

# The Influence of Exogenous Testosterone on the Dynamics of Nestling Provisioning in Dark-Eyed Juncos

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## Abstract

In many songbird species, application of exogenous testosterone (T) during the breeding season has the general effects of reducing male parental investment and increasing allocation of time and energy to mating. Most studies record the number of feeding trips made by males as a function of their hormone treatment, but few have investigated the ways in which testosterone affects the dynamics of male and female provisioning behavior or the quantity of food delivered by males. We attempt to fill these gaps in our understanding of testosterone and male parental effort by utilizing data from a long-term study on the behavioral endocrinology of the dark-eyed junco (*Junco hyemalis*). We found that male and female feeding rates covaried positively, although to different degrees, throughout the nestling period, but that this relationship was degraded in pairs in which males were given T implants. We also found that the coefficients of variation in the duration of intervals between successive feeding trips by males and females were highly positively related in broods of older nestlings. Male hormone treatment, however, had no effect on the coefficients of variation in either male or female feeding intervals. Finally, we examined the quantity of prey delivered by males and found no significant effect of hormone treatment.

## Introduction

In bird species with biparental care, optimal levels of parental effort differ between males and females. Provisioning of young by both sexes is strongly affected by the energetic needs of the offspring, and therefore is related to brood size and brood age (Hatchwell & Davies 1990; Yasukawa et al. 1990; Sanz & Tinbergen 1999). Provisioning may be particularly influenced by extrinsic factors such as food availability and predation risk and, in the case of males, opportunities for polygyny or extra-pair matings (Ketterson & Nolan 1994; Whittingham & Robertson 1994; Magrath & Elgar 1997; Ghalambor & Martin 2000). Both males and females vary their parental effort in response to the contributions of their mate (Houston

& Davies 1985; Winkler 1987; Hinde 2005). Males, however, are generally less likely to increase their effort when female effort decreases (Slagsvold & Lifjeld 1990; Sanz et al. 2000).

Experimental studies on the dynamics of biparental care in birds have utilized a range of manipulations, including removal of one partner (Bart & Tornes 1989; Hatchwell & Davies 1990; Wolf et al. 1990) and physical handicapping (Wright & Cuthill 1989, 1990; Slagsvold & Lifjeld 1990). Another fruitful approach has been to manipulate steroid hormone levels. It has been repeatedly demonstrated that the application of the androgen testosterone (T) suppresses male parental effort (Silverin 1980; Hegner & Wingfield 1987; Oring et al. 1989; Ketterson et al. 1992; Stoehr & Hill 2000; Peters

et al. 2002; Schwagmeyer et al. 2005; but see Lynn et al. 2002). More recent studies have taken a similar approach with females (De Ridder et al. 2002; Clotfelter et al. 2004). The exact mechanism by which testosterone reduces parental effort is not clear, but one alternative, that it directly affects prolactin levels or prolactin binding sites in the brain, has not received support (Oring et al. 1989; Schoech et al. 1998). Regardless of the physiological mechanisms involved, males with elevated testosterone (hereafter T-males) typically allocate more time and energy to singing, territory defense, and the pursuit of additional matings than do their control counterparts (hereafter C-males) (Wingfield 1984; Chandler et al. 1994; De Ridder et al. 2000; Stoehr & Hill 2000; Peters 2002). Females mated to T-males often increase their parental effort to compensate for their mates' behavior (Ketterson et al. 1992; Hunt et al. 1999; Stoehr & Hill 2000).

Several questions remain, however, regarding the complex compensatory relationship between male and female parental behavior and how this relationship is affected by elevated testosterone. Our goal was to test the following predictions using data derived from a study of dark-eyed juncos (*Junco hyemalis*) obtained over parts of a 15-year period. First, we predicted that male and female provisioning behavior in control pairs would covary negatively during the early brood stage when females are obligated to spend time brooding nestlings, and positively during the late brood stage when nestling demands are highest (Wolf et al. 1990; Nolan et al. 2002). Second, given recent data suggesting that parental behavior is insensitive to elevated testosterone when nestling need is great (Van Duyse et al. 2000; Lynn et al. 2002; Clotfelter et al. 2004), we predicted that provisioning behavior by T-males would be similar to C-males in the early and late brood stages, but would covary negatively with female provisioning rates during the middle brood stage when females are most able to meet the brood's needs alone. Third, we predicted greater variation in between-feeding intervals (BFIs) (Grieco 2001, 2002) in males treated with T compared with control males, as T-males would be more likely to pursue extra-pair matings (Raouf et al. 1997; Reed et al. 2006). As a consequence of changes in male behavior, we predicted the opposite would be true of females, that they would become more regular (i.e. less variable) in their provisioning behavior. Finally, based on previous research showing a prey-size bias in T-males when foraging for themselves (Clotfelter et al. 2001), we tested the hypothesis that T-males

might compensate for reduced provisioning rates by increasing the quantity of food delivered per visit. Thus, we predicted that T-males might bring fewer, larger prey items to their young than did C-males (cf. Schoech et al. 1998).

## Methods

### Study Site and Species

We have studied a color-banded population of dark-eyed juncos (*Junco hyemalis carolinensis*) at the Mountain Lake Biological Station in Giles County, VA, USA (37°22'N, 80°32'W) since 1983. Chandler et al. (1994) give a detailed description of the study area. Dark-eyed juncos (Order Passeriformes, Family Emberizidae) are socially monogamous birds with biparental care. Brood size is typically 3–4 nestlings, which remain in the nest for approximately 12 d, during which they are fed primarily arthropods (Nolan et al. 2002).

### Hormone Implants

In 1987, we initiated a study of adaptive variation in testosterone levels. The rationale for this study and a summary of the major results are given by Ketterson et al. (2001). The implantation methods we used have been reported elsewhere (Ketterson et al. 1991, 1992), but are outlined briefly here. We caught males in mist nets or baited Potter traps in April and early May of each year. Males were randomly assigned to one of two treatment groups: testosterone (T) or control (C). Males of both treatments were implanted subcutaneously with two 12-mm implants (i.d. = 0.58 mm, o.d. = 0.77 mm) made of Silastic® tubing sealed with Silastic glue® (Dow Corning, Midland, Michigan, USA). T implants were packed with crystalline testosterone (Sigma-Aldrich, St. Louis, Missouri, USA) and C implants were empty. Assays have demonstrated that T implants maintain plasma levels of testosterone at the normal spring maximum levels (Ketterson et al. 1991). Females were not treated, but are often referred to by the category to which their mate was assigned (e.g. t- or c-female). We use lower-case letters to distinguish them from other studies in which females themselves were implanted with testosterone (T-females; Clotfelter et al. 2004).

After implantation we released all males at their capture sites, monitored their behavior, and located their nests in the subsequent days and weeks. Following clutch completion and a 12-d incubation period, nests were checked daily for hatched eggs. The

day on which nestlings hatched was designated day 0. For the feeding observations described below, observers used portable blinds, vegetation, or automobiles to conceal themselves.

### Covariance in Feeding Rates

We observed the rates at which nestlings were fed by T- and C-males and their respective mates during three brood intervals: early (days 0–3), middle (days 4–7), and late (days 8–11). Because of predation and failure to locate some nests until after hatching, nests from later brood intervals are only a partial subset of nests from earlier intervals. During each feeding watch, which began when both adults ceased alarm calling, we counted food deliveries by each parent over a 1- to 2-h period (determined a priori). These observations were conducted between 06:00 and 12:00 hours EDT during the 1987–1988 breeding seasons.

### Between-Feeding Intervals

We observed nestling feeding rates by T- and C-males and their respective mates in 1995–1997 to measure the coefficient of variation (CV) in intervals between successive feedings. We used CV as our measure of variation because of the considerably different mean feeding rates among males and between males and females. BFIs were calculated when nestlings were 6 and 9 d old. We conducted feeding watches at various times between 07:00 and 19:00 hours EDT. Each feeding watch was 90 or 120 min in duration (determined a priori) and began when both adults ceased alarm calling. For each feeding visit to the nest, the time (to the nearest minute) and the sex of the parent were recorded. BFIs were measured as the number of minutes between feeding trips. We excluded from our analyses the intervals at the beginning (before the first feeding) and end (after the last feeding) of each observation period. Analyses not reported here show that the inclusion of these 'truncated' intervals yields similar results.

### Prey Load Sizes

We applied neck ligatures to nestling juncos in 1999 and 2000 to determine the quantity and size of prey delivered by T- and C-males. These manipulations were performed when nestlings were 6 or 7 d old. Before each observation we caught the female in a mist net and put her in a holding cage away from the nest. Females were removed so that we collected

only prey items provided by males. We attached black plastic ligatures (3 × 100 mm cable ties; Mellott & Woods 1993), which were tightened until snug around the neck of each nestling in the brood, after which the ends of the ligatures were trimmed away. We then monitored nestlings for 5 min before returning them to the nest. If a nestling appeared distressed, we immediately removed the ligature, waited 5 min, and applied another one. The entire process took 15–20 min. We returned to the nest after 60 min. From each nestling we extracted the food bolus (if any) with forceps. We removed the ligatures, returned the nestlings to the nest, and released the female. In no case was the female absent from the nest for more than 90 min, and there was no mortality associated with this procedure. This procedure was conducted with the approval of Indiana University's Institutional Animal Care and Use Committee. The prey items we retrieved from nestlings were preserved in ethanol; they were later dried for 24 h at 80°C and weighed to the nearest mg. In addition to total prey loads, we calculated the mean mass of intact prey items brought by each male. Partial prey items were not included in the latter analysis.

### Statistical Analyses

We conducted analyses (major-axis regressions, linear regressions, and ANCOVA) using SPSS (SPSS, Chicago, Illinois, USA) and SYSTAT (SYSTAT Software, Richmond, CA, USA). For the BFI data, we conducted stepwise backward regressions ( $p = 0.10$  to enter model,  $p = 0.15$  to leave) and included male hormone treatment (0 = control, 1 = testosterone), study year (1995–1997), time of day, Julian date, observation duration (90 or 120 min), and brood size (2–4) as independent variables. Mean values are presented  $\pm$ SE; differences were considered significant at  $p < 0.05$ .

## Results

### Covariance in Feeding Rates

We recorded feeding rates and per capita feeding rates by males and females during the early ( $n = 46$  nests), middle ( $n = 43$  nests), and late ( $n = 42$  nests) brood intervals over two breeding seasons (1987–1988). These data are summarized in Table 1. Among C-pairs, and with brood size statistically controlled in a multiple regression, there were significant positive relationships between male and female provisioning rates at both the brood and per capita levels, particularly during the first two brood intervals. For those

**Table 1:** Partial correlations (and p-values) between male and female feeding rates in control (C-pairs) and testosterone (T-pairs) pairs at each brood interval (early = days 0–3 post-hatching, middle = days 4–7, and late = days 8–11)

Brood interval	n	Feeding rates	Per capita rates
Early			
C-pairs	20	0.59 (0.008)	0.65 (0.001)
T-pairs	26	−0.14 (0.52)	−0.16 (0.43)
Middle			
C-pairs	16	0.59 (0.019)	0.70 (0.007)
T-pairs	27	0.19 (0.38)	0.22 (0.30)
Late			
C-pairs	17	0.25 (0.33)	0.42 (0.14)
T-pairs	25	−0.24 (0.27)	−0.33 (0.13)

brood intervals in which control pairs exhibited a correlation between male and female effort, we quantified the slope of this relationship with major-axis regression (Sokal & Rohlf 1995). There were significant major axes relating male and female feeding rates in the early interval ( $\beta = 1.06$ ,  $\chi^2 = 7.57$ ,  $p = 0.024$ , describing 79.6% of the overall variation in feeding rates) and middle interval ( $\beta = 2.06$ ,  $\chi^2 = 6.63$ ,  $p = 0.024$ , 81.2%). Although male and female feeding rates were not correlated significantly in the late brood interval, the major-axis pattern was similar ( $\beta = 3.40$ ). When provisioning was measured as a per capita rate, there were significant major axes during the early ( $\beta = 0.84$ ,  $\chi^2 = 14.77$ ,  $p = 0.007$ , 87.8%), middle ( $\beta = 1.06$ ,  $\chi^2 = 7.67$ ,  $p = 0.008$ , 82.9%), and late ( $\beta = 2.47$ ,  $\chi^2 = 9.14$ ,  $p = 0.01$ , 84.2%) brood intervals. Pairs of juncos in which males had been treated with testosterone showed no significant correlations, positive or negative, between male and female provisioning behavior at any stage of nestling development (Table 1).

**Table 2:** Factors that affect the coefficient of variation (CV) in male and female between-feeding intervals (BFI) to broods of dark-eyed juncos at 6 and 9 days post-hatching

Brood interval	Dependent variable	Overall model	Parameters in model
Day 6	CV in male BFI	$r^2 = 0.48$ $F_{2,13} = 5.98$ $p = 0.014$	Julian date: $\beta = 2.96$ , $p = 0.001$ Study year: $\beta = 0.18$ , $p = 0.014$ Time of day: $\beta = -0.001$ , $p = 0.008$
	CV in female BFI	$r^2 = 0.54$ $F_{2,13} = 7.58$ $p = 0.007$	Study year: $\beta = 0.19$ , $p = 0.005$ Observation duration: $\beta = 0.009$ , $p = 0.028$
Day 9	CV in male BFI	$r^2 = 0.38$ $F_{1,16} = 9.89$ $p = 0.006$	CV in female BFI: $\beta = 0.99$ , $p = 0.006$
	CV in female BFI	$r^2 = 0.38$ $F_{1,16} = 9.89$ $p = 0.006$	CV in male BFI: $\beta = 0.38$ , $p = 0.006$

Results are from multiple regressions with backward selection criteria of  $p = 0.10$  to enter the model and  $p = 0.15$  to leave. Sample sizes are 17 and 20 broods at days 6 and 9 respectively.

## Between-Feeding Intervals

We recorded BFIs for 32 pairs (12 C-males and 22 T-males) over three breeding seasons (1995–1997) on nestling day 6 and/or day 9. To determine the effects of male hormone treatment and partner contribution on the CV in male and female BFI, we conducted stepwise backward regressions, the results of which are summarized in Table 2. The coefficients of variation in male and female BFI were strongly positively related when nestlings were 9 d old. Male hormone treatment had no significant effects on the CV in BFIs of either males or their mates (Table 2).

## Prey Load Sizes

We measured prey delivered by males to nestlings from 23 nests (16 C-males and seven T-males) in 1999 and 2000. The size and quantity of prey retrieved from the mouths of nestlings was not affected by the hormone treatment of the attending male. The total dry mass of prey delivered by T-males ( $79 \pm 15$  mg) was comparable with that delivered by C-males ( $96 \pm 12$  mg; ANCOVA  $F_{1,16} = 0.08$ ,  $p = 0.78$ ). The average size of individual prey items was also similar,  $38 \pm 8$  mg for T-males and  $29 \pm 6$  mg for C-males (ANCOVA  $F_{1,16} = 0.20$ ,  $p = 0.66$ ). Of the covariates included in our model, only brood size had any effect; males brought larger prey to larger broods ( $\beta = 0.011$ , partial- $t = 2.19$ ,  $p = 0.045$ ).

## Discussion

Among unmanipulated pairs of juncos (Wolf et al. 1990) or pairs in which males receive empty implants (Ketterson et al. 1992), males and females provision nestlings at approximately equal mean

rates. Our results presented here show significant positive covariation between males and females in feeding rates and in the variability in BFIs. We interpret these positive relationships as the common response of pair members to among-pair variation in factors that influence provisioning rates, including food availability, their own need for food, and nestling need (Hussell 1988; Naef-Daenzer & Keller 1999; Sanz & Tinbergen 1999; Grieco 2002). Such positive among-pair covariation may be necessary to maintain stable patterns of biparental care over a range of environmental conditions. Not only are male and female feeding rates positively correlated, the positive covariation accounts for the majority (in some cases more than 80%) of the overall variation in feeding rates among pairs of juncos. This suggests that in control pairs, males and females respond very similarly to the environmental factors that influence provisioning rates.

Why does this positive covariation in male and female feeding rates degrade when males are implanted with testosterone? There exists ample evidence that male birds treated with T (including juncos) have larger territories and home ranges, spend more time singing, and acquire more extra-pair matings than do control males (Silverin 1980; Wingfield 1984; Chandler et al. 1994; Raouf et al. 1997; Peters 2002; Schwagmeyer et al. 2005; Reed et al. 2006). Therefore, it is likely that testosterone altered the males' responsiveness to the cues that influence provisioning, suppressing their responses to cues that enhance provisioning or enhancing their responses to cues that trigger alternative behavior. It is also possible that t-females perceive their mates to be of higher phenotypic quality, and thus maintain high provisioning rates even in the face of decreased male effort (Burley 1988; de Lope & Møller 1993). In either case, the result is the disassociation of male and female provisioning behavior.

There was no effect of male hormone treatment on the CV in BFIs at either nestling day 6 or day 9. Thus, if T-males were using the nestling period to pursue additional extra-pair mating opportunities, that tendency was not manifested in long absences from the nest that were more variable in duration than those seen in control males. Said another way, T-males were no less predictable in their provisioning behavior than C-males. When nestlings were 9 d old and approaching their asymptotic mass (Nolan et al. 2002), male and female CV in BFI were highly positively correlated. That is, members of a pair tended to resemble one another in the regularity or irregularity of their provisioning behavior. As with

the findings on mean provisioning rate, we conclude that external contingencies such as food availability have similar effects on the ways males and females structure their time.

Male birds with elevated testosterone might somehow compensate for fewer provisioning trips by increasing the quantity or size of prey brought to the nest (for a different approach to this same question see Schoech et al. 1998). Previous laboratory studies on dark-eyed juncos have provided some support for this hypothesis. T-males selected larger prey for themselves than C-males in an experiment by Clotfelter et al. (2001). This relationship was not supported by the current study; we found no evidence of greater load sizes delivered by T- vs. C-males. Thus, there was no evidence of compensatory feeding as has been shown in polygynous males of some species (Sejberg et al. 2000). Rather, our findings are consistent with studies of house finches (*Carpodacus mexicanus*) that have shown positive correlations between nest visitation rate and quantity of food delivered to nestlings (Nolan et al. 2001; Stoehr et al. 2001). If T-males brought back larger, more indivisible prey it could have resulted in increased nestling competition (Mock 1984), which might have explained reduced nestling survivorship in nests of T-males (Raouf et al. 1997). Our analysis of the prey items retrieved from nestlings revealed no significant bias in the average size of prey brought by T-males.

What does the current study contribute to our understanding of the relationship between testosterone and provisioning in male birds? We now know that positive covariation in male and female feeding rates dissociates with the application of exogenous testosterone. We found no evidence that T- and C-males differed in the variability of the timing of their visits to the nest, or the quantity of prey they delivered. These data suggest that reduced nestling survivorship in nests of T-males (Hegner & Wingfield 1987; Raouf et al. 1997) is probably unrelated to long intervals between feeding trips or to competition over large prey items.

The temporal dynamics of provisioning is an important area for future research. Despite myriad studies of parental provisioning rates, relatively few have focused on the intervals between feeding trips (Naef-Daenzer & Keller 1999; Grieco 2001, 2002) or temporal variability in feeding. In the current study, we focused on BFIs and prey load sizes but were unable to study them simultaneously, nor did we examine sex differences in prey loads (Krebs et al. 1999; Grieco 2001, 2002). Future studies should attempt to fill these gaps. Another important variable

that has received little attention, because of the relative difficulty of tracking birds, is the distance traveled by provisioning parents (see Naef-Daenzer & Keller 1999). No data are available for comparing T- and C-males in this regard. Such information would be particularly valuable for testing the predictions of central-place foraging theory (Orians & Pearson 1979; Houston 1985) in the context of hormone manipulation because T-males typically have larger territories than their control counterparts (Chandler et al. 1994).

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