

Effects of Nestling Age and Brood Size on Nestling Care in the Bachman's Sparrow (*Aimophila aestivalis*)

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ABSTRACT.—Effects of nestling age and brood size on parental food delivery and brood attention time were studied in the Bachman's sparrow (*Aimophila aestivalis*) in central Arkansas from 1983-1985. Nestlings received an increase in food mass with age because both parents increased the size of foods they delivered and because females increased the number of feeding trips and food items delivered. Males delivered a greater percentage of lepidopteran larvae to 0-2 day-old nestlings than to older nestlings. Nestling attentive time for both parents decreased with nestling age. Nestlings of large broods received approximately the same food mass as small brood nestlings because both parents increased the number of feeding trips and food items delivered. Brood size had no effect on the types of foods fed to nestlings. Small brood nestlings received more attentive time than large brood nestlings. Although females spent more time at the nest than males, they delivered roughly the same amount of food.

INTRODUCTION

In altricial birds, parental food delivery rates may change to meet needs of growing nestlings and varying brood sizes. Parents can change food delivery rates by altering their feeding frequency and/or number of food items per feeding trip. They also can change their food selection habits and deliver foods with varying masses. Altering food delivery, however, may affect time available for brooding, shading, nest guarding, self-maintenance, and possibly other activities (e.g., defending territory, extra-pair copulations). How do parents balance these conflicting needs so that they can achieve maximum reproductive success? Do the sexes differ in how they meet these needs? Recent studies of passerines have shown variation in interspecific and intersexual nestling care (Biermann and Sealy, 1982; Johnson and Best, 1982; Bédard and Meunier, 1983; Knapton, 1984; Carlson and Moreno, 1986; Grundel, 1987), but reasons for this variation are unclear. Further, parental care patterns have been closely linked with theories dealing with the evolution of mating systems (Emlen and Oring, 1987; Wittenberger, 1979). Therefore, additional studies can help elucidate causes of variation in parental care patterns and possible factors leading to the evolution of various mating systems.

Bachman's sparrow (*Aimophila aestivalis*) is a monomorphic, double-brooded species that nests and forages on the ground in open pine forests and over-grown fields in south and central portions of eastern United States (American Ornithologists' Union, 1983; Haggerty, 1988). Although a few studies have reported on nestling care in Bachman's sparrow (Brooks, 1938; Meanley, 1959; Wolf, 1977), these reports were brief and not quantitative. The objectives of this research are to (1) examine the effects of nestling age and brood size on food delivery rates, nestling diet and nest attentive time, and (2) compare the roles of the sexes in caring for nestlings. Because reports indicate Bachman's sparrow populations are declining (Tate, 1986), information concerning its biology is of special importance.

STUDY AREA AND METHODS

Research was conducted during spring, summer and autumn of 1983-1985 in Hot Spring Co., Arkansas, approximately 16 km S of Malvern. Fourteen tracts owned by International

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Paper Company and used to grow shortleaf (*Pinus echinata*) and loblolly (*P. taeda*) pines were the principal study areas. Adult sparrows were captured in mist nets, sexed by presence or absence of cloacal protuberance or brood patch, and marked with unique combinations of colored leg bands. Nest observations took place from a blind 4–8 m from the nest. A spotting scope with 20–45× eyepiece, 7 × 35 binoculars, and a stopwatch were used to monitor food delivery and attentive behavior. Nestling care data were collected from 35 nests of 19 monogamous pairs during 201 h of observation over 3 breeding seasons. The average observation time per nest was 162 ± 12.9 (SE) min. Observation time per nest varied primarily because of nest predation. I observed 823 feeding visits and delivery of 1008 food items.

Adults delivering food usually landed on bare patches of ground in front of the nest and paused for a few seconds, allowing most food items to be identified. Rarely were both parents seen at the nest together. If a parent was at the nest when its mate returned, "chitter" calls were usually exchanged and the parent at the nest usually left before its mate reached the nest. Occasionally, males delivered food to attending females who then delivered it to nestlings.

Food delivery rate was assessed by measuring food mass, number of food items per feeding trip, and number of feeding trips per hour. I used adult bill length (average length from anterior nares to tip, 8.5 ± 0.06 [SE] mm, $n = 37$) to classify food items into four length classes (1–10 mm, 11–20 mm, 21–30 mm, 31–40 mm) and then calculated an approximate mass value for an item from each length class using the formula: $\text{mass}(\text{mg}) = 0.0305 \text{ length}(\text{mm})^{2.62}$. This formula is the result of linear regression following logarithmic transformation of 500 individual insect body weights and lengths (Rogers *et al.*, 1976; *see also* Hegner, 1982). Midpoint lengths for each size class (*i.e.*, 5.5, 15.5, 25.5, 35.5 mm) were used in the formula and converted values were 2.7 mg, 40.1 mg, 147.7 mg, and 351.5 mg. Food mass per hour was obtained by adding the converted mass values for each feeding trip, then adding the mass values for all feeding trips for 1 h. Average food length approximations for each observation period were made by multiplying the number of food items within each size class by the midpoint lengths for each size class, then dividing by the total number of food items delivered for the observation period. Attentive time includes time spent feeding, brooding, shading and/or guarding nestlings. Nestling period was divided into three classes: 0–2, 3–5 and 6–9 days old. Two or three nestlings were considered small broods and four or five nestlings were considered large.

Data for the same nest and day were pooled, averaged, and analyzed as an independent observation (n -values). Observations from different nests but from the same pairs were considered independent because of spatial and temporal differences between nests. Due to predation, only two nests were observed throughout the nestling period; and thus in order to make comparisons between the sexes for the whole nestling period, observations from eight randomly chosen nests were selected from each age class. These observations were then combined into one data set for analysis.

Initial analyses (Kruskal-Wallis one-way ANOVA) showed no significant differences in adult nestling care behavior among years and time of day, so these data were pooled. Data that were not normally distributed were transformed using logarithmic (number of food items, number of feeding trips, number of food items per trip), square root (food mass) and arcsin (percent attentive time and proportions of food types) transformations before one-way ANOVAs (general linear model), t -tests, or paired-comparison's t -tests were performed (Zar, 1974). Data that could not be transformed successfully were analyzed with the Kruskal-Wallis one-way ANOVA test (chi-square approximation), Mann-Whitney U -test (normal approximation) and Wilcoxon's signed-ranks tests (normal approximation). When a sig-

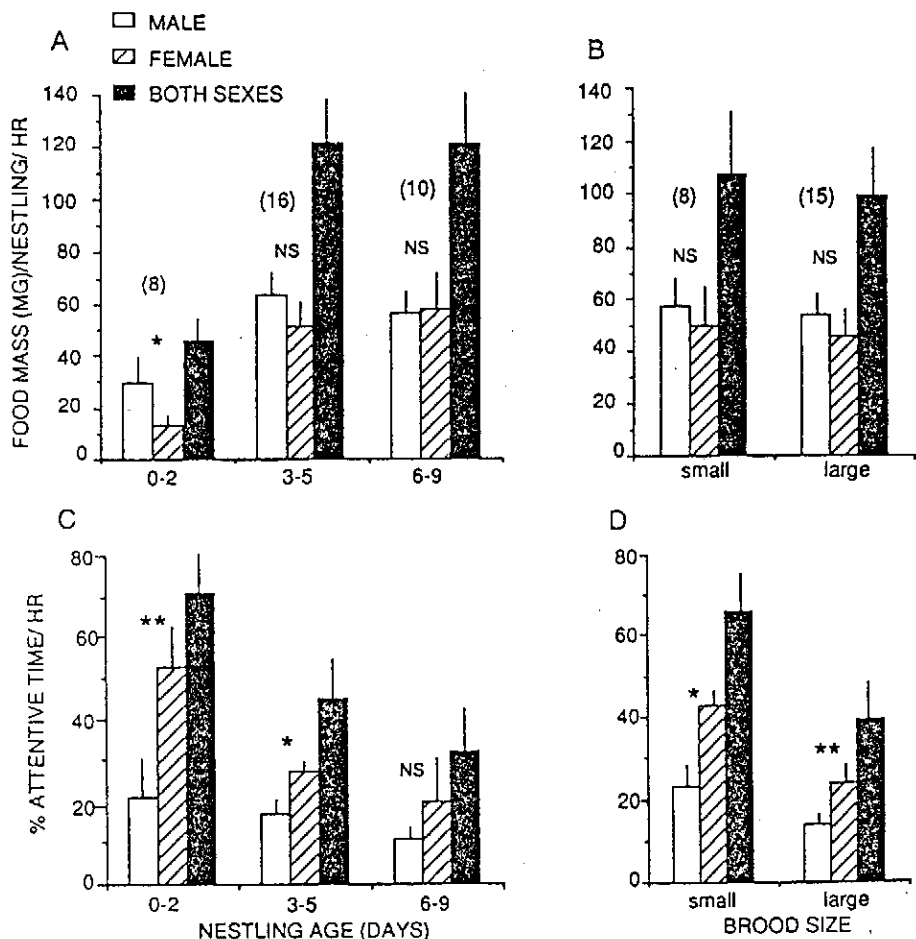


FIG. 1.—Mean adult food mass delivery per nestling per hour to three age classes (A), and two brood size classes (B). Mean parent percent attentive time per hour to nestlings of different ages (C), and brood sizes (D). Vertical lines indicate one standard error and numbers in parentheses (*n*) are the number of nests observed. Asterisks denote significant difference between sexes using paired-comparisons *t*-test (* = $P < 0.05$, ** = $P < 0.01$, NS = not significant)

nificant difference was found between the nestling age classes, Duncan's multiple range test was used to determine which classes were significantly different. All tests were two-tailed and statistical significance was set at $P < 0.05$. Statistical Analysis System software (version 5.18) and Statview SE+Graphics (version 1.03) were used for statistical analyses.

RESULTS

Effects of nestling age.—Nestling age affected the combined food mass delivered to nestlings by parents ($F_{2,11} = 6.1$, $P = 0.01$) because both sexes (females: $F_{2,11} = 6.9$, $P = 0.003$; males:

TABLE 1.—Effects of nestling age on mean (SE) number of food items delivered, number of food items/trip, number of feeding trips and food size delivered. Asterisks signify statistical difference ($P < 0.05$) between sexes using paired-comparisons t-test. Sample size (n) is the number of nests observed

Nestling age (days)	n	Food items/nestling/h			Food items/trip	
		Male	Female	Both sexes	Male	Female
0-2	8	0.9 (0.2)	0.4 (0.1)*	1.3 (0.2)	2.1 (0.3)	1.4 (0.1)*
3-5	16	1.0 (0.1)	0.8 (0.1)*	1.8 (0.1)	2.1 (0.1)	1.6 (0.1)*
6-9	10	1.1 (0.2)	0.9 (0.2)	2.0 (0.2)	1.8 (0.2)	1.6 (0.2)
Statistic*		0.5	4.2	3.7	2.2	0.9
P value		0.6	0.02	0.04	0.3	0.6

* F value (one-way ANOVA) except for food items/trip which is χ^2 approximation value from Kruskal-Wallis test

$F_{2,31} = 6.6$, $P = 0.004$) delivered a greater food mass to 3-5 and 6-9 day-old nestlings than to 0-2 day-olds (multiple range test, $P < 0.05$, Fig. 1A).

Nestling age also affected the combined number of food items per nestling per hour delivered by parents (Table 1). Nestlings 0-2 days old received significantly fewer food items than 6-9 day-olds (multiple range test, $P < 0.05$, Table 1). When the sexes were examined separately, however, this difference between age classes was only significant for females (multiple range test, $P < 0.05$, Table 1).

Nestling age had no effect on the number of food items per trip delivered by males or females (Table 1), but did affect the combined number of feeding trips per nestling per hour made by parents (Table 1). Nestlings 0-2 days old received significantly fewer feeding trips than 6-9 day-old nestlings (multiple range test, $P < 0.05$). This difference between age classes was primarily due to an increase in the number of feeding trips by females to 6-9 day-old nestlings (multiple range test, $P < 0.05$, Table 1).

Size and type of food items delivered by parents was also affected by nestling age. Nestlings 0-2 days old received smaller food items than 3-5 and 6-9 day-olds from males, females and both parents combined (multiple range test, Table 1). Together, parents delivered 47% more lepidopteran larvae to 0-2 day-olds than to nestlings of the older age classes ($\chi^2 = 8.4$, $df = 2$, $P = 0.01$, Fig. 2A). When the sexes were examined separately, however, only males significantly increased the percentage of lepidopteran larvae among age classes (female: $\chi^2 = 2.3$, $df = 2$, $P = 0.3$; male: $\chi^2 = 7.7$, $df = 2$, $P = 0.02$). The percentages of other food types delivered to nestlings did not differ significantly between age classes for males, females or both sexes combined (Fig. 2A).

Nestling age inversely affected the combined parent attentive time ($F_{2,31} = 8.1$, $P = 0.001$), but when the sexes were examined separately, only female attentive time was inversely affected significantly (females: $F_{2,31} = 8.6$, $P = 0.001$; males: $F_{2,31} = 1.2$, $P = 0.3$, Fig. 1C). Females spent more attentive time at 0-2 day-old broods than at 3-5 or 6-9 day-old broods (multiple range test, $P < 0.05$, Fig. 1C).

Effects of brood size.—Although not significant, substantial increases in food mass delivery by both sexes to large brood nests were responsible for nestlings of large broods receiving approximately the same food mass as nestlings of small broods (t-test, sexes combined: $t = 0.3$, $df = 21$, $P = 0.8$; male: $t = 0.2$, $df = 21$, $P = 0.8$; female: $t = 0.1$, $df = 21$, $P = 0.9$, Fig. 1B).

Together, parents significantly increased the number of food items they delivered to large

TABLE 1.—Extended

Feeding trips/nestling/h			Food size (mm)		
Male	Female	Both sexes	Male	Female	Both sexes
0.6 (0.1)	0.3 (0.02)*	0.9 (0.1)	12.3 (1.5)	12.7 (1.3)	12.4 (1.4)
0.6 (0.0)	0.5 (0.0)	1.1 (0.1)	16.3 (0.9)	16.4 (0.7)	16.3 (0.8)
0.7 (0.1)	0.7 (0.1)	1.4 (0.1)	16.4 (1.1)	16.6 (1.1)	16.5 (1.1)
0.9	5.7	4.4	3.4	4.2	3.6
0.4	0.01	0.02	0.04	0.02	0.04

brood nests compared to small brood nests (Table 2). When the sexes were examined separately, increase in the number of food items to large brood nests was nonsignificant for both sexes (Table 2), but was great enough to enable large brood nestlings to receive approximately the same number of food items as small brood nestlings (1.6 ± 0.1 vs. 1.9 ± 0.2 , $t = 1.4$, $df = 21$, $P = 0.2$).

Brood size had no effect on the number of food items per trip delivered by males or females (Table 2).

Parents made significantly more feeding visits to large brood nests than to small brood nests (Table 2). This increase in feeding trips resulted in large brood nestlings receiving roughly the same number of feeding trips as small brood nestlings (1.1 ± 0.1 vs. 1.2 ± 0.1). When the sexes were examined separately, however, even though males made a greater number of feeding trips to large brood nests (Table 2), large brood nestlings still received significantly fewer feeding visits from males than small brood nestlings (0.53 ± 0.04 vs. 0.67 ± 0.05 , $t = 2.1$, $df = 21$, $P = 0.04$). Females made approximately the same number of feeding trips to large brood nestlings as they did to small brood nestlings (0.59 ± 0.1 vs. 0.51 ± 0.1 , $t = 0.07$, $df = 21$, $P = 0.5$).

Brood size had no effect on the size (Table 1) or type (Fig. 2B) of food items delivered by male, female, or both sexes combined.

Small broods received significantly more combined parent attentive time than large broods ($t = 3.5$, $df = 21$, $P = 0.01$). This difference, however, was primarily due to females spending more time at small brood nests than at large brood nests (female: $t = 3.3$, $df = 21$, $P = 0.005$; males: $t = 1.7$, $df = 21$, $P = 0.10$, Fig. 1D).

Comparison of the sexes.—Comparison of the sexes for the whole nestling period, (nestling age and brood size classes pooled) showed that they delivered approximately the same food mass to nestlings (male: $51 \text{ mg} \pm 5.2$, female: $46 \text{ mg} \pm 8.2$, paired-comparisons t -test, $t = 1.6$, $n = 24$, $P = 0.1$). A comparison within each nestling age and brood size class, however, showed that males delivered a significantly greater food mass to 0–2 day-olds than did females (Fig. 1A). No sexual differences in food mass delivery were found within the other age or brood size classes (Fig. 1A, B).

For the entire nestling period males delivered more food items than females (1.0 ± 0.1 vs. 0.8 ± 0.1 , paired-comparisons t -test, $t = 2.2$, $n = 24$, $P = 0.04$). Within each class, males delivered more food items to 0–2 and 3–5 day-olds, but not to 6–9 day-olds (Table 1). No significant differences in the number of items delivered were found between the sexes within either brood size class (Table 2).

For the whole nestling period, males delivered a significantly greater number of food

TABLE 2.—Effects of brood size on mean (SE) number of food items delivered, number of food items/trip, number of feeding trips and food size delivered. Asterisks signify statistical difference ($P < 0.05$) between sexes using paired-comparisons *t*-test. Sample size (*n*) is the number of nests observed

Brood size	n	Food items/brood/h			Food items/trip	
		Male	Female	Both sexes	Male	Female
Small broods (2-3 nestlings)	8	2.7 (0.3)	2.1 (0.3)	4.8 (0.4)	2.0 (0.3)	1.7 (0.2)
Large broods (4-5 nestlings)	15	3.5 (0.3)	3.1 (0.4)	6.6 (0.5)	1.7 (0.2)	1.5 (0.1)*
Statistic ^a		2.0	1.8	2.4	0.2	1.4
P value		0.06	0.08	0.03	0.9	0.2

^a *T* values except for food items/trip which is *Z* value from Wilcoxon 2-sample test (normal approximation)

items per trip than females (male: 1.9 ± 0.1 , female: 1.6 ± 0.1 , paired-comparisons *t*-test, $t = 2.7$, $n = 24$, $P = 0.01$). When the sexes were compared within each nestling age and brood size class, males delivered a greater number of food items per trip than females to 0-2 and 3-5 day-olds (Table 1), and to large broods (Table 2).

No significant difference in the number of feeding trips was found between the sexes for the entire nestling period (male: 0.66 ± 0.05 , female: 0.53 ± 0.06 , paired-comparisons *t*-test, $t = 1.9$, $n = 24$, $P = 0.07$), but when each class was examined separately, males made more feeding trips than females to 0-2 day-olds (Table 1). No other intersexual differences were found within the other classes (Tables 1 and 2).

For the whole nestling period, males and females delivered food items of approximately the same size (paired-comparisons *t*-test, $t = 0.5$, $n = 24$, $P = 0.64$) and type (Wilcoxon's signed-ranks test; orthopterans: $Z = 0.65$, $n = 24$, $P = 0.5$; arachnids: $Z = 0.4$, $n = 24$, $P = 0.7$; coleopterans: $Z = 1.1$, $n = 24$, $P = 0.3$; lepidopteran larvae: $Z = 1.1$, $n = 24$, $P = 0.3$; lepidopteran adults: $Z = 1.8$, $n = 24$, $P = 0.1$). When the sexes were compared for 0-2 day-old nestlings, however, males delivered a greater percentage of lepidopteran larvae ($Z = 1.9$, $n = 8$, $P = 0.04$) and females delivered a greater percentage of orthopterans ($Z = 2.5$, $n = 8$, $P = 0.01$). No other significant intersexual differences were found within the other age or broodsize classes.

Only females brooded young but both sexes shaded and guarded nestlings. For the entire nestling period, females spent significantly more time at the nest than males (females: $34\% \pm 0.05$, males: $15\% \pm 0.02$, paired-comparisons *t*-test, $t = 4.2$, $n = 24$, $P = 0.0004$). Within each nestling age and brood size class, females spent more time at nests than males within all classes except the 6-9 day-old class, where there was no difference (Fig. 1C, D).

DISCUSSION

Effects of nestling age.—As in other passerines (Bédard and Meunier, 1983; Breitwisch *et al.*, 1986; Grundel, 1987), Bachman's sparrow parents increased food mass delivery as nestlings aged, especially during the first two thirds of the nestling period when most growth occurred (Haggerty, 1986). This overall food increase was achieved somewhat differently by the sexes. Males increased their food delivery primarily by increasing item size. The number of items males delivered remained relatively constant throughout the nestling period because their feeding rate and the number of items they delivered per trip were not significantly altered. A similar positive relationship between nestling age and food size has been reported in some species (Willson, 1966; Morehouse and Brewer, 1968; Best, 1977; Johnson

TABLE 2.—Extended

Feeding trips/brood/h			Food size (mm)		
Male	Female	Both sexes	Male	Female	Both sexes
1.6 (0.2)	1.3 (0.2)	2.9 (0.3)	14.9 (1.5)	14.6 (1.4)	14.7 (1.4)
2.1 (0.2)	2.4 (0.3)	4.5 (0.4)	16.0 (0.9)	16.1 (0.6)	16.0 (0.7)
2.3	2.7	3.1	0.7	1.1	0.7
0.04	0.01	0.01	0.5	0.3	0.5

and Best, 1982; Bédard and Meunier, 1983; Knapton, 1984; Moreno, 1987), but not in others (Royama, 1966; Biermann and Sealy, 1982).

Bachman's sparrow males may have altered their food selection habits to increase item size. They fed a greater proportion of lepidopteran larvae (smaller foods) during the 1st 3 days of the nestling period, while orthopterans and ground spiders (larger foods) were fed in greater proportions (although not significantly) after that period. Changes in item size and in diet composition as broods age has been described for other species (Willson, 1966; Moreno, 1987; Meunier and Bédard, 1984). Although males may have changed their food selection habits in response to increasing energy demands of growing nestlings, inability of newly hatched young to swallow and digest certain foods (Best, 1977; Fagerstrom *et al.*, 1983), and changes in food availability during the nestling period (Pinkowski, 1978; Wittenberger, 1982; Meunier and Bédard, 1984), could also have had an effect. In addition, nestlings, as they develop, could require changes in their diet to receive required nutrients (Carlson and Moreno, 1986; Moreno, 1987).

Females increased their food mass delivery with nestling age by increasing the overall number and size of food items delivered. The increase in item number was due to an increase in feeding rate while maintaining a relatively constant number of items delivered per trip. Numerous studies have documented increased feeding frequency with nestling age (*e.g.*, Nolan, 1978; Pinkowski, 1978; Walsh, 1978; Wittenberger, 1982; Heagy and Best, 1983; Grundel, 1987; Moreno, 1987; Wolf *et al.*, 1990). The increase in food delivery with nestling age by females was probably closely linked with their reduced attentive time during the same period (Fig. 1A, C). As the young aged and became more homeothermic, females spent less time brooding, shading and guarding young, and more time foraging and feeding nestlings. This apparent conflict between meeting the attentive and nutritional needs of young nestlings has been noted by others (Best, 1977; Johnson and Best, 1982; Bédard and Meunier, 1983; Grundel, 1987; Wolf *et al.*, 1990).

Although males did increase their delivery of larger food items as nestlings aged, they did not deliver more items per trip or make more trips. This could indicate that males were working close to their maximum rate and that the increase in the number of feeding trips and food size by females during the later half of the nestling period may have been critical for normal nestling growth and survival (Table 1).

Effects of brood size.—Brood size also affected parental behavior of Bachman's sparrow. Unlike some species in which large broods received less food per nestling than small broods (Best, 1977; Johnson and Best, 1982; Carlson and Moreno, 1986; Grundel, 1987), nestlings from large broods received roughly the same amount of food as nestlings from small broods (*see also* Wolf *et al.*, 1990). This lack of disparity between brood sizes was due to both sexes

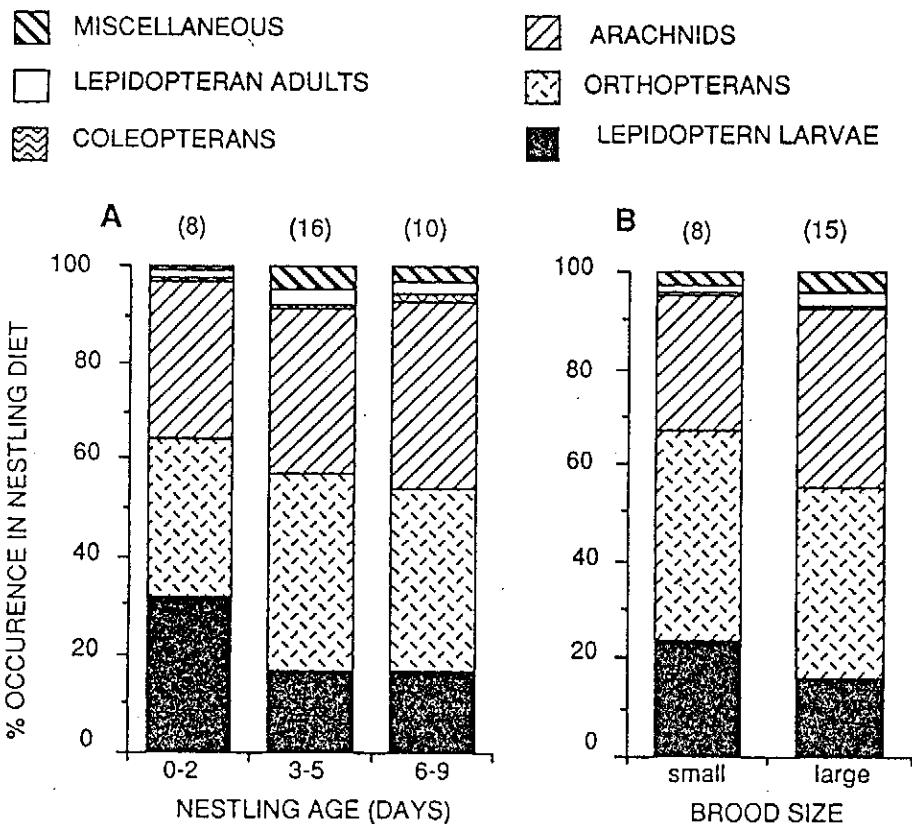


FIG. 2.—Diet composition delivered to nestlings of three age classes (A), and two brood size classes (B) by both male and female adults. Numbers in parentheses (n) are number of nests observed

increasing the number of food items they delivered. This was accomplished by increasing their feeding frequency, not by increasing the number of items delivered per trip. Others have found a similar relationship between feeding frequency and brood size in passerines (Royama, 1966; Morehouse and Brewer, 1968; Best, 1977; Johnson and Best, 1982; Wittenberger, 1982; Moreno, 1987), but some investigators have found no relationship (Seel, 1969; Pinkowski, 1978; Knaption, 1984). Although this lack of a relationship could be due to larger brood nestlings requiring less food owing to their lower surface-to-volume ratio (Royama, 1966; Mertens, 1969; Seel, 1969), caution seems warranted in using this explanation since feeding frequency alone is not a reliable measure of parental food contribution (Walsh, 1978; Bédard and Meunier, 1983; Grundel, 1987). Although both parents increased the size of foods they fed to larger broods and this increase probably affected food mass delivery, the difference between the two brood sizes was not significant. Unlike some species (Meunier and Bédard, 1984), brood size had no effect on the types of food items fed to nestlings.

Bachman's sparrow parents, especially females, spent more time at small brood nests than at large brood nests. This dissimilarity in parent attention time between brood sizes

could be due to differences in food requirements and surface-to-volume ratios between nestlings of the two brood sizes. Smaller broods required less food and therefore parents could spend more time brooding, shading and guarding small brood nestlings. It is interesting to note, however, that no difference in nesting success (*i.e.*, nests that fledged at least one young) was found between the two brood size classes (Haggerty, 1988). In addition, large brood nestlings had a reduced surface-to-volume ratio and therefore possibly required less brooding (Ricklefs, 1983).

Relative parental care and conclusions.—As predicted for monogamous species, both Bachman's sparrow parents contributed substantially to nestling care (Emlen and Oring, 1977). Although both sexes delivered roughly the same food mass, female nest attentive time was substantially greater. This difference in attentive time can be attributed to the fact that only females had a brood patch and brooded young. The disparity in nest attentive time between the sexes could explain why males tended to deliver more items to nestlings than females. Because of their greater nest attentiveness, females could have reduced the time spent foraging. In addition, since female foraging time is limited by the attentive needs of the young, their reduced number of items per trip could be due to their eating collected food items to take care of their own nutritional needs (Grundel, 1987). Females may have compensated for this reduced number in food items by selecting larger items. Moreno (1987) attributed a gender difference in food items per trip to a difference in bill size, but no bill size difference was found for Bachman's sparrows (Haggerty, 1986).

It has been suggested that under conditions when nestlings require less care (*e.g.*, when broods and young are small), males may reduce their relative contribution, allowing more time and energy to pursue additional matings (Westneat, 1988; Carey, 1990). This was not the case for Bachman's sparrow males. Males delivered more food than females during the first third of the nestling period and there was no difference in relative food contribution between the sexes between brood size classes (Fig. 1, Tables 1 and 2). This lack of reduction in male care could have been due to a low probability of extrapair matings and/or a potential increase in the proportion of young dying if male care was reduced (Westneat, 1988). If females must increase their feeding contribution because of a reduction in male care, then nestlings will be left unattended for longer periods of time, possibly increasing the chance of predation and exposure to temperature extremes. Although recent experiments with dark-eyed juncos (*Junco hyemalis*) found no difference in entire brood loss to predators between female-only broods and broods with male assistance, female-only broods did sustain a greater partial loss due to exposure and starvation (Wolf *et al.*, 1988; *see also* Ricklefs, 1983). In addition, females that must expend more energy collecting food due to a reduction in male care, may have fewer reserves for re-nesting attempts after nest failures or successful nests. Although I found evidence that females could raise a brood independently (*pers. observ.*), a female selecting an unmated male that will contribute substantially to nestling care may be able to attempt more nests, have greater annual and lifetime fecundities, and a greater reproductive success than an unaided or poorly assisted female. Recent studies provide evidence that aided females do have greater reproductive success than unaided females (Arcese, 1989; Wolf *et al.*, 1990; Webster, 1991).

Finally, the presence of bachelor and floating males in my study area indicates a possible male-biased breeding-adult sex ratio (Haggerty, 1988). This could have allowed females the option to desert males that reduce their care and select new mates (Breitwisch *et al.* 1986). Although I found no evidence of female desertion in my study, the threat of desertion could have also contributed to the substantial contribution of Bachman's sparrow males to nestling care.

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