Effects of testosterone on use of space by male dark-eyed juncos when their mates are fertile

C. RAY CHANDLER*, ELLEN D. KETTERSON† & VAL NOLAN JR†

*Department of Biology, Georgia Southern University
†Department of Biology, Indiana University

Abstract. Testosterone is an important determinant of spatial activity in male birds. Using radio-telemetry, male dark-eyed juncos, *Junco hyemalis*, were followed during the period when their mates were fertile to investigate the relationship between testosterone and behaviours (territoriality, consorting with female) through which males might guard paternity. Males with experimentally elevated testosterone levels (T-males) and control males (C-males) did not differ significantly in their use of space during this period. T-males and C-males occupied similar home ranges, used similar-sized core areas (areas enclosing 95% of all activity), spent similar amounts of time close to their mates, and experienced similar intrusion rates onto their territories. Experimentally elevating testosterone above control levels did not detectably affect the spatial activity of male juncos during the female fertile period, although earlier studies have shown that its effects are pronounced during other stages of the nesting cycle.

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Experimental manipulation of testosterone levels significantly affects the use of space by males in a variety of vertebrates (Watson & Moss 1971; Watson & Parr 1981; Wingfield 1984; Moore 1987; Zielinski & Vandenbergh 1993). In birds, the link between testosterone and space use may be particularly important because the size of a male's territory and the proportion of time he spends close to his mate are commonly considered adaptations to reduce the risk of extra-pair copulations (reviewed by Birkhead & Møller 1992). If so, testosterone levels may be a proximate mechanism through which natural selection shapes appropriate paternity guards. Few studies, however, have addressed the effects of testosterone on free-ranging male birds at the time their mates are fertile. Those that have done so suggest that when mates are fertile, testosterone should increase territorial defence (Moore 1984) or increase time spent with females (Saino & Møller 1995).

In a study of spatial activity in dark-eyed juncos, *Junco hyemalis*, we (Chandler et al. 1994) found that, during the incubation and nestling stages of the nesting cycle, males with experimentally elevated testosterone occupied larger home ranges, made more long-distance movements and visited the nest less often. We do not know, however, whether testosterone has similar effects when female juncos are fertile, a time when the benefits of guarding females may constrain male movements. Testosterone can increase range size and territorial behaviour (e.g. Watson & Parr 1981; Moore 1984; Wingfield 1984; Chandler et al. 1994) or increase time spent with the female (Saino & Møller 1995). There is no consensus on how testosterone might be expected to mediate these potentially conflicting (cf. Dunn 1992; Møller 1992) behaviours. Therefore, we addressed three specific questions. (1) When their mates are fertile, do males with elevated testosterone range over larger areas than control males? (2) Does elevated testosterone affect the proportion of time a male spends near his mate? (3) Given potential differences in range size or proximity to their mates, do males of different treatments experience different intrusion rates onto their territories?

Correspondence: C. R. Chandler, Department of Biology, Georgia Southern University, Statesboro, GA 30460-8042, U.S.A. (email: chandler@gasou.edu). E. Ketterson and V. Nolan, Jr are at the Department of Biology, Indiana University, Bloomington, IN 47405, U.S.A.

METHODS

Study Site and Subjects

This study was conducted during the summers of 1993 and 1994 at Mountain Lake Biological Station of the University of Virginia, Giles County, Virginia (37°22′N, 80°32′W). Dark-eyed juncos are common breeding birds at this site in the Allegheny Mountains of southwestern Virginia. Approximately 150–200 juncos, each ringed with a United States Fish and Wildlife Service aluminium ring and marked with a unique combination of coloured plastic leg bands, are monitored on our study site each summer. Most male juncos establish territories in March or April, pair with a single female and contribute as much as the female to feeding nestlings (Wolf et al. 1990). Details of the breeding biology of juncos at Mountain Lake are provided by Hostetter (1961) and Wolf et al. (1988); a description of the study area is provided by Chandler et al. (1994).

Hormone Manipulation

The protocol for manipulating testosterone levels in free-ranging juncos has been described elsewhere (Ketterson et al. 1991, 1992). In brief, we captured most male juncos on the study area in April and implanted them with two 10-mm lengths of silastic tubing (Dow Corning; 1.47-mm internal diameter, 1.96-mm outer diameter). We inserted the implants subcutaneously along the flank of lightly anaesthetized birds (methoxy-fluorane). Testosterone-treated males (T-males) received implants filled with testosterone (Sigma Chemical); control males (C-males) received empty implants.

After a brief peak in April, testosterone levels of C-males fall rapidly to relatively low levels for the remainder of the breeding season. T-males, on the other hand, maintain testosterone levels similar to naturally occurring spring maxima for at least 40 days and have significantly higher levels than C-males throughout the summer (for seasonal profiles see Ketterson et al. 1991; Ketterson & Nolan 1992). During the time that we conducted our radiotelemetry (May and early June; 30–70 days post implantation), T-males had higher testosterone levels than C-males (Ketterson & Nolan 1992). We also know that for males mated to fertile females (egg-laying period), T-males have
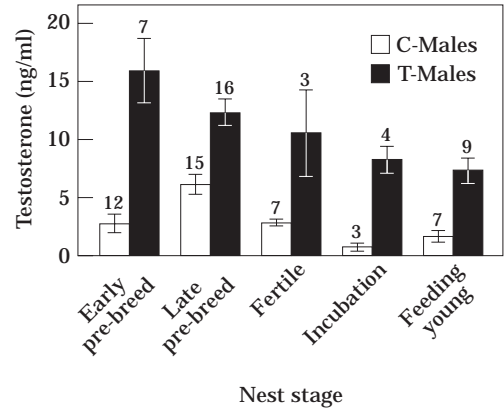

Figure 1. $\bar{X} \pm$ SE testosterone levels for control (C-males) and testosterone-treated (T-males) male dark-eyed juncos during different stages of the nesting cycle. Early pre-breeding is prior to 27 March. Late pre-breeding is 27 March–15 April. Other stages are from May–July. Sample sizes are given above the error bars. T-males had significantly higher levels than C-males ($F_{2,81}=43.7$, $P<0.001$), and levels vary with stage of the nesting cycle ($F_{4,78}=4.28$, $P=0.004$). Among C-males only, levels did not differ significantly between the fertile, incubation and nestling periods (Tukey's HSD). Data are from juncos captured March–July 1989 (E. D. Ketterson and V. Nolan, Jr, unpublished data).

significantly higher testosterone levels (ng/ml) than C-males (T-males: $\bar{X} \pm$ SE$=10.4 \pm 3.87$, $N=3$; C-males: 2.89 ± 0.32, $N=7$; $t=3.2$, $P=0.013$; Fig. 1). C-males maintain testosterone levels well below spring maxima throughout the nesting period (Fig. 1).

Similar numbers of T-males and C-males were implanted each year (approximately 40–50 birds in each treatment group), and their territories were interspersed on the study site. Treatment status was assigned randomly at each of several capture sites around the study area. We periodically checked retention of implants and replaced any missing implants. No males lost implants during the radiotracking reported here. With few exceptions, implants were removed at the end of the summer (Nolan et al. 1992).

Radiotelemetry

During May and early June, we quantified the use of space during the female's fertile period in a sample of 13 implanted males (seven T-males, six C-males). Each male was radiotracked for

5–6 days when it was reasonable to assume his mate was fertile (2–3 days before egg-laying through the end of the day on which the third egg was laid; most female juncos lay four eggs). Pairs were selected opportunistically, although we attempted to alternate between males of different treatments to avoid chance seasonal bias in tracking effort.

Males were captured near their nests in nets or traps and fitted with a radiotransmitter using a technique modified from Raim (1978). From capture to release, the transmitter attachment took approximately 30 min (Chandler et al. 1994). The transmitters (Wildlife Materials Inc.) were $12 \times 8 \times 8$ mm and weighed approximately 1 g ($\bar{X}=1.02$, range=0.9–1.1). At this size, transmitters were approximately 5% of a male junco's body mass ($\bar{X}=4.74\%$, range=4.6–5.1). Each transmitter had a 15-cm antenna and produced signals detectable, with a Wildlife Materials Merlin-24 receiver and a Yagi hand-held antenna, at distances of 100–500 m.

Beginning 2–3 days prior to egg-laying (based on the progress of nest building), we located males every 0.5 h by following transmitter signals until we saw the birds. We recorded the behaviour of the male (e.g. singing, foraging, sitting), whether that male's mate was present (within 20 m of the male), distance (estimated to the nearest metre) between the male and his mate (if she was present) and presence of potential intruders (males within 20 m of the focal male). We also marked the location of the male (with flagging on which we noted the date and time). In practice, males were either relatively close to their mates (within 20 m) and showed evidence of maintaining contact with them (following, flying towards them as they moved away), or females were not seen at all. T-males were tracked an average of 92.9 times (range=67–134); C-males were tracked an average of 97.3 times (range=75–133). When radiotracking was completed, we mapped all tracking locations (and the nest site at the time of radiotracking) onto a bicoordinate system using a compass, metre tape and known landmarks. Bivariate coordinates were estimated to the nearest metre.

Manipulation of Female Status

Whenever possible, we located nests early in construction (i.e. at the onset of the female's fertile period), captured the male associated with that nest and radiotracked him through his mate's fertile period. Nests at the appropriate stage were often unavailable, however, or particular males could not be caught in a timely fashion. Therefore, we induced re-nesting in some pairs by removing eggs from nests early in incubation. In these cases, we first captured the male and attached a radiotransmitter. We then removed eggs from the nest the following day and monitored re-nesting by the female. We began radiotracking prior to the onset of egg-laying in the new nest. In all cases, re-nesting occurred within 1 week of induced nest failure (juncos re-nest repeatedly in the face of high natural predation rates at Mountain Lake; Ketterson & Nolan 1992). The frequency with which we used these two methods was similar between treatment groups (three T-pairs, two C-pairs).

Data Analysis

We calculated two measures of range size in male juncos. Overall home range was measured using minimum convex polygons (Stickel 1954). These polygons enclosed all tracking locations (including any off-territory or long-range movements) and, thus, represented the maximum estimate of home-range size. A more intensively used core area was identified using a non-parametric estimation technique (Anderson 1982; Wilkinson 1985). Using this technique, we estimated the size of the area enclosing 95% of a male's activity (MAP(95)). We consider this a closer approximation of territory size, although territory size is difficult to estimate directly because male juncos sing infrequently during the female fertile period (Titus et al., in press), and overt aggression between males is uncommon.

Although sample sizes were small for a rigorous test, these two variables showed no evidence of non-normality within treatment groups (Lilliefors test: $P=0.67$–0.99). Variances appeared heterogeneous between treatments, however (F-test: $P=0.08$ and 0.04 for home range and MAP(95), respectively). Log-transformation did not affect normality and eliminated heterogeneity of variances ($P=0.27$ and 0.09, respectively). Therefore, we used one-way analysis of variance on log-transformed variables to quantify the effects of testosterone on home range and MAP(95). Power of these tests was calculated (Zar 1984) using an

Table I. Estimates of $\bar{X} \pm$ SE home-range size, time spent near female and intrusion rates for control (C-males) and testosterone-treated (T-males) male dark-eyed juncos during their mate's fertile period

	N	Home range (ha)	MAP (95) (ha)	% of time seen with female	Mean distance from female (m)	% of observations with intruders present
C-males	6	2.11 ± 0.22 (1.43–3.89)[a]	0.38 ± 0.04 (0.29–0.59)	81.0 ± 3.6 (68.1–90.0)	5.97 ± 0.33 (4.98–7.04)	4.8 ± 1.5 (1.2–10.8)
T-males	7	2.95 ± 0.45 (1.28–4.87)	0.55 ± 0.08 (0.28–0.96)	76.7 ± 3.1 (69.3–91.2)	6.32 ± 0.30 (5.14–7.52)	6.1 ± 1.6 (1.4–13.5)
Power[b]		0.91	0.99	0.87	0.74	0.55

[a]Extreme values are given in parentheses.
[b]Power to detect a 100% change in home range, MAP (95), or intrusion rates, and a 20% change in time spent near the female or distance from the female.

effect size (100% change in range size) half of the smallest effect observed in our earlier studies (Chandler et al. 1994).

Percentage of time spent near the female and intrusion rates were estimated as the proportion of tracking fixes for each individual during which we observed males with their mate or an intruding male, respectively. A mean distance between a male and his mate was calculated based on only those observations for which the female was seen with the male (females could not be located on other occasions). These three variables were normally distributed within treatment groups (Lilliefors test: $P=0.74$–0.99) and showed homogeneous variances between treatment groups (F-test: $P=0.64$–0.81). We used one-way analysis of variance to quantify the effects of testosterone on these variables. Power was calculated (Zar 1984) with subjectively chosen effect sizes of 20% (time near female, distance from mate) and 100% (intrusion rates). A larger effect size for intrusion rates was chosen because of the low overall intrusion rates. All statistical analyses were conducted using SYSTAT (Wilkinson 1989).

RESULTS

Range Size

Although T-males ranged over slightly larger areas, treatment with testosterone did not significantly affect size of a male's home range during the fertile period (log-transformed data; $F_{1,11}=1.9$, $P=0.20$; Table I). A male's core area within this home range, MAP(95), also did not

differ between treatments (log-transformed data; $F_{1,11}=3.3$, $P=0.10$; Table I).

Proximity to Female

Male juncos spent about 80% of their time with their mates (Table I). If male and female positions were independent of one another and restricted to a 0.5-ha area, we would expect them to be within 20 m of one another approximately 12% of the time (computer simulation, $N=100$). Male juncos spent a greater percentage of their time close to females than expected by chance. Furthermore, the percentage of tracking fixes during which males were observed together with their mates did not differ between T-males and C-males ($F_{1,11}=0.4$, $P=0.54$; Table I). When both pair members were visible, male juncos were, on average, approximately 6 m from their mates. Proximity to the female did not differ between T-males and C-males ($F_{1,11}=0.6$, $P=0.44$; Table I).

Intrusion Rates

Potentially intruding males were seen during approximately 5% of our tracking observations (Table I). Intrusion rates did not differ for T-males and C-males ($F_{1,11}=0.4$, $P=0.56$; Table I). When intruders could be seen well enough to be individually identified, they were usually males from nearby territories. These intrusions rarely precipitated overt aggression (fighting, chases) between males. Intruders often foraged close to territory owners and their fertile mates. Territory
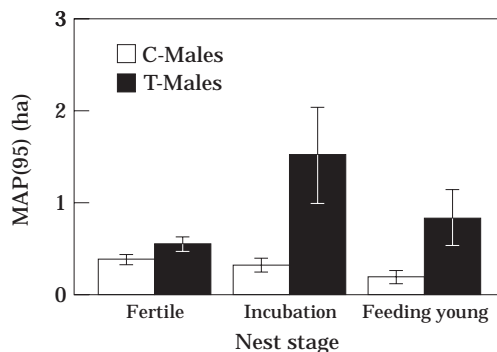
Figure 2. $\bar{X} \pm$ SE size of the areas encompassing 95% of male activity when females were fertile (egg laying), during incubation and while feeding young, for control (C-males) and testosterone-treated (T-males) male dark-eyed juncos. Data for incubation and feeding young are from Chandler et al. (1994).

owners responded with displays such as tail spreading and ptiloerection, and by remaining close to females. Although sample sizes were small (because of the low rate of intrusions), male juncos were closer to their mates when intruders were present (C-males: $\bar{X} \pm$ SE$=2.2 \pm 0.41$ m, T-males$=2.7 \pm 0.53$ m) than at other times (Table I).

DISCUSSION

Home range size in control male juncos at the time their mates are presumed fertile was similar to that observed at other stages of reproduction (Fig. 2). Although Chandler et al. (1994) showed that T-males had dramatically enlarged home ranges during the incubation and nestling periods, experimentally elevated testosterone did not influence male home range size during the female's fertile period (Fig. 2). Despite elevated testosterone, T-males occupied restricted home ranges and used relatively small core areas when their mates were fertile. Males from both treatment groups occupied ranges similar to, or only slightly larger than, those occupied by C-males during incubation (Fig. 2; Chandler et al. 1994). Treatment also did not affect the proportion of time males spent near their mates or observed intrusion rates into their territories (power for this test was low).

The presence of a fertile female appears to be an effective restraint on the wide-ranging behaviour

that testosterone induces in male juncos during later stages of the nesting cycle. Because males are at substantial risk from extra-pair fertilizations in this population of juncos (Ketterson et al. 1996, in press), a high percentage of time spent with the female is consistent with the need for male juncos to guard paternity. Although male juncos do not maintain the proximity to their mates seen in some mate-guarding species (e.g. Møller 1985), they do remain closer to females than expected by chance and they reduce this distance further when intruders are present (suggesting that they respond to the threat of extra-pair copulations). There are, however, other possible reasons for frequent consorting between males and fertile females (Johnson & Burley, in press). Whatever the reason, spatial activity in the fertile period was indistinguishable between T-males and C-males. Increasing testosterone beyond control levels does not increase the proportion of time males spend with their mates (cf. Saino & Møller 1995) or the size of a male's home range.

One possible explanation for these results is that early in the breeding season (May–June), or briefly during the fertile period, testosterone levels in C-males were naturally elevated and therefore similar to those of T-males. If so, the failure to detect a difference in spatial activity between treatments might reflect the facultative ability of male juncos to raise their testosterone levels at key times in the reproductive cycle (Wingfield et al. 1987; Beletsky et al. 1995). We know, however, that during the period analysed here (1–2 months after implantation in April), testosterone levels are significantly higher in T-males than in C-males (Ketterson & Nolan 1992), and during the egg-laying period (i.e. when females are fertile), T-males have significantly higher testosterone levels than C-males (Fig. 1). Testosterone levels in C-males did not vary significantly from the fertile period to the nestling period (Fig. 1). Our protocol is effective in elevating testosterone levels during the period and stage of the nesting cycle analysed here, but this elevation does not significantly affect the spatial activity of male juncos.

Our results, together with those of Chandler et al. (1994), are also relevant to the overall complex of behaviours male birds exhibit during the nesting cycle. Møller (1990, 1991, 1992) argued that during the female fertile period males should sing often, occupy larger territories and guard females. Behaviour of male juncos,

regardless of testosterone levels, is only partially consistent with this view. Male juncos do not sing significantly more often during the fertile period (Titus et al., in press; cf. Rodrigues 1996) and do not appear to expand territorial boundaries (Fig. 2; Chandler et al. 1994). Instead, their behaviour and movements are 'female-centred' with males spending most of their time in relatively close proximity to their mates.

This behaviour may be related to the thick woodland habitat occupied by most juncos. If male juncos are indeed guarding paternity, territory-based paternity guards might be relatively ineffective in this habitat because it is easy for intruders to move about unseen (male juncos will even roost on their neighbour's territory; Chandler et al. 1995). Intrusions occur on a regular, if infrequent, basis in this population (Table I; Chandler et al. 1994). A male's best strategy may be to follow his mate unobtrusively, taking advantage of the cover that the habitat provides. The lack of overt aggression seen in many encounters between males and intruders suggests that in a habitat where it is easy to lose sight of both intruders and mates it may be important for males to remain near their mates. Even if male juncos consort for reasons other than mate guarding, density of the vegetation should still accentuate the trade-off between benefits that a male might gain from remaining close to a female (Johnson & Burley, in press) versus benefits that might accrue from more wide-ranging behaviour (extra-pair copulations, larger territories).

Overall, our results suggest that the proximate role of testosterone in determining spatial activity in male juncos varies with stage of the nesting cycle. Although the presence of nestlings did not constrain testosterone-induced increases in spatial activity of male juncos (Chandler et al. 1994), the presence of a fertile female apparently did. Despite elevated testosterone levels (Fig. 1), male juncos appear to remain flexible in their use of space depending on the nature of competing stimuli. Our results also highlight differences in the apparent effects of experimentally elevated testosterone between species that differ in mating system and life-history traits (Wingfield et al. 1990; Beletsky et al. 1995). Additional data are needed from species with diverse life-history characteristics and from diverse habitats to understand better how testosterone mediates the use of space by male birds.

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