Effects of testosterone on spatial activity in free-ranging male dark-eyed juncos, *Junco hyemalis*

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Abstract. Several of the reported costs and benefits of testosterone-induced changes in avian breeding behaviour may be mediated by the hormone's effects on spatial activity. Therefore, radiotelemetry was used to monitor the effects of experimentally elevated testosterone on the movements of free-ranging male dark-eyed juncos. Juncos were located every 0·5 h over periods of 3–5 days. During the incubation period and while feeding nestlings, males with testosterone-filled silastic implants (T-males) showed significant changes in spatial activity compared with males with empty implants (C-males). On average, T-males had home ranges approximately 200% larger, and within these home ranges occupied core areas (areas encompassing 95% or 50% of all activity) over 300% larger, than those occupied by C-males. T-males were at the nest less often, were found at greater maximum distances from the nest, and sang more often than C-males. Males with experimentally elevated testosterone are less attentive to their nests and young, but may benefit from reduced intrusion rates by other males onto their territories, attraction of females to their large territories, or greater opportunities for extra-pair copulations within their expansive home ranges.

Testosterone mediates many aspects of behaviour in male birds (Balthazart 1983; Wingfield & Moore 1987; Ketterson & Nolan 1992) and other vertebrates (e.g. Crews 1980; Moore 1987; Stacey 1987). In free-living male birds, testosterone affects such fundamental aspects of breeding biology as territory size (Watson & Moss 1971; Watson & Parr 1981; Wingfield 1984a), levels of aggression (Watson & Moss 1971; Watson & Parr 1981; Moore 1984; Wingfield 1984b, 1985), parental care (Silverin 1980; Hegner & Wingfield 1987; Oring et al. 1989; Ketterson et al. 1992), and song (Silverin 1980; Ketterson et al. 1992). In general, experimentally elevated testosterone levels cause males to shift effort away from care of current offspring and into aggressive or sexual behaviour (Silverin 1980; Hegner & Wingfield 1987; Oring et al. 1989; Ketterson et al. 1992). Inducing these behavioural shifts in male birds by experimentally manipulating testosterone levels provides the opportunity to quantify the costs and benefits of alternative reproductive behav-

iour, as well as the factors that shape patterns of testosterone secretion.

Several of the potential costs and benefits of testosterone-induced changes in reproductive behaviour are likely to be mediated by a male's use of space. For example, the probability of obtaining extra-pair copulations, defending a large territory, providing effective mate guarding, or defending the nest depends on a male's particular pattern of spatial activity. However, no studies have quantified testosterone's effects on overall use of space. Because testosterone is likely to influence a trade-off between nest-centred activity (e.g. mate or nest defence) and wider-ranging activity at or beyond territory boundaries (e.g. territory defence, mate attraction), we sought to quantify the effects of experimentally increased testosterone on the use of space by male birds.

Using radiotelemetry, we monitored the movements of male dark-eyed juncos, a territorial and socially monogamous passerine bird. We know that elevated testosterone decreases parental care by male juncos and increases their song rates (Ketterson et al. 1992). However, because these effects have been observed primarily at the nest

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(Ketterson et al. 1992), it is unknown whether elevated testosterone has important consequences for wider-ranging activity. Therefore, we quantified the effects of testosterone on overall use of space by determining whether male juncos with experimentally elevated testosterone had significantly larger home ranges, ranged further from the nest, or engaged in more off-territory activity than did control males.

METHODS

Study Site

We studied juncos during the summers (May–July) of 1990 and 1991 at the University of Virginia's Mountain Lake Biological Station in the Allegheny Mountains of southwestern Virginia (Giles County; 37°22'N, 80°32'W). The study area ranged in elevation from 1000 to 1330 m and was dominated by montane deciduous forest of oak, *Quercus* spp., maple, *Acer rubrum* and *A. saccharum*, hickory, *Carya* spp., birch, *Betula* spp., beech, *Fagus grandifolia*, and tulip poplar, *Liriodendron tulipifera*. Pines, *Pinus strobus* and *P. virginiana*, were patchily distributed in the area, and hemlock, *Tsuga canadensis*, dominated along the margins of Mountain Lake and larger streams. Understory plants included, depending on soil and moisture, ericaceous shrubs (e.g. *Rhododendron*, *Vaccinium*, *Kalmia*), striped maple, *A. pensylvanicum*, hobblebush, *Viburnum alnifolium*, shadbush, *Amelanchier laevis*, and a variety of ferns (e.g. *Pteridium, Osmunda*).

Above 1000 m, dark-eyed juncos, *J. h. carolinensis*, are one of the most common breeding birds in this area. They nest in virtually all available habitats, including woodlands, wood edges along powercuts and roadways, and openings around human habitation (sometimes nesting directly on ledges of buildings). Males establish territories in March or April and pair with a single female (there are rare exceptions; Wolf et al. 1990); both adults contribute equally to feeding nestlings (Wolf et al. 1990). Juncos are sufficiently common that almost all territories are bordered by two or three neighbouring pairs. Since 1983, all but a few of the 150–200 individuals occurring on the study area each summer have been ringed with United States Fish and Wildlife Service aluminium rings and marked with a unique combination of coloured plastic leg bands.

Hormone Manipulation

Each spring prior to and during territory formation, we captured (in mist nets and Potter traps) most of the males on the study area (65–70 individuals annually) and implanted them with 20 mm of silastic tubing (Dow Corning; 1·47 mm internal diameter, 1·96 mm outer diameter). After anaesthetizing the birds (Methoxyfluorane; trade name Metofane), we inserted the implants subcutaneously along the left or right flank. Testosterone-treated males (T-males) received implants filled with crystalline testosterone (Sigma Chemical); control birds (C-males) received empty implants. T-males maintain testosterone levels similar to naturally occurring spring maxima for at least 40 days and have significantly higher levels of testosterone than C-males throughout the summer (see Ketterson et al. 1991; Ketterson & Nolan 1992). T-males and C-males were implanted in approximately equal numbers, and their territories were interspersed on the study area. Interspersion of territories was largely at random (i.e. treatment status was assigned randomly at each of several capture sites on the study area), but was subject to the vagaries of settlement among implanted males. We checked retention of implants by recapturing males periodically, and any missing implants were replaced. Few males lost implants (none in 1991) and no males lost implants during the radiotracking that was the basis of the experiment described here. With few exceptions, implants were removed at the end of the breeding season (Nolan et al. 1992). Details of the experimental protocol can be found in Ketterson et al. (1991, 1992).

Radiotelemetry

Once nesting began (May), we quantified the use of space in a sample of 20 implanted males (seven in 1990, 13 in 1991; 10 T-males and 10 C-males). We monitored the movements of individuals over periods of 3–5 days. Within each treatment group, five males were radiotracked while their mates were incubating and five were radiotracked after their eggs had hatched and the nestlings required food. Males to receive radiotransmitters were selected opportunistically, although we attempted to alternate between males from different combinations of treatment (T versus C) and nesting stage (incubation versus

nestling) in order to avoid chance seasonal bias in tracking effort.

Males were captured in mist nets or traps near their nest sites, transported immediately to the laboratory, and fitted with a transmitter (employing a method modified from Raim 1978). Using a single loop of cotton thread, we tied a rectangular piece of light cotton cloth (cut slightly larger than the base of the transmitter) to the transmitter. The thread was sewn through the edges of the cloth, looped over the top of the transmitter, and knotted; the knot was sealed with a small drop of cyanoacrylate. The cloth provided a surface for attaching the transmitter to the bird. We then clipped feathers from the bird's upper back (leaving 1–2 mm at the base of the shaft) to expose an area of skin slightly larger than the size of the cloth. By clipping carefully along the upper back where the spinal pteryla narrows (and the lateral apteria are prominent), we minimized the number of clipped feathers. After clearing the clipped area of any loose feathers, we glued a rectangular piece of chiffon to the bird's back with eyelash glue. We were careful to keep the chiffon smooth as it dried and, when the glue was partially set, placed the bird in a holding cage for 2–3 min. The chiffon acted as an attachment surface for the cloth to which the transmitter was affixed; interposing the chiffon between the transmitter package and the bird facilitated removal of the transmitter at the conclusion of tracking (cf. Johnson et al. 1991). Finally, the cotton cloth on the transmitter was soaked lightly with cyanoacrylate and pressed against the chiffon. A blunt probe was used to press the edges of the cotton cloth into firm contact with the chiffon. When positioned properly, the transmitter rode high on the bird's back and was almost completely covered by the remaining feathers of the neck and back. The antenna projected directly over the tail. We then checked the transmitter signal and released the bird at the capture site. From capture to release, birds were held for approximately 30 min.

The transmitters were obtained from Wildlife Materials Inc., Carbondale, IL in 1990 and from AVM Corp., Livermore, CA in 1991. Transmitters (12 × 8 × 8 mm) weighed approximately 0·8–1·1 g. These units were no more than 5·0% of any subject's body mass and sometimes were as low as 3·5%. Each unit had a 15-cm antenna and

produced signals that were detectable, with a Wildlife Materials Merlin 24 receiver and hand-held Yagi antenna, at distances of 100–500 m (depending on the position of the bird and the nature of the terrain).

When released, juncos preened and pecked at the transmitter or antenna. However, they adjusted quickly and behaved normally within a few hours. Beginning 2–3 h after release we located males every 0·5 h by following transmitter signals until we saw the birds or, rarely, until an unseen bird's position was unequivocal (e.g. a signal coming from directly overhead in a thick conifer). In only six of 1251 tracking attempts (four for one T-male, and two for another T-male) could we not locate an individual; these attempts were omitted from analysis. Assuming that these two T-males were beyond the areas they usually occupied, omission of these instances should result in conservative estimates of their use of space. We recorded the behaviour of birds that were visible (singing, foraging, perching, flying, etc.) each time they were located. We then marked the site with surveyor's flagging and with permanent ink wrote the date and time on the flagging. We monitored males from approximately dawn to dusk for 3–5 days (usually 3–4), restricting our tracking to these brief periods in order to get a 'snapshot' of movements during standardized segments of the nesting period. When we finished tracking an individual, we recaptured him and removed the transmitter by carefully working the chiffon away from the skin. Subjects that were recaptured in the autumn or in the following year had molted normally and showed no ill effects from the transmitters.

In July and August, we mapped the tracking locations (and the nest site at the time of radiotracking) of all males. This involved mapping each tracking location onto a bicoordinate system by using a compass and metre tape, and by making reference to landmarks whose spatial relations were known and had been mapped previously. The mapping allowed us to assign bivariate coordinates (estimated to the nearest metre) to each tracking location.

Data Analysis

We calculated three different measures to quantify the size of the areas used by male juncos. Home range was measured by using minimum

convex polygons (Stickel 1954), a measure that encloses all tracking locations for an individual and, thus, represents the maximum estimate of home-range size. Areas used more intensively were identified using the non-parametric estimation technique of Anderson (1982; see also Wilkinson 1985). This method estimates the spatial distribution of an individual's activity by fitting a Fourier transformation to the observed tracking data. The areas enclosing a particular percentage of an individual's estimated activity can then be calculated (Anderson 1982; Wilkinson 1985). We selected areas that enclosed 95% of a male's activity (Map (95)) and 50% of a male's activity (Map (50)), respectively, considering these to be core areas within the home range.

These three variables were normally distributed within (Lilliefors test; $D=0.181-0.328$, $P=0.08-0.99$), but showed pronounced heterogeneity of variance among ($F_{max}=19.6-80.7$, $Ps<0.05$), each treatment–nest stage combination. Log-transformation improved the fit to normality ($D=0.135-0.230$, $P=0.73-0.99$) and eliminated heterogeneity of variances ($F_{max}=3.6-6.6$, $Ps>0.05$). We used two-way analysis of variance (on log-transformed variables) to quantify the effects of treatment (testosterone versus empty implants) and nesting stage (incubation versus nestling) on home-range size, Map (95), and Map (50). Variance components were estimated following Winer (1971). The relative sizes of core areas (as a percentage of home-range size) were compared using a two-way Kruskal–Wallis test (Zar 1984), because transformations did not improve the non-normality of these variables.

To explore the distribution of activity within the home range, we also quantified the distance between each tracking location of a male and that male's nest site. For each individual, we calculated the mean of these distances (Dist) as a measure of the average dispersion of his activity around the nest. Log-transformed Dist was normally distributed within ($D=0.18-0.27$, $P=0.33-0.99$) and showed homoscedascity among ($F_{max}=1.96$, $P>0.05$) treatment–nest stage combinations. We used two-way analysis of variance to quantify the effects of treatment and nesting stage on this measure of activity. The collective distributions of tracking locations around the nest site were compared between treatment–nest stage combinations using a Kolmogorov-Smirnov two-sample test. Samples consisted of the mean proportion of

tracking locations at successive 20-m intervals around the nest for five individuals from each treatment–nest stage combination.

We compared the frequency with which T-males and C-males were seen foraging, singing and at the nest site. We selected these three behaviour patterns because others were seen infrequently (e.g. fights, displays) or were of ambiguous significance (e.g. perching). Because individuals may have been disturbed occasionally by the approach of the observer, we considered our observations to be minimum estimates of the time devoted to each behaviour. The proportion of total tracking observations per individual accounted for by each behaviour was compared between treatments using a two-way analysis of variance. Behavioural variables were normally distributed within ($D=0.14-0.34$, $P=0.06-0.99$) and showed homoscedascity among ($F_{max}=7-14$, $Ps>0.05$) treatment–nest stage combinations. Because our primary interest was behavioural differences between treatment groups, we tested only the treatment effect (using nest stage as a blocking factor).

All analyses were conducted with SYSTAT (Wilkinson 1989). In cases of multiple related tests, significance levels were adjusted (to maintain an experimentwise error of $P=0.05$) using Hochberg's sequential Bonferroni adjustment (Hochberg 1988; Wright 1992).

RESULTS

Spatial Activity and Tracking Effort

The number of tracking locations varied between individuals. Nevertheless, there was no significant correlation between home-range size and number of tracking locations for C-males ($r=-0.21$, $df=9$, $P=0.56$; nest stages pooled) or T-males ($r=0.39$, $df=9$, $P=0.27$). The same was true for Map (95) (C-males: $r=-0.49$, $P=0.15$; T-males: $r=0.55$, $P=0.10$) and Map (50) (C-males: $r=-0.42$, $P=0.22$; T-males: $r=0.45$, $P=0.19$). The difference in sign between treatment groups for the relationship between range and tracking effort was attributable to the large number of tracking locations obtained for one individual with an exceptionally large range (a T-male, 95 tracking locations) and one individual with an unusually small range (a C-male, 82 tracking locations). Omitting these two individuals yielded

Table I. Spatial activity of control (C-males) and testosterone-treated (T-males) male dark-eyed juncos as a function of nesting stage

	N	Home range (ha)	Map (95) (ha)	Map (50) (ha)	Dist (m)
Incubation					
C-males	5	1·96 ± 0·356	0·33 ± 0·070	0·09 ± 0·022	49·1 ± 8·84
		(0·65–2·75)	(0·16–0·54)	(0·05–0·16)	(29·2–79·5)
T-males	5	6·36 ± 2·106	1·51 ± 0·523	0·31 ± 0·096	107·3 ± 20·67
		(1·99–13·84)	(0·52–3·48)	(0·11–0·66)	(49·3–174·1)
Nestling					
C-males	5	1·31 ± 0·235	0·20 ± 0·074	0·04 ± 0·026	31·72 ± 5·82
		(0·68–2·09)	(0·05–0·22)	(0·01–0·15)	(15·1–45·0)
T-males	5	3·31 ± 1·213	0·83 ± 0·314	0·21 ± 0·078	66·24 ± 18·51
		(1·05–7·97)	(0·13–1·94)	(0·04–0·49)	(30·6–137·0)

Use of space was quantified ($\bar{X} \pm$ SE) by measuring overall home range (minimum convex polygon), area of 95% activity (Map (95)), area of 50% activity (Map (50)), and mean distance from nest site (Dist). Ranges are given in parentheses.

similar relationships between range and tracking effort for the two treatment groups (e.g. Map (50) in C-males: $r = -0·29$, $P = 0·43$; T-males: $r = -0·15$, $P = 0·78$). Furthermore, there was no significant difference ($F_{1,18} = 0·25$, $P = 0·62$) in the number of tracking locations obtained for T-males and C-males (C-males: $\bar{X} \pm$ SE = 63·8 ± 4·39, range = 46–88; T-males: 61·3 ± 5·21, range = 42–95). For these reasons, tracking effort was not considered as a covariate in further analyses.

Size of Home Range and Core Areas

Males with elevated testosterone had significantly larger home ranges than control males ($F_{1,16} = 9·9$, $P = 0·006$; Table I). On average, T-males ranged over areas about three times as large as those of C-males. Although the mean size of home ranges decreased from the incubation to the nestling stage (Table I), the decrease was not significant ($F_{1,16} = 3·2$, $P = 0·09$). The treatment effect accounted for approximately 42% of the variation in home-range size, while only about 10% was attributable to differences between nest stages.

The core areas used by T-males were also larger than those of C-males (Table I); Map (95) areas of T-males averaged over four times the size of those of C-males ($F_{1,16} = 9·8$, $P = 0·001$). As with home-range size, Map (95) areas decreased from the incubation to the nestling stage (Table I), but again not quite significantly so ($F_{1,16} = 2·6$, $P = 0·06$). Treatment accounted for approximately

52% of the variation in Map (95) size; nest stage accounted for about 11%. The pattern for Map (50) was similar (Table I): T-males had significantly larger Map (50) areas than C-males ($F_{1,16} = 13·8$, $P = 0·002$). There was also a significant, albeit small, effect of nest stage ($F_{1,16} = 4·9$, $P = 0·04$). Treatment accounted for 47% of the variation in Map (50) size, while nest stage accounted for about 14%.

For all three measures of range size there were no significant interactions between treatment and nest stage (Ps = 0·6, 0·9 and 0·3, respectively), indicating that the effect of testosterone on use of space was consistent across nest stages. A sequential Bonferroni adjustment for this family of tests ($k = 9$) does not alter the conclusions for the effects of treatment, but the effect of nest stage on Map (50) becomes non-significant ($P = 0·24$).

Map (95) areas expressed as a percentage of the home range tended to be larger in T-males (T-males: $\bar{X} \pm$ SE = 26·2 ± 4·7%; C-males: 16·4 ± 2·8%) but not significantly so ($H = 3·02$, $df = 1$, $P = 0·08$). The relative size of Map (50) areas also did not differ significantly ($H = 2·76$, $df = 1$, $P = 0·09$) between treatments (T-males: $\bar{X} \pm$ SE = 6·0 ± 1·1%; C-males: 4·6 ± 1·0%). Nest stage had no significant effect on the relative size of core areas (Ps > 0·80), nor were there significant interactions between treatment and nest stage.

Distribution of Activity Around Nest

The distribution of activity of T-males was often qualitatively distinct from that of C-males,
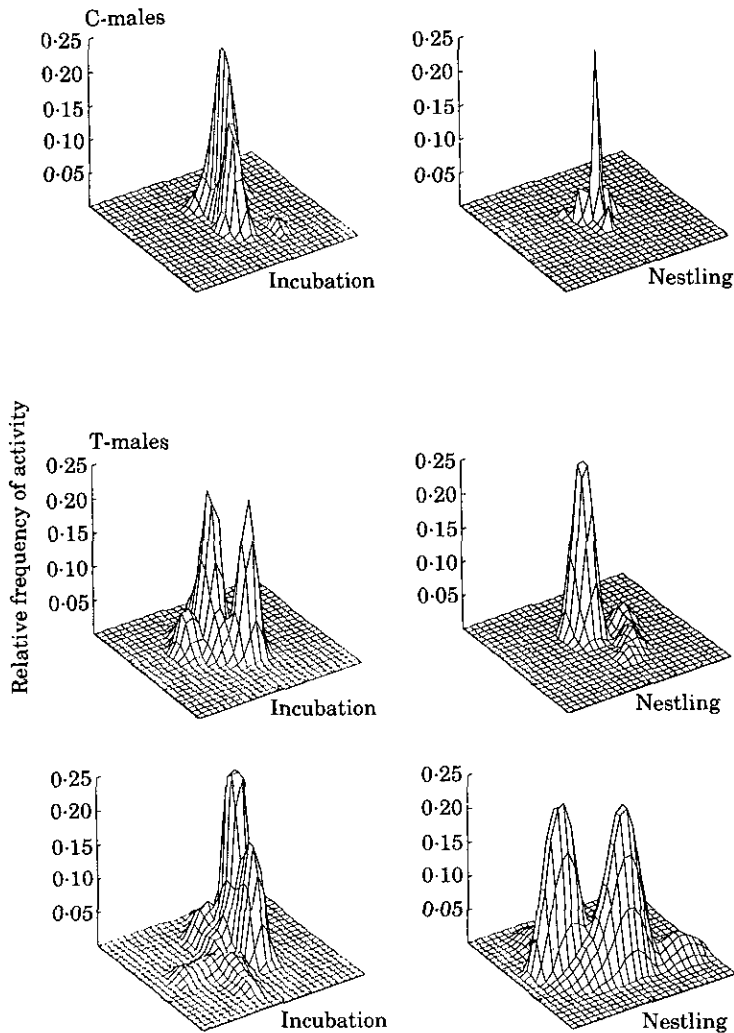
Figure 1. Examples of spatial activity in two control (C-males) and four testosterone-treated (T-males) male juncos. Stage of the nesting cycle is identified for each male. The grids are 600 m on each side and the height of the surface describes the relative frequency of activity at that coordinate.

including movements to areas outside the principal home range and bimodality of activity (Fig. 1). For those T-males with bimodal activity, one of the two peaks corresponded to favoured sites at or near the nest, but the second peak did not always correspond to an area of obvious significance (e.g. an area with a fertile female present).

The mean distance that males were found from their nests (Dist; Table I) was significantly greater for T-males than for C-males ($F_{1,16} = 11\cdot6$, $P = 0\cdot004$; log-transformed data). There was also a tendency in both treatment groups for Dist to be

greater during incubation than during the nestling stage ($F_{1,16} = 5\cdot4$, $P = 0\cdot03$; log-transformed data). There was no interaction between treatment and nest stage ($F = 0\cdot03$, $P = 0\cdot9$).

To visualize the overall distribution of male activity, we calculated the proportion of tracking locations occurring at various distances from the nest (Fig. 2). The activity of T-males was distributed significantly further from the nest than that of C-males, both during incubation ($D = 0\cdot387$, $P < 0\cdot001$, one-tailed) and during the nestling stage ($D = 0\cdot263$, $P = 0\cdot015$, one-tailed). Unlike C-males,
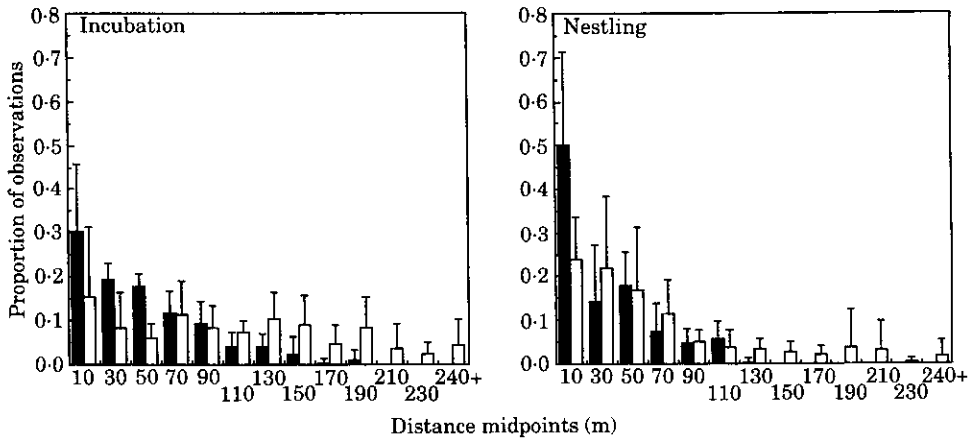
Figure 2. Proportion of tracking locations at varying distances (m) from the nest site for control (●) and testosterone-treated (○) male juncos during the incubation and nestling stages. Values are means for five individuals from each treatment group; standard errors are given by the vertical bar.

T-males often ranged further than 150 m from the nest and were occasionally found up to 550 m away at locations known to be on the territories of neighbouring males (personal observation). Within treatment groups, the activity of T-males was distributed further from the nest during incubation than during feeding of nestlings ($D=0.327$, $P=0.002$, one-tailed), whereas this was not the case for C-males ($D=0.196$, $P>0.05$, one-tailed).

Sequential Bonferroni adjustment for the family of tests dealing with dispersion around the nest ($k=7$) had two effects. The significance of the effect of nest stage on Dist became marginal

($P=0.09$), as did the treatment effect on overall distribution of activity around the nest site during the nestling stage ($P=0.06$). The treatment effect on Dist and overall distribution of activity during the incubation stage remained significant ($P=0.02$ and $P<0.007$, respectively).

Behaviour

Changes in the use of space by male juncos were associated with changes in other behaviour (Table II). T-males sang more often ($F_{1,16}=11.8$, $P=0.003$) and were at the nest site less often

Table II. Estimates of the proportion of time spent singing, foraging and at the nest by control (C-males) and testosterone-treated (T-males) male dark-eyed juncos as a function of nesting stage

	N	Singing	Foraging	At nest
Incubation				
C-males	5	0·08 ± 0·012	0·41 ± 0·048	0·04 ± 0·012
		(0·04–0·11)	(0·29–0·56)	(0·00–0·07)
T-males	5	0·26 ± 0·053	0·26 ± 0·063	0·02 ± 0·016
		(0·14–0·44)	(0·09–0·41)	(0·00–0·08)
Nestling				
C-males	5	0·04 ± 0·017	0·35 ± 0·077	0·19 ± 0·037
		(0·00–0·10)	(0·05–0·47)	(0·10–0·30)
T-males	5	0·20 ± 0·083	0·32 ± 0·051	0·07 ± 0·035
		(0·02–0·48)	(0·17–0·43)	(0·00–0·19)
Stages combined				
C-males	10	0·06 ± 0·012	0·38 ± 0·044	0·12 ± 0·030
T-males	10	0·23 ± 0·047	0·29 ± 0·039	0·04 ± 0·020

Estimates ($\bar{X} \pm$ SE) were calculated for each individual as the proportion of tracking observations (42–95 observations for each male) at which the male was seen performing each behaviour. Ranges are given in parentheses.

($F=6.9$, $P=0.019$) than C-males. There was no difference between treatments in the proportion of time spent foraging ($F=2.0$, $P=0.177$). Sequential Bonferroni adjustment for multiple tests ($k=3$) had no effect on these conclusions.

Transmitters and Body Mass

C-males did not lose body mass while carrying transmitters (before attachment: $\bar{X} \pm \text{SE} = 20.9 \pm 0.19$ g; after removal: 20.9 ± 0.21 g, $N=10$). The same was true for T-males (before attachment: $\bar{X} \pm \text{SE} = 21.0 \pm 0.22$ g; after removal: 21.1 ± 0.20 g, $N=10$). Furthermore, the body mass of C-males and T-males did not differ significantly at the time of transmitter attachment ($F_{1,18}=0.34$, $P=0.57$) or at the time of transmitter removal ($F=0.28$, $P=0.61$).

DISCUSSION

Testosterone and Spatial Activity

Elevated testosterone levels significantly increase (Watson & Moss 1971; Watson & Parr 1981; Moore 1984; Wingfield 1984a, b, 1985; Wingfield et al. 1987; Beletsky et al. 1990) or prolong (Trobec & Oring 1972; Silverin 1980) aggression and territorial behaviour in free-ranging male birds. This suggests that testosterone has a significant effect on males' use of space as well. However, only in the case of red grouse, *Lagopus lagopus scoticus*, and song sparrows, *Melospiza melodia*, has territory size been measured and males with experimentally elevated testosterone been found to occupy larger-than-normal territories (Watson & Moss 1971; Watson & Parr 1981; Wingfield 1984a). Our experiment shows that testosterone has a significant effect on several aspects of spatial activity in free-ranging male dark-eyed juncos. T-males had larger home ranges, and occupied larger core areas within these home ranges, than C-males. They also spent less time at the nest and were found further from the nest than C-males. T-males sometimes showed pronounced bimodality of activity (Fig. 1).

The shift in spatial activity of T-males was accompanied by a shift in behaviour; T-males sang more than C-males. However, T-males did not forage more frequently than C-males (if anything, T-males foraged less frequently during the incubation stage; Table II) and their body mass did not differ from that of C-males. This suggests that the observed changes in spatial activity were not the consequence of a possible testosterone-induced increase in metabolic rate (Hännsler & Prinzinger 1979; Feuerbacher & Prinzinger 1981) and, therefore, foraging demands. Overall, experimentally increased testosterone levels caused male juncos to shift their use of space from the vicinity of the nest site to more distant areas. This view conforms to the findings of Ketterson & Nolan (1992) who reported that T-males studied in other years fed their young less frequently than controls.

Benefits and Costs of Testosterone-induced Changes in Spatial Activity

If male juncos were to maintain elevated levels of testosterone throughout the nesting cycle, they might derive a number of potential benefits from testosterone-induced shifts in spatial activity. Some of the most likely benefits would be advantages derived from possessing a larger territory. Although we did not quantify defence of space by male juncos, it seems likely that T-males did, in fact, defend larger areas within their home ranges than C-males. Testosterone is known to increase territorial aggression and territory size in other species (Watson & Moss 1971; Wingfield 1984a, b, 1985). T-males had larger (presumably defended) core areas than C-males (Table I), and T-males showed more territorial behaviour in the form of singing than C-males (Table II; cf. Ketterson et al. 1992).

Defence of larger areas might produce advantages related to resources (Hinde 1956; Schoener 1969), mating success (Davis & O'Donald 1976; Price 1984), or certainty of paternity (Hinde 1956; Møller 1987, 1990). Any fitness advantages of defending a larger resource base would seem to be offset by the fact that T-males feed their nestlings less often than C-males (Ketterson et al. 1992). However, females mated to T-males increase the rate at which they feed nestlings (Ketterson et al. 1992) and may benefit from a larger resource base in their efforts to compensate for reduced male effort. If territory size influences mate choice in female juncos, T-males may enjoy an advantage during pair formation. Any female preference for larger territories, however, is insufficient to induce females to pair polygynously with T-males (Ketterson et al. 1992; cf. Wingfield 1984a).

Finally, because extra-pair fertilizations do occur in this population (Ketterson & Nolan 1992; P. Parker, E. D. Ketterson & V. Nolan Jr, unpublished data), reduced intrusion rates by neighbouring males (resulting in greater certainty of paternity) might be an important benefit for T-males defending a large territory (Møller 1990, 1992; cf. Dunn 1992). To explore this possibility, we are currently quantifying spatial activity of males during the period in which their females are fertile.

Whereas larger territories of T-males may reduce intrusion rates and the risk of being cuckolded, their larger home ranges may increase their opportunities for obtaining extra-pair copulations. T-males range far beyond their core areas and, unlike C-males, are frequently found over 150 m (and occasionally up to 550 m) from the nest (Fig. 2). Such long movements consistently placed T-males at locations known to be on the territories of neighbouring males (personal observation). In at least two cases, T-males were tracked to areas where neighbouring females were building nests or had nests in which laying of the clutch was in progress. Because unguarded females are vulnerable to extra-pair copulations in several species of birds (Björklund & Westman 1983; Møller 1987; Birkhead et al. 1989; cf. Björklund et al. 1992), wide-ranging T-males may encounter such females more frequently than do C-males and have more opportunities to gain extra-pair copulations. However, preliminary paternity analysis indicates that both T-males and C-males successfully obtain extra-pair fertilizations; there is as yet no evidence that T-males are more successful than C-males (Ketterson & Nolan 1992; P. Parker, E. D. Ketterson, V. Nolan Jr, unpublished data).

There are also some potential costs to the changes in spatial activity exhibited by T-males. Because they range further from the nest (Fig. 2) and are at the nest site less often (Table II), T-males are less likely than C-males to be available for nest defence. Female juncos mated to T-males are probably more likely to face potential nest predators on their own. This may be an important cost because rates of nest predation are high for juncos (Wolf et al. 1990); both sexes vigorously mob potential nest predators such as eastern chipmunks, *Tamias striatus*, often driving them away (Ketterson et al. 1992). Furthermore, in some passerines, it is the male that usually performs the greater share of nest defence (Curio 1980; Regelmann & Curio 1986). Nevertheless, there is no evidence that nest predation rates differ between treatment groups (Ketterson & Nolan 1992) and, despite the potential risk of defending nests without male assistance, females mated to T-males do not have lower survivorship than females mated to C-males (Ketterson et al. 1992).

In addition to being in a less favourable position for nest defence, T-males feed their nestlings less often than C-males (Ketterson et al. 1992). Our observations during radiotracking suggest that this is not attributable to a reduction in time spent foraging, at least during the nestling period (Table II). Reduced provisioning seems to be a consequence of the fact that T-males use space differently to C-males. Because they are further from the nest, T-males may receive fewer signals from the young that stimulate food delivery, or competing behaviour associated with wide-ranging activity may make T-males less responsive to these signals even when they receive them.

Finally, because of their wide-ranging behaviour, T-males may be less effective at mate guarding and, thus, be more frequent victims of extra-pair fertilizations. The critical question is whether by defending larger areas T-males reduce intrusions by neighbouring males (Møller 1990, 1992) or, instead, whether their expansive home ranges actually subject them to higher rates of intrusion and reduced certainty of paternity (Dunn 1992). We emphasize that we as yet have no radiotracking data from the period when female juncos are fertile, but we do know that T-males and C-males both achieve and are victimized by extra-pair fertilizations (Ketterson & Nolan 1992; P. Parker, E. D. Ketterson, V. Nolan Jr, unpublished data).

Nest Stage and Spatial Activity

Although stage of the nesting cycle had few significant effects on the use of space, all measures of spatial activity tended to decrease from incubation to the nestling period. Decreasing territory size with the progress of the nesting cycle is known for many species of birds (e.g. Odum & Kuenzler 1955; Stegner & Falls 1959; Stefanski 1967; Yarrow 1970; Tryon & MacLean 1980; Møller 1990). Our results (specifically, the absence of significant interactions between treatment and nest stage for our measures of spatial activity) suggest that, whatever the reasons for use of

smaller space during the nestling period (Møller 1990), declining testosterone levels are not necessarily a proximate cause. In juncos, the home range and core areas tend to be smaller during the nestling period even when testosterone levels are artificially maintained at their spring maximum.

Conclusions

Our results demonstrate that testosterone is a proximate mechanism influencing a trade-off between activity in the vicinity of the nest and wide-ranging activity at or beyond territory boundaries. The net cost or benefit of testosterone-induced changes in spatial activity is probably frequency dependent. The success of wide-ranging behaviour will depend not only on an individual's movements, but also on the use of space by his neighbours. A male with elevated testosterone may experience dramatically different paternity-related costs and benefits when surrounded by other wide-ranging T-males, as opposed to C-males. That is, predicting whether or not a novel phenotype with elevated testosterone would spread in a population would require knowledge of its frequency. We are currently investigating this problem by exploring the paternity of young on territories with neighbouring males of different treatment status.

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