FEMALE CONDITION AND DELAYED BENEFITS TO MALES THAT PROVIDE PARENTAL CARE: A REMOVAL STUDY

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ABSTRACT.—In Dark-eyed Juncos (*Junco hyemalis*), we have shown that male participation in care of the young usually has a small effect on the number of nestlings that leave the nest and markedly improves survival of fledglings to the age of independence. Here we ask whether male participation also improves male reproductive success by enhancing female condition for future reproductive efforts. We captured males when their eggs hatched, then released one group immediately (controls) and held the other group (experimentals). The mates of experimental males were therefore deprived of help in rearing their broods. Removed males were quickly replaced by new males, which rarely fed the young of the experimental males but usually mated with the experimental females for later nesting attempts. We compared experimental (unaided) and control (aided) females for differences in the potential costs of their respective reproductive efforts. As measures, we used percent loss of mass during the nestling period and absolute mass at nest-leaving. Mass was regarded as a potential correlate of physical condition that might affect subsequent reproductive success. We also considered whether aided and unaided females were equally likely to attempt a subsequent brood and whether subsequent broods were produced equally rapidly and were of similar quality.

When data were combined over years and across brood sizes, unaided females lost more mass and weighed less when their young left the nest. However, the differences were significant in only one year. Unaided females that raised large broods lost more mass than those that raised small broods, whereas brood size did not influence mass in aided females. Treatment groups did not differ in the probability of nesting again after producing fledglings. After nest failure, if females renested, the brood interval was 18% (1.3 days) longer for unaided females; after success and rearing of young to independence, the brood interval of unaided females was ca. 21% (3.4 days) longer. Neither difference was statistically significant. In both groups when first-brood nests succeeded, size of the brood was not correlated with the brood interval. Finally, neither number nor mean mass of eggs in the subsequent clutch differed between unaided and aided females.

Even if the greater loss of mass and the somewhat longer brood intervals of unaided females can be interpreted as reflecting poorer physical condition, these apparently had little effect on future reproduction. Instead we suggest that the impact of the absence of male parental care was largely on female success in raising fledglings of the current brood. If so, delayed benefits are not likely to have been important in selecting for paternal behavior in juncos. *Received 5 January 1990, accepted 30 October 1990.*

RECOGNITION that the reproductive interests of the sexes are potentially in conflict (e.g. Davies 1989) has led students of reproductive behavior to question more critically why males in some vertebrate species help their mates care for their young (Trivers 1972, Dawkins and Carlisle 1976, Maynard Smith 1977, Gowaty 1983, Beissinger 1987). The question is especially pertinent to passerine birds, which unlike other vertebrates typically couple monogamy, or apparent monogamy, with biparental care (Lack 1968, Verner and Willson 1969, Møller 1986). At present we assume that sharing of parental care indicates that males achieve higher fitness through this behavior than they would if they pursued some other reproductive option, and we ask in what way this greater fitness might be achieved.

The usual approach to this question has been to assess the extent to which biparental care is necessary to raise any or all young of a single brood. The method is to remove males and compare the reproductive success of unaided and aided females (see Wolf et al. 1988 for review of studies of passerines; also Bart and Tornes

1989, Dunn and Hannon 1989). Any difference in success of the two groups of females is interpreted as the increment normally attributable to male help. In some species, females whose mates were removed raised as many young to nest-leaving (hereafter, fledging) as did pairs (Richmond 1978, Smith et al. 1982, Gowaty 1983, Greenlaw and Post 1985, Wolf et al. 1988). In other species, loss of male parental care lowered reproductive success at fledging but still was not essential to the production of some fledglings (e.g. Weatherhead 1979, Alatalo et al. 1982, Smith et al. 1982, Lyon et al. 1987, Bart and Tornes 1989). Only Dunn and Hannon (1989) found male passerines to be essential to the production of at least one fledgling. In the period of dependence following fledging, the success rate of unassisted females in raising young to independence has been reported for only three passerine species, and even at this stage success did not fall to zero (Greenlaw and Post 1985, Smith et al. 1982, Wolf et al. 1988).

Various studies have explored the relationship between biparental care and the survival of young in the current brood. However, better understanding of the evolution of male parental behavior also requires investigation of possible delayed benefits arising from improved success of subsequent broods (Gowaty 1983). Consequently, we ask whether males that share the work load of rearing young help to maintain the physical condition of females and thereby reduce the cost of reproduction to females and improve their future reproductive success. Obviously the question is relevant to male fitness only if females tend to remate with the same males for subsequent attempts and if females are not easily replaced.

The reason male-removal studies have been slow to address the question of delayed benefits is probably because of the difficulties of obtaining the data. We recognize two such difficulties. First, in open-nesting passerines nest predation is intense (Ricklefs 1969, Nolan 1978), and not all females succeed in rearing even one brood, much less try to raise two. Second, the male-removal method necessarily prevents the female from renesting with her original mate. Only if removed males are quickly replaced, and only if experimental females then form pairs with the replacement males, can the question of delayed benefits be addressed. These conditions appear to be satisfied very rarely.

A breeding population of Dark-eyed Juncos (*Junco hyemalis*) that we studied provided a system well suited for the investigation of delayed benefits by use of the male-removal method, for several reasons. First, pairs usually remain together for the season (Hostetter 1961, Ketterson et al. in prep.) and often for subsequent seasons (Ketterson et al. in prep.). They raise two and occasionally three broods per year, provided predators do not destroy early broods and force renesting; and males help care for nestlings and fledglings. Second, when males are removed experimentally at about the time the eggs hatch, or when males occasionally disappear naturally, females can raise nearly as many young to fledging as pairs working together (Wolf et al. 1988). They accomplish this by doubling the rate of food delivery to nests and reducing the time spent brooding (Wolf et al. 1990). This unusual effort clearly has the potential for affecting female condition and therefore future reproduction and survival (Williams 1966, Charnov and Krebs 1974). Third, the disappearance of a male from his territory is almost always followed within a few hours or, at most, days by the appearance of a replacement male, which takes over the territory but rarely helps the female feed her current young. When the nest succeeds or fails, the female usually mates with the replacement male for her next nest attempt. This provides the requisite opportunity to investigate the effects that the efforts made by unaided females have on their subsequent reproduction. Finally, unlike males, females are not easily replaced. A male that loses his mate usually takes weeks to acquire another, and sometimes he remains unmated for the rest of the season (pers. obs.), which indicates that the sex ratio is probably biased in favor of males. Under these circumstances, in which opportunities for males to acquire replacement females may be few, we would expect any delayed benefits to the male resulting from biparental care to be potentially more important (Maynard Smith 1977).

Loss of condition by an unaided female while she attempted to rear nestlings to fledging or fledglings to independence might lower her success immediately. For example, it might reduce the number or quality of members of her current brood. Alternatively, or in addition, it might have adverse effects on her subsequent broods. Wolf et al. (1988) found that in most

years unaided females and females assisted by males did not differ significantly in number of young fledged from the current brood. However, significantly fewer fledglings of unaided females reached independence. Among fledglings that did reach independence, survival until the following breeding season, as measured by return to the study area, was the same for both treatment groups. Here we focus on whether male help in rearing nestlings affected female condition at fledging. We compared females for loss of mass during the nestling period and at fledging. To determine if any differences in female condition influenced subsequent reproductive success, we compared treatment groups for the probability of renesting, the time elapsed before laying of the first egg, the clutch size, and the mean mass of eggs in the clutch. We predicted that the body mass and subsequent reproductive performance of unaided females would be inferior to that of aided females in some or all of the enumerated variables.

METHODS

Species, location, and sample.—The study was conducted from early May to mid-August, 1983–1986, at the University of Virginia's Mountain Lake Biological Station in the Allegheny Mountains of southwestern Virginia (site described in Wolf 1987). Female juncos build the nest and perform all the incubation and brooding. Clutch size is usually three or four eggs, rarely two or five. Males do approximately half the feeding of nestlings and fledglings (Wolf et al. 1990 and pers. obs.). If there is a second brood, females quit caring for the first brood when they begin incubating the second clutch, and males assume responsibility for the first clutch for the remainder of the period of dependence. The timing of the transition to independence varies somewhat from brood to brood, but we have found that young that survive for 14 days after fledging can care for themselves, and we treat that as the age of independence (Wolf et al. 1988).

We worked with nests begun at all times of the breeding season and chose pairs for study when the eggs in a nest (Clutch 1) hatched, and male care became a possibility. The next clutch (Clutch 2) was produced after Clutch 1 failed or succeeded (produced at least one fledgling). All birds were banded with USFWS aluminum bands and with unique combinations of colored plastic bands.

We divided mated pairs into an experimental and a control group. Using nets and traps, we captured experimental males on hatching day (day 0) or within 3 days of hatching, and we held them until the end of the breeding season. Control males were captured at the same stage and released immediately after processing (banding if necessary, etc.). Experimentals and controls were treated similarly in all other ways (e.g. daily weighing of young). Originally, in an attempt to match pairs of experimental and control broods for date, brood size, and habitat, we selected the experimental member of the matched pair at random. However, the nest of at least one member was frequently lost to predators before the young fledged. Therefore, for analysis we simply grouped broods according to treatment.

Four males that we did not remove disappeared naturally near the time their eggs hatched, and in one case an unremoved putative father remained but did not feed his young. We treated these instances as experimental. The territories of 51 of the 54 removed males were taken over by replacement males, which followed and courted the females as they cared for their young. Five such replacement males began to feed the nestlings late in the nestling period, but the five females whose broods were adopted were omitted from the analyses because the extent of male help may have differed from that of fathers. In all but one instance in which experimental females renested after nest failure or success, they paired with the replacement males. An exceptional female, which we included in the sample, moved to another male's territory to renest. We weighed all nestlings daily until they could no longer be handled without risk of causing them to leave the nest prematurely (day 8). We treated all disappearances of fledglings up to 14 days after fledging as deaths during the period of dependence (data in Wolf et al. 1988).

Female mass.—To measure mass females lost while they cared for nestlings, we netted females on—or within 2 days after—the day their eggs hatched (caught on hatching day, unaided females, $n = 9$, aided females, $n = 23$; caught 1 or 2 days after hatching, unaided females, $n = 15$, aided females, $n = 13$). We removed young from the nest at day 12 (hatching day $= 0$) and caught the females at that time or within 1 day of fledging (the day before fledging, unaided females, $n = 0$, aided females, $n = 6$; at fledging just before or after the young left the nest, unaided females, $n = 26$, aided females, $n = 46$; the day after fledging, unaided females, $n = 1$, aided females, $n = 3$). For females caught both at hatching and at fledging, we computed the percentage of mass lost (percentages arcsine transformed), to standardize for individual differences in initial mass and in overall body size. In some additional cases we caught females only at fledging. To take advantage of the increased sample size produced by inclusion of these individuals, we also compared absolute mass of treatment groups at fledging. Because we predicted that unaided females would lose more mass and weigh less, tests for dif-

ferences between treatment groups are one-tailed. Statistics follow Sokal and Rohlf (1981); analyses were performed using SPSS software (Nie et al. 1975, Hull and Nie 1981). Only the main effects are reported from ANOVAs, unless there were significant interactions.

Females were caught at all hours of the day (0700–2100). When capture times at hatching and at fledging were used as covariates in comparisons of the treatment groups for percentage of loss, hour of capture was not significant (ANCOVA, $P > 0.90$). In comparisons of mass at fledging, hour of capture was a significant covariate (ANCOVA, $P = 0.01$). We accounted for its effect in comparisons at that stage of reproduction.

For unaided but not for aided females, percentage of mass lost varied according to year (ANOVA with effect of year: unaided females, $F = 3.33$, df = 3, 20, $P = 0.04$; aided females, $F = 0.2$, df = 2, 33, $P = 0.80$). We compared treatment groups for each year separately, and when we combined years, we used year as a factor in ANOVA. In female mass at fledging there was no significant annual variation within either treatment group (ANOVA, effect of year with capture time as a covariate: unaided females, $F = 2.1$, df = 3, 23, $P = 0.13$; aided females, $F = 0.01$, df = 3, 51, $P = 0.97$), so years were combined to compare treatments.

To examine the effect of brood size on percentage of mass lost, it was necessary to control for the fact that the number of nestlings in individual nests sometimes varied over the nesting interval because a brood member died or disappeared. From nests whose brood size we knew on each day from hatching to fledging, we calculated effective brood size (J. Hengeveld pers. comm.) by computing the number of nestling-days the female cared for young. Number of nestling-days was the sum of the numbers of nestlings in the nest on each day of the 12-day nestling period, divided by 12.

To examine the relationship between effective brood size and female mass loss in each treatment group, we used linear regression. To see how annual variation, treatment, and brood size interacted to influence percentage of mass lost, we performed an ANOVA with all three factors. Effective brood size was treated as a categorical variable by grouping broods into four categories: ≤1.5 nestlings, 1.6–2.5 nestlings, 2.6–3.5 nestlings, and 3.6–4.0 nestlings.

Probability of attempting a second brood.—After each nest fledged, we visited the territory almost daily to determine the number of young still alive and to learn whether the female had begun a second-brood nest (Wolf et al. 1988). We excluded cases in which the first brood succeeded after approximately 15 July, when many females—regardless of treatment group—quit breeding. We used Fisher's exact test to compare likelihood of attempting a second brood, according to treatment.

Brood intervals.—When Clutch 1 was unsuccessful (failed on or after day 3 after hatching), the brood interval was the number of days between its failure and the laying of the first egg of Clutch 2. When Clutch 1 was successful, the interval was the number of days between fledging of the young of Clutch 1 and laying of the first egg of Clutch 2, provided at least one young from Clutch 1 survived to independence. We excluded cases in which all young that left the nest died before reaching independence, because variability in times of disappearance made such cases difficult to characterize in small samples. Occasionally we found Clutch 2 only after incubation had begun, but we could estimate the brood interval by backdating, provided the eggs subsequently hatched. Samples were too small to make year-by-year comparisons, so we combined years and used one-tailed t-tests to compare brood intervals; we predicted that unaided females would take longer to renest. We used regression to consider the possibility that size of the first brood affected the brood interval.

Characteristics of the subsequent clutch.—We examined the number of eggs and mean egg mass of Clutch 1 and Clutch 2 of females for which we had data on both clutches. Because an effect of treatment on female condition would probably not be detectable until the lapse of a few days after male removal, we excluded from both treatment groups cases in which Clutch 1 failed before day 6 of the nestling period. We weighed eggs to the nearest 0.1 g with a 10-g Pesola spring scale (usually on laying day and always within 2 days of clutch completion) and calculated the mean for the clutch. No annual variation was revealed in mass or egg number of either clutch, and we combined years for analysis. For both experimental and control females, clutch size decreased slightly as the season progressed.

When we compared clutch size and mean egg mass, first we asked whether Clutch 1 or Clutch 2 differed between treatment groups. Because we chose females randomly for treatment, we expected no difference in Clutch 1. Therefore in the absence of a difference in Clutch 2 the conclusion would be that our experimental treatment had no effect on Clutch 2. Second, we compared clutch size and egg mass of Clutch 1 and Clutch 2 within each treatment group. If we detected no difference in either group, or if we found parallel differences in both groups, again the conclusion would be that Clutch 2 of the experimental group was unaffected by the treatment. Between treatment groups we used Mann-Whitney U-tests to compare clutch size and t-tests to compare mean egg mass. Within treatment groups, we used Wilcoxon signed-rank test for paired observations to compare clutch sizes, and we used t-tests for matched pairs to compare mean egg mass of Clutch 1 and Clutch 2. We predicted that the condition of unaided females would deteriorate more than that of aided females, and comparisons between treatment groups were one-tailed.

TABLE 1. Percentage of body mass lost by females during the nestling period and female mass (g) at fledging of the young, according to treatment and year.[a] Sample sizes are in parentheses; * $P < 0.05$, ** $P < 0.25$, *** $P < 0.001$, one-tailed tests between groups, ANOVA.[b]

	Unaided females		Aided females	
	% mass lost ($\bar{x} \pm$ SE)	Mass at fledging ($\bar{x} \pm$ SE)	% mass lost ($\bar{x} \pm$ SE)	Mass at fledging ($\bar{x} \pm$ SE)
1983	8.2 ± 0.03 (2)	19.7 ± 0.80 (2)	8.0 ± 0.03 (7)	20.1 ± 0.32 (11)
1984	12.8 ± 1.26 (12)	19.2 ± 0.26 (12)	9.9 ± 0.80 (16)***	20.1 ± 0.26 (16)**
1985	8.9 ± 0.98 (6)	19.8 ± 0.37 (7)	8.6 ± 0.95 (13)	20.2 ± 0.23 (20)
1986	6.3 ± 2.40 (4)	20.2 ± 0.46 (6)	—	20.0 ± 0.33 (8)
Total	10.4 ± 0.93 (24)	19.6 ± 0.17 (27)	8.6 ± 0.56 (36)**	20.2 ± 0.16 (55)**

[a] Data include all brood sizes.

[b] Hour of day at capture is a covariate for comparisons of mass at fledging. Year is a factor for both percent mass lost and mass at fledging, when years are combined. Percentages are arcsine transformed.

RESULTS

Female mass.—As expected, female mass when the eggs hatched did not differ between experimental and control females (experimental females, $\bar{x} \pm$ SE = 21.9 ± 0.20 g, $n = 24$, control females, $\bar{x}$ = 22.0 ± 0.19 g, $n = 36$; ANOVA with year as a factor: effect of treatment, $F = 0.5$, two-tailed $P = 0.50$). While caring for nestlings, unaided females tended to lose a greater percentage of their body mass than aided females (when data were combined across years, 10.4% vs. 8.6%; Table 1), and the effects of both treatment and year were significant (ANOVA, effect of treatment: $F = 4.3$, df = 1, 53, one-tailed $P = 0.02$; effect of year, $F = 3.0$, $P = 0.04$).

In both treatment groups, the highest percentage of mass was lost in 1984, which was also the only year in which unaided females lost significantly more mass than aided females in year-by-year comparisons (Table 1). The difference between treatments in 1984 was 2.9%, as compared with 0.2% in 1983 and 0.3% in 1985 (Table 1).

Mean absolute mass when their young fledged was less for unaided than aided females by 0.4 g in 1983, 0.9 g in 1984, 0.4 g in 1985, and −0.2 g in 1986 (Table 1). Here also mass was significantly lower in unaided females only in 1984 and when years were combined (Table 1; ANOVA, time of day as a covariate, effect of treat-

TABLE 2. Possible effects of male parental care on female's next nest attempt, according to treatment.

	Unaided females ($\bar{x} \pm$ SE)	Aided females ($\bar{x} \pm$ SE)	P
% renesting after success[a] of Clutch 1	100 ± — (17)	91 ± — (33)	>0.2[b]
Mean brood interval (days)			
After failure	8.6 ± 2.9 (5)	7.3 ± 2.0 (7)	>0.4[c]
After success (independence)	19.3 ± 2.5 (6)	15.9 ± 1.1 (23)	>0.1[d]
Mean clutch size (n eggs)[e]			
Clutch 1	3.9 ± 0.14(8)	4.0 ± 0.31(22)	>0.3[f]
Clutch 2	3.5 ± 0.27(8)	3.7 ± 0.10(22)	>0.1[f]
Mean mass of eggs (g)[g]			
Clutch 1	2.5 ± 0.08(8)	2.6 ± 0.11(11)	>0.3[h]
Clutch 2	2.7 ± 0.06(8)	2.6 ± 0.41(11)	>0.1[h]

[a] Nest produced at least one fledgling.

[b] Fisher's exact test on females that reared at least one young to fledging.

[c] Student's *t*-test, one-tailed.

[d] Student's *t*-test, one-tailed.

[e] Includes only cases for which data from both Clutch 1 and Clutch 2 were known.

[f] Mann-Whitney *U*-test, two-tailed.

[g] Includes only cases for which data from Clutch 1 and Clutch 2 were known.
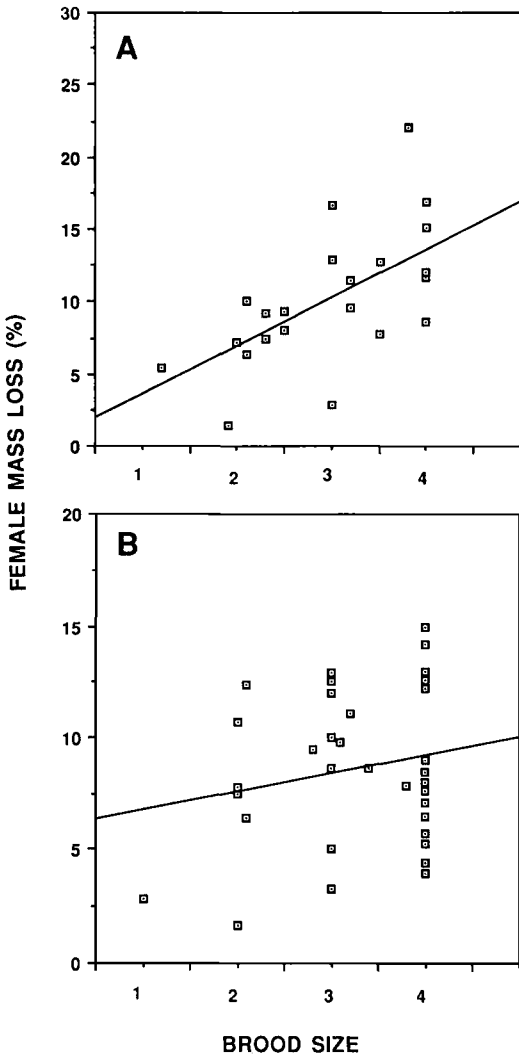
[h] Student's *t*-test, one-tailed.

Fig. 1. Linear regression of percent loss of mass by females on effective brood size (see Methods). (A) Unaided females, $r = 0.61$, $P = 0.002$. (B) Aided females, $r = 0.26$, $P = 0.12$. (Note difference in scale of y-axes of A and B.)

ment: partial $F = 4.6$, df $= 1, 80$, one-tailed $P < 0.02$).

Effect of brood size on female mass.—The only year in which unaided females lost significantly more mass than aided females (1984) was also the year in which they reared the largest broods (Wolf et al. 1988: table 4), which raises the question of the relationship between loss of mass and brood size. Regression of percentage of mass lost on effective brood size indicated that unaid-

ed females that raised larger broods lost more mass than those that raised smaller broods (Fig. 1A). A similar trend also appeared in controls but was nonsignificant (Fig. 1B). We suggest (see Fig. 1) that unaided females lost more mass than aided females only when unaided females attempted to raise larger broods (i.e. greater than three). When they raised smaller broods, there was little to indicate a difference between treatment groups in mass loss.

Probability of raising a second brood.—There was no indication that successful unaided females were less likely than successful aided females to attempt a second brood. Replacement males were present on 17 territories on which unaided females succeeded in producing at least one fledgling before 15 July, and all 17 females renested (Table 2). Under the same conditions, 30 of 33 aided females attempted to raise a second brood.

Brood interval after failure or success.—Although the interval between the failure of Clutch 1 and the laying of the first egg in Clutch 2 was slightly longer for unaided than for aided females (Table 2, ca. 1.3 days or 18%), the difference was not significant (one-tailed $P > 0.4$). The brood interval, measured from date of fledging, of females that reared at least one young to independence was 3.4 days or 21% longer for unaided females than for aided females (Table 2). However, again the difference was not significant (one-tailed $P > 0.4$).

Because unaided females tended to produce fewer fledglings and because they lost significantly more of them in the 2 weeks after fledging (Wolf et al. 1988), we tested if the absence of a difference in brood interval resulted from the fact that unaided females had fewer young to rear, which presumably reduced their work load. However, when treatments were combined, brood interval was unaffected by brood size at fledging or at independence (regression, $P = 0.984$, $P = 0.921$).

Influence of male aid on size and mean mass of subsequent clutch.—In a comparison of the size of Clutch 1 and Clutch 2 within treatment groups, we found a slight trend toward a smaller Clutch 2 in each group (matched pairs, unaided females, $n = 8$, one-tailed $P > 0.10$; control females, $n = 22$, two-tailed $P > 0.10$; Table 1).

As expected, there was no tendency across groups for Clutch 1 to differ in size (two-tailed $P > 0.3$; Table 2). The same was true of Clutch

2 (3.5 vs. 3.7 eggs, one-tailed $P > 0.1$; Table 2), which indicates no delayed effect of male aid on the size of the second clutch.

Finally, there was no significant difference in mean egg mass of Clutch 1 and Clutch 2 within either treatment group (Table 2, comparisons between Clutch 1 and Clutch 2, paired t-tests: experimental females, $t = 1.6$, one-tailed $P > 0.10$; control females, $t = 0.1$, two-tailed $P > 0.90$), and neither Clutch 1 nor Clutch 2 differed in mass across groups ($P > 0.3$, $P > 0.1$; Table 2).

DISCUSSION

Female mass.—In this study, as in others (Alatalo et al. 1982, Sasvári 1986, Lyon et al. 1987, compare Schifferli 1976), females that raised young without male help lost more mass than aided females and were lighter when their young fledged. However, the differences observed were not great and are difficult to interpret (Ricklefs and Hussell 1984). Should they be taken to indicate a greater cost of reproduction in unaided females and thus lead us to expect delayed effects on future reproductive efforts? Although it has commonly been assumed that body mass in breeding birds reflects their condition (Ricklefs 1974, Bryant 1979, Ross and McLaren 1981, Sasvári 1986), evidence that relates body mass to survival (i.e. to rate of return to last year's breeding site) of adult birds is scarce (Perrins 1965, Nur 1984). In fact, a difference in mass between treatment groups does not necessarily imply a cost. It might simply reflect a neutral response by unaided females to their greater work load, without indicating that they were in poorer condition (Ricklefs and Hussell 1984). Late in the nestling period, unaided female juncos average 12 deliveries of food to the nest per hour compared with <6 for aided females (Wolf et al. 1990). If, as some authors have suggested, loss of mass improves efficiency of flight (Freed 1981, Norberg 1981, Ricklefs and Hussell 1984), the loss we observed could even be interpreted as advantageous.

Even if we suppose that the lower mass of unaided females reflects deterioration in physical condition, we should be cautious before we conclude that male parental care is favored because it lowers the cost of reproduction (i.e. increases the female's future success—and hence the male's, if the female continues as his

mate). A female's condition at the time her current young fledge may well have a greater impact on whether those young survive to independence than it has on her future reproductive efforts. This seems especially likely in our experiment as unaided female juncos lost significantly more fledglings before independence than did aided females (Wolf et al. 1988), and as just reported, we detected no significant differences between controls and experimentals in probability of renesting, timing of renesting, or quality of Clutch 2.

Brood size and the cost of reproduction.—Consideration of the relationship between brood size and loss of mass may suggest how the treatment-related difference in mass loss should be interpreted. In many species in which the male helps feed the young, brood size is correlated with loss of mass by females during the nestling interval, or with lower mass of females at fledging (Hussell 1972, Askenmo 1977, Bryant 1979, Westerterp et al. 1982, Nur 1984, Hegner and Wingfield 1987), but in others this relationship is absent (DeSteven 1980, Moreno 1989).

Our finding that loss of mass increased with brood size in unaided females but not in aided females parallels an earlier finding. Unaided females fed larger broods more frequently than they fed smaller ones, whereas the feeding rate of aided females did not vary with brood size (Wolf et al. 1990). This indicates that female juncos do not ordinarily adjust their parental efforts to brood size because males buffer them against the need to do so. Rearing full-sized broods of fledglings would probably be especially taxing without male participation (Morehouse and Brewer 1968, Tyrvainen 1969, Smith 1978, Moreno 1984, Buitron 1988), and unaided female juncos only occasionally brought full broods to independence (Wolf et al. 1988). If unaided females were to rear full-sized broods more frequently, the difference in condition might be considerably greater, with potentially more conspicuous effects on future reproduction. We think it likely that unaided female juncos face the alternatives: (1) accept lower success in the number of young brought to independence from Clutch 1, but at a cost of reproduction not obviously greater than the cost paid by aided females, or (2) bring as many Clutch-1 young to independence, but at greater cost for the future. If this correctly states the choices, unaided female juncos evidently usu-

ally adopt the first alternative. Accordingly, the more important benefit the male junco derives from his parental care is immediate. Although his assistance improves the success of the current brood, it reduces delayed costs only slightly or possibly not at all.

Brood intervals.—Gowaty (1983) compared brood intervals of unaided and aided female Eastern Bluebirds (*Sialia sialis*) and found that females deprived of their mates took longer to renest (33 days vs. 20 days for aided females), but the difference was not significant. Our samples for this comparison were extremely small because so few unaided females met the criterion for inclusion (i.e. rearing at least one young to independence on a date early enough to permit another nesting). Even among individuals that met the criterion, we were not always able to find the subsequent nest in time to determine the brood interval. Unaided females delayed renesting after nest-failure 1.3 days (18%) longer than control females and, after successfully raising at least one young to independence, 3.4 days (21%) longer. Although neither difference was statistically significant, the trend was strongly in the expected direction in the case of the successful females. This delay in attempting a second brood may represent a real cost of the absence of male help with the first brood. The brood interval of successful unaided females might have been even longer if they had not lost significantly more fledglings before independence (Wolf et al. 1990). Hypothetically, full-sized broods of fledglings might require more time to reach independence, although we did not observe a relationship between brood size and brood interval. This relationship exists in other species (Smith and Roff 1980, McGillivray 1983, Hegner and Wingfield 1987, Tinbergen 1987, Arcese and Smith 1988).

We observed that unaided and aided females rarely fed the first-brood fledglings after the initial egg was laid in the second clutch, and that they never fed them after incubation was initiated. Males of aided females fed first-brood fledglings while their mates incubated, and it would seem likely that this would increase survival of the first-brood young. However, among young brought to independence by unaided females and control pairs, we observed no difference in overwinter survival (Wolf et al. 1988).

Quality of Clutch 2.—If the condition of females was affected by whether they received

male help, that fact was not reflected in Clutch 2. Some studies have shown that clutch or egg size reflects female condition at the time of formation of eggs for the next clutch (Jones and Ward 1976, Askenmo 1982, see Winkler and Walters 1983 for review, Bancroft 1985, Murphy 1986, Arcese and Smith 1988, Eldridge and Krapu 1988), and that these variables can affect success of the brood (Parsons 1970; O'Connor 1976, 1979; Ankney and MacInnes 1978; Nisbet 1978; Nolan and Thompson 1978). Furthermore, in some species the effort devoted to raising early broods will affect the subsequent clutch (McGillivray 1983, Hegner and Wingfield 1987). However, there is evidence that females of some small passerines can utilize food and minerals shortly before and during egg formation and quite rapidly regain condition to produce the next clutch (Freed 1981). We place juncos in this last category, and we suggest that even if unaided females suffer a decline in condition while caring for nestlings of the first brood, they recover the deficit by the time they lay their next clutch.

Further consideration of delayed effects of uniparental care in juncos requires that we know how male removal influences female survival between the current breeding season and the next. Only three studies, including our work in progress on survivorship of female juncos, have examined this question. All investigators have suggested that unaided females do not suffer greater annual mortality than aided females (Smith et al. 1982, Gowaty 1983, Ketterson et al. unpubl. data). Based on the results presented here, it is unlikely that the reproductive success of surviving females would be affected in subsequent years because so little effect was detected in the year of removal. If so, male parental care does not affect the male's fitness through improving his mate's condition in those cases in which they re-pair in the following year.

If male juncos were to desert their young, would any resulting fitness costs be immediate, delayed, or both? If their deserted mates succeeded in rearing full-sized broods to independence, thus avoiding immediate costs, delayed costs might be considerable. But our results indicate that few deserted females would succeed in rearing full-sized broods, and that the cost of male desertion would be largely immediate. We conclude that maintaining the condition of

the female for future reproductive attempts does not appear to have been primary among the selective pressures that led to the evolution of male parental care in Dark-eyed Juncos.

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