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TESTOSTERONE AND AVIAN LIFE HISTORIES: EFFECTS OF
EXPERIMENTALLY ELEVATED TESTOSTERONE ON
BEHAVIOR AND CORRELATES OF FITNESS IN THE
DARK-EYED JUNCO (*JUNCO HYEMALIS*)

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Abstract.—Hormones influence many aspects of organismal behavior, physiology, and morphology, and thus hormones may lie at the root of many life-history trade-offs. By manipulating hormones we can create novel phenotypes (i.e., perform phenotypic engineering) and attempt to relate phenotypic variation to fitness. We report the effect of testosterone treatment on parental behavior and vocal behavior of adult male dark-eyed juncos. Testosterone partially suppressed paternal behavior and increased the frequency of song. When we compared treated males and controls for nine potential correlates of fitness (offspring growth and survival to the age of 10 d, condition of females, length of the interval between consecutive nestings, size of subsequent clutches and broods, mate retention within and between breeding seasons, and survival rate), we found no statistical differences. In some measures treated males outperformed controls, but in most the reverse was true. The power of some of our tests was not great enough to detect small differences. At this stage of our investigation, three interpretations of our results seem almost equally probable: (1) a broad range of behavioral phenotypes is selectively neutral in the junco, (2) male parental behavior is beneficial to males only in some years or habitats, or (3) we have yet to measure the correlates of fitness that are most strongly affected by the behavioral changes induced by elevated testosterone.

Because the physiological and behavioral mechanisms that lead to life-history trade-offs are frequently under hormonal control (Stearns 1989), hormonal manipulations may allow investigators to perform a kind of phenotypic engineering in which they produce novel phenotypes. Comparisons of the attributes and relative fitness of these novel phenotypes to those of existing phenotypes provide an experimental approach to life-history evolution. By documenting the concerted effects of hormones on morphology, physiology, and behavior and relating these effects to survival, mate choice, and fecundity, it may be possible to determine why existing phenotypes persist (i.e., what maintains the status quo).

In birds, the hormone testosterone (T) affects parental behavior (Silverin 1980; Hegner and Wingfield 1987; Oring et al. 1989), vocal behavior (Wada 1981, 1982, 1986; Gyger et al. 1988; Harding et al. 1988; Nowicki and Ball 1989), and aggres-

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sive behavior (Balthazart 1983; Wingfield et al. 1987, 1990; Archawaranon and Wiley 1988; Beletsky et al. 1990), as well as locomotor activity (Wada 1982, 1986). It also influences metabolic rate (Hännöslér and Prinzingér 1979; Feuerbacher and Prinzingér 1981), lipid storage (Wingfield 1984; Ketterson et al. 1991*a*), and the timing and even the occurrence of prebasic molt (Runfeldt and Wingfield 1985; Schleussner et al. 1985; Nolan et al. 1992). Examples of other effects on birds are summarized by Wingfield et al. (1990), and examples from other vertebrate groups can be found elsewhere (Fox 1983; Townsend and Moger 1987; Marler and Moore 1988*a*, 1988*b*, 1989).

Manipulations of T in free-living male birds have shown that the physiological and behavioral effects of T can influence the major components of fitness, namely, the ability to acquire mates (see, e.g., Watson and Parr 1981; Wingfield 1984), produce offspring (Hegner and Wingfield 1987), and survive until the following year (Dufty 1989; Nolan et al. 1992). Some of these impacts on fitness are negatively correlated; for example, T increases the number of mates acquired in song sparrows (*Melospiza melodia*) but decreases survival in brown-headed cowbirds (*Molothrus ater*), which indicates the potential for antagonistic effects (Williams 1957; Studd and Robertson 1988). Only a few studies have addressed the simultaneous effects of T on both behavior and a wide array of fitness measures in a single species (Hegner and Wingfield 1987; Beletsky et al. 1990).

It is the general objective of this study to examine the relationships between hormones, behavior, and life histories in dark-eyed juncos (*Junco hyemalis*: Emberizidae) in order to increase understanding of how hormones influence behavior, how hormonal systems evolve, and the nature of the mechanisms involved in the evolution of trade-offs in life histories.

To ask how selection might act on individuals with hypothetical mutations that affect T secretion, we altered plasma concentrations of T in male juncos and induced behavioral changes. In this species, as in other songbirds, T rises in early spring, remains high during territory acquisition and pair formation, but then declines later in the breeding season (Wingfield and Moore 1988; E. D. Ketterson et al., unpublished observations). With T implants, however, it is possible to sustain T at peak physiological levels for the entire breeding season (Ketterson et al. 1991*a*).

The fate of an altered phenotype having high plasma T will depend on the relationship between hormone-induced behavioral and physiological changes and fitness. If high T causes male juncos to compete more effectively for mates or to be more attractive to females and if it influences no other traits, then a mutant phenotype might be expected to spread. If high T depresses parental behavior, as it does in some species, it might slow the growth of young or lower their survival, and counterselection might prevent spread. If females compensate for diminished male parental care by feeding young more frequently, but the extra effort influences their condition, females might delay their next broods, produce smaller clutches, or change mates. In such cases fitness of males with high T might be negatively affected.

We would expect deviant phenotypes to be at a net disadvantage when fitness measures are considered collectively, even if the deviants outperform the norm

on particular measures. It is possible, however, that physiological and behavioral changes would produce no detected changes in fitness, and in that case we might ask whether we were studying the right correlates of fitness or were working at a time or place in which selection was soft. Alternatively, we might conclude that within a broad range of phenotypes there are no detectable differences in fitness.

PREDICTIONS BASED ON EARLIER STUDIES OF JUNCOS

Since 1983 we have investigated a junco population having a male-biased sex ratio. In an earlier male-removal study the effects of depriving a female of her mate and thus of assistance in rearing young were investigated (Wolf et al. 1988, 1990, 1991). In the present study we treated males with T and, as we anticipated, reduced the level of male parental care. Our methods also differed from the male-removal work in that, instead of allowing nestlings to leave the nest, we took them late in nest life (simulating predation), hand-reared them to independence, and released them. Except where these methodological differences preclude meaningful comparisons, we expected our results to be similar to those of male removal.

In the removal study male juncos were caught and caged at the time their eggs hatched. Removed males were quickly replaced, and replacement males courted the now-unmated females, but they only rarely helped to care for the young. Unaided females doubled their feeding rates, which therefore equaled the rates of control pairs working together, and they devoted less time to brooding (Wolf et al. 1990). Their young weighed slightly less than control young at nest leaving (fledging), and fledgling survival was considerably lower (Wolf et al. 1988). Unaided females also lost more mass than controls, but there were no detectable effects on their subsequent nest attempts (usually as mates of the replacement males) such as effects on clutch size, egg size, time before reneating (Wolf et al. 1991), or survival to the following year (E. D. Ketterson, V. Nolan Jr., L. Wolf, unpublished manuscript).

However, in comparison to control females with mates, unaided females were more likely to leave the territory (and the replacement male) after nest failure in midseason and to pair elsewhere for the next nest attempt. Even those that did not move in midseason and that survived until the following year returned to their former breeding sites at a lower rate than did aided females (E. D. Ketterson et al., unpublished manuscript). Further, males whose females did not remate with them the following year were more likely to obtain no mate at all than were males whose mate from the previous year was still alive (E. D. Ketterson et al., unpublished manuscript). We hypothesized that the lower within- and between-year site fidelity in unaided females might be attributable to the fact that they had been required to care for their young without male help. If these females assessed the level of help they had received and associated the breeding location with low probability of male aid there, movement to a new location might be a good strategy to obtain greater male contribution in the future. In this view, females would be a selective agent enforcing male parental care, and paternal behavior could be viewed as a sexually selected trait.

METHODS

Species, Study Area, and Treatment

Dark-eyed juncos are socially monogamous (i.e., a male almost always consorts with one female), although we (in collaboration with P. Parker Rabenold) are at present gathering evidence showing that extrapair fertilizations (hereafter EPFs) occur. Only females build nests, incubate eggs, and brood nestlings. Males help feed nestlings and fledglings. We studied a nearly sedentary race at Mountain Lake Biological Station near Pembroke, Giles County, Virginia, from 1986 through 1989. The study area (described in Wolf 1987) is in the Appalachian Mountains, where juncos breed above approximately 1,000 m and usually make short movements to winter at lower elevations (Ketterson et al. 1991*b*). Males that survive winter almost invariably return to their territories of the previous year, and females also show considerable site fidelity. There are always unmated territorial males (E. D. Ketterson et al., unpublished manuscript), some for the full season and some for days or weeks, and at times their proportion may be as high as 10% of all males with territories (E. D. Ketterson et al., unpublished manuscript).

All pairs were color banded for individual identification. Testosterone (Sigma Chemical) was administered by subcutaneous implants of silastic tubing (Dow Corning, i.d. = 1.47 mm, o.d. = 1.95 mm, sealed with silastic glue) placed along the left flank while the subjects were under anesthesia. Implants of controls were identical but empty. In 1986, our pilot year, implant length varied from 18 to 24 mm. In 1987 and 1988, implants were 20 mm long. We refer to males implanted with T as T-males and to controls as C-males and for convenience apply T and C to their mates and young as well, even though only males received treatment.

During 1986 we treated six males, and all were given T. During 1987 there were 17 T-males and 14 C-males, while in 1988 we had 15 T-males and 17 C-males. Treatment was determined by the toss of a coin; for males studied in more than 1 yr, we reversed treatment between years. We inserted implants while the males' mates were incubating (late May to late June) and observed behavior at the nest after the eggs hatched. Implants were removed at the end of breeding (15 July–10 August).

We captured males and females just before their young were ready to leave the nest (day 10; hatching day = day 0), bled them for hormone assays (about 200 μ L from the alar vein), and weighed them (Pesola spring balance, nearest 0.1 g). The effect of the implants on plasma concentrations of T has been reported elsewhere (Ketterson et al. 1991*a*). In brief, T implants elevated T within 24 h and were effective for at least 40 d. Mean plasma concentration of T in T-males was 6.42 ng/mL, as compared to 2.1 ng/mL among controls (Ketterson et al. 1991*a*). This plasma concentration in T-males was like that in C-males and unimplanted males during the early spring maximum (Ketterson and Nolan 1992).

Observations at the Nest

We and our assistants observed the behavior of adults at 52 nests between 23 May and 16 July (years pooled). Observers did not know the treatment group of

the birds they watched. Watches took place during the morning, from cars or blinds or from distances that did not detectably affect the birds' behavior. They lasted between 1 and 2 h, typically 1.5 h, and the duration of each was decided before it was begun. We counted feeding trips to the nest by the male and the female, time spent brooding by the female, and songs sung by the male. We divided the nestling interval into thirds (days 0–3, days 4–7, days 8–10) and observed each nest once during each third, unless it was destroyed by a predator. Junco nestlings usually leave the nest on day 11–12 (Wolf et al. 1988).

Growth and Survival of Nestlings, Female Condition, Remating Frequency, Renesting Interval, and Size of Replacement Clutch

Clutch A of the pair was the first clutch known to have hatched that season (i.e., the clutch for which we treated the male and removed the young; see below), and clutch B was the next one produced by the female. We report clutch size only for nests that we found prior to laying and that were not parasitized by brown-headed cowbirds. Young in clutch A were counted and weighed (nearest 0.1 g using 10- or 50-g Pesola spring balances) during the afternoon on day 3, day 6 (when they were banded), and day 10. For analysis of growth we summed the mass of all members of the brood and computed the brood's mean. To estimate female condition, we captured and weighed females on day 10 of nestling life. To simulate predation, we removed the young from the nest at day 10 and reared them by hand.

After removing the young we followed pairs to determine whether the female renested and, if so, with what male. Pairs seen together 14 or more days after nest failure were considered to have remated, although we occasionally failed to find the nest. If we found the nest, we counted the number of days between removal of the young and laying of the first egg in clutch B (hereafter called the renesting interval) and the number of eggs in clutch B.

Mate Retention and Annual Rates of Return

In the year following treatment, we noted which males and females returned to the study area and, when both were alive, whether they remated. An occasional bird that we had injured was not considered in determining return rates. Because the sample for between-season mate fidelity was quite small, for one analysis we augmented the controls by adding a set of pairs in which the males had been unimplanted.

Statistical Analyses

We found no significant annual or seasonal variation in the dependent variables, so we pooled data across years and breeding seasons. All comparisons were two-tailed, and we used one standard error as the measure of variation about the mean. With one exception (see next paragraph), we set Type I error at 0.05, two-tailed. We performed analyses using the Statistical Package for the Social Sciences (SPSS) or SYSTAT (Evanston, Ill.).

Statistical analyses of behavior at the nest were of two kinds. First, within each third of the nestling interval we compared treatment groups and/or sexes

using *t*-tests. No individuals were observed more than once during each third, so the observations may be treated as independent for the particular third under consideration. However, because many of the individuals that we observed in the three periods were the same, we corrected for multiple comparisons by applying the Bonferroni correction (three tests; significance criterion 0.05 divided by 3 = 0.017). Second, we employed a repeated-measures ANOVA. This procedure has the advantage of avoiding repeated tests of significance on data collected from the same individuals at different times and of testing simultaneously the effects of age of young (third of the nestling interval) and treatment (or sex) of parent on behavior. However, it has the disadvantage of reducing the sample by restricting it to nests observed during all thirds of the nestling interval (i.e., nests not lost to predators). The two types of analyses gave similar results with two exceptions, which we note in the Results.

We assessed relative fitness of T- and C-males by comparing them for clutch size, mass of young, mass of female, renesting interval, mate retention within and between breeding seasons, and annual rates of male and female return in the year following treatment. The data for certain variables called for Mann-Whitney *U*-tests, which we performed. However, we also wished to calculate the power of these results. Because we are not aware of power tables for Mann-Whitney *U*-tests, we used the tables for *t*-tests in Cohen (1988) to determine the power of our tests to detect differences of 10%, 20%, and 30% between means of the two treatment groups (Type I error set at 0.05, two-tailed). We also used Cohen's tables to calculate the sample sizes that would have been required to detect treatment effects of 10%, 20%, and 30% with a power of 80%.

We compared return rates of males and females using a chi-square test of independence. For these contingency tables, we also determined degree of association, which can be expressed as a product-moment correlation coefficient, ϕ , and is equal to the square root of the chi-square value divided by the sample size. The square of ϕ is interpretable as a coefficient of determination (i.e., the proportion of variation shared by the two variables in the contingency table). For example, a ϕ of 0.5 relating treatment to return rate would indicate that 25% of the variation in return rate could be accounted for by treatment. We used the tables in Cohen (1988, table 7.3.15) to determine our power to detect various values of ϕ and thus ϕ^2 . We also determined the sample sizes that would have been required to detect ϕ 's of 0.1, 0.3, and 0.5 (Cohen 1988, table 7.4.6). We assessed mate retention during the season of experimental treatment and in the year following treatment with Fisher's exact test. We are not aware of any tables to calculate the power of Fisher's exact test.

RESULTS

Behavior at the Nest

Singing.—During all three nestling intervals, T-males sang more audible songs than did C-males (fig. 1). The effect of T on song rate was significant in one of the thirds of the nestling interval (*t*-tests, by thirds, $P = .008, .045, .110$), but it

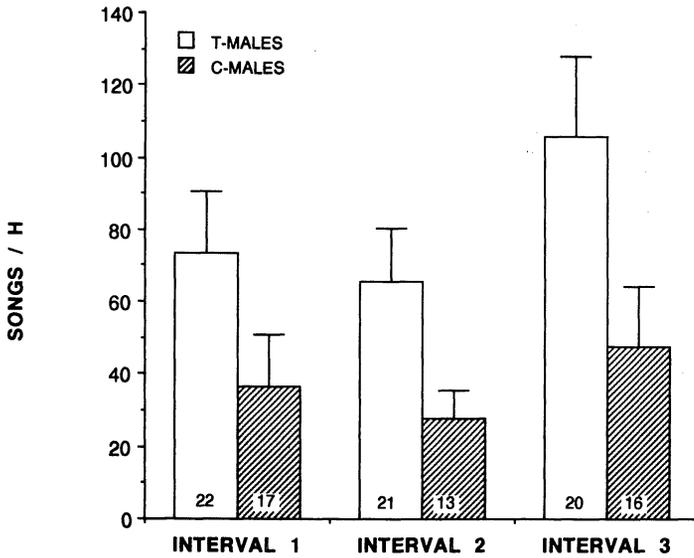


FIG. 1.—Effect of testosterone treatment on male song rate (mean \pm 1 SE). Intervals are thirds of the period between hatching and day 10 of nestling life. Sample sizes are shown at base of bars.

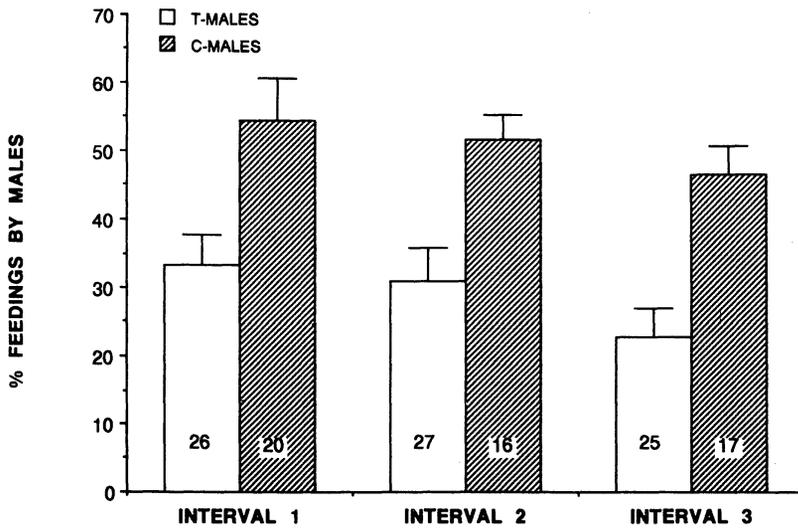


FIG. 2.—Effect of testosterone treatment on percentage of male feeding trips to the nest relative to feeding trips by female (mean \pm 1 SE). See caption to fig. 1.

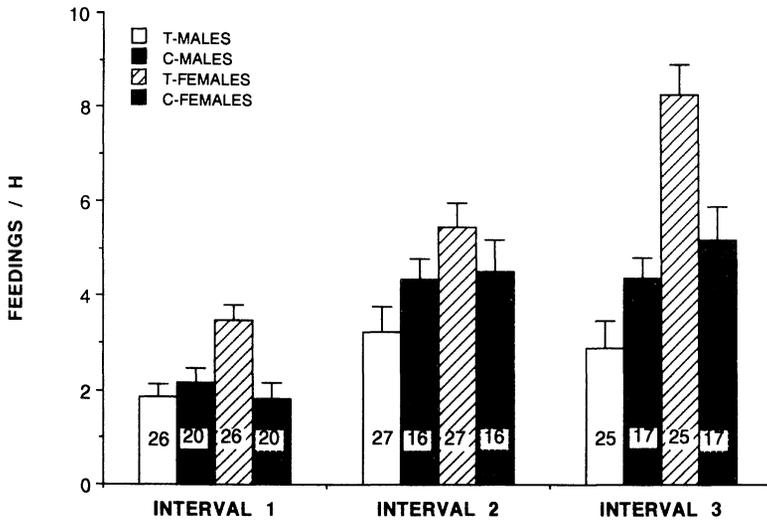


FIG. 3.—Effect of testosterone treatment on rate of food delivery to the nest by treated males and their untreated mates (mean \pm 1 SE). See caption to fig. 1.

was not significant in the repeated-measures ANOVA ($N = 26$, treatment $P = .186$, interval $P = .035$, interaction $P = .681$).

Feeding of young.—The proportions of the pair's total feeding trips to the nest contributed by T-males, according to thirds of the nestling interval, were 33.3%, 31.0%, and 22.8%, while the percentages by C-males were 54.5%, 51.7%, and 46.6%, respectively (fig. 2; t -test, by thirds, $P = .007$, .004, and .000; repeated-measures ANOVA, $N = 37$, treatment $P = .000$, interval $P = .089$, interaction $P = .746$). Thus, the percentage of feeding trips by T-males was significantly lower than that by C-males, and there was a tendency for the percentage to fall during the last third of the nestling stage.

When males were compared for number of feeding trips per hour (fig. 3), again according to thirds of the nestling interval, T-males came to the nest with food 1.8, 3.2, and 2.9 times per hour, as compared to 2.1, 4.3, and 4.4 times per hour for C-males (fig. 3; t -test, by thirds, $P = .50$, .18, .04; repeated-measures ANOVA, $N = 37$, treatment $P = .037$, interval $P = .000$, and interaction $P = .250$). The hourly feeding rate of T-males was significantly lower than that of C-males when the nestling interval was considered as a whole, and males, regardless of treatment, fed young more frequently as young grew older.

Among T-females, the feeding rates per third were 3.5, 5.5, and 8.3 trips per hour, while for C-females they were 1.8, 4.5, and 5.2 (fig. 3). Mates of T-males fed their young significantly more frequently than mates of controls during the first and final thirds of the nestling interval and also when the nestling interval was considered as a whole. Both groups fed more frequently as young grew older (t -tests, by thirds, $P = .002$, .257, and .003; repeated-measures ANOVA, $N = 37$, treatment of mate $P = .008$, interval $P = .000$, interaction $P = .096$).

When we compared males to their mates within treatment groups, T-males made feeding trips to the nest less frequently than T-females during all three thirds of the nestling interval (paired *t*-test, by thirds, $P = .004$, $P = .002$, $P = .000$; repeated-measures ANOVA, $N = 46$, sex $P = .000$, interval $P = .000$, interaction $P = .000$), whereas there were no differences between C-males and their mates (paired *t*-test, by thirds, $P = .308$, $P = .774$, $P = .274$; repeated-measures ANOVA, $N = 28$, sex $P = .741$, interval $P = .000$, interaction $P = .557$).

Finally, when we compared the pooled feeding efforts of males and their females according to treatment, T-pairs tended to feed young more frequently than C-pairs during the first and third intervals and only slightly less often during the middle interval, but none of the comparisons was statistically significant (interval 1: T-pairs, $N = 26$, 5.35 ± 0.46 , C-pairs, $N = 20$, 3.96 ± 0.59 , *t*-test, $P = .070$; interval 2: T-pairs, $N = 25$, 8.68 ± 0.82 , C-pairs, $N = 16$, 8.84 ± 1.02 , $P = .908$; interval 3: T-pairs, $N = 25$, 11.17 ± 0.83 , C-pairs, $N = 17$, 9.56 ± 0.95 , $P = .215$; repeated-measures ANOVA, $N = 35$, treatment $P = .501$, interval $P = .000$, interaction $P = .451$).

Brooding.—During the first third of the nestling interval, T-females brooded $57.5\% \pm 4.3\%$ of the time, as compared to $51.4\% \pm 5.2\%$ for C-females ($N = 27, 20$; *t*-test, $P = .370$). During the second third the respective percentages were $27.3\% \pm 5.3\%$ and $25.0\% \pm 4.8\%$ ($N = 26, 16$; *t*-test, $P = .769$), and during the final third they were $4.9\% \pm 3.8\%$ and $6.9\% \pm 2.8\%$ ($N = 24, 15$; *t*-test, $P = .643$). Thus, the percentage of time spent brooding (by females) declined with the age of nestlings but did not vary with male treatment (repeated-measures ANOVA, $N = 33$, treatment $P = .556$, interval $P = .000$, interaction $P = .998$).

Growth and Survival of Nestlings, Female Condition, Renesting Interval, and Size of Replacement Clutch

Treatment had no significant effect on size of clutch A (table 1; $P > .1$) or on number of eggs that hatched from clutch A (table 1; $P = .696$). The average brood size of day-10 young produced by T-pairs and C-pairs, 3.1 and 3.3, respectively, was also quite similar (table 1; $P = .460$), as was mean mass of these young, 16.9 g versus 17.2 g (table 1; $P = .390$). At the time we removed young on day 10, females from both treatments were nearly identical in mean mass: 20.4 g for T-females and 20.3 g for C-females (table 1; $P = .680$). The renesting interval for T-pairs was 8.2 d versus 7.1 d for C-pairs (table 1; $P = .350$). Also similar was the size of clutch B: 3.6 eggs for T-pairs and 3.8 eggs for C-pairs (table 1; $P = .560$). Finally, the number of eggs hatching in clutch B did not differ between T-pairs and C-pairs: 3.2 versus 3.4 (table 1; $P = .870$).

Among the eight comparisons in table 1, we did not expect the first two to differ because the birds were not implanted until after the eggs had been fertilized and laid. Of the remaining six, C-pairs performed better than T-pairs on five, and T-pairs performed better on the other one. As stated, we calculated (1) the power of our tests to detect 10%, 20%, and 30% differences in the means and (2) the sizes of the samples that would have been required to make these same detections with a power of 80% (table 2; see Cohen 1988). If we use the criterion 80% power

TABLE 1

COMPARISONS OF FITNESS CORRELATES ACCORDING TO TREATMENT, T-PAIRS VERSUS C-PAIRS

	T-PAIRS			C-PAIRS			<i>P</i>
	\bar{X}	<i>N</i>	SE	\bar{X}	<i>N</i>	SE	
No. of eggs laid, clutch A	3.8	25	.09	4.1	17	.15	.104
No. of eggs hatched, clutch A	3.5	27	.12	3.5	18	.22	.696
No. of nestlings at day 10	3.1	26	.18	3.3	15	.25	.460
Nestling mass (g), day 10	16.9	21	.26	17.2	15	.28	.360
Female mass (g), day 10	20.4	20	.26	20.3	14	.22	.680
Renesting interval (d)	8.2	16	.95	7.1	15	.66	.350
No. of eggs laid, clutch B	3.6	14	.13	3.8	10	.20	.560
No. of eggs hatched, clutch B	3.2	9	.41	3.4	11	.25	.870

NOTE.—Comparisons by Mann-Whitney *U*-test except for nestling mass, female mass, and renesting interval, in which *t*-tests were used.

to detect a 30% difference, we may conclude that treatment with T had no effect on the mean number of young surviving to day 10, nestling mass at day 10, female mass at day 10, and number of eggs in clutch B. Only the renesting interval (power = 42%) and the number of eggs hatching in clutch B (power = 51%) fail to meet this criterion. If we raise the criterion and require the ability to detect a 10% difference in the means with a power of 80%, two variables meet the criterion: nestling mass at day 10 and female mass (table 2).

Mate Retention and Annual Rates of Return by Females

Female within-season desertion of males after nest failure did not differ according to treatment. One of 21 females mated to T-males left the territory after we removed their young, as compared to 0 of 13 females mated to C-males (table 3; Fisher's exact test, two-tailed $P = 1.000$).

Estimating minimum annual survival rate as the proportion of males that returned to breed in the year following treatment, we found no difference in survival of T- and C-males. Of 32 males treated with T, 22 were present in the year after treatment (69%). For C-males the comparable numbers were 15 of 29 (52%) (table 3; $\chi^2 = 1.847$, $df = 1$, NS). The association between treatment and return, ϕ , is 0.0174. The power of the test to detect a ϕ of 0.1 is 12%; for 0.3, it rises to 64%; and for 0.5 it is 97% (P set at .05, $df = 1$). Sample sizes that would have been required to detect ϕ of these same values with a power of 80% are 785, 87, and 31, respectively. Our sample was 61. In other words, given the small observed difference in return rate, our sample was adequate to detect only relatively large effects on return rate.

When we compared female rates of return to the study area in the year following treatment of their mates, we found 14 of 36 T-females (39%) and 12 of 26 C-females (46%) returning to breed ($\chi^2 = 0.327$, $P = .567$). The correlation coefficient between treatment and return, ϕ , was 0.0073. The power of the test and the sample sizes required to detect various levels of association were nearly identical to the values just presented for males.

TABLE 2
POWER OF TESTS REPORTED IN TABLE 1*

Variable and Percentage	N'	σ'	Power (%)	N
No. of eggs laid, clutch A:				
10	20.2	.550	63	30
20			99	<9
30			>99	<9
No. of eggs hatched, clutch A:				
10	21.6	.794	30	85
20			80	19
30			98	10
No. of nestlings at day 10, clutch A:				
10	19.0	.943	18	137
20			55	33
30			88	13
Nestling mass, day 10:				
10	17.5	1.139	>98	<9
20			>98	<9
30			>98	<9
Female mass, day 10:				
10	16.5	1.007	>97	<9
20			>97	<9
30			>97	<9
Renesting interval:				
10	15.5	3.238	8	351
20			22	86
30			42	38
No. of eggs laid, clutch B:				
10	11.7	.564	14	96
20			88	8
30			>99	<7
No. of eggs hatched, clutch B:				
10	10	1.049	11	39
20			27	39
30			51	21

* Column symbols are defined as follows: Percentage refers to postulated levels of detectable differences in the means of the two treatment groups; N' refers to our observed sample sizes, adjusted to take account of the fact that groups were unequal in size; σ' refers to the mean square of the SDs of the treatment groups; power is the power to detect differences between the means of treatment groups at the postulated levels using the data actually observed; N is the sample size that would have been required for each treatment to detect differences of 10%, 20%, and 30% with a power of 80%, given the observed σ . (See Cohen 1988, tables 2.3.5 and 2.4.1.)

Comparing mate fidelity of returning females whose mates of the preceding year had also returned, eight of nine returning T-females remated with the same male (89%); the ninth female (11%) is the one that had deserted her mate and joined another male during the previous year (table 4). If she is excluded because she had already relocated in the year before returning, then 100% of the T-females rejoined their mates. Of seven returning C-females whose former mates were also present, five remated with their former mates (71%), and two (29%) changed mates. Interestingly, one of these two had been a secondary female in a polygy-

TABLE 3
ANNUAL RATE OF RETURN BY MALES AND FEMALES

	RATE OF RETURN (%)			
	T		C	
	Return*	No Return	Return*	No Return
Between seasons:				
Males	69 (22)	31 (10)	52 (15)	48 (14)
Females	39 (14)	61 (22)	46 (12)	54 (14)

NOTE.—Numbers in parentheses are sample sizes.

* Return refers to breeders in 1 yr that were captured or sighted on the study area during the next year.

TABLE 4
MATE FIDELITY OF FEMALES

	MATE FIDELITY (%)			
	T-FEMALES		C-FEMALES	
	Faithful*	Not Faithful	Faithful*	Not Faithful
Within seasons	95 (20)	5 (1)	100 (13)	0 (0)
Between seasons	89 (8)	11 (1)	71 (5)	29 (2)

NOTE.—Numbers in parentheses are sample sizes.

* Faithful females are those that remained with their mate for repeated breeding efforts in the same season or that mated with their previous year's mate, when that mate also returned. Males that returned invariably occupied all or part of their territory of the preceding year.

nous association in the preceding year. Treatment had no detectable effect on mate fidelity (Fisher's exact test, two-tailed $P = .550$).

We broadened the last comparison by adding to the C-females a set of returning females that had been mated to returning males that were untreated during the three years of the study (1986–1988). In this augmented sample, 11 of 14 females that were not mated to T-males were mate-faithful (79%), as compared to the eight of nine for T-males (89%) (Fisher's exact test, two-tailed $P = 1.000$).

DISCUSSION

Testosterone and Vocal Behavior

Testosterone-implanted male juncos sang more often than C-males (fig. 1), significantly so in one analysis. Testosterone also led to more frequent song in the pied flycatcher *Ficedula hypoleuca* (Silverin 1980) and the house sparrow *Passer domesticus* (Hegner and Wingfield 1987). Presumably this effect results

from the action of T on the vocal centers in the brain and/or the periphery (Arnold 1982; Kelley and Tobias 1989).

While frequent song is also a striking characteristic of unmated, untreated male juncos, singing T-males behaved somewhat differently than unmated males. Unmated males tend to sing from high perches, often just below the canopy, while mated T-males with nestlings tended to sing from perches not far above the nest, which for juncos is usually on the ground. Furthermore, although we did not quantify amplitude, songs of T-males were frequently muted, whereas "advertising" unmated males usually sing at full volume.

The increase in song frequency might possibly cause T-males to attract more mates. Experimentally elevated T has led to polygyny in avian species that are normally monogamous (Watson and Parr 1981; Wingfield 1984), but this effect was not observed in pied flycatchers, in which bigamy is common even in the absence of experimental manipulation (Silverin 1980). We observed no cases of polygyny among treated males. We implanted our subjects after territories had been established, and this fact as well as the male-biased sex ratio may have caused polygyny to be unlikely. (However, our more recent studies of males implanted in early spring before they became territorial also did not result in polygyny [Ketterson and Nolan 1992].)

Testosterone and Parental Behavior

As in pied flycatchers (Silverin 1980), house sparrows (Hegner and Wingfield 1987), and spotted sandpipers (*Actitis macularia*) (Oring et al. 1989), experimentally elevated T interfered with parental behavior of male dark-eyed juncos. When food deliveries by both members of the pair were combined, T-males made a smaller percentage of food deliveries to the nest. They also fed their broods less frequently than C-males, particularly as the young grew older.

When one parent reduces its delivery of food to nestlings, the other parent is expected to compensate but, according to theory, not completely (Houston and Davies 1985; Winkler 1987). The total number of feeding trips to young juncos, however, was the same regardless of male treatment because T-females did compensate fully and consistently fed young more frequently than C-females. The T-females also spent as much time brooding as C-females.

Comparing our results to those from other species in which male participation was experimentally reduced but not eliminated, we note that in pied flycatchers T-females did not increase their feeding frequency (Silverin 1980), whereas T-female house sparrows did so (Hegner and Wingfield 1987). Female starlings (*Sturnus vulgaris*) mated to males that provided reduced care because lead weights had been glued to their tail feathers (Wright and Cuthill 1989) also increased their rate of feeding, although, like female house sparrows, not to values that were fully compensatory.

Interestingly, the feeding rate of female juncos mated to T-males was intermediate between those of the normally aided and the entirely unaided females in an earlier male-removal study (fig. 4) (Wolf et al. 1990). In steplike fashion, female juncos work least when their mates contribute their full share, more when their mates participate at a reduced level, and most when forced to rear young alone.

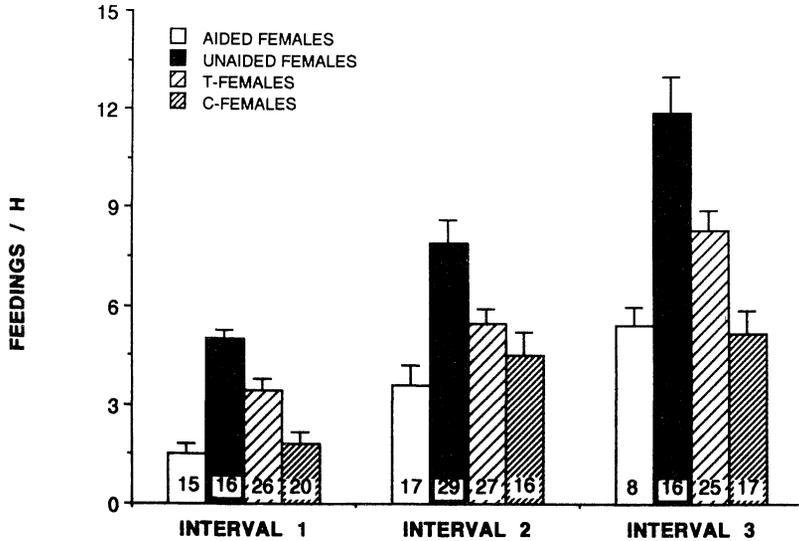


FIG. 4.—Comparison of female feeding rates according to treatment of their mates (mean \pm 1 SE). See caption to fig. 1. Unaided females were mates of males removed in an earlier study (Wolf et al. 1990); aided females were their controls and were helped by their mates. The T- and C-females are as described in text.

Thus, despite considerable natural variation in weather, brood size, and food availability, one of the most important variables (as opposed to cues) that determine feeding rates by female juncos is the contribution of the male. It also seems clear that under ordinary circumstances female juncos hold in reserve much of their capacity to deliver food. Put otherwise, pairs of juncos could feed larger clutches than females in fact produce. We speculate that this less than all-out effort may reduce predation on females while foraging and also permit them to remain at or near the nest and thus detect and defend against nest predators. (Females as well as males often drive away chipmunks [*Tamias striatus*] that they see near the nest; chipmunks are the most common nest predator in our study area.) It also seems likely that time pressures imposed by the heavy nest predation may be more important in shaping clutch size in juncos than the factors traditionally invoked to explain limits to clutch size (reduced growth and survival of young belonging to larger broods). That is, an increase in clutch size prolongs the nesting cycle by 1 d per egg laid, which raises both the probability of predation and the probability that there will be no time left to nest again if predation occurs.

What cues do females use to set their levels of parental effort? For the junco it appears probable that the behavioral mechanism responsible for female compensation involves the begging calls of the young (von Haartman 1953; Hussel 1988). Hungrier young presumably call longer or more loudly when a parent visits, and these calls presumably stimulate further foraging and food delivery. In this view, the dynamic, so long as young are hungry, is one of positive feedback: the more an adult feeds, the more often it hears begging. If T-males are

slower than their mates to return after a feeding, then females are likely to hear hungry young during a greater proportion of visits to the nest, and they will be stimulated to feed more frequently.

However, there is an alternative, though less likely, possible stimulus of the increased feeding by T-females. Tape-recorded song stimulates nest building in captive female canaries (*Serinus canaria*) (Hinde and Steel 1976; Kroodsma 1976), and exposure to the somewhat more frequent song of T-males may have an analogous effect on feeding of nestlings by female juncos (cf. Silverin 1980).

Rates of feeding and brooding are, of course, only two components of provisioning young and parental care. Size of the load delivered, quality of food items brought, and level of nest defense are other important considerations (see, e.g., Nolan 1978, pp. 269–270), and these components may have differed between treatment groups.

Testosterone and Correlates of Fitness

Nestling survival.—The T-pairs raised as many young to age 10 d as C-pairs, and the young were of comparable mass, apparently because of the capacity of female juncos to respond to alterations in the behavior of their mates. Because we removed young when they were ready to leave the nest, we cannot compare survival of T- and C-fledglings between nest leaving and independence. Male-removal studies have shown that female juncos have considerably lower success when attempting to rear fledglings alone than when they have male help (Wolf et al. 1988), and this is an important fitness correlate that we are now measuring in T-pairs.

Correlates of female condition.—There was little evidence for a decline in condition of T-females. Mass of T- and C-females did not differ at day 10 of the nestling period, unlike the result when females receive no male assistance at all (Wolf et al. 1991). There were also no differences in probability of reneating, time elapsed before reneating, or size of the clutch in the subsequent nests (although, as noted, the power of some of these comparisons was quite low). These results resemble comparisons of house sparrows whose mates were or were not treated with T (Hegner and Wingfield 1987). Finally, there was little indication that the increased feeding effort of T-female juncos affected their long-term survival, since females of both treatment groups returned at similar rates to breed the next year (T-females, 39%; C-females, 46%). The 46% return rate by C-females was nearly identical to the rate observed in our earlier study of female juncos whose mates we removed (E. D. Ketterson et al., unpublished manuscript). Since we did not detect a lower return rate in these females that were entirely unaided, it is likely that the nonsignificant difference observed in the present study is attributable to chance. This result differs from that of Askenmo (1979), who found a negative relationship between reproductive effort and return rate in pied flycatchers. The rate among males that fed experimentally enlarged broods was 18% as compared to 38% for males with normal broods.

It may be, when we allow young to leave the nest (in work that we have just begun) and compare C- and T-pairs, that the efforts of T-females to raise fledglings to independence will affect female condition, even if brood size at independence

is unaffected. However, in a male-removal study of entirely unassisted females, no significant effects were found on probability of reneating, reneating interval, size and quality of clutch B, or, as just noted, female return rate the next year (Wolf et al. 1991; E. D. Ketterson et al., unpublished manuscript).

Minimum survival rates in males.—Dufty (1989) reports reduced rates of return to his study area by T-implanted male cowbirds, but in the present study the rate of return of T-males was actually somewhat higher than in C-males. Nevertheless, plasma corticosterone of T-males was elevated (Ketterson et al. 1991a), which may indicate stress that could influence survival (Siegel 1980; Silverin 1982). Although we found no effect of T on male survival, we believe that survival might fall if we varied the time of inserting T implants or removing them. Elsewhere (Ketterson et al. 1991a) it is reported that fat stores of T-males treated in early spring quickly dropped to breeding-season levels (no subcutaneous fat detectable), whereas C-males delayed reduction of fat until the start of breeding. This response to early T could be costly in years when harsh late-spring weather produces unexpected energy demands that require fat reserves; such weather is not uncommon at the altitudes at which these juncos breed. At the other extreme, T-males whose implants were not removed until October delayed postnuptial molt (Nolan et al. 1992), and those whose implants were not removed at all returned next year at a significantly lower rate than normal. Thus, the timing of administration of T appears to have an important bearing on conclusions about its effects on fitness.

Do Females Enforce Male Parental Care in Dark-eyed Juncos?

Females of T- and C-pairs were equally unlikely to switch mates, both within and between seasons. Recalling that there are always unmated territorial males, we find the absence of within-season mate desertion by T-females especially interesting. Unmated males or their territories may be inferior for some reason, but we have observed individual males that have been unmated in 1 yr and have had mates at the same site in earlier or later years. This suggests that the failure of T-females to desert their mates was not caused by a shortage of suitable alternative options, although females may have imperfect information about the locations of unmated males (e.g., see the search-cost model of Searcy and Yasukawa [1989] to explain the occurrence of territorial polygyny; cf. Nolan 1978, p. 363). Furthermore, even if T-females were unaware of alternative males in the current year, they had the option to change mates at the beginning of the following breeding season, and yet they rarely did.

Why do females remain mated to males that provide reduced parental care? The simplest explanation is that the advantages of nesting in a familiar location outweigh the costs of mating with a male that has proved to be a poor father. If so, maintenance of male parental care is not likely to be attributable to sexual selection (i.e., female preference for males that feed offspring). Another hypothesis is that females use song frequency to assess a male's attractiveness and that the tendency of T implants to increase song rate triggered this mechanism and thus influenced mate fidelity. Burley (1986) has suggested that females should work harder when mated to males that are attractive, in order to produce high-

quality sons (differential allocation hypothesis); perhaps the same is true for mate fidelity. If T is also correlated with sperm production (for a review see Lofts and Murton 1973, but see Desjardins and Turek 1977), frequent song might serve as an indicator of fertility and similarly foster mate fidelity in females.

Testosterone and Avian Life Histories

If a novel phenotype were to arise, characterized by elevated T levels throughout the breeding season, would that phenotype spread? Obviously, this would require heritable variation in patterns of T secretion, a subject that has received little study in birds. Several bird species exhibit heritable variation in aggressive behavior (Boag 1982; Moss et al. 1982), which depends on T, and studies have demonstrated that T-related traits respond to selection (Sefton and Siegal 1975; Cunningham and Siegal 1978). Therefore, it seems probable that natural variation in T has some genetic basis.

The question, then, is whether T-induced behavioral differences are reflected in fitness and, if so, whether benefits outweigh costs. To the extent that selection must act on the whole phenotype (Travis 1989), changes that are advantageous when considered alone will be selected for only to the extent that they are not counterbalanced by disadvantageous changes in other traits. Thus, predicting the course of a phenotype with elevated T requires consideration of the role of selection on all correlated traits.

In fact, we observed little effect of behavioral alterations on survival or reproduction, although we have pointed out aspects of our data that are not very robust. If we simply compare means, controls outperformed experimentals on six of our nine correlates of fitness. But the power of our tests was variable and in some analyses (e.g., renesting interval and number of eggs hatching in clutch B) was quite low. If we assume our tests did have sufficient power, how can we account for our failure to find that T affected fitness? First, the data would be consistent with the view that a wide range of equally fit phenotypes can exist (see, e.g., Stearns 1989). Alternatively, the fitness of the high-T phenotype may differ, but the differences (1) were too small for us to detect or (2) were nonexistent in this study but would be detectable in other years or other environments. (A male-removal study revealed annual variation in the effect of removal on mass of fledglings [Wolf et al. 1988] and on female mass at fledging [Wolf et al. 1991].) Yet another possible explanation for our failure to find an effect of T on fitness is that (3) the measures of fitness we used were not the ones that are sensitive to the behavioral changes we induced.

It seems almost certain that there are spatial and temporal differences in the balance of costs and benefits of male parental behavior (and therefore of underlying levels of T). Two environmental variables that are likely to be important and that would favor flexibility in male parental behavior are density of nest predators and availability of food. In years when nest predation is high, females are forced to renest frequently, the population becomes highly asynchronous in stage of reproduction, and at any given time a number of females may be fertile. In such years, males might have much to gain from seeking fertile females and EPFs (Westneat et al. 1990), although the heavy nest predation would reduce the num-

ber of surviving young fathered in this way. On the other hand, in years when food is in short supply, males might improve their reproductive success by tending the offspring of their own mate rather than by diverting time and energy to the search for EPFs. When we learn the effect of treatment with T on survival of the male's fledglings and on EPFs, we may then be able to make more confident statements about the expected fate of novel phenotypes.

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