EFFECTS OF BROOD SIZE AND NESTLING AGE ON PARENTAL CARE BY MALE FIELD SPARROWS (*SPIZELLA PUSILLA*)

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ABSTRACT.—Relative to their mates, male Field Sparrows (*Spizella pusilla*) disproportionately altered their contribution to nestling care as the demand for such care varied. In small broods (1-2 nestlings), males made significantly fewer trips to the nest, brought fewer food items, and brought items of a size equal to those of females. In larger broods (3-4 nestlings), males made significantly more trips, brought more items, and brought significantly larger items. A similar, though less significant, pattern was noted as nestlings aged. Relative to their mates, males made significantly fewer trips to young nestlings. These trends in male nestling care are consistent with the hypothesis that, under conditions of reduced demand for care, males will disproportionately reduce care (Westneat 1988). The time and energy gained could be allocated towards additional mates or extrapair copulations. *Received 6 October 1989, accepted 17 February 1990.*

IN a survey of passerine bird species, Lack (1968) concluded that ~90% mated monogamously. A similar proportion was reported by Verner and Willson (1969) in North American passerines. Since these surveys, polygyny has been found regularly in other species (e.g. Carey and Nolan 1975, 1979; Nolan 1978; Seastedt and MacLean 1980; Smith et al. 1982; Moller 1986). However, monogamy remains by far the most common mating system in passerines. A primary factor in passerine monogamy is the large parental investment (PI) needed to raise altricial young (Orians 1969, Oring 1982). In birds, this investment (except for egg laying) can be performed equally by males and females. In fact, the high PI requirements are thought, at times, to entail heavy investment by both parents to raise young successfully. This renders investment in multiple matings on the part of either parent detrimental to fitness (Lack 1968).

Asymmetries in the parental investment between sexes may lead to different behavior between the parents (Trivers 1972, van Rhijn 1984). A smaller investment in sperm relative to eggs may make it advantageous for males to seek additional inseminations. This might be accomplished with additional mates. Although females in such situations may lose some male PI, they may successfully raise their young alone (see Richmond 1978; Smith et al. 1982; Gowaty 1983; Wolf et al. 1988, 1990). Alternatively, males might seek extrapair copulations (EPCs) (see Ford 1983; Gowaty and Karlin 1984; Westneat 1987a, b, 1988; Moller 1988; Sherman and Morton 1988). Either behavior requires an investment of the male's time and energy, which is not available to young of his primary mate.

Westneat (1988) modified a PI model devised by Maynard Smith (1977) to describe the fitness trade-offs between the male's contributing parental care and seeking additional inseminations. According to this model, withholding male parental care is favored if $pNb > qR$, where p is the probability of achieving a mating, N the availability of matings, b the number of young from a given mating, R the number of current offspring in the male's nest, and q the proportion of young dying due to reduced parental care. If, at any time in the breeding cycle, parental investment requirements are high, the male may necessarily be required to invest heavily in his current young. However, if PI requirements at the current nest are reduced, the male is likely to reduce his investment and seek additional mates or EPCs.

In all passerines and other altricial bird species, the nestling and fledgling periods are a time of high parental investment. Feeding the young is energetically very costly (Ricklefs 1974; Biedenweg 1983; Walsberg 1983a, b; Finch 1984). Thus males of most passerine species aid their mates in feeding young. In a few species, males help incubate eggs, an activity with much lower investment (Verner and Willson 1969, Moller 1986). Feeding costs will vary. Fewer young or smaller young will require less food. In such situations, males might be expected to reduce investment relative to the care provided by their mates. Similarly, larger broods or older young correlate with greater relative male investment. I tested these expected changes in relative male investment by observing parental care activities of both sexes during the nestling period in a monogamous population of Field Sparrows (*Spizella pusilla*) during three breeding seasons (1987-1989) in an old field habitat in northeastern Pennsylvania.

METHODS

Study area.—The study area is a series of old fields, 10.63 ha in area, expanded to 15.99 ha in 1988. The fields are located 1.5 km east of LaPlume, Benton Township, Lackawanna County, Pennsylvania, adjacent to the western boundary of Lackawanna State Park. Most fields had been undisturbed for at least 10 yr, except for fox-hunt trails mowed through portions of them after the breeding season. New fields added in 1988 had not been mowed in 2 years. Characteristic vegetation is a lush ground cover of grasses and other forbs, primarily goldenrod (*Solidago* sp.). Scattered throughout are clumps of small woody vegetation (mean height ~ 1.5 m), especially dogwood (*Cornus* spp.), blackberry (*Rubus* spp.), vibernum (*Vibernum* spp.), spirea (*Spiraea* spp.), ash (*Fraxinus* spp.), and honeysuckle (*Lonicera* spp.). The rectangular study area is surrounded on three sides by mature forest and on one side by a hayfield. The fields are on a southwesterly facing slope and range in elevation from 298-344 m.

Species.—The Field Sparrow is monomorphic, builds open nests and is common in early successional habitats in the eastern United States. In northeastern Pennsylvania, males first appear in mid-April, females ca. 1 May. Pairing is rapid, and nest construction starts ca. 10 May. Only females build nests, and while doing so they are followed closely by the males. May nests are built on or near the ground (mean [±SD] height = 15.8 ± 23.4 cm, $n = 44$), primarily in grasses or honeysuckle. June/July nests are elevated, usually in dogwood or ash saplings (mean height = 53.3 ± 24.2 cm, $n = 64$). Only females incubate eggs and brood young. Feeding activities are shared by the parents (Best 1977a and below). On the study area nest predation was considerable, but there was no Brown-headed Cowbird (*Molothrus ater*) parasitism. Approximately 60% of the nests fledged young in all years, and second broods were common. No new nests were begun after 20 July. For additional data on Field Sparrow breeding biology, see Walkinshaw (1936, 1939, 1968) and Best (1977a, b, 1978).

Data collection.—The study was carried out between 1 May and 1 August, 1987-1989. I used mist nets to capture nearly all Field Sparrows that bred on the area, and I individually color-banded them. Individuals were sexed by the presence of a brood patch (female) or cloacal protuberance (male), and by differences in wing length (most males, >65 mm; most females, less). Behavior confirmed gender. I canvassed fields regularly to follow territory settlement and pairing. Nesting activities of each pair were then followed daily throughout the summer.

With the exception of two 5-egg clutches, all nests ($n = 108$) contained either 3 or 4 eggs (mean clutch = 3.6). In 10 nests, unhatched eggs or piecemeal egg loss reduced the number of hatchlings to 1 or 2 (mean number of hatchlings at nests which survived to hatching = 3.2). To increase the number of nests that contained only 1 or 2 nestlings, I removed eggs from 10 other nests on the day before expected hatching. There were no significant differences in nestling care between manipulated and unmanipulated nests (t-tests, $P > 0.05$). Thus both types were pooled for subsequent analyses.

During the *nestling period* (the time between the hatching of the first young [day 1] and the fledging of the last), a canvas blind was erected 5-10 m from each nest. Nests were observed from the blinds for 30-min periods daily in the nestling period. Observation days ranged from 28 May through 31 July. Of 483 such observations, 470 were between 0600 and 1300 EDT; later hours were used only if rain prevented morning observation. I recorded the number of feeding trips and the number, type, and size (length in mm) of food items brought by each sex. Accuracy of visual estimations of food type and size was checked periodically by collecting food items from day 6 nestlings that had pipe cleaner ligatures placed around their necks. Through day 6 of the period, nestlings were weighed (±0.1 g) after daily nest observations. On day 6, nestlings were banded, after which they were not handled. Normal fledging occurred on day 9 or 10.

I followed 12 breeding territories in 1987, 17 in 1988, and 21 in 1989. In 1987, 19 of 31 nests produced young; 18 nests survived to fledging. In 1988, 25 of 38 nests produced young; 23 survived to fledging. In 1989, 29 of 39 nests produced young; 23 survived to fledging. Only nests observed 6 times at a constant brood size and with both parents present ($n = 60$) were used for analyses. These criteria excluded all predation-related nest failures from the analysis. Due to a shortage of blinds in 1987, I had no day 1 observations at 13 of 17 nests. In 1988-1989 I sampled day 1 in 40 of the 43 nests.

Single mean values per individual bird were used in determining the overall means in all tables. I used the Wilcoxon matched-pairs signed-ranks test for intersex comparisons, and single classification ANOVA for all others. If ANOVA indicated significant differences, further comparison of means was done by Sheffe's test. Data were analyzed using the SAS System, SAS Institute Inc. Significance level for all analyses was $P < 0.05$.

TABLE 1. Mean parental activities of Field Sparrows (30-min observation period) according to sex and brood size (all nestling ages pooled).[a] Levels of significance (between sexes): * = $P < 0.05$; ** = $P < 0.01$ (Wilcoxon signed-ranks test).

Brood size	Pairs (*n*)	Sex	Trips	Food items	Item size	Total food	Nest time
1	7	m	0.94*	0.99	15.38	15.38	0.69**
		f	1.44	1.31	14.77	18.91	13.90
2	13	m	1.27**	1.30**	15.60*	20.30*	0.66**
		f	1.99	1.82	14.29	26.15	14.97
3	20	m	2.24*	2.46**	16.45**	40.81**	1.26**
		f	1.86	1.75	14.36	25.61	11.44
4	18	m	2.23	2.62*	17.29**	45.01**	1.12**
		f	2.28	2.20	15.17	34.52	11.18

[a] Definitions: *trips*—mean number of trips to the nest made by each individual during the 30 minute observation period; *food items*—mean number of food items delivered by each individual in a 30 minute period; *item size*—mean length (mm) of food items delivered to the nest by each individual; *total food*—mean (food items)(item size) for each individual; *nest time*—mean time (min) spent at the nest by each individual in a 30-min. period.

RESULTS

The parental activities of male and female Field Sparrows varied according to brood size and showed a general decrease in relative male nestling care with decreasing brood size (Table 1). At brood sizes of 3 or 4, male feeding activities were greater, usually significantly so, than that of their mates. At lower brood sizes, relative male feeding activities were lower. In both sexes, the number of food items delivered was roughly equivalent to the number of trips, which indicates one food item per trip.

Female total food delivery increased significantly as brood size increased ($F_{3,54} = 4.47$, $P < 0.005$). In pairwise comparisons (Sheffe's test), female total food increased significantly between brood sizes of 1 and 2 and again between 3 and 4. Male total food deliveries also increased significantly as brood size increased ($F_{3,54} = 18.06$, $P < 0.001$). In pairwise comparisons (Sheffe's test), male total food deliveries increased significantly between brood sizes of 2 and 3.

Only females brooded young and repaired the nest. On rare occasions, males shaded young for short periods, but this was primarily a female activity. Thus at all brood sizes, females contributed significantly more nest time than males. There were significant differences in female nest time according to brood size ($F_{3,54} = 3.70$, $P < 0.025$). In pairwise comparisons (Sheffe's test), there was a significant increase in nest time as brood size decreased from 3 to 2.

Per-nestling food deliveries by both parents according to brood size differed (Table 2). There were significant brood size effects on all parameters except item size (ANOVAs, $P < 0.05$). In pairwise comparisons (Sheffe's test), total food delivered to broods of one was significantly greater than that delivered to larger broods. There was no significant difference (ANOVAs, $P > 0.05$) in increases in mass of young relative to brood size through day 6 (Fig. 1).

Two nests survived to fledging without a male present (Table 3). Both started with brood sizes of 4. One was decreased to 3 young on day 4. In this latter nest, a neighboring male entered the territory on day 6 and made 62% of the feeding trips on days 7 and 8. The females of the male-less nests compensated fully for the lack of male help. Unaided female total food was equivalent to that of both sexes at nests with 3 and 4 young. The unaided females increased food deliveries partially at the cost of reduced nest time (e.g. brooding). They also appeared to choose relatively larger food items and often had multiple prey loads ($\bar{x} = 1.38$ items/trip). Mean day-6 mass of young from unaided female nests (8.29 g) was roughly equal

TABLE 2. Nestling feeding rate of Field Sparrows (30-min observation period) relative to brood size (both parents and all nestling ages pooled).

Brood size	Pairs (*n*)	Trips	Food items	Item size	Total food
1	7	2.38	2.30	15.08	34.59
2	13	1.61	1.56	14.94	23.35
3	20	1.37	1.40	15.40	22.01
4	18	1.13	1.21	16.23	19.88

to the mass of young from comparable broods of biparental nests (7.92 g).

Only in food size were there significant food differences between sexes relative to nestling age (Table 4). Males brought significantly larger food items to young of all ages. This, in turn, increased significantly total food delivered by males compared with that of their mates. I had a poor sample of day 1 feeding activities in 1987 (see methods). Thus I reanalyzed the data using only 1988/1989 observations. Results of this analysis were generally the same as those in Table 4, with one exception. Males in 1988/1989 made significantly fewer trips to nests containing 1-3 day old nestlings than did their mates (Wilcoxon signed-ranks test, $T_s = 163.5$, $n = 31$, $P < 0.05$).

Both males and females increased food delivery significantly as nestlings aged. Older nestlings received significantly more and larger food items from both parents (ANOVAs, $P < 0.05$). Female nest time relative to nestling age also changed significantly ($F_{2,119} = 84.69$, $P < 0.001$); Sheffe's test indicated significant decreases in nest time through each of the three age classes.

The number of laying females changed over time as did feeding trips of the parents (Table 5). Laying females were present throughout the breeding season—most at the beginning, fewest in late July. Males made fewer trips than their mates made in May, though with small sample size, the difference was not significant. Males made significantly fewer trips to the nest in early June.

DISCUSSION

These data support both predictions of the Westneat (1988) model. At typical brood sizes (3-4), males made significantly more trips and delivered significantly more food than did their mates. At broods of 1 or 2, males did less (Table 1). Females spent significantly more time brooding at nests with fewer young. This reduced further the male's relative contribution to small broods. A similar, though nonsignificant, brood size effect was noted by Best (1977a) in an Illinois population. The differences between sexes in food delivery relative to nestling age were not as great as differences due to brood size (Table 4). However, males made significantly fewer trips to nests with young nestlings (1988/1989 data only). Females spent more time at nests with young nestlings, which reduced relative male contribution to younger nestlings. As predicted, when feeding demands of nestlings were reduced, male Field Sparrows disproportionately reduced their relative contribution to nestling care.

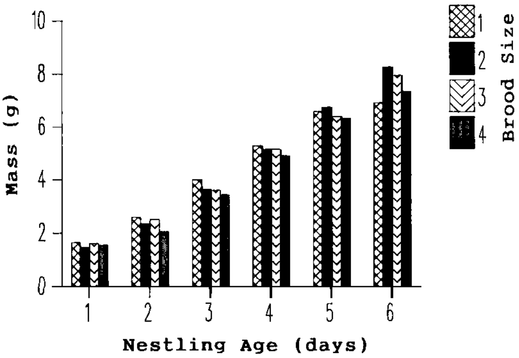

Fig. 1. Mean mass (g) of nestling Field Sparrows by brood size and age (day 1 is day first young hatched).

In some monogamous passerines, reduced brood size leads to reduced relative male contribution (Howe 1979, Johnson and Best 1982, Grundel 1987, Westneat 1988). In others, brood size had no effect on relative parental contributions (Biermann and Sealy 1982, Breitwisch et al. 1986, Leffelaar and Robertson 1986, Moreno 1987, Smith et al. 1988). In a few species, males increased relative contribution to smaller broods (Hegner and Wingfield 1987, Buitron 1988). Westneat (1988) reported reduced relative male contribution to younger nestlings. Typically, though, passerine males fed relatively more to younger nestlings (Howe 1979, Johnson and Best 1982, Grundel 1987, Hegner and Wingfield 1987, Buitron 1988). In other species, nestling age had no effect on relative parental contributions (Biermann and Sealy 1982, Breitwisch et al. 1986, Leffelaar and Robertson 1986, Moreno 1987).

TABLE 3. Nestling care activities of 2 unaided female Field Sparrows at nests (30-min observation period), compared with mean activity at nests of similar brood size (3-4) with males present.

	Unaided female	Male & female	Aided female only
Trips	3.20	4.29	2.06
Food items	4.43	4.50	1.96
Item size	16.12	15.80	14.74
Total food	71.41	71.10	28.89
Nest time	7.61	—	11.32

TABLE 4. Parental activities of Field Sparrows (30-min observation period) according to sex and nestling age (Day 1 is hatching day of the first young); all brood sizes pooled. Levels of significance (between sexes): * = $P < 0.05$; ** = $P < 0.01$ (Wilcoxon signed-ranks test).

Age (days)	Pairs (*n*)	Sex	Trips	Food items	Item size	Total food	Nest time
1-3	42	m	1.43	1.43	11.90**	17.04*	1.30**
		f	1.56	1.31	10.51	13.79	17.72
4-6	42	m	1.94	2.20	18.27**	40.21**	1.00**
		f	2.01	1.86	16.26	30.60	12.35
7-9	38	m	2.54	2.85	19.83*	56.89	0.85**
		f	2.64	2.69	18.97	50.99	5.64

Feeding of nestlings is only one component of male investment during the nestling period. Another major component is brood defense. In 50% of unmanipulated small broods, random reduction in eggs appeared to be caused by predation. My manipulations simulated this predation. Predators might return to nests where they were successful. It may benefit male Field Sparrows to decrease feeding reduced broods and allocate more time to their defense. This would not change overall nestling parental investment. Knight and Temple (1986) manipulated American Goldfinch (*Carduelis tristis*) brood sizes, and found that males defended larger broods more strongly. The general trend is for males to defend more strongly as brood size and nestling age increase (Breitwisch 1988, Montogmerie and Weatherhead 1988). If male Field Sparrows follow these patterns in nest defense, then reduced feeding investment would be accompanied by reduced defense investment. Consequently, there is a disproportionate reduction in overall nestling investment in smaller broods and younger nestlings.

According to the Westneat (1988) model, reductions in male contributions to nestling care should produce minimal harm to the nestlings. This criterion would be met if females compensated for male reductions. In Field Sparrows, males showed no significant increase in total food delivery as brood size increased from 1 to 2, while females did (Table 1). This pattern was reversed between brood sizes of 2 and 3. As a result, there were few significant differences in per-nestling total food according to brood size (Table 2), and no significant differences in nestling mass with brood size through day 6 (Fig. 1). Even without male aid, two female Field Sparrows raised large broods to fledging with no decrease in total food (Table 3) or day-6 nestling mass.

TABLE 5. Numbers of female Field Sparrows laying first eggs in nests and mean feeding trips of males and females by date. Levels of significance (between sexes): * = $P < 0.05$ (Wilcoxon signed-ranks test).

Date	Egg-laying females	Male trips	Female trips	Pairs (*n*)
12-31 May	49	1.04	1.83	4
1-15 June	21	1.65	1.88*	23
16-30 June	21	1.77	1.78	15
1-15 July	15	2.17	2.14	20
16-31 July	2	1.87	1.78	11

Males might benefit from a reduction in attention to nestlings. Males could allocate more time and energy to additional inseminations, either through polygynous matings or extrapair copulations (Westneat 1988). There is no evidence of polygyny in Field Sparrows (Walkinshaw 1968, Best 1977b). With one possible exception (a polyterritorial male), I found no polygynous males in this population. Thus, if there is benefit for male Field Sparrows, it must be extrapair copulations. Field Sparrow EPCs have been observed (Walkinshaw 1968). Petter et al. (In press) reported that ~18% of nestling Field Sparrows were not fathered by the male whose territory contained their nests.

If the reduction in male nestling care functions to gain access to extrapair copulations, such reductions would most likely be expected when receptive females are most common. Laying females were most common at the initiation of breeding in May and decreased through July (Table 5). As expected, the proportion of trips to nests made by males increased as the breeding season progressed, though male feeding trips were significantly less than their mates only in early June. There were no significant differences during the rest of the summer.

My results support Westneat's (1988) model. Male Field Sparrows reduced relative parental contribution when brood size and nestling age were low, apparently without harm to the nestlings. In addition, the reduction was greatest early in the season when receptive females were most abundant. Male Indigo Buntings (*Passerina cyanea*) reduced nestling care in a similar manner (Westneat 1988), and, as expected, the species is occasionally polygynous (Carey and Nolan 1979) and has relatively high extrapair copulation rates (Westneat 1987a, b). Not all monogamous species have males that reduce nestling care in this manner. For example, Black-billed Magpie (*Pica pica*) males increased relative contribution to small broods and young nestlings (Buitron 1988). A lack of male nestling care in Magpies can result in death of the nestlings (Dunn and Hannon 1989). Lack of reduction in a species might also correlate with fewer opportunities for EPCs. Further study of these and other monogamous species is needed to understand the relationships among male nestling care, nestling survivorship, and opportunities for additional inseminations.

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