

## **Behavioural response of female dark-eyed juncos to the experimental removal of their mates: implications for the evolution of male parental care**

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**Abstract.** Male dark-eyed juncos, *Junco hyemalis*, are monogamous and normally help females feed nestlings. We removed males at hatching of their eggs and examined female parental behaviour in response to male removal. We compared parental behaviour of unaided females (experimentals) with that of (1) females aided by their mates (control females) and (2) females and their mates working together (control pairs). Unaided females fed their young at least twice as often as did aided females and as often as the combined efforts of pairs. The increased rate of food delivery by unaided females was accompanied by a decrease in time brooding the young and an increase in the amount of time the female's nest was unattended, suggesting that feeding and brooding are competing parental behaviours. Feeding rates of both unaided females and pairs increased as brood size increased, but the response to brood size was stronger in unaided females than in either aided females or pairs. An earlier study indicated that, despite their compensatory feeding rates, unaided females experienced greater partial brood loss than did pairs. Perhaps males bring more food per feeding trip, or food of a different quality. It seems likely that males can improve fledging success by bringing food to the young, both during the early nestling stage when brooding is crucial and also later, during the period of rapid growth.

Biparental care is a common pattern of reproduction in many bird species but is relatively uncommon in other vertebrates (Perrone & Zaret 1979; Gittleman 1981; Kleiman & Malcom 1981; Wells 1981; Møller 1986). Because the sharing of parental care is prevalent in birds, it was generally assumed that in most avian species two parents are necessary for successful reproduction (Lack 1968). However, recent experimental studies have shown that many female passerines whose mates were removed were able to raise at least some young to the nest-leaving stage (hereafter referred to as fledging), often producing fledglings of comparable number and mass as two parents produce when working together (Richmond 1978; Gowaty 1983; Greenlaw & Post 1985; Wolf et al. 1988). This apparent ability to dispense with male assistance led us to ask how females alter their behaviour facultatively when they lose their mates. Elucidation of female responses to the absence of male help will improve our understanding of why male parental care is so prevalent among passerine birds.

In a previous paper (Wolf et al. 1988) we reported removal of male dark-eyed juncos, *Junco hyemalis*, at the time their eggs hatched, and we compared the growth and survival of young in female-only broods and in control, two-parent broods. Juncos are typically monogamous passer-

ines in which only females incubate and brood, but the sexes share about equally in feeding the young (Hostetter 1961; this study). We found that only about 2% of experimental females deserted their nests (a rate no higher than among mated females) and that, unless a brood was lost entirely to predators, unaided females were always able to raise at least one young to fledging. Some unaided females raised full broods, and in these cases their nestlings grew in mass as much as nestlings in broods raised by pairs. In contrast, nestlings from female-only broods in which one or more young were lost to starvation or piecemeal predation were lighter than nestlings in comparably reduced broods of two parents and also than nestlings in intact broods.

In this paper we compare the feeding rate of unaided females, of female members of pairs (aided females), and of male and female members of pairs combined. In order to compensate fully for the absence of the male, a female would have to increase her feeding rate without decreasing the time devoted to other activities, such as brooding or watching for potential predators. Since this is probably impossible and some compromise among competing activities would be predicted, we also compare the time spent brooding by unaided and aided females and the amount of time experimental

and control nests were probably out of the sight of any parent. We would expect the likelihood of nest predation to be greater when nests were unattended.

## METHODS

### Species and Location

The study was conducted from early May to mid-August, 1983–1986, at the University of Virginia's Mountain Lake Biological Station in the Appalachian Mountains of southwestern Virginia (see Wolf 1987 for description of the study site).

Juncos normally form monogamous mating associations and, if no nests are lost to predators, pairs commonly raise two broods per season in this population (Hostetter 1961; Wolf et al. 1988). Clutch size is three, four or rarely five eggs. Males typically take over the care of dependent fledglings when females begin incubating a second clutch. When a male is removed or disappears from his territory, a new male usually replaces him within a few hours or days, takes over the territory, and follows and courts the female but usually ignores the young of his predecessor.

### The Sample

We studied nests throughout the breeding season. Adults were caught with mist nets and in Potter traps baited with corn and millet. Each adult was ringed with United States Fish and Wildlife Service aluminium rings and a unique combination of coloured plastic leg rings.

Pairs were divided into an experimental and a control group. Experimental males were captured on the day their eggs hatched ( $N=16$  broods) or within the following 2 days ( $N=9$  broods) and were held until the end of the breeding season. Control males were allowed to remain with their mates and young ( $N=22$  broods). Controls included pairs whose nests were found before the fourth day after hatching of the young. We originally assigned birds to a treatment group by matching pairs as closely as possible for hatching date, brood size and habitat (forest, roadside edge and clearings), but so many broods were lost to predators that it became necessary to group broods within each treatment for analysis.

In five cases the male parent either disappeared before his brood hatched or he did not feed the

nestlings. We treated these cases as experimental, which increased the number of experimental broods to 30. In one experimental brood the replacement male began to feed the female's young on their ninth day of life (hatching day = day 0). We therefore included this nest in the experimental group before day 8 but omitted it following the onset of care by the replacement male because such males may not behave like true fathers. The numbers of experimental and control nests observed in each of the 4 years of the study were: 1983, two experimentals, zero controls; 1984, six experimentals, six controls; 1985, 10 experimentals, 11 controls; and 1986, 12 experimentals, five controls. Because the parental behaviour of males and females varied with the weather, behavioural variation among years, if there was any, was overridden by the high within-year variation. Statistical differences in behaviour among years either were not significant ( $P > 0.05$ ), or annual samples were too small to compare.

Using binoculars, we observed experimental and control nests from day 0 until either nest destruction or fledging of the young (day 11 or 12). Observers sat in the open 20 m or more from the nest, in a car, or in a portable blind about 15–20 m from the nest. Parental behaviour varies greatly with hour of day among many small birds (Nolan 1978), including juncos. To control for this variation, nests were observed between 0600 and 1200 hours Eastern Standard Time for a period of 1–2 h in all weather except steady rain. The duration of the watch was decided in advance and therefore was not influenced by the behaviour observed. Nests were inspected at the termination of each observation, and the number of young was recorded.

The number of feedings by each parent and the time the female spent brooding were recorded in all years (Table 1). Because parental behaviour changes with age of the nestlings (e.g. delivery of food increases with nestling age), we divided the nestling period into three age intervals and treated each interval as a separate test in which experimentals and controls were compared. The three age intervals were: days 0–3 (interval 1), days 4–7 (interval 2) and days 8–11 (interval 3). For cases in which a brood was observed more than once during an interval, we averaged the data within that interval so that each brood provided one independent case.

Both male and female juncos frequently perch

**Table I.** Number of observations in which feeding rate was recorded for experimental (female-only) and control (two-parent broods), according to three nestling age increments and to brood size at the time of the observation

Brood size	Experimental broods				Control broods			
	Nestling age			% of total observations	Nestling age			% of total observations
	Day 0-3*	Day 4-7	Day 8-11†		Day 0-3	Day 4-7	Day 8-11†	
2	5	11	11	28	1	1	0	05
3	3	14	6	24	5	3	5	30
4	17	22	7	48	11	10	7	65
Total	25	47	24	96	17	14	12	100

\* Day 0: hatching day of first egg.

† Broods usually fledged on day 11 or day 12; the designation of day 11 here indicates fledging day.

above the nest, evidently guarding it and attacking predators such as eastern chipmunks, *Tamias striatus*, that approach (usually driving chipmunks away). In 1985 and 1986 we recorded unattended time, i.e. time during which we could not detect any parent near the nest. We may have overestimated this measurement if an unseen parent was in fact nearby. On some watches, feeding rate, brooding time, unattended time or some combination of these could not be confidently determined because the nest or its vicinity was not in full view. In these instances, data for the incompletely observed behaviour were omitted from the analyses, causing differences in sample sizes among some variables.

### Analyses

To compare feeding rates between treatment groups, we calculated (1) the number of feeding visits to the nest per hour (the per-brood rate) and (2) the number of feeding visits per nestling per hour (the per-caput feeding rate). Using two-tailed Mann-Whitney *U*-tests, we compared feeding rates of unaided females within each age interval with those of (1) aided, control females and also of (2) the combined efforts of control pairs working together. Using two-tailed *t*-tests, we also compared the percentage of time that unaided and aided females spent brooding and the percentage of time the nest was unattended by any parent. Percentage data were arcsine transformed (Sokal & Rohlf 1981). The transformed data met the assumptions of *t*-tests.

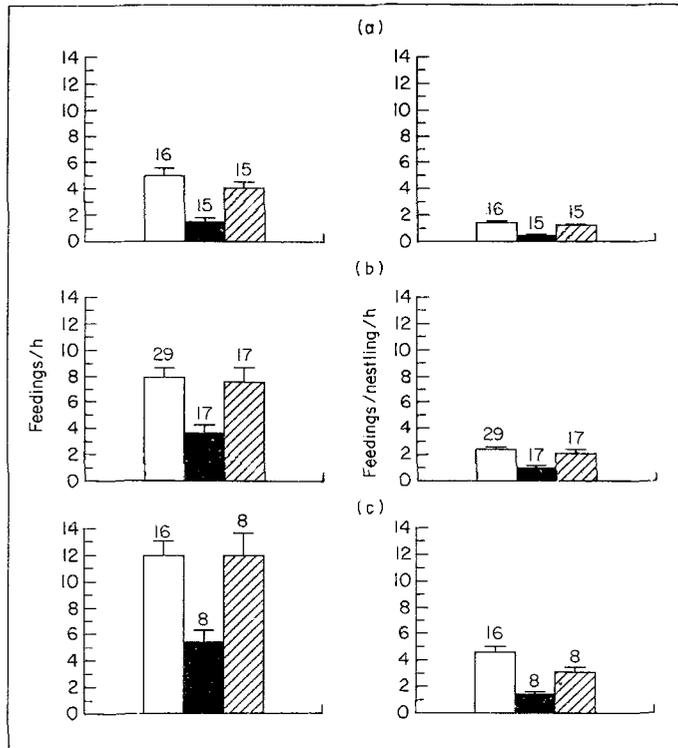
We also investigated the effect of brood size on parental behaviour. If females raising small broods are able to compensate fully for the absence of males but those raising larger broods are not, then selection might act on males to contribute parental care only when raising larger broods. In order to investigate whether the female's response to male removal was dependent on brood size, we regressed feeding rate on brood size within each treatment group, including nestling age as a variable in the regression (Nie et al. 1975; Hull & Nie 1981). Data were square-root transformed and met the assumptions of parametric tests. Brood size was the number of young present in a nest during each watch. To assure independence of cases, we selected only one watch per nest. Watches were chosen by matching age as closely as possible between experimental and control broods within the year of observation. For depiction (Figs 4 and 5), we present data according to nestling age interval. Sample sizes were too small for statistical comparisons of parental behaviours among brood sizes within nestling age intervals.

## RESULTS

### Feeding Rates, Brood Sizes Combined

#### *Unaided versus aided females*

When data from all brood sizes are combined, unaided females made significantly more feeding trips to the nest than did aided females during all three nestling age intervals (Fig. 1,  $P < 0.001$ ). The feeding rate of unaided females in interval 1 was



**Figure 1.** Mean per-brood (left side) and per-caput (right side) feeding rates of unaided females (□), aided females (■), and the combined efforts of pairs working together (▨) during the three nestling age intervals. (a) Interval 1, day 0 (=hatching day)-3. (b) Interval 2, day 4-7. (c) Interval 3, day 8-11 (fledging day). Number of observations in the sample are shown in each bar. Vertical bars indicate 1 SE. See text for statistics.

5 feedings/h, in contrast to the rate of aided females, which was only 1.5 feedings/h. In interval 2, the respective rates were 7.9 feedings/h and 3.6 feedings/h, and in interval 3, 11.9 feedings/h and 5.4 feedings/h. The per-caput feeding rate in each nestling age interval was also significantly greater for unaided than for aided females (interval 1, 1.4 feedings/nestling/h versus 0.44 feedings/nestling/h; interval 2, 2.4 feedings/nestling/h versus 1.0 feedings/nestling/h; interval 3, 4.6 feedings/nestling/h versus 1.4 feedings/nestling/h;  $P < 0.0001$ , Fig. 1). Thus, unaided females increased their feeding rates to at least double those of females with male help, even when the needs of the nestlings increased with age.

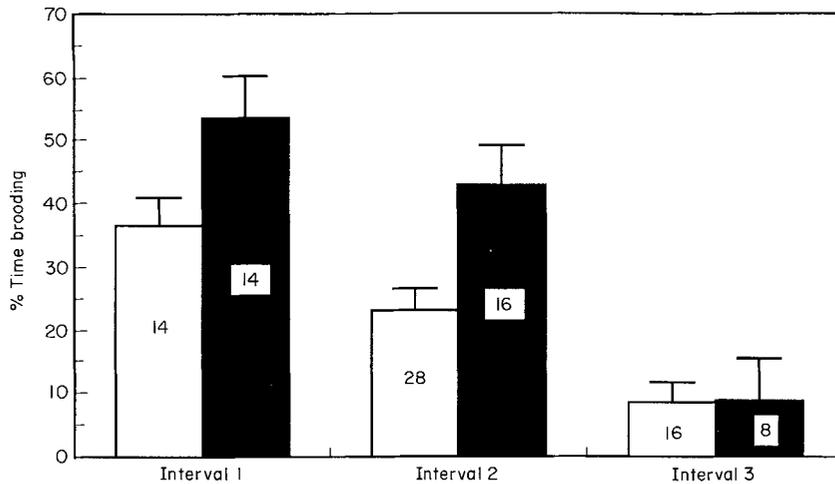
#### *Unaided females versus pairs*

When feeding rates of unaided females were compared with feeding rates of pairs working together, with brood sizes combined, there were no

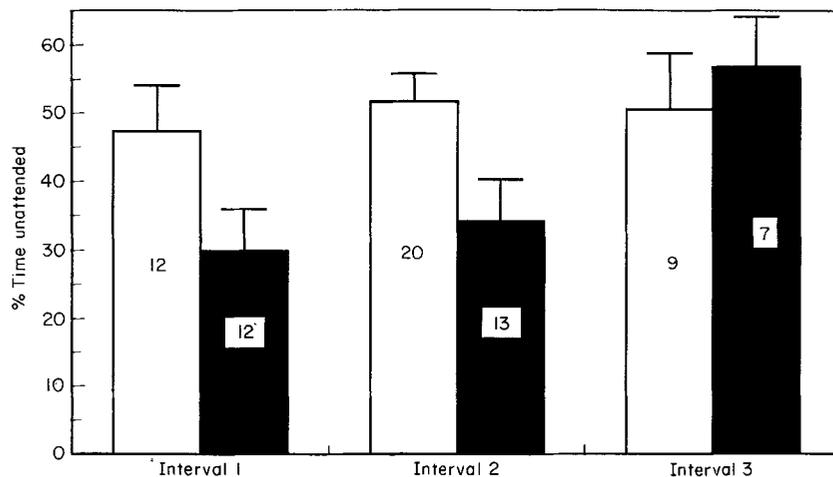
differences in either the per-brood or the per-caput rates in any age interval (Fig. 1,  $P > 0.08$ ). The rates of unaided females (see preceding section) should be compared with the following rates of combined male and female control pairs: per-brood feeding rate, interval 1, 4.1 feedings/h, interval 2, 7.6 feedings/h, and interval 3, 11.9 feedings/h; per-caput feeding rate, interval 1, 1.2 feedings/nestling/h, interval 2, 2.1 feedings/nestling/h, and interval 3, 3.1 feedings/nestling/h. Therefore, by working at least twice as hard as females with mates, females without mates were able to compensate fully in frequency of feeding trips to the nest.

#### **Brooding and Nest Attendance**

When brooding was analysed according to the three nestling age intervals, unaided females brooded only 68 and 54% as much as aided females during the first two intervals, respectively, but thereafter they did not brood less than aided



**Figure 2.** Mean percentage of time spent brooding by unaided (□) and aided (■) females during each of the three nestling age intervals. See text for statistics.



**Figure 3.** Mean percentage of time during which no parent was in the nest vicinity during each of the three nestling age intervals. □: unaided females; ■: the combined behaviour of aided females and their mates. See text for statistics.

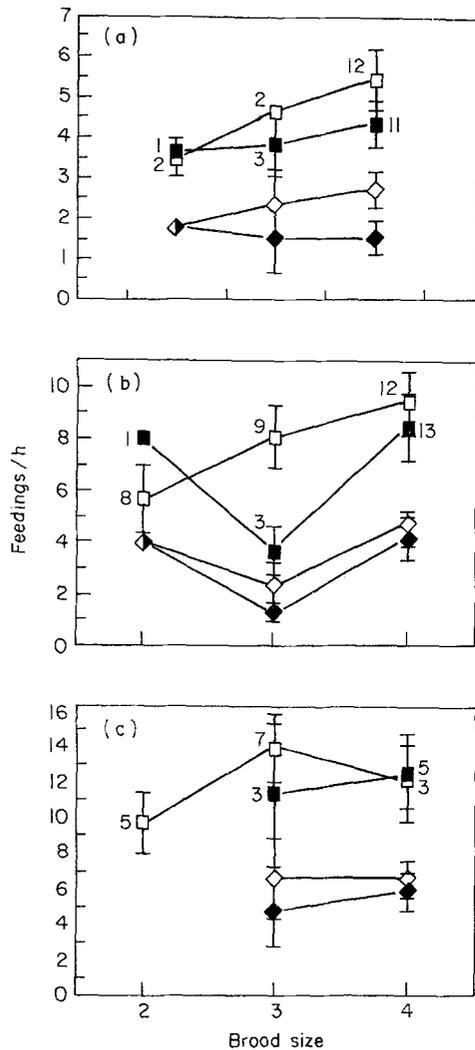
females (Fig. 2). In interval 1 unaided females brooded 37% of the time, whereas aided females brooded 53% of the time ( $P=0.053$ ); in interval 2 the respective percentages were 23 and 43% ( $P=0.02$ ); and in interval 3 they were 8 and 9% ( $P>0.9$ ).

The percentage of time the nest was unattended by any parent (Fig. 3) in interval 1 was 47% for experimental broods, whereas control broods were

left for 30% of the time ( $P=0.10$ ). In interval 2 the respective figures were 52 and 34% ( $P=0.017$ ), and in interval 3 they were 51 and 58% ( $P>0.50$ ).

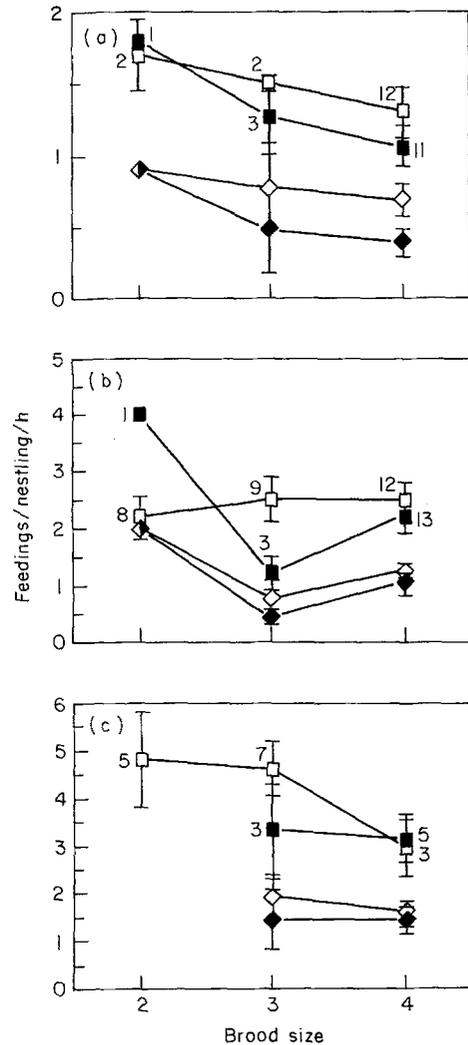
#### Effect of Brood Size on Feeding Rate

Since time devoted to foraging and to delivering food probably increases with brood size, we asked whether unaided and aided females responded



**Figure 4.** Mean per-brood feeding rates of unaided females (□), aided females (◆), males (◇) and combined efforts of pairs working together (■) for brood sizes of two, three and four during each of the three age intervals. Number of observations is shown at each point. For controls, sample size is shown on the curve for pairs working together. Vertical bars represent 1 SE. (a) Interval 1; (b) interval 2; (c) interval 3.

differently as number of nestlings increased. There were many more experimental than control broods of two young, making direct comparison of treatment groups impossible. Therefore, for each treatment group we performed linear regressions with



**Figure 5.** Mean per-caput feeding rates of unaided females, aided females, males and pairs working together for brood sizes of two, three and four during each of the three nestling age intervals. Data and symbols as in Fig. 4.

both brood size and nestling age as independent variables (see Methods).

Unaided females made more per-brood feeding trips when feeding larger than smaller broods (Fig. 4;  $P=0.001$ ), consequently similar numbers of per-caput trips (Fig. 5;  $P>0.5$ ). Aided females did not significantly alter either their per-brood or per-caput feeding rate with increased brood size

(Figs 4 and 5; per-brood rate,  $P > 0.15$ ; per-caput rate,  $P > 0.8$ ). However, when the rates of pairs are considered, there was a strong tendency to increase the per-brood feeding rate with brood size ( $P > 0.06$ ). The per-caput rate of pairs together did not change with increased brood size ( $P > 0.7$ ). The absence of a significant correlation of per-brood feeding rate and brood size in control pairs may be due to the small number of broods of two that were raised by pairs.

In sum, our results show that unaided females worked harder when raising larger broods than did aided females. Unaided females raised broods of two more often than did aided females, but even when feeding such reduced broods, unaided females worked at least as hard as aided females feeding broods of three and four. In addition, individual young in large broods were fed as often, on average, as individuals in smaller broods, regardless of whether they were being tended by one parent or two.

## DISCUSSION

Unaided dark-eyed junco females compensated for the lack of a male by making as many feeding trips to the nest as pairs working together. However, quantity or quality of the food delivered by males and females may not be equal (Martin 1974; Nolan 1978, pp. 269–270; Weatherhead 1979; Biermann & Sealy 1982; Bédard & Meunier 1983; Carlson & Moreno 1986; Sasvári 1986; Jones 1987; Lyon et al. 1987); if so, doubling the feeding rate may not have compensated fully for the male's absence. The increase in feeding by unaided females was accompanied by a decrease in brooding time, and the combination of these alterations may have been the cause of slower growth and lower survival of the nestlings in some broods (Wolf et al. 1988). The fact that experimental females increased their feeding rates even though replacement males were present on their territories indicates that female juncos respond directly to the demands of the young rather than to the presence of a male (Bengtsson & Rydén 1983; Sasvári 1986; Hüssel 1988; compare with Silverin 1980).

Increase in female feeding rate in the absence of the male has been found to be fully compensatory in some bird species in which males normally care for the young (house sparrows, *Passer domesticus* (Schifferli 1976); prairie warblers, *Dendroica disco-*

*lor* (Nolan 1978: Table 85 and page 263); savannah sparrows, *Passerculus sandwichensis* (Weatherhead 1979); song sparrows, *Melospiza melodia* (Smith et al. 1982), but only partly so in others (pied flycatchers, *Ficedula hypoleuca* (Alatalo et al. 1982); tree swallows, *Tachycineta bicolor* (Leffelaar & Robertson 1986); blue tits, *Parus caeruleus*, and great tits, *P. major* (Sasvári 1986); snow buntings, *Plectrophenax nivalis* (Lyon et al. 1987); black-billed magpies, *Pica pica* (P. Dunn & S. Hannon, personal communication)). Studies of fish in which both parents care for the young have also shown (appropriate) compensatory changes in parental behaviour after removal of a mate Rechten (1980; Mrowka 1982).

Females of bird species in which males do not usually feed young have exhibited different patterns. In the polygynous redwinged blackbird, *Agelaius phoeniceus*, and marsh wren, *Cistothorus palustris*, in which males feed the young facultatively, females do not significantly increase their feeding when unaided (Patterson 1979; Muldal et al. 1986; Leonard & Picman 1988; K. Yasukawa, unpublished data). Male pied flycatchers are often bigamous and normally assist only the primary female. A study (Silverin 1980) in which males were injected with testosterone (T) resulted in a significant decrease in their feeding rate, but monogamous and primary mates of testosterone-injected males did not compensate by increasing their feeding rate. Secondary females fed significantly more often than both monogamous (therefore, assisted) and primary assisted females. The reason for differences in female response to absence of a helping male both within and among species is not clear. Comparative study of the reproductive investment strategies of both the male and female among polygynous and monogamous bird species (or populations) might provide insight into factors underlying the variation in female responses.

### Brooding and Absence from Nest Vicinity

The relative decrease in brooding by experimental females during the first two age intervals probably occurred because they were forced to devote more time to foraging. Because time spent brooding decreases substantially late in the nestling period, after the nestlings are able to thermo-regulate, the similarity in brooding by experimental

and control females during the late nestling period is not surprising.

Feeding and brooding behaviour of unaided females were negatively correlated. Because males of some altricial bird species have been observed to feed very young nestlings more than females do, i.e. when females spend greater time brooding, it has been suggested that brooding and feeding compete for the female's time and energy (Moreau 1947; Royama 1966; Seel 1969; Johnson & Best 1982; Wittenberger 1982; Fagerström et al. 1983; McGilivray 1984; Carlson & Moreno 1986; Martin 1987). Our results are in accord with this view. Male juncos often bring food to the young while the female broods, especially when the nestlings are young and/or during inclement weather when the female tends to spend more time on the nest (personal observation). Thus, male assistance probably enables the female to brood when it is necessary (compare prairie warblers, Nolan 1978, pp. 263–264).

A decrease in brooding by unaided females has also been found in pied flycatchers (Alatalo et al. 1982), savannah sparrows (Weatherhead 1979) and prairie warblers (Nolan 1978, pp. 252–263), but brooding did not change in unaided female black-billed magpies (P. Dunn & S. Hannon, personal communication) and actually increased in song sparrows (Smith et al. 1982).

The reason experimental nests were left unattended more than control nests during the first two age intervals is most probably because aided females brooded more. Later, however, when brooding had decreased, the high food demands of the young probably required increased foraging, resulting in longer periods of absence from the nest vicinity by parents in both treatment groups. Not only can prolonged absence from the nest result in exposure of nestlings and thus in their decreased growth or even death (see Ricklefs 1983), but it also probably increases the risk of predation. Since juncos are sometimes able to prevent predation by small predators such as chipmunks, male parental care in the form of nest guarding may apparently reduce the likelihood of partial brood loss (but see Wolf et al. 1988).

#### **Influence of Brood Size on Feeding Rate**

Unaided females and pairs working together increased their per-brood feeding rates with brood size, but aided females, almost all of whose broods

numbered three or four, did not do so. Although the elevation of the feeding rate of large broods was greater in experimental females than in control pairs together, young of control pairs were nevertheless heavier at fledging and suffered less starvation (Wolf et al. 1988). If these differences were not due to chance, they suggest that unaided females brought less (or inferior) food per trip to the nest.

Per-caput feeding rates of unaided females, aided females and pairs together did not change significantly as brood size increased. As a result, nestlings in large and small broods were fed equally often, regardless of treatment group.

The findings that unaided females fed large broods more often than they fed small broods, and that this rate equalled or exceeded that of pairs together, may largely explain why some experimental females were able to raise full broods to fledging age. The ability of some females to raise large broods without male help may depend on several factors, such as age, condition, experience and territory or habitat quality (Perrins & Moss 1974; Carey & Nolan 1975; Martin 1987; Lifjeld 1988), all of which may affect a female's efficiency and the amount of energy she can invest in a brood. Some females may work at their maximum capacity but still be unable to rear the full brood to fledging (e.g. Smith et al. 1982; Leffelaar & Robertson 1986), while others are successful in doing so.

#### **Parental Investment of Unaided Females**

Do normally aided females work at maximum capacity, or do they conserve energy while the male contributes the remaining care? In dark-eyed juncos it appears that aided females do not work at their maximum capacity. Our data indicate that females can invest more than they usually do. However, the higher incidence of partial brood loss and lower mean mass of nestlings in experimental broods (Wolf et al. 1988) suggest that compensation in feeding rate alone is not sufficient to make up for the absence of the male.

How might the extra effort of unaided female juncos affect their fitness? They may incur delayed costs in the form of higher mortality or decrease in future reproduction (Williams 1966; Kluyver 1970; Trivers 1972; Askenmo 1979; Bryant 1979; Gowaty 1983; Nur 1984), although our data to date do not support this possibility (Ketterson et al., unpublished data). Further work is needed to assess these

potential long-term costs, which may enable us to evaluate more fully the effect of the male's care on both his own and his mate's lifetime fitness.

### ACKNOWLEDGMENTS

We wish to thank Krissy Bruner, Laura Ziemer, Charles Ziegenfus, Ken Jones, Adrienne Massey and Braven Beaty for the special help they provided. Many researchers, post-doctoral fellows and graduate students at Mountain Lake Biological Station kindly contributed ideas and help that made the project run more smoothly. We also thank the Mountain Lake Resort Hotel and several of its employees for kindly allowing us the use of their land: F. Stanford Foutz, J. W. McMillin, Bill Kenney and Mike Surtoski. M. A. Sydlik and an anonymous referee made helpful comments on the manuscript. This project was supported by the Herbert and Betty Carnes Research Award, the Frank M. Chapman Memorial Fund, the Josselyn Van Tyne Award, Sigma Xi Grant-in-Aid of Research, Indiana Academy of Science Research Grants, Mountain Lake Biological Station Pre-doctoral Research Fellowship, summer fellowships from the Department of Biology at Indiana University, Indiana University graduate Grant-in-Aid of Research Award, BRSG Grant S07 RR07031 by the Biomedical Research Support Grant Program and NSF BRS-87 18358.

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(Received 5 October 1988;  
initial acceptance 8 December 1988;  
final acceptance 13 February 1989;  
MS number: A 5401)