

Paternal influence on growth and survival of dark-eyed junco young: do parental males benefit?

LICIA WOLF, ELLEN D. KETTERSON & VAL NOLAN JR
Department of Biology, Indiana University, Bloomington, Indiana 47405, U.S.A.

Abstract. Recent studies of typically monogamous passerine birds have suggested that the fitness benefits males derive by caring for their young may not be as great as was previously thought. This study was conducted to determine whether parental care by male dark-eyed juncos, *Junco hyemalis*, serves to increase either the quantity or quality of young that they produce. Over a 4-year period, males were caught at the time their eggs hatched, and the subsequent growth and survival of the young of unaided females and control pairs were compared. Broods raised by unaided females gained body mass more slowly and fledged at slightly lower mass than those raised by two parents. However, fledging mass was not correlated with survival to independence. There were no differences in tarsus growth between the two treatment groups. Entire brood loss to predators occurred as often among females without male help as it did among those with male help. However, partial brood loss was more common among female-only broods than among controls; this difference was largely attributable to higher rates of starvation and exposure in female-only broods. There appeared to be an interaction between growth and predation. Female-only broods that were below the median mass of combined treatment groups at 5 days of age were more likely than all other broods to experience partial or complete predation. Male impact on offspring survival varied with age of the offspring. When years were combined, males tended to increase survival during the first half of the nestling period, but their impact at the time of nest-leaving was minimal. In all years, from nest-leaving to independence (ca. 2 weeks), broods without male help survived only about half as well as did those with male help. Independent young raised by one parent were as likely to return the following spring as were young raised by two parents. Thus, paternal care benefits males by improving the survivorship of their fledglings, and may also act as a buffer against poor female parental quality and inclement weather. However, the magnitude of these benefits is such that bigamous males might achieve greater reproductive success than monogamous males. Various possible male strategies are discussed.

The question of the adaptive basis of bi-parental care in vertebrates has generated much interest in recent years (Kleiman 1977; Nisbet et al. 1978; Perrone & Zaret 1979; Lenington 1980; Martin et al. 1985). Birds are unusual among vertebrates in that many species (most passerines) exhibit bi-parental care, which is usually associated with the most common avian mating system, monogamy (Verner & Willson 1966; Lack 1968; Silver et al. 1985; Møller 1986). The apparent cooperation between the sexes has been assumed to be beneficial to both parents; presumably both increase their reproductive success above what could be attained if only one parent raised the young (Lack 1968; but see Trivers 1972; Maynard Smith 1977; Wittenberger & Tilson 1980). Indeed, bi-parental care has been shown to be essential in many species (e.g. Rivolier 1958; Cade & MacLean 1967; Kemp 1978; see Oring 1982 for review).

Although all passeriform birds have an altricial mode of development, not all exhibit bi-parental care. In only about 70% and 88% of North American species do males feed their nestlings and fledglings, respectively (Verner & Willson 1966, 1969; Carey & Nolan 1975; Patterson 1979; Payne 1979; Richter 1984; for comparison with European species see Møller 1986). Most of the species in which males do not feed the young have a polygynous mating system. Interestingly, females of several monogamous species that are normally aided by their mates are able to raise their young to nest-leaving alone (Schifferli 1976; Nolan 1978; Richmond 1978; Weatherhead 1979; Smith et al. 1982; Gowaty 1983; Björklund & Westman 1986; Lyon et al. 1987). This apparent success of single-parent broods has led workers to reconsider the assumed advantage of bi-parental care among passerine birds (Richmond 1978; Gowaty 1983; Greenlaw &

Post 1985). Measures of reproductive success in most studies, however, terminated at nest-leaving and thus ignored the 2- to 4-week period of dependence that followed. Only two studies have compared fledgling survivorship between female-only and two-parent broods (Post & Greenlaw 1982; Smith et al. 1982), and both suggested that fledglings in female-only broods do not survive as well as those in two-parent broods. Moreover, no study of a passerine has measured a long-term influence of male parental care, such as survival of the offspring to reproductive age.

We examined the benefits that males of a monogamous passerine, the dark-eyed junco, *Junco hyemalis*, derive from caring for their nestlings and fledglings. We removed males of mated pairs at the time their eggs hatched and compared the reproductive success of unaided and aided females, on the premise that any deficit in reproductive success of unaided females would represent the marginal benefit accruing to males as a result of caring for their young. We characterized any such benefit as direct, in contrast to other imaginable indirect advantages to males, such as maintaining their mates' condition or accelerating re-nesting after nest failure or between broods. We will consider these indirect advantages elsewhere (unpublished data). In this paper we examine the effects of male parental care on the growth of nestlings and survival of the young to nest-leaving (fledging) and independence in the course of raising a single brood. We also look at survivorship of these young to reproductive age. In addition, sources of mortality of the young are examined in order to gain insight into the role played by the male in caring for his young.

METHODS

Study Species and Location

The dark-eyed junco is an abundant North American emberizid that breeds at high latitudes and high altitudes in the United States and Canada (Tanner 1958; Hostetter 1961; Bent 1968). Females build the nest, incubate the eggs and brood the nestlings; both parents share roughly equally in feeding and defending the young, a pattern common to many passerine birds (Kendeigh 1952; Verner & Willson 1969; Nolan 1978; Bédard & Meunier 1983; Breitwisch et al. 1986). In the population we studied, pairs commonly rear two

broods per year (the most common brood size is three to four), and the male typically takes over the care of the first-brood fledglings while the female re-nests. Juncos in our study area usually nest on or near the ground, but occasionally build unstable nests in elevated places such as in trees, on boulders, or on buildings (Hostetter 1961; personal observation). The study was conducted in the Allegheny Mountains of the eastern United States, within a 3.3 km radius of the University of Virginia's Mountain Lake Biological Station, elevation 1185 m, located near Pembroke, Virginia (37°22'N, 80°32'W). The area is dominated by deciduous and mixed deciduous-coniferous forests, interspersed with roads and fields. A more detailed description may be found in Wolf (1987).

Field Methods

The study was conducted from early May to mid-August from 1983 through 1986. Nests were found throughout the breeding season from the nest-building stage onwards, but many were destroyed by predators before fledging. Thus, data for some broods included the entire period between hatching and independence, while data from destroyed broods included only the period preceding their death. All known pairs of adult birds, as well as most adults from neighbouring territories, were caught in mist nets or in traps baited with grain and were ringed with United States Fish and Wildlife Service aluminium leg rings and a unique combination of coloured plastic leg rings. Nestlings' claws were marked with coloured nail polish until they were 7 days of age, when we ringed them as we did adults.

Mated pairs were divided into an experimental and a control group. In the experimental group, we captured the male within 1 day of hatching ($N=40$) or within the following 2 days ($N=16$) and held him until the end of the breeding season. In the control group, nests were found on or before day 2, and the male was captured, ringed (unless he was already ringed) and released and allowed to remain with his mate and young. Some broods were excluded from the study because of possible confounding effects of brood parasitism by brown-headed cowbirds, *Molothrus ater*, and for other reasons discussed below.

We removed a total of 9, 17, 17 and 14 males from broods in 1983, 1984, 1985 and 1986, respectively. In 1984, two females each raised two broods

unaided; these four broods were treated as independent cases. In addition, some males either disappeared naturally during incubation or did not feed the young (one exceptional case): one each in 1984, 1985 and 1986. Therefore, we added these broods to the experimental group. Males that were removed were almost invariably replaced by new males; these males usually ignored the nestlings. However, six of these replacement males eventually did feed the nestlings of unaided females late in the nestling stage (two in 1983, both nests were parasitized, and two each in 1984 and 1985). Because it was not clear whether foster fathers cared for the young in the same manner as real fathers, these families were omitted from the study.

We assigned birds to experimental or control groups by choosing pairs of newly hatched broods matched by hatching date, brood size and habitat, as best as we could. Because of predation, members of many matched pairs of broods did not survive to fledging, and, therefore, we grouped the broods within each treatment for analysis.

With the exception of 1983, we attempted to equalize brood size of experimental and control broods at hatching by creating similar numbers of broods with three and four young in each treatment group. When an occasional brood was smaller than the modal size (because some eggs did not hatch or were removed by predators or brown-headed cowbirds), we transferred young of similar ages among nests to produce broods of normal size. Transfers, except in three cases, occurred within 48 h of hatching (15% of 56 experimental broods, and 6% of 101 control broods). Juncos at Mountain Lake that are parasitized by brown-headed cowbirds rear these heterospecifics along with their own young (Wolf 1987). Because of this apparent lack of nestling recognition and because we did not observe differential treatment or survivorship of very young nestlings by the foster parents, we believe that no bias was introduced into the study by performing these transfers.

Nests containing nestlings at ages day 0 (hatching day) to day 7 were visited daily and the young were examined between 1200 and 1800 hours Eastern Standard Time. Young were weighed with 10-g and 50-g Pesola spring scales (± 0.1 g) in 1983–1985, and their tarsus lengths were measured with dial calipers (± 0.1 mm) in 1984 and 1985. Nestlings were ringed on day 6. Because handling nestlings older than 8 days may cause them to leave the nest prematurely, nestlings older than 8 days

were inspected daily but left untouched until fledging, usually on day 11 or 12. In 1983, nestlings were allowed to leave the nest naturally and were then caught and weighed. However, the difficulty in finding and capturing such fledglings prompted us in subsequent years to remove young from the nest on day 11 or day 12 (the usual fledging age of juncos at Mountain Lake). We discerned no difference in subsequent survival of naturally fledged young and those forced out by us (48% of 21 experimental broods fledged naturally; 60% of 37 control broods fledged naturally, tests within both treatment groups for naturally fledged versus forced-out young, number surviving to independence versus number that died, chi-squared tests, $P > 0.3$).

To determine survivorship of young to independence, we monitored fledglings, which usually remained on or near the natal territory, for 14 days after fledging. By that age they could feed themselves and appeared to fly as well as adults. Therefore, we considered them independent even if they still associated with their parents. A fledgling was assumed to be dead if it was not seen for 2 or more days of observation during which the rest of the family was seen. Some families were not monitored after fledging because we could not follow them in rough terrain, and these cases were omitted from the survivorship calculations. We may have underestimated the true survival of fledglings in both treatment groups; one fledgling (the only one in its brood) that we assumed dead the year it was hatched was discovered the following spring breeding about 1.3 km away. Since treatment of the two groups was identical and we were able to monitor families of each group equally well, it is unlikely that our estimate of survivorship is biased toward either treatment group.

Growth Analyses

Because no overall differences between or within treatment groups could be detected in mass or tarsus length of first and second broods, or between these and broods of unknown status (Mann-Whitney *U*-tests comparing first and second broods for mass and tarsus length at all ages, $P > 0.05$), we included first and second broods, as well as some broods of unknown status, in the study (female-only broods: $N = 26$ first broods, $N = 3$ second broods, $N = 6$ unknown; two-parent broods: $N = 38$ first broods, $N = 15$ second broods, $N = 16$ unknown).

Body mass and tarsus length of young were compared between treatment groups for each age (day 0 through day 7 and at fledging) using Mann-Whitney *U*-tests. Variances between and within treatment groups were sometimes heterogeneous, and, therefore, we used the mean value of the mass and tarsus length of the surviving nestlings for each brood at each age as the datum (mean nestling mass and mean nestling tarsus length per brood). We predicted that young in female-only broods would grow more slowly and survive less well than those raised by two parents; accordingly, we used one-tailed tests in comparisons of growth and survival between female-only and two-parent broods; all such comparisons are noted in the text. All other statistical comparisons, if not noted as one-tailed, were two-tailed tests.

Mortality Assessment

Because differences in the causes of nestling mortality between treatment groups may provide insight into the importance of paternal care, sources of nestling mortality between groups were considered. Broods as a whole were classified according to one of three outcomes: all young were lost prior to fledging (failure), fewer than all young were lost (partial brood loss), and all young fledged (success). These outcomes were analysed in a three-way goodness-of-fit test of outcome by year and treatment (Sokal & Rohlf 1981).

Nest failure occurred in two ways, predation and desertion. Predation was said to have occurred when (1) the entire brood disappeared from the nest between successive visits, or (2) members of apparently healthy broods disappeared between successive visits until no young remained. Desertion was rare and occurred when a complete brood was left unattended for several days and subsequently died. Partial brood loss was used to describe broods in which one or more young disappeared between daily visits but from which at least one young ultimately fledged. The causes of partial brood loss were often difficult to ascertain. Sometimes a dead nestling was found in or near the nest (and occasionally an uninjured nestling was found near its nest), but more often one or two young were simply gone. The three most common causes of partial brood loss appeared to be predation, starvation and exposure, and to distinguish among them we used the following criteria. A nestling was treated as having starved if it either

lost or failed to gain body mass between 2 consecutive days and either was found dead or had disappeared by the next day. Death was categorized as caused by exposure if a nestling younger than 5 days old was found uninjured but dead in the nest and had shown no previous sign of starvation. Deaths treated as exposure always occurred during or shortly following a rainstorm in which ambient temperature fell below about 10°C. Death was attributed to predation if one or more nestlings disappeared between daily nest inspections and there was no indication that starvation was the cause. This was probably the most common explanation for these disappearances, but other causes were possible; for example, a nestling may have accidentally fallen out of an elevated nest or become ill, died, and been removed by a parent. The last category, 'other', includes cases that could not be properly distinguished from predation that but differed in appearance. The category includes instances in which nestlings were found dead and starvation or exposure did not appear to be the cause. The causes in these few cases were puzzling; we occasionally found young with puncture wounds, both in and out of the nest, some dead, others alive. Also included in this category are two cases in female-only broods in which one nestling disappeared by day 2, a period too short to determine whether starvation had occurred. We counted any live young found outside the nest as dead, as they would have quickly died of exposure, since parents do not return displaced young to the nest. We replaced such young in these nests for the purposes of growth analyses. We rarely found ectoparasites on junco nestlings, and thus mortality due to this factor was probably infrequent at most.

Survivorship Analyses

We analysed survivorship to ringing age (day 6), fledging and independence from 1983 through 1986 using Mann-Whitney *U*-tests in two ways (methods I and II). Survivorship in broods whose initial sizes were three and four young was analysed separately. In method I, we considered only those broods in which at least one young survived either to day 6 or to fledging and noted the number of young alive in each brood at each age. This allowed us to omit broods that had failed and to compare the number of young in surviving broods between treatment groups. At independence, we compared

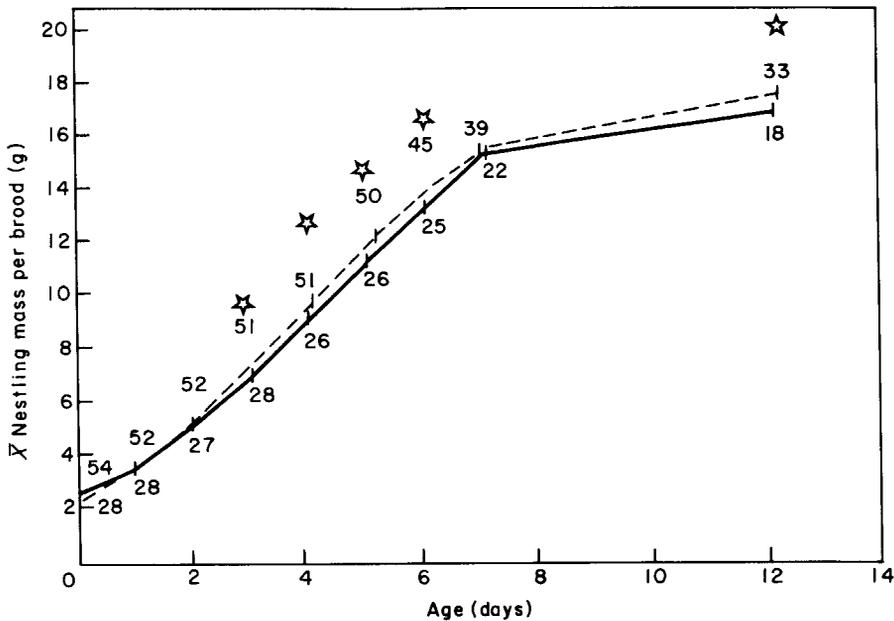


Figure 1. Nestling mass, according to age, of young raised by aided (---) and unaided (—) females, 1983 through 1985 pooled. Points represent mean nestling mass per brood. Mass was significantly lower in one-parent broods from day 3 to day 6 and at fledging, indicated by stars (one-tailed Mann-Whitney U -tests, $P < 0.025$). Sample size is shown below the line for female-only broods and above the line for two-parent broods. Vertical bars indicate ± 1 SE; if no SE bar is shown, the length of the SE was smaller than the width of the line. Increases in sample sizes are the result of failure to weigh some broods each day; sample size generally decreased over time as broods were lost to predators.

survival only in broods in which at least one young had fledged, including cases in which entire broods were lost after fledging.

In method II, we considered all broods for each age, including those that failed before that age. We computed the percentage of each brood alive at each age and ranked these percentages according to treatment group (Mann-Whitney U -tests). When a brood failed, its percentage fell to 0 and was carried forward for purposes of comparisons at later ages. This method of analysis allowed us to quantify the effects of male removal while including effects of complete nest predation. However, it should be pointed out that parents of failed broods in fact began to re-nest while the parents of surviving broods were still engaged in parental care.

Statistical procedures were performed with Statistical Package for the Social Sciences (Nie et al. 1975; Hull & Nie 1981), SPSSX Information Analysis System (1986) and Microstat microcomputer software; G -tests were calculated from Sokal & Rohlf (1969).

RESULTS

Growth of Nestlings

Gain in mass

Nestling mass was not affected by brood size in either female-only or two-parent broods (mean nestling mass per brood did not differ among broods of two, three or four, at any age, for either female-only or two-parent broods, Mann-Whitney U -tests, $P > 0.05$). Consequently, data from broods of two, three and four were combined in analyses of nestling mass.

As expected, mass at hatching did not differ between treatment groups (Fig. 1; mean nestling mass per brood, experimental broods $\bar{X} \pm \text{SE} = 2.5 \pm 0.07$ g, $N = 28$; control broods $\bar{X} \pm \text{SE} = 2.4 \pm 0.04$ g, $N = 54$; Mann-Whitney $U = 717.5$, $P > 0.3$). Experimental nestlings weighed significantly less than control nestlings from ages day 3 through day 6, the period of most rapid growth (Fig. 1). Mass was equivalent between treatment groups on day 7, but experimental broods were

Table I. Number of female-only and two-parent broods that either fledged all or lost one or more young, according to whether they were above or below the median mass of combined treatment groups on day 4, and loglinear analysis models

	Mass	Lost one or more young	Intact at fledging
Type of brood			
Female only	Above median	4	5
	Below median	12	1
Two-parent	Above median	11	16
	Below median	9	11
Terms in model*			
S	<i>df</i>	χ^2	<i>P</i>
S, S × T	3	12.08	0.007
S, S × M	2	6.45	0.040
S, S × T, S × M	2	8.72	0.013
S, S × T, S × M	1	4.07	0.044
S, S × T, S × M, S × T × M	0	0.00	1.000

* S: success; T: treatment group; M: mass

again lighter at fledging (Fig. 1; Mann-Whitney *U*-tests, one-tailed $P < 0.02$).

We asked whether the reduction in mean nestling mass in experimental broods was caused by starving young whose mass decreased the mean value of their broods. To do this, we excluded broods in which at least one young starved (five female-only broods and one two-parent brood) from the analysis and again compared mass of experimental and control broods. The results were identical to those in which starved young had been included; experimental broods were significantly lighter on days 3-6, and at fledging (Mann-Whitney *U*-tests, one-tailed $P < 0.05$). Thus, the presence of starving young was not the cause of reduced mass in female-only broods.

Because the demands of raising a full brood to fledging for a single parent could conceivably be greater than either raising a reduced brood alone or raising a full brood with help, we next compared across treatment groups the sub-samples of broods in which no young were lost to predation during the entire nestling period. We expected experimental broods in which all young fledged to exhibit even greater reduction in mass than controls. To our surprise, however, no differences in mass occurred between treatment groups at any age in broods that escaped predation (Mann-Whitney *U*-tests, $P > 0.05$). This suggested that the experimental broods experiencing predation (partial or com-

plete) were primarily those that were lighter than controls. Therefore, we compared the mass of experimental and control broods that lost at least one young to predation prior to fledging (again, excluding broods in which nestlings starved). In such broods, experimentals were lighter than controls during the rapid-growth stage, days 2-5, although not at fledging (Mann-Whitney *U*-tests, $P < 0.05$). Further, within experimental broods, those that lost at least one young to predation were lighter than those in which all young fledged on days 2-6 (Mann-Whitney *U*-tests, $P < 0.045$). Within control broods, however, those that lost at least one young were lighter than those in which all young fledged only on day 6 (Mann-Whitney *U*-test, $P < 0.05$). Thus, there was an unexpected interaction among treatment, mass and predation.

To test whether this interaction was significant, we categorized broods according to treatment, whether they were above or below the median mass of combined treatment groups on day 4, and whether they fledged all young or lost one or more young to predation (Table I; recall that broods were weighed in only 3 of 4 years). We looked at the mass of young on day 4 because at this age the nestlings are growing rapidly and the consequences of inadequate nutrition would be detectable. We then ran a logit form of the loglinear analysis (SPSSX) in which survival was the dependent variable. The various models and their chi-squared

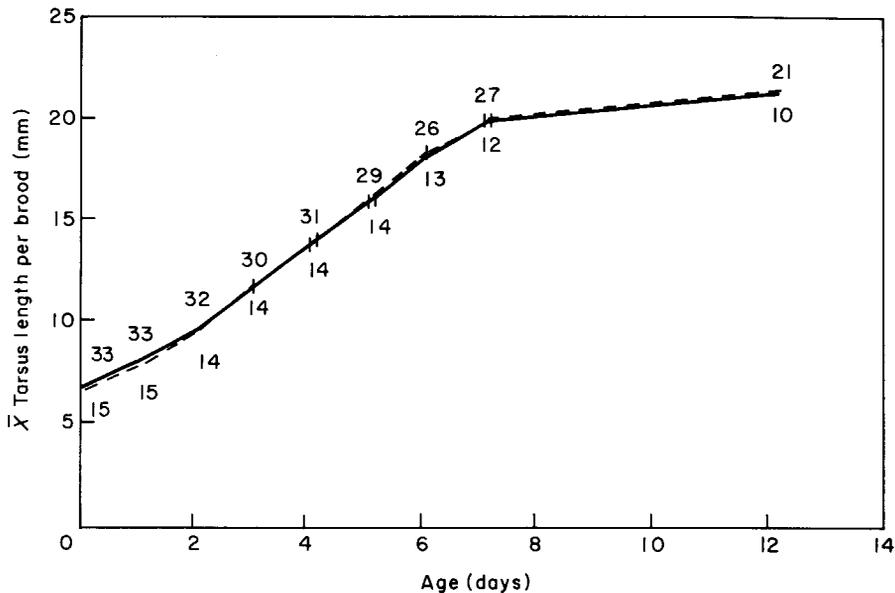


Figure 2. Tarsus length of nestlings, according to age, of young raised by aided (---) and unaided (—) females, 1984 and 1985 pooled. Points represent mean tarsus length per brood. One- and two-parent broods did not differ in tarsus growth (one-tailed Mann-Whitney U -test, $P > 0.025$). Sample size labels are the same as in Fig. 1. Vertical bars indicate ± 1 SE; see Fig. 1. Increases in sample sizes were the result of failure to measure some broods each day. Sample size generally decreased over time as broods were lost to predators.

values show that the only model that provides an adequate fit to the data is the saturated model, indicating that the influence of both mass and treatment are necessary to account for the observed pattern of success (Table I). The presence of a three-way interaction between success, treatment and mass means that the effect of treatment on success depended on whether the brood was above or below the median mass. In other words, the effect of mass on survival depended upon treatment. Pairwise chi-squared analyses within treatment groups indicated that success depended on mass in experimental broods (mass above or below day 4 median, reduced versus intact broods, $\chi^2 = 3.97$, $P = 0.046$), but not in control broods (mass above or below day 4 median, reduced versus intact broods, $\chi^2 = 0.021$, $P > 0.89$). These results suggest that some females raising broods without help were not able to supply adequate food, and, perhaps, that increased calling of the hungry young may have attracted predators. Because female-only broods were attended less than two-parent broods (unpublished data), nest-defence in female-only

broods was probably decreased and predators attracted by the calling may have located the young more easily.

Tarsus growth

Tarsus length was not influenced by brood size (broods of two, three and four) at any age, for either female-only or two-parent broods (Mann-Whitney U -test, $P > 0.1$). Consequently, brood sizes were combined for the analyses.

The pattern of tarsus growth was different from that of gain in mass. No differences in mean nestling tarsus length per brood were found between female-only and two-parent broods (Fig. 2; Mann-Whitney U -tests, one-tailed $P > 0.05$).

Variation in body mass and tarsus length

To gain further insight into the effects of paternal care on nestling growth, we examined the variance between treatment groups in mean nestling mass and mean tarsus length per brood, using F -tests. We reasoned that some individuals might be better

Table II. Fates of broods from hatching to fledging from 1983 through 1986 in female-only and two-parent broods*

	Female-only broods						Two-parent broods					
	1983	1984	1985	1986	Total	% Total	1983	1984	1985	1986	Total	% Total
Successful†	2	7	1	3	13	23	8	13	13	2	36	33
Partially successful‡	1	5	6	4	16	29	5	5	2	1	13	19
Failed§	2	6	10	8	26	46	13	12	10	8	43	48
Deserted	0	0	1	0	1	2	0	0	2	0	2	2
Total	5	18	18	15	56	100	26	30	27	11	94	100

* Broods of all sizes are included.

† All young fledged.

‡ Broods that produced at least one fledgling, but at least one nestling was lost before fledging.

§ Broods in which all nestlings eventually disappeared, probably due to predation. Included are nests in which nestlings disappeared on separate days.

parents than others (e.g. first-year versus experienced breeders) and that, without a second parent to contribute, female-only broods might exhibit more variable growth in response to variability in maternal care and environmental conditions. Variance in mean nestling mass per brood was higher for experimental broods than for controls on day 1 and from days 3–7 (F -tests, $P < 0.05$). Variance in mean tarsus length per brood, however, differed between treatment groups only on day 1 (F -test, $P < 0.05$). Thus, while the acquisition of body mass in growing juncos appears to have been depressed and more variable in broods raised by one parent, growth and variance of the tarsus was much less affected by lack of a male parent.

Fates of Broods and Sources of Mortality

Table II reports the fates of female-only and two-parent broods at the end of the nestling interval. To determine whether fate (success, failure, including desertion, and partial brood loss) was dependent on treatment group and also whether fate varied with year, we performed a three-way goodness-of-fit test. Fate depended on treatment but not on year ($P > 0.25$); consequently we combined data across years.

Among experimental broods, 23% were successful, 29% were partially successful and 46% failed. The corresponding percentages among controls, 33%, 19% and 48%, reveal three things. First, outcome was affected by male removal ($\chi^2 = 6.39$,

$df = 2$, $P = 0.041$). Second, the proportion of broods that fledged all the young was greater among two-parent broods while the proportion that suffered partial loss was greater in female-only broods. Third, male removal had no measurable impact on the proportion of broods lost in their entirety.

To ask how the presence of two parents reduced partial brood loss and increased the likelihood that all members of a brood would fledge, we took a closer look at the causes of mortality in reduced broods. We examined the wholly and partially successful broods and their nestlings according to fate (Table III). Considering broods first, the most obvious difference between experimentals and controls, beyond the greater percentage of intact broods produced by the latter, was that 17% of experimental broods were reduced by starvation or exposure, whereas starvation or exposure occurred in only 2% of comparable control broods (Fisher's exact, $P = 0.049$). Other sources of mortality associated with partial brood loss did not appear to be more or less frequent when the male was present or absent.

Focusing on nestlings as opposed to broods (Table III), nine individual young met our criteria for starvation or exposure (eight experimental nestlings and one control). The eight represented 14% of the 57 nestlings hatched in female-only broods that experienced partial brood loss or 8% of the 96 nestlings from the combination of partially reduced and intact female-only broods. The comparable percentages for controls were 2% ($N = 48$)

Table III. Percentage of wholly or partially successful broods and nestlings within them, classified according to outcome

	Female-only % (N)	Two-parent % (N)
Broods		
100% fledged	45 (13)	73 (36)
Reduced by predation†	21 (6)	17 (8)
Reduced by starvation or exposure‡	17 (5)	2 (1)
Reduced by other§	17 (5)	8 (4)
Total number of broods	(29)	(49)
Nestlings		
Survivors of wholly successful broods	41 (39)	71 (118)
Survivors of reduced broods	30 (29)	17 (29)
Died from predation	11(11)	7 (12)
Died from starvation or exposure	8 (8)	1 (1)
Died from other	9 (9)	4 (6)
Total number of nestlings	(96)	(166)

* Table excludes broods that were completely destroyed by predators. broods of all sizes are included. See text for statistics.

† Nestlings that were found partially eaten or that disappeared between nest visits and had not shown previous signs of starvation.

‡ Nestlings were treated as starved if they failed to gain or lost mass over 2 consecutive days and then disappeared or were found dead. Nestlings were considered to have died of exposure if they were found dead in the nest, usually before day 4, but had not shown previous signs of starvation. Exposure always occurred during or shortly following rainstorms.

§ Includes cases that could not be attributed to either of the other categories. Included are two cases in which one nestling died before day 2.

and less than 1% ($N=166$), respectively. A Fisher's exact test applied to both comparisons indicated that although starvation was rare in general, it was more common among female-only nestlings (partially reduced broods only, $P=0.058$, all broods fledging young, $P=0.003$). Much of this individual nestling loss occurred during or after prolonged rainstorms accompanied by cold temperatures, which probably forced unaided females both to leave their nests more frequently and to forage for themselves for longer periods. As before, no other cause of partial brood loss was experienced disproportionately by female-only nestlings. Based on the interaction between day 4 mass and later predation, we had expected that males might diminish the probability of partial brood loss to predators, but that effect did not show up in this analysis.

Nestling Survival

Despite our efforts to standardize brood size between the treatment groups at hatching, female-only broods were significantly larger at hatching

than were two-parent broods (female-only broods $\bar{X} \pm SE = 3.6 \pm 0.09$ young, $N=51$; two-parent broods $\bar{X} \pm SE = 3.4 \pm 0.08$ young, $N=93$; sample includes all brood sizes for which we knew the number at hatching; Mann-Whitney $U=1889.5$, $P<0.03$). Therefore, we analysed survival of nestlings for broods of three and four separately, excluding broods of one and two.

In experimental broods of three that were not lost entirely to predators (method I), the mean number of young per brood surviving to day 6 and to fledging was significantly smaller in female-only than in control broods in 1983 and in the combined years; however, the result in 1983 may be an artefact of the very small sample size (Table IV). On average, unaided females lost 1.0 young and aided females lost 0.1 young between hatching and fledging.

In broods of four (method I), significantly fewer young in female-only broods survived to day 6 in 1985 and in combined years, but no significant differences occurred at fledging (Table IV). On average, unaided females lost 1.1 nestlings per

Table IV. Mean number \pm SD (N = number of broods) of young surviving to various ages in broods that hatched three and four young, raised by one and two parents†

	Female-only broods			Two-parent broods		
	Day 6	Fledging	Independence‡	Day 6	Fledging	Independence
Brood Size 3						
1983	2.0 (1)	2.0 (1)	—	3.0 \pm 0 (10)***	3.0 \pm 0 (5)**	3.0 \pm 0 (3)
1984	3.0 (1)	3.0 (1)	—	3.0 \pm 0 (5)	2.7 \pm 0.5 (4)	3.0 \pm 0 (2)
1985	3.0 (1)	—	—	3.0 \pm 0 (7)	2.8 \pm 0.4 (5)	2.2 \pm 1.0 (4)
1986	2.0 (1)	1.0 (1)	0 (1)	3.0 (1)	—	—
Total	2.5 \pm 0.6 (4)	2.0 \pm 1.0 (3)	0 (1)	3.0 \pm 0 (23)***	2.9 \pm 0.4 (14)**	2.7 \pm 0.7 (9)*
Brood size 4						
1983	3.5 \pm 0.7 (2)	3.0 (1)	2.0 (1)	3.2 \pm 1.0 (8)	3.4 \pm 0.5 (5)	3.5 \pm 0.6 (4)
1984	3.4 \pm 0.9 (14)	3.1 \pm 1.1 (10)	1.4 \pm 1.2 (8)	3.8 \pm 0.4 (14)	3.4 \pm 1.0 (12)	3.1 \pm 0.8 (9)**
1985	3.0 \pm 0.6 (6)	2.8 \pm 0.5 (4)	0.2 \pm 0.5 (4)	3.9 \pm 0.3 (11)**	3.4 \pm 1.2 (8)	1.6 \pm 1.5 (8)*
1986	3.2 \pm 1.1 (5)	2.5 \pm 1.7 (4)	1.0 \pm 1.4 (2)	3.7 \pm 0.5 (4)	3.0 \pm 0 (2)	2.0 \pm 1.4 (2)
Total	3.3 \pm 0.9 (27)	2.9 \pm 1.1 (19)	1.0 \pm 1.1 (15)	3.7 \pm 0.6 (37)**	3.4 \pm 0.9 (27)	2.6 \pm 1.3 (23)***

† Means for day 6 and fledging include only broods in which at least one young survived to the designated age.

‡ Means for independence include all broods whose fate was known, in which at least one young fledged. Dashes indicate ages for which there were no data.

One-tailed Mann-Whitney U -tests compare number of young per brood surviving in female-only and two-parent broods. * $P < 0.05$; ** $P < 0.025$; *** $P < 0.001$.

brood before fledging, whereas aided females lost 0.6 nestlings.

Using data from combined years, we examined the average percentage of young surviving per brood at day 6 and fledging, including failed broods in the sample (method II). In general, methods I and II yielded similar results. In method II, for broods of both three and four, female-only broods survived less well to day 6 than did two-parent broods (Figs 3a and 3b; percentage surviving to day 6, brood size 3, experimentals = 37%, controls = 74% brood size 4, experimentals = 59%, controls = 71%). However, at fledging, no significant difference occurred between treatment groups for broods of three or four (Figs 3a and 3b; percentage surviving to fledging, brood size 3, experimentals = 22%, controls = 44%; brood size 4, experimentals = 37%, controls = 47%). Methods I and II led to different conclusions only for broods of three at fledging. We summarize as follows. The effect of male removal was more apparent half-way through the nestling interval than it was at fledging. By the time the young left the nest, removal was associated with a significant reduction in survival

only in broods of three and then only after removing from consideration broods lost to predators. Thus, the effect of the male at fledging is measurable, but it is minimal.

Fledgling Survival

The number of young surviving from fledging to independence was significantly reduced (both methods I and II) for young raised by unaided females, regardless of brood size at hatching, over the 4 years combined (Table IV, Fig. 3; brood size 3, combined years, mean number surviving, experimentals = 0, controls = 2.7; percentage surviving, experimentals = 0%, controls = 32%; brood size 4, combined years, mean number surviving, experimentals = 1.0, controls = 2.6; percentage surviving, experimentals = 12%, controls = 33%). When years are examined separately for broods of four, female-only broods experienced significantly lower survival from fledging to independence only in 1984 and 1985 (Table IV). Three of 16 female-only and three of 32 two-parent broods were completely

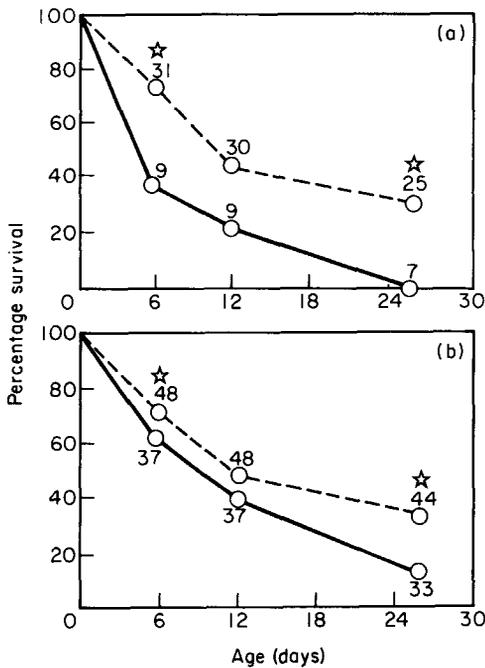


Figure 3. Survivorship of young raised by one (—) and two (---) parents from hatching to independence, 1983–1986 pooled. At hatching, 100% were alive. Values were calculated as the percentage of each brood surviving from hatching to independence, retaining 0 values for broods in which all young died; the mean of these values constitutes each point. Sample size is shown at each point. Broods whose fates were unknown following fledging were excluded from the sample at independence. Stars indicate $P < 0.05$ (one-tailed Mann–Whitney U -tests). (a) Broods with three hatchlings. On day 6, $P < 0.05$; at independence, $P < 0.01$. (b) Broods with four hatchlings. On day 6, $P < 0.05$, at independence, $P < 0.025$.

lost shortly after fledging (within about 2 days), but the difference between treatment groups was not significant (test of proportions, one-tailed $P = 0.089$). On average, unaided females raised fewer than half the number of independent young that aided females did.

Sources of fledging mortality were difficult to determine because we rarely witnessed the death of young or found their remains. On three occasions, we did find remains of newly fledged young within 10 m of the nest; the predators were most probably eastern chipmunks, *Tamias striatus*, or red squir-

rels, *Tamiasciurus hudsonicus*, the most common predators of nestlings at Mountain Lake (personal observation). Adult juncos show great alarm (by calling and mobbing) at the presence of these rodents near their nests or young.

Influence of Fledging Age and Mass on Survival to Independence

In some cases, young left the nest early, i.e. before day 11. Although more experimental than control broods fledged early (six of 29 female-only broods, five of 46 two-parent broods), experimental broods were not statistically more likely to fledge early than were controls ($\chi^2 = 0.6$, $df = 1$, $P > 0.4$). However, if nestlings instead of broods are treated as independent events, experimental young were significantly more likely to fledge early than were control young (Table V).

The probability of surviving to independence was reduced significantly for early-fledging young, both experimental and control (Table V; number of young surviving versus number that died, fledging before day 11 compared to on day 11 or day 12; female-only young, $\chi^2 = 6.0$, $df = 1$, $P < 0.02$; two-parent young, $\chi^2 = 36.1$, $df = 1$, $P < 0.0001$). Of the 25 young that fledged before day 11, experimental young were less likely to survive to independence than were early-fledged control young (number surviving versus number that died, compared across treatment groups, $\chi^2 = 5.2$, $df = 1$, $P = 0.022$). Of the 73 young that fledged on day 11, there was a trend for reduced survival to independence of female-only compared with two-parent young (number surviving versus number that died, compared across treatment groups, $\chi^2 = 3.5$, $df = 1$, $P > 0.05$). Similarly, of the 41 young that fledged on day 12, female-only young survived significantly less well to independence than did two-parent young (number surviving versus number that died, compared across treatment groups, $\chi^2 = 6.1$, $df = 1$, $P = 0.014$).

We conclude that young juncos are less likely to survive to independence (1) if they fledge early, regardless of whether they are reared by one or two parents, and (2) if they are reared by one parent, regardless of fledging age.

Because of lower survival of early-fledged young, we excluded broods that fledged before day 11 in analysing the effect of fledging mass on survival to

Table V. Number of young that survived to independence or died during the fledgling period in female-only and two-parent broods, with respect to age at nest-leaving (young from broods of all sizes are included)*

Age at nest-leaving	Female-only young			Two-parent young		
	Survived	Died	% Survived	Survived	Died	% Survived
Before day 11†	1	12	8	7	5	58
On day 11	7	8	47	44	14	76
On day 12†	8	5	62	27	1	96
Total	16	25	39	78	20	87

† χ^2 test for female-only and two-parent young that survived to independence versus those that died during the fledgling period: $P < 0.025$.

* Three-way G -test indicated lack of independence among fledging age, treatment, and survival to independence ($G = 49.5$, $P < 0.001$). All pairwise interactions were significant in χ^2 tests; survival by treatment, survival by age, and treatment by age, $P < 0.025$.

independence. Among female-only broods, fledging mass of young that survived to independence did not differ from that of fledglings that died, although the survivors tended to be lighter at fledging (survived: $\bar{X} \pm \text{SE} = 16.5 \pm 0.72$ g, $N = 13$; died: $\bar{X} \pm \text{SE} = 17.7 \pm 0.80$ g, $N = 6$; Mann-Whitney $U = 83.0$, $P > 0.09$). Interestingly, two-parent young that survived to independence also tended to be lighter at fledging than did two-parent young that died (survived: $\bar{X} \pm \text{SE} = 17.6 \pm 0.16$ g, $N = 58$; died: $\bar{X} \pm \text{SE} = 18.0 \pm 0.20$ g, $N = 14$; Mann-Whitney U , $P > 0.05$), but the difference was again non-significant.

Because juncos that hatched early in the season tended to fledge at a lighter mass than did those that fledged later in the season (Kruskal-Wallis one-way ANOVA, fledging mass by four seasonal quarters, $\chi^2 = 7.2$, $df = 3$, $P = 0.07$), we asked whether the seasonal effect on fledging mass could account for the inverse relationship of fledging mass and survivorship to independence; i.e. whether young fledged early in the season were more likely to survive. Therefore, we partitioned the season into four quarters and performed chi-squared tests of number of young that survived to independence or died by quarter of season, both within treatment groups and for combined treatment groups. We found no evidence that young fledging earlier in the season were more likely to survive to independence than young fledging in

later quarters of the season (four seasonal quarters by number that survived versus number that died, combined treatment groups, $\chi^2 = 1.96$, $df = 3$, $P = 0.58$).

Survival Beyond the Period of Dependence

Of the 265 nestlings ringed in the study from 1983 to 1985, 26 (10%) were known to be alive on the study area during the first spring of their adult life (16 females, nine males, one sex unknown), most of them breeding. Of these, we already knew that some had fledged or had reached independence because we had been able to follow them in their natal year. Of 68 experimental and 185 control young known to have fledged, four (6%) female-only and 19 (10%) two-parent individuals were known to be alive the following spring. There was no statistical difference in the return rate between treatment groups ($\chi^2 = 0.9$, $P > 0.4$); however, a statistical difference might have been detected with a larger sample. Of 20 female-only and 103 two-parent young known to have reached independence, three (15%) one-parent and 16 (15%) two-parent offspring were known to be alive the following spring ($\chi^2 = 0.03$, $P > 0.8$). These data suggest that although male parental care improves offspring survival during the period of dependence, lack of paternal care does not decrease survivorship of the offspring after they reach independence.

DISCUSSION

Nestling Growth

Gain in mass and tarsus length

Although young from female-only broods tended to weigh less than young from two-parent broods, the differences were significant only during the exponential growth stage and again at nest-leaving. However, since fledging mass was not positively correlated with survival to independence, it is questionable whether this difference in fledging mass is biologically important.

The difference in growth, however, may have influenced the likelihood of predation. Contrary to expectation, when we examined only broods in which all young fledged there were no differences in mass between treatment groups at any age, whereas experimental broods that did lose young tended to be lighter than those that did not and than all control broods. We also found that experimental broods that were lighter than the overall median mass on day 4 were highly subject to predation, whereas heavier experimental broods and both light and heavy control broods were not. This suggests that some unaided females were less able to provide for their young than others, and that hungry nestlings in these lighter broods may have called more and attracted certain kinds of predators. Hungry young that were cared for by two parents may also have called, but two parents may have been more likely to observe the predator and drive it away from the nest. This interpretation is not inconsistent with the fact that experimental and control broods were equally likely to suffer complete predation, because the complete predators could have been animals such as squirrels, foxes and raccoons, which are too large for a junco to deter. However, this interpretation would have led us to expect less partial predation on control broods by deterrable predators such as chipmunks, and we did not observe this.

Why were some experimental females able to raise their entire broods to fledging while others were not? We suspect that individual females that suffered partial brood loss may have been less able to care for their young for any of several possible reasons: inexperience of first-year birds, poor physical condition, poor territory quality, or inability to cope with some environmental stress (Smith et al. 1982; Lyon et al. 1987). Another finding supports the notion that female parental quality was variable and that this variation was realized to

a greater extent in female-only broods: variance in nestling mass among female-only broods was higher than that among two-parent broods. This suggests that without a male to buffer variability in female care, different parental abilities among unaided females produced variable effects in their nestlings.

Tarsus growth did not differ between experimental and control nestlings at any age. This result evidently reflects a low phenotypic response of tarsus length to the environmental effects created by our experiment. One reason for this lack of response may be that tarsus growth is highly canalized, i.e. is under strong genetic control with little variation among individuals. Alternatively, high heritability or a large maternal effect could create low within-brood variance and high among-brood variance, thus overriding the effect of our treatment. Several investigators have found high heritability in tarsus length of birds (Smith & Zach 1979; Dhondt 1982; Boag 1983; Alatalo et al. 1984; Alatalo & Lundberg 1986). Junco tarsi are fully grown by nest-leaving (Smith & Andersen 1982; this study); thus, one could compare tarsus length of parents and their fledglings in order to examine heritability of this trait. Resolution of this problem will require further study.

Nestling Survival

Both methods I and II showed that, in general, nestling survival was reduced in female-only compared to control broods by the end of the first half of the nestling period. At fledging, however, few statistical differences between treatment groups remained (only for broods of three, combined years, method I). The reasons for the pattern of early nestling loss by unaided females are not entirely clear, but we suggest that starvation and exposure, which nearly always occurred early, were part of the cause. Among broods suffering partial brood loss, starvation and exposure were responsible for significantly more deaths of experimental than control nestlings. By day 6, female-only broods had already lost more young than two-parent broods, and subsequent reduction in brood size in both groups was most often caused by total or piecemeal predation, not starvation. In our study, males were apparently only weak preventors of predation.

Why do males help care for nestlings if their efforts bring so little return? One reason appears to

be simply that they are useful early in the nestling stage and again later after the young fledge, so there may be little to be gained from withholding parental care for a short period late in nestling life. We worked in years of very high predator density and the predators may have overwhelmed the defence mechanisms of even two parents. In years of lower predator density, male defence against piecemeal predators might be more effective. Similarly, in years of sustained bad weather, the male's help in permitting the female more time to brood might result in greater protection from starvation or exposure.

Some degree of annual variability with respect to the effect of male parental care did occur in this study (Tables II and III). Nestling survival was decreased in experimental broods to a greater extent in 1985 than 1984 and 1986. If some females are less able to raise young alone than others, then males that provide care to their young may benefit by buffering against environmental effects of year-to-year differences, reflected in factors such as weather or food availability (Lyon et al. 1987).

Survival to Independence and Return Rate the Following Spring

Survivorship from fledging to independence (ca. 27 days of age) was consistently lower in broods raised by one parent. This difference was significant in some years and highly significant when years were combined. We suggest a possible reason for this finding. The young disperse from the nest after fledging and soon become active. They probably require more food at this stage than during the nestling stage (Tyrväinen 1969; Smith 1978; Moreno 1984; Sullivan 1988; McGowan, personal communication), and we have observed a similar species studied (Ebenman & Karlsson 1984; Moreno 1984; Sullivan, in press; McGowan, personal communication), and we have observed a similar pattern in this population. Juncos are poorly developed when they fledge and most cannot yet sustain flight. Since food must be delivered to fledglings that are spatially scattered, single females may be unable to attend to more than about two fledglings. It thus appears that the male's care is not necessarily crucial for increasing the survival of his young during the nestling period, but is extremely important during the period between fledging and independence.

We considered whether young raised by one parent might suffer decreased physical condition and thus have lower survivorship after they reached independence. We found no difference in overwinter survival between female-only and two-parent young of either those known to have fledged or those known to have reached independence. We had expected a lower return rate of experimental young between fledging and the following spring, because survival from fledging to independence was reduced. That no statistical difference was detected may have been an effect of the small sample size of returning nestlings. However, the fate of the young that were not found in their first spring is unknown. The possibility remains that experimental and control juveniles may have dispersed differentially.

Influence of Mass at Fledging on Survival to Independence

It is usually assumed that mass is an index of condition and thus probable survival. Although positive correlations of fledging mass and survival have been demonstrated in several studies (Perrins 1965; O'Connor 1976; Nur 1984a), other studies have failed to find such a correlation (Ross & McLaren 1981; Groves 1984; Nur 1984a; Harris & Rothery 1985; Sullivan, personal communication). In this investigation, juncos that were lighter at fledging tended to survive better than did those that were heavier, contrary to expectation if greater mass indicates better condition. We considered above whether this finding might have been due to a confounding factor such as an effect of season on survival, but early-season and late-season fledglings were equally likely to die during the fledging period. Some other confounding effect that we did not measure may have caused this pattern, but, alternatively, the negative correlation of fledging mass and survival may have been real. Conceivably, heavier young may have suffered reduced mobility and thus may have been more susceptible to predation.

Comparisons with Other Studies

Other studies of monogamous passerine species in which males contribute parental care report varied results, which are summarized in Table VI. The summary is confined to passerines because

Table VI. Summary of results of male-removal studies performed on songbirds

Species	Mass of young	Tarsus length of young	Survival to nest-leaving	Survival to independence	Source
Group I†					
Tree swallow, <i>Tachycineta bicolor</i>	+	0	+	0	Robertson & Stutchbury (unpublished data)
Tree swallow, <i>Tachycineta bicolor</i>	+	0	+	0	Quinney (unpublished data)
Blue tit, <i>Parus caeruleus</i>	+	0	+	0	Sasvari (1986)
Great tit, <i>Parus major</i>	+	0	+	0	Sasvari (1986)
Great tit, <i>Parus major</i>	+	+	+	0	Björklund & Westman (1986)
Eastern bluebird, <i>Sialia sialis</i>	+	0	+	0	Robertson (personal communication)
Pied flycatcher, <i>Ficedula hypoleuca</i>	+	+	+	0	Alatalo et al. (1982)
Savannah sparrow, <i>Passerculus sandwichensis</i>	+	0	+	0	Weatherhead (1979)
Yellow-headed blackbird, <i>Xanthocephalus xanthocephalus</i>	0	0	+	0	Rutberg & Rohwer (1980)
House sparrow, <i>Passer domesticus</i>	+	0	0	0	Schifferli (1976)
Snow bunting, <i>Plectrophenax nivalis</i>	+	0	+	0	Lyon et al. (1987)
Group II†					
Eastern bluebird, <i>Sialia sialis</i>	=	0	=	0	Gowaty (1983)
Northern cardinal, <i>Cardinalis cardinalis</i>	=	0	=	0	Richmond (1978)
Seaside sparrow, <i>Ammodramus maritimus</i>	=	0	=	+	Greenlaw & Post (1985)
Dark-eyed junco, <i>Junco hyemalis</i>	+	=	=/+	+	Present study
Song sparrow, <i>Melospiza melodia</i>	+	0	=	=	Smith et al. (1982)
White-throated sparrow, <i>Zonotrichia albicollis</i>	+	0	=	0	Whillans-Browning & Falls (unpublished data)

Symbols: + indicates value significantly greater when male present, = indicates no significant difference when male present or absent, 0 indicates no data (or data were not presented in a manner that permitted comparison), =/+ indicates male made measurable contribution in some years but not in others.

* Represents mass or tarsus length of young as late-stage nestlings or at nest-leaving.

† Group I consists of species where removal decreased 'quality' or quantity of young; in group II, removal had little or no measurable effect prior to nest-leaving.

differences in the nature of parental care between passerines and non-passerines preclude direct comparison of male-removal studies (see Goforth 1964; Burley 1980; Pierotti 1980; Hannon 1984; Hitchcock & Mirarchi 1984; Martin et al. 1985; Martin & Cooke 1987). The reasons for different findings among the studies in Table VI are unclear, but possibilities include (1) methodological differences, (2) temporal and spatial variability in the importance of male parental care (some studies may have occurred in habitats or years in which male care was critical while other studies may have occurred in situations in which it was not), and (3) real, consistent differences among species in the impor-

tance of male parental care. Methodological considerations include differences in (1) sample sizes on which conclusions as to whether the male improves growth and survival of the young were based, and (2) the oldest age at which survival of young raised with and without a male was compared. Many studies in Table VI were based on small samples and most measured survival only until nest-leaving. However, the two studies in which fledgling survival was assessed (Smith et al. 1982; Greenlaw & Post 1985) agree with our findings: fledgling mortality tended to be comparatively high in female-only broods.

We have organized Table VI into two groups

according to whether the male was important for the growth and survival of his young. Group I consists of studies in which male-removal significantly decreased growth and/or nestling survival, and group II consists of species in which the male made little or no statistical difference. A pattern of note is that most species in group I are either cavity-nesters or breed at high latitudes; both are conditions that may increase the importance of the male's care. First, cavity-nesters tend to lay larger clutches than do open-nesters of comparable body size, a possible result of lower vulnerability of cavity-nesters to predation (Perrins 1965; Lack 1968; DeSteven 1980; Nur 1984a). Open-nesters may undergo greater selection for reduced clutch size because high predation rates force females to re-nest frequently, and the cost of egg laying may limit the production of too many large clutches. If males can help prevent predation of the young, then clutch size might increase and species with large initial brood sizes might benefit more from male parental care. Second, birds that breed at higher latitudes probably face more severe temperature stress, especially during the early-nestling period before the young become endothermic (Ricklefs 1983). Prolonged absence of the female from the nest in a cold climate (passerine males do not usually incubate or brood the young) could result in hypothermic, slow-growing nestlings (Nolan 1978; Bryant & Gardiner 1979; Murphy 1985); thus, the male's provisioning of food to the young may be important in allowing the female more time to brood them. In some monogamous species, females lose more body mass during the first half of the nestling period, when brooding is crucial; this may indicate the extent of the conflict between brooding and foraging (Westerterp et al. 1982; Nur 1984b).

Relationship of Mating Systems and Bi-parental Care

If the number of young that a male can produce with more than one female exceeds the number he produces as a monogamist, then a male will gain in fitness if he is polygynous (Maynard Smith 1977). In our study, the number of young reaching independence in two-parent broods that escaped predation was about 2.5 times that in female-only broods. This suggests that male juncos could increase their fitness if they could attract two females and feed the offspring of at least one. What

then constrains males to monogamy? Male-male competition may prevent males from acquiring sufficient resources to attract two females or females may simply accept only unmated males as mates. Still another explanation may hold in our population where predation is common and the sex ratio appears to be male-biased. Under these circumstances, females may have a choice of mates and the potential to enforce male parental care. If male aid is not adequate for the female during her first brood, she apparently has the option to re-nest with the same male or desert the territory and find a new male (Breitwisch et al. 1986). In this way, females conceivably could select for males that care for their young. We are currently testing this explanation experimentally.

Investigators have only just begun to assess the complexity of mating systems and their relationship to bi-parental care. Further studies are needed to explore the effects of males on survival of their offspring to the termination of parental care and also to identify the reproductive options of both the male and the female.

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