980) found, as we did, that replacements of monogamous male passerines removed during the breeding season seldom provided food to young of their new mates. One Song Sparrow male, however, did feed his foster young after an initial delay. One other case of care of foster young occurred in 1978, when a female left the territory of her previous mate accompanied by two fledglings. She paired with a neighbor whose previous mate had disappeared after her first brood. The new male fed the foster fledglings while the female began to incubate her second clutch. In both these cases, it is not clear that feeding foster young actually constituted altruism. The size of the first brood determines the interval between broods in Song

Sparrows (Smith and Roff 1980). By assisting a new female to care for young sired by a previous male, a male may speed up the initiation of a breeding attempt with the new female and hence gain an advantage. Some time may be required for hormonal priming of the male parental response (Emlen 1975). In our male removal experiment, most of the foster fathers were occupied in caring for young of their primary female and hence were less likely to feed their foster young.

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