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The role of testosterone in male downy woodpeckers in winter home range use, mate interactions and female foraging behaviour

JAMES S. KELLAM*, JEFFREY R. LUCAS* & JOHN C. WINGFIELD†
*Department of Biological Sciences, Purdue University
†Department of Biology, University of Washington

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Studies of the role of testosterone (T) in birds have typically focused on sexual or aggressive behaviours of males during the breeding period, but males of nonmigratory species may invest in mate and territory long before breeding, and the influence of T in facilitating nonbreeding-season behaviours is poorly understood. We gave free-living male downy woodpeckers, *Picoides pubescens*, T-implants during the winter to determine whether elevated levels of T increased a male's ability to exclusively occupy territory-based resources, and whether elevated T strengthened a male's investment in an existing pair bond relationship. We also explored how a female's foraging efficiency might be affected by her mate's behaviour if he had elevated T. We found little difference between control and T-implanted males with regard to home range exclusivity. Surprisingly, male–male display rates were significantly lower in T-implanted males than in controls. Regarding male–female interactions, T-implanted males that experienced high incursion rates from other males maintained more frequent spatial association with their mate, suggesting that T facilitates male behaviours that could restrict the mate's access to other male birds. Female mates of T-males showed reduced foraging rates, but because male–female aggression was similar between treatment groups, the cause for this reduction is unknown. The results indicate that exogenous T during winter affects a variety of behaviours in male woodpeckers, and proximate influences on pair bond maintenance in winter may be a fruitful avenue for future research.

Hormones have a vital influence on avian mate choice and life history. For example, male courtship, mate guarding, defence of breeding territory, the number of female mating partners per season and female choice of males depend on testosterone (T) levels in males to some degree (Moore 1984; Wingfield & Farner 1993; Enstrom et al. 1997). However, relatively few studies have examined T's contribution to facilitating male social behaviours outside the traditional breeding season, even though, in resident species, both defence of breeding territory and pairing activities may take place. In some species, T and related control mechanisms may regulate these nonbreeding-season behaviours (Wingfield et al. 1997; Hau et al. 2004). Thus, if behaviours related to defence of breeding territory and maintenance of the pair bond relationship in the nonbreeding period increase a male's fitness (and/or the fitness of his existing or future mate), increases in plasma T before the breeding period could also be advantageous.

At the same time, elevated and prolonged T levels could have significant fitness costs. These may include physical wounding or depredation resulting from aggressive or otherwise conspicuous behaviours, immunosuppression and heightened energetic demands (Wingfield et al. 1997; Buchanan et al. 2001). High male T levels might also lower the fitness of the male's mate, a possibility that is often overlooked. Increased interaction between mates could lead to increased levels of interference competition, which in some species particularly affects the female partner (Kilham 1970; Hogstad 1978; Kellam 2003). There is thus a potential trade-off between any T-mediated benefits of pair bond maintenance and the cost of increased pair interaction.

Correspondence and present address: J. S. Kellam, Department of Biology, Franklin & Marshall College, Lancaster, PA 17604, U.S.A. (email: jkellam@fandm.edu). J. R. Lucas is at the Department of Biological Sciences, Purdue University, 915 W. State Street, West Lafayette, IN 47907-2054, U.S.A. J. C. Wingfield is at the Department of Biology, University of Washington, 106 Kincaid Hall, Box 351800, Seattle, WA 98195-1800, U.S.A.

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We used T-implants in free-living male downy woodpeckers, *Picoides pubescens*, during winter to evaluate the effect of T on pair interactions and the possible effect of those interactions on female foraging behaviour. We also evaluated the influence of T on male–male interactions during this time.

Downy woodpeckers are socially monogamous with biparental care. Nests in our population are initiated in early May, and individuals remain within the breeding home range throughout the nonbreeding period (Kellam 2003). We showed earlier that male T levels in faeces were generally low but variable in winter, and male–male interactions were infrequent but sometimes intense (Kellam et al. 2004). Likewise, male–female interactions were infrequent in winter but mated pairs were in spatial association during about 30% of observations. Faecal T did not appear to correlate with the seasonal frequency of mate association or with the frequency of male–male conflicts (Kellam et al. 2004). However, our hormone-sampling rate was lower than our behaviour-sampling rate, and short-term relations between T and intraspecific interactions could have been missed. Regardless, the relatively low levels of T and social behaviour in our study population provide the opportunity to explore the function of T in winter by comparing the behaviour of implanted males (T-males) and their unmanipulated mates (T-females) with a control group (C-males and C-females).

We first evaluated two general hypotheses based on studies of different bird species reported in the literature. The hypotheses are not mutually exclusive, but they represent the two most commonly proposed functions of T in male birds, at least during the breeding period. In both cases, we modified the predictions of the hypotheses to address nonbreeding social behaviour in our own study species, *P. pubescens*. One hypothesis is the ‘resource defence’ hypothesis, which states that males with elevated T during winter can occupy and defend a territory to a greater degree than other males. Furthermore, expansion of the home range could lead to an increased opportunity for males to interact with nonmate females, who may be higher in quality than the current mate (cf. Raouf et al. 1997). We predicted that under the resource defence hypothesis, T-males would expand their home range, occupy space more exclusively of other males, associate with more females over time and interact more frequently with other males than would controls. T-implants in the spring have these effects in other species (Silverin 1980; Hegner & Wingfield 1987; Wingfield & Farner 1993; Ketterson et al. 1996). As a consequence of these T-influenced effects, males also neglect their mate and offspring (Ketterson et al. 1996; Hunt et al. 1999; Schwagmeyer et al. 2005). Therefore, a secondary prediction we made under the resource defence hypothesis is that T-males and T-females will associate with each other less often than control pairs do. Mate association frequencies among experimental pairs may also be low if T-males become more aggressive towards their mate. Little is known about the effects of T on male–female aggression in birds, but male woodpeckers are known to displace females from high-quality foraging sites when resources are scarce (Kilham 1970, 1974). Thus, T-males could show higher mate-displacement rates than controls, and the foraging rates of T-females could be reduced because of their efforts to avoid displacements by their mates.

A second hypothesis is the ‘pair bond’ hypothesis. Testosterone might improve a male’s potential for future reproductive success by facilitating investment in a current or future pair bond rather than, or in addition to, an expanded home range and resource base (e.g. Enstrom et al. 1997; Alonso-Alvarez 2001; Peters 2002). The hormonal state of one partner affects that of the other (Wingfield & Farner 1993; Wingfield & Monk 1994), and hormonal synchrony early in the breeding season improves reproductive success (Hirschenhauser et al. 1999). Thus, in species in which mates have the opportunity to interact in winter, higher winter T levels could hasten the start (or increase the frequency) of male–female interactions. Under the pair bond hypothesis, we predicted that T-pairs would show a higher mate association frequency and greater home range overlap between mates than would controls. We further predicted that T-females would have greater foraging efficiency than C-females as a consequence of more frequent mate association. Studies on avian pair behaviour during winter have documented male protection of females against predators and conspecific food competitors (*P. pubescens*: Sullivan 1984, 1985; Kellam 2003; other examples: Lens & Dhondt 1993; Hogstad 1995; Fusani et al. 1997). As males become more vigilant when near the mate, female foraging efficiency improves. This helps prevent mate loss by lowering the risks of female starvation and depredation.

Both the resource defence and pair bond hypotheses are based on the findings of studies conducted on a variety of bird species, usually during the breeding period. However, the results that we report here for *P. pubescens* in winter do not tend to support either a priori hypothesis, even though our treatment groups showed several significant behavioural differences. We therefore conclude our paper posing a third hypothesis for the function of T in males during nonbreeding periods: the mate-guarding hypothesis. We use our results to suggest that T may help males in the nonbreeding period prevent mate loss stemming from female-initiated mate switches or desertion before mating. This hypothesis contrasts with the pair bond hypothesis, which predicts that males and females would benefit similarly from a nonbreeding social relationship.

METHODS

Our experiment was conducted at the Ross Biological Reserve, Tippecanoe County, Indiana, U.S.A., during winter periods from 5 January to 31 March 2001–2002. The reserve is bordered on two sides by unfavourable habitat (the Wabash River and a golf course), but patchy forestland extends beyond the reserve’s borders to the east and west. We captured 21 male and 20 female downy woodpeckers using manually operated traps mounted on tree trunks. Individuals studied in winter 2001 were different from those studied in 2002 with the exception of two males. Both were control birds in 2001 and members of the experimental group in 2002, with a different mate each year (see 'Testosterone manipulation'). Based on these interyear differences, we considered data collected on these males in 2001 to be independent of data collected in 2002.

Traps were baited with a commercial suet product during and 2 days before the trapping sessions. Bait was removed from each trapping site as soon as trapping at the site was complete to reduce the influence of bait on the foraging behaviour of woodpeckers. No behavioural data were collected from woodpeckers within 40 m of a baited trap.

Testosterone Manipulation

Female woodpeckers were equipped and released with a 1.1-g radiotransmitter (BD-2, Holohil Systems, Carp, Ontario, Canada; battery life ca. 32 days; transmitter:body mass ratio = 4%) using a leg-loop harness. Male woodpeckers were transported a short distance to a laboratory at the field site and anaesthetized intramuscularly with ketamine and xylazine in saline solution (62.5 μg ketamine and 12.5 μg xylazine administered per gram of body mass). Eleven of the males received a single subcutaneous implant filled with crystalline T and another 11 males received an empty implant. We flipped a coin to assign a treatment group to the first-captured male of each year and then alternated between T-filled and empty (control, C) implants as additional males were captured. This resulted in a relatively even distribution of T- and C-males throughout the study site. Based on home range boundaries, each T-male had a mean ± SE of 1.6 ± 0.3 T-male neighbours and 2.4 ± 0.5 C-male or unmanipulated male neighbours. Similarly, each C-male had an average of 2.0 ± 0.4 T-male neighbours and 1.3 ± 0.3 C-male or unmanipulated male neighbours. T-implants were made from Silastic tubing (Dow Corning, Midland, Michigan, U.S.A.; effective length: 7 mm, 1.47 mm i.d., 1.96 mm o.d.) sealed at both ends with Silastic medical adhesive (Dow Corning). Implants constructed in the same way delivered a relatively constant dose of T over a period of more than 40 days in dark-eyed juncos, *Junco hyemalis* (Ketterson & Nolan 1992). The implant procedure took less than 10 min to complete, but to ensure recovery from anaesthesia, we held the implanted males for 3 h in a recovery room heated to 27 °C. Before release, we attached radiotransmitters to the males and offered supplementary food (Kaytee Exact Hand-Feeding Formula; Kaytee, Chilton, Wisconsin, U.S.A.). All woodpeckers were released at least 3 h before sunset to allow adequate foraging time before roosting.

In March, as radiotransmitter batteries failed, we recaptured all individuals and removed the radios. To assess the function of T-implants, we measured cloacal protuberance length (a T-dependent morphological trait; Soma et al. 2000) and collected faecal samples from both experimental and control males. Faecal samples were later analysed for T using radioimmunoassay. Previous work using this technique showed that faecal T significantly correlated with plasma concentrations of androgen (Kellam et al. 2004). Following collection of faeces, implants were removed from males using the same procedures outlined above. All implant procedures, capture, handling and observation of woodpeckers were approved by the Purdue University Animal Care and Use Committee under protocol number 97-084-2.

Home Range

Starting on the third day following capture, we tracked each radioed woodpecker once per day for the life of the transmitter. The initial delay in data collection minimized any residual effect of transmitter attachment on the woodpeckers' behaviour. When first seen on each day, we recorded the individual's location in reference to pre-established grid markers spaced every 40 m throughout the study site. Location data were analysed using the Animal Movement program in ArcView (Hooge & Eichenlaub 1997). Home ranges for each individual were constructed from an average of 33 coordinate locations (range 17–52). We excluded six males from analysis that had fewer than 15 locations. These males lived at the north and south boundaries of our study site and could not be tracked regularly. We used a random-walk site fidelity test (Hooge & Eichenlaub 1997) to confirm that all home ranges were stable over time.

We characterized space use in several ways. First, we calculated home range size using the minimum convex polygon technique (MCP) to provide some context with previous literature (Harris et al. 1990). However, MCP can be a poor indicator of space use because unsuitable habitat is often scattered throughout the home range. To exclude these areas from our characterization of space use, we used a fixed kernel estimator using least-squares cross-validation to determine the smoothing factor (Hooge & Eichenlaub 1997). With this technique, we calculated the size of core-use areas within the 95%, 75%, 50% and 35% isopleths (Harris et al. 1990). These 'use areas' represent the percentage of an individual's activity taking place within the specified area.

Once use areas were plotted for each woodpecker, we overlaid the home ranges and calculated the proportion of a male's home range (using different use areas in separate analyses) overlapped by its mate's home range. Significant overlap between mates in the experimental group would be predicted by the pair bond hypothesis. However, the resource defence hypothesis would not necessarily predict a reduction in overlap between mates. Instead, a T-male may expand his home range to encompass both his mate's home range as well as space not used by the mate. Thus, we devised an additional way to evaluate our hypotheses by examining the activity of males within their home ranges. We used ArcView to calculate the geographical centre of each male's 75% and 35% core-use areas and the geographical centre of the mate's 75% use area. Then we calculated the vector of a line drawn from a male's 35% use area centre to the male's 75% use area centre. If T-males shifted activity away from their own home range centre towards the home range centre of the mate, then the 75% use area should bulge disproportionately in the direction of the mate's home range. This finding would support the pair bond hypothesis. Alternatively, consistent spatial bias in T-male activities in directions away from the mate's home range centre would support the resource defence hypothesis, because those males would be defending places not used by the mate.

The lack of home range overlap between males was used to characterize the degree to which males occupied space exclusive of other males. We calculated a proportion of exclusivity by dividing the area of a focal male's home range not overlapped by the home ranges of other males by the total size of the focal male's home range. We used the 75% core-use area to examine male overlaps because there was almost no overlap between male 35% and 50% use areas (J. Kellam, unpublished data). We did not construct home ranges for six marked (but not studied) males living just to the north and south of our study area, so for T- and C-males living near these six, the proportion of home range not overlapped by other males may be an overestimate. This problem affected four males, half T-males and half controls. This even split means that our results are unlikely to be biased in a particular direction.

An additional way to test whether T-males, as predicted by the resource defence hypothesis, used space more exclusively than controls was to count the number of intrusions neighbouring males made into another male's 75% core-use area during our winter study periods. Dividing by the size of the focal male's 75% use area, this gave a relative index of how frequently one males' home range was used by other males (hereafter 'neighbour incursion rate'). We calculated neighbour incursion rates using 50% and 35% use areas in like manner.

Focal Observations

After obtaining a home range location from an individual woodpecker, instantaneous scans were conducted every 10 min during a 30-min focal observation to document the identity and distance of conspecific associates. Woodpeckers loosely associated with a particular member of the opposite sex during our studies, and we considered these to be mates. We confirmed these partnerships each spring by finding nests. To characterize the cohesion of mated pairs during our study, we calculated four seasonal indexes of mate association for each male. Each index was equal to the proportion of focal observations during which mates were seen within 10, 20, 30 and 40 m of each other, respectively.

Occasionally, males and nonmate females came within 40 m of one another. Like the mate association indexes, we calculated the proportion of focal observations during which nonmate females were seen within 10, 20, 30 and 40 m of each male. This was to gauge whether T-males had more opportunity to assess and interact with nonmate females than did C-males. We calculated comparable association indexes to describe how often males associated with other males and how often females associated with nonmate males.

During instantaneous scans, we also recorded the width of substrate (such as a tree trunk or limb) where the bird was seen. A previous study at this site showed that substrate width affects downy woodpecker foraging behaviour (Kellam 2003).

Time Budget and Instantaneous Behaviours

We conducted time budget analyses during the same 30-min focal observations described above to estimate male–male display rate and female foraging efficiency. The behaviours of pecking, moving, looking and other activities of individuals were recorded in the field using a lapel microphone and an audiocassette recorder. These audiocassettes were later transcribed in real time using event recorder software (a C++ program written by J.R.L.) to time the duration of each behaviour. Time budgets for each bird were constructed from 6.9 ± 2.4 SD focal observations taking place over at least 5 days, with each focal including an in-view observation time of 8.2 ± 3.7 min (only focal observations with in-view times lasting at least 3 min were used in analyses).

Male displays and chases involving other males could be timed and were used when assembling time budgets. We calculated the proportion of the total time observed that was spent in male–male display by combining bill-waving and wing-flicking displays, mid-air grapples, chases and male–male displacements that occurred in rapid succession (behaviours defined in: Jackson & Ouellet 2002; Kellam et al. 2004).

To evaluate whether T-males had a negative or positive effect on female foraging efficiency (as proposed by our two respective hypotheses), we devised two ways to measure foraging behaviour that appeared to be reliable indicators of foraging efficiency (Kellam 2003). First, we determined the number of food patches visited per focal by counting the number of times that a woodpecker travelled between places where pecking was observed (any behaviour involving bill-down behaviour, excluding communicative drumming). Thus, each pecking place was considered a food 'patch'. To calculate patch visit rate, we divided the number of patches visited during each focal observation by the combined period during the focal observation that the woodpecker was travelling between patches (i.e. moving or flying). We calculated a second component of foraging efficiency, visit duration, to account for time spent in each patch. Visit duration was the average time spent pecking at a patch, calculated as the total time spent pecking during a focal observation divided by the number of patches visited. Lima (1983, 1984) showed that woodpeckers remained in patches longer when food value was high. Thus, longer visit durations suggest higher foraging efficiency. However, visit duration and patch visit rate must be considered together to estimate foraging efficiency. For instance, long visit duration combined with low patch visit rate would represent high foraging efficiency only if the number of food items within each patch was high. Although we could not measure the density of food items within a patch, a relatively low density of food items per patch seems more likely, because the majority of visit durations in a previous study of our population lasted less than 30 s (Kellam 2003). A combination of high patch visit rate and long visit duration can be assumed to indicate high foraging efficiency. This is true because, in a previous study, these variables positively correlated with total foraging time (proportion of time spent pecking across all focal observations), and total foraging time was highly correlated with woodpecker body condition: woodpeckers that spent a relatively large amount of time foraging were also relatively heavy for their size (Kellam 2003).

Coinciding with the resource defence hypothesis, we predicted that T-treatment could lead to more aggressive interactions between mates, so during focal observations we documented male displacements of their mates. Displacements were treated as instantaneous events, and we found a seasonal male mate-displacement rate by dividing the number of displacements by the total duration of focal observations conducted on an individual.

Statistical Analyses

We used Student's t tests assuming equal variances to determine whether T-males differed from C-males in the mean values of the following variables: faecal T concentration, cloacal protuberance length, social association rates (for mate and nonmate females), characteristics of home range use and time spent in male–male display. Equality of variances was tested in SAS using Brown & Forsythe's (1974) modification of a Levene's test. Data on male mate-displacement rate were not normally distributed, so the nonparametric Wilcoxon two-sample test was used to determine whether mean values differed between treatment groups. We further evaluated whether T- and C-males differed by using Hotelling's one-sample test (Batschelet 1981) to determine whether male usage of home range space was nonrandom with regard to its orientation to the mate's home range.

We used general linear models (PROC GLM; Johnston 1993) to test whether a significant amount of variance in male mate association indexes and male space use parameters was explained by one or more of the following independent variables: T-treatment, neighbour incursion rate, distance between home range centres of mates and interaction terms when significant. The number of locations used to construct each home range did not correlate with home range size (indicating that we had an adequate sample for all birds), so we did not use this parameter in our models. General linear models (GLM) were also used to explain variation in association rates of females and nonmate males as related to T-treatment, neighbour incursion rate and an interaction term.

Where repeated measurements of birds were included in our analyses, we used repeated measures analysis of covariance (ANCOVA) models with first-order autoregressive structure (PROC MIXED; Littell et al. 1996). These models were designed to test whether individual differences in the two estimates of female foraging efficiency calculated for each focal were explained by one or more of the following independent variables: T-treatment of the mate, substrate width, mate association, time of day (morning, midday or afternoon) and interaction terms. We log-transformed patch visit rate and double log-transformed visit durations ($\log(\log x+1)$) to ensure that assumptions of normality were met. In models with categorical variables (T-treatment of the mate, mate association and a treatment-by-mate association interaction), we used contrast analyses to determine whether least-squares means of the dependent variable significantly differed between groups.

Power analyses were conducted on selected tests following Cohen (1988). For each power analysis, we state in the Appendix how we determined an appropriate effect size. We considered power greater than 0.80 adequate for detecting differences between treatment groups. Two-tailed tests ($\alpha = 0.05$) were used for all tests. All means are reported with standard errors unless otherwise noted.

RESULTS

Implant Efficacy

Mean faecal testosterone of T-males was significantly higher than that of C-males (T-males: 15.16 ± 2.32 pg/mg, C-males: 5.52 ± 1.04 pg/mg; Student's t test: $t_{10} = 3.80$, $P = 0.003$) and was similar to peak breeding-season levels found in an unmanipulated population during April (Kellam et al. 2004). Cloacal protuberance lengths of T-males from January through March also differed significantly from controls (T-male: 8.9 ± 0.9 mm, C-male: 2.5 ± 0.5 mm; $t_{11} = 6.22$, $P < 0.0001$).

Nonmate Female Associations

Under the resource defence hypothesis, we predicted that T-males would associate with nonmate females more frequently than would C-males. Contrary to the hypothesis, we found no significant difference between T- and C-males in the rate at which they were observed within 40 m of a nonmate female (T-males: $\overline{X} \pm \mathrm{SE} = 0.16 \pm 0.03$ nonmate females per focal; C-males: 0.11 ± 0.02 nonmate females per focal; Student's t test: $t_{12} = 1.29$, $P = 0.22$). Analyses performed using smaller association thresholds also failed to find significant differences. However, power was too low for us to consider the importance of these results (power using 40-m threshold = 0.44).

Home Range

Our results on nonmate female associations were inconclusive, but if, according to the resource defence hypothesis, elevated T leads males to seek out and interact with nonmate females, T-males should have larger home ranges. Contrary to the hypothesis, we found little evidence that T-treatment resulted in an enlarged home range. With sufficient statistical power, we found that the 95% range area of T-males did not differ from that of C-males (Table 1). We also found no differences between groups in the size of core-use areas other than 95% within the home range, but power in those tests was lower.

Table 1. Mean ± SE home range sizes of male downy woodpeckers calculated using minimum convex polygon (MCP) and kernel estimators at different core-use levels

	Home range size (ha)				
Home range size calculation	T-males (*N*=9)	C-males (*N*=6)	t_{13}	*P*	Power*
35% use area	1.5±0.3	1.4±0.2	0.17	0.87	0.70
50% use area	2.9±0.6	2.5±0.4	0.36	0.72	0.55
75% use area	7.9±1.6	5.8±0.8	0.99	0.34	0.50
95% use area	17.5±2.8	16.9±1.7	0.16	0.87	0.90
MCP	16.6±4.0	16.8±3.0	0.04	0.97	0.67

*See Appendix for details on power analyses.

The lack of power resulted from high variability in core-use area sizes, particularly among T-males at the 75% use level (Table 1). However, differences in variances between T- and C-males were only marginally significantly different at the 75% use level (Levene's test: $F_{8,5} = 5.81$, $P = 0.07$). To better determine whether the T-implants had an effect on home range sizes, we compared data from four males tracked in two consecutive winters between 2000 and 2002. Each occupied the same home range area between years, and each received a T-implant during the second winter. There was no consistent increase in home range size across individuals in the second year (Table 2).

T-treatment did affect the way male woodpeckers used space within their home ranges. On average, 75% core-use areas of T-males were 5.4 ± 0.3 times larger than their 35% use areas, while 75% use areas of C-males were only 4.2 ± 0.3 times larger (hereafter, we refer to this relationship between 75% and 35% use areas as the range ratio). The treatment-dependent difference in range ratio was significant (Student's *t* test: $t_{13} = 2.71$, $P = 0.018$). This means that T-males concentrated their activities over a greater area than did C-males relative to the size of their respective home ranges (Fig. 1). The more dispersed T-male activity patterns could suggest that T-males patrolled their territory more than did C-males to defend resources from other individuals. If true, this behaviour would support the resource defence hypothesis. Conversely, T-males may stray further from their 35% core-use area if, by doing so, they are able to increase the frequency of mate association under the pair bond hypothesis. We address the former possibility first by examining male–male interactions more closely.

Table 2. Comparison of home range sizes in the year before, and the year during, a T-manipulation in four individual male downy woodpeckers

Male	1st winter (no T-implant)*	2nd winter (T-implant)	T/C ratio†
Kernel home range: 35% use area (ha)			
ymym	1.3	0.5	0.38
mlml	1.1	1.3	1.18
gobo	0.9	1.7	1.89
mcbc	1.4	1.1	0.79
Kernel home range: 75% use area (ha)			
ymym	4.8	3.0	0.63
mlml	6.6	8.8	1.33
gobo	4.2	9.1	2.17
mcbc	5.1	6.3	1.24
Minimum convex polygon (ha)			
ymym	6.4	6.1	0.95
mlml	6.0	20.9	3.48
gobo	17.3	24.1	1.39
mcbc	26.1	8.0	0.31

*Males ymym and mcbc were studied in the year before our experiment began; they did not receive implants of any kind. Males mlml and gobo received empty implants.

†The ratio relates the changes in home range size from the year of the T-implant to the year before. If all males had values greater than 1.00, that could suggest that T-implants caused home range size to expand. However, two of the four males generally had smaller home range sizes during the year of the T-implant (T/C < 1.00).

Male–Male Interactions

If T-male home ranges overlapped neighbouring male home ranges to a smaller degree than C-male home ranges, then that might indicate that T-males were more territorial. However, T-treatment had no significant effect on the proportion of the 75% core-use area used exclusive of neighbouring males (T-male exclusivity: $\overline{X} \pm \mathrm{SE} = 0.66 \pm 0.08$, C-male exclusivity: 0.78 ± 0.09; *t* test: $t_{13} = 0.87$, $P = 0.40$; power = 0.78; see Appendix). There were also no treatment differences between males in neighbour incursion rate within the 75% use area (Table 3). Tests for a treatment effect on neighbour

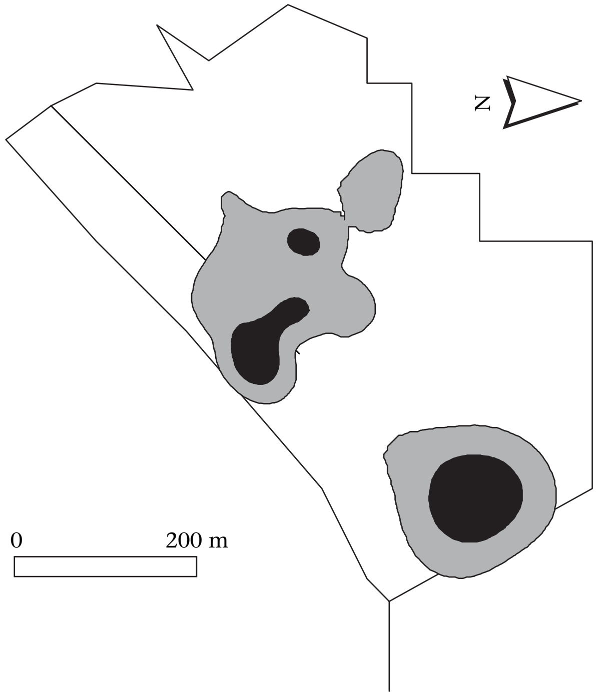

Figure 1. Home ranges of an example T-male (upper left) and C-male (lower right) showing the difference in range ratio. The 75% core-use areas of each male are shaded grey; 35% use areas are black.

Table 3. Mean ± SE neighbour incursion rates (incursions per hectare) onto focal male downy woodpeckers' home ranges calculated over the winter season for different core-use areas

Kernel home range	Incursions per hectare T-males (*N*=9)	C-males (*N*=6)	t_{13}	*P*	Power*
35% use area	0.22±0.08	0.24±0.06	0.14	0.89	0.50
50% use area	0.17±0.05	0.19±0.05	0.32	0.76	0.68
75% use area	0.24±0.04	0.20±0.04	0.65	0.52	0.90

*See Appendix for details on power analyses.

incursion rates using smaller core-use areas were inconclusive. However, neighbour incursion rates were fairly constant, regardless of which usage area was considered. This result suggests that the 35% and 50% use areas were not defended against neighbouring males any more than were the 75% use areas.

Under the resource defence hypothesis, we predicted that T-males would aggressively interact more with other males than would controls. This result would be expected if T-males approached nonmate females more (assuming that those females would be accompanied by other males), or if T-males maintained larger or more exclusive territories than did C-males. Contrary to our prediction, T-males associated with fewer males per focal observation than did C-males (30-m threshold, T-male associates: $\overline{X} \pm \mathrm{SE} = 0.052 \pm 0.015$, C-male associates: 0.138 ± 0.032; Student's *t* test: $t_{12} = 2.67$, $P = 0.020$). Perhaps as a result, T-males spent significantly less time displacing, chasing and displaying to other males than did control males (time spent in displays as proportion of total observation time, T-males: 0.004 ± 0.0013, C-males: 0.0146 ± 0.004; $t_{14} = 2.77$, $P = 0.015$).

Pair Interactions

We predicted under the pair bond hypothesis that the frequency of association between members of T-pairs would be higher than between members of C-pairs. There was little support for this prediction. T-implants did not generate a difference in mate association frequency compared to control males (proportion ± SE of focal observations with T-male within 40 m of the mate: 0.34 ± 0.06; C-males: 0.26 ± 0.05; Student's *t* test: $t_{12} = 0.96$, $P = 0.36$), although the power for this test was low (power $= 0.63$; see Appendix). Similarly, experimental and control groups did not differ significantly in home range overlap with the mate (75% core-use area: T-males: 0.64 ± 0.10; C-males: 0.65 ± 0.09; $t_{10} = 0.05$, $P = 0.96$), but the power for this test was low as well (power $= 0.56$).

An alternative method of testing our hypotheses using home range data was to look for a bulge in the 75% core-use area of T-males in the direction of their mates' 75% use area. Presence of a bulge, signifying a bias of male activities towards the mate's home range, would support the pair bond hypothesis. However, there was no apparent female-biased shift (Hotelling's one-sample test: $T^2_{2,12} = 1.69$, $P = 0.51$). In fact, some males in both the experimental and control groups expanded their 75% core-use area away from the mate's home range (negative values for 'male shift' in Fig. 2). Male home ranges with the greatest spatial shift away from their mate's home range had the greatest range ratio values (i.e. size of 75% use area divided by 35% use area; Table 4, Fig. 2). This result is reflected by an inverse relationship between mate association frequency and range ratio (Fig. 3, Table 5). Thus, males that frequently associated with their mate appear to have had a lower frequency of wide-ranging activities, resulting in a smaller range ratio than that for males who interacted less with their mate. This pattern could relate to a male's effort (in either treatment group) to restrict its mate's access to other males visiting locations within the home range (Eason & Hannon 2003). Generally, males with high neighbour incursion rates had high mate association frequencies, and a significant interaction between implant type and neighbour incursion rate indicated that the pattern was strongest among the T-males (Fig. 4, Table 5). Thus, T-treatment exaggerated the response of males to high neighbour incursion rates. At the same time, as neighbour incursions onto a focal male's home range increased, the frequency at which nonmate males associated with the focal male's mate decreased (GLM: $F_{1,11} = 8.90$, $P = 0.018$; Fig. 5). The two findings together (cf. Figs 4, 5) suggest that males defended their mates more intensely when male incursion on their home range was relatively common.

Given that some (but not all) T-males associated with their mate with relatively high frequency, we predicted under the resource defence hypothesis that T-females would experience greater interference competition from males and be subject to more displacements than would C-females. However, male mate displacements were infrequent (range 0.0–2.4/h), and means of the two treatment groups did not differ (LS means: T-male displacements/h: 0.116 ± 0.140, C-male displacements/h: 0.176 ± 0.217; Wilcoxon two-sample test: $W = 52.50$, $N = 15$, $P = 0.62$).

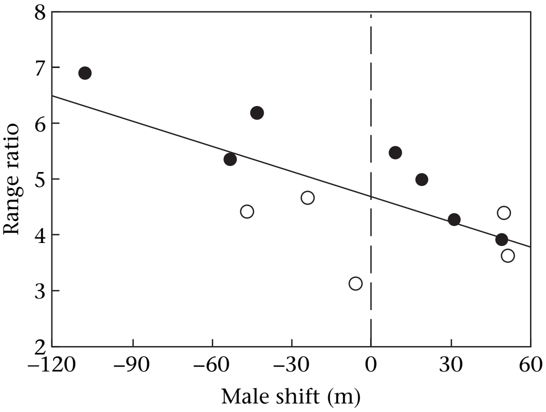

Figure 2. Relationship between range ratio and male shift. See Table 4 for significance of the model and the definition of 'male shift'. ●: T-males; ○: control males.

Table 4. Analysis of male downy woodpecker range ratio (size of the 75% core-use area of the home range divided by the 35% use area) using a general linear model

Independent variable	Estimate	$F_{1,11}$	P
Distance between mates*	0.003	1.13	0.32
Male shift†	−0.016	7.04	0.033
Implant type‡	−1.073	9.67	0.017
Implant×male shift interaction	0.012	2.36	0.17

*Distance between the geographical centres of the male's and female's 75% core-use areas.

†Distance between the geographical centres of male's 35% use area and his mate's 75% use area minus the distance between mates (as above*). Larger values would indicate that a male's non-core space use is skewed towards his mate's home range.

‡Subcutaneous implants were either filled with testosterone or empty. This variable was included in the model because T-implanted males had previously been found to have higher range ratios than controls.

Effect of Male Testosterone on Female Behaviour

Under the pair bond hypothesis, we predicted that increased mate association (as was found among some T-males) would increase female foraging efficiency because of male protection behaviour. Overall, our data were not consistent with this hypothesis. When time of day and foraging substrate width were held constant, T-females visited fewer food patches per hour and spent less time pecking at each patch than did C-females (repeated measures ANCOVA, visit durations: $F_{1,19} = 5.44$, $P = 0.031$; patch visit rate: $F_{1,14} = 4.54$, $P = 0.051$; Fig. 6).

DISCUSSION

We tested two hypotheses regarding the function of testosterone (T) in male downy woodpeckers during winter. The resource defence hypothesis states that exogenous T-treatment enables males to dominate territorial space to a greater degree than controls. This investment into resource defence could be an important contributor to future reproductive success because males use the same home ranges throughout the year, and loss of spatial dominance in winter could limit resource availability in the spring. The pair bond hypothesis states that male T could facilitate social interaction between mates, which could aid female survivorship and eventually increase male and female reproductive success. Both hypotheses have been supported in previous studies, albeit in different species (Wingfield & Farner 1993). However, our results suggest that neither hypothesis is a good descriptor of how T influences the interactions of downy woodpecker pairs during the nonbreeding season. We will first address the unique predictions from each of these

Table 5. Analysis of the proportion of focal observations during which mates were spatially associating within a given distance threshold, using a general linear model

Independent variable*	Estimate	$F_{1,13}$	P
Mate association (40-m threshold)			
Range ratio	−0.078	6.93	0.027
Neighbour incursion rate	0.126	11.74	0.008
Implant type	0.119	1.35	0.27
Implant×incursion interaction	−0.108	6.23	0.034
Mate association (30-m threshold)			
Range ratio	−0.084	5.20	0.049
Neighbour incursion rate	0.145	5.55	0.043
Implant type	0.240	3.57	0.092
Implant×incursion interaction	−0.168	9.82	0.012
Mate association (20-m threshold)			
Range ratio	−0.079	5.73	0.040
Neighbour incursion rate	0.119	6.07	0.036
Implant type	0.158	1.91	0.20
Implant×incursion interaction	−0.122	6.45	0.032

*See text for description of variables.

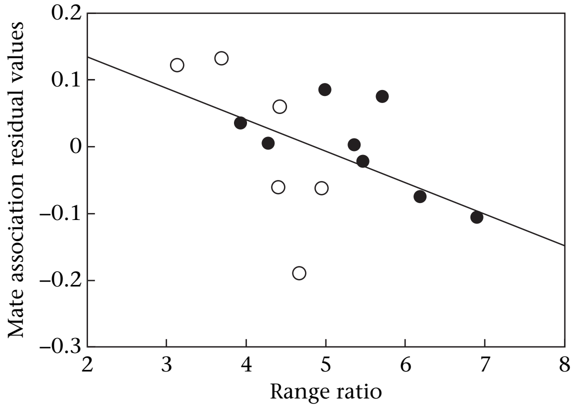

Figure 3. Residual values produced by a general linear model including neighbour incursion rate, implant type and an interaction term, plotted against range ratio. This shows the negative relationship between mate association frequency (using a 40-m threshold) and range ratio detected by the model referred to in Table 5. ●: T-males; ○: C-males.

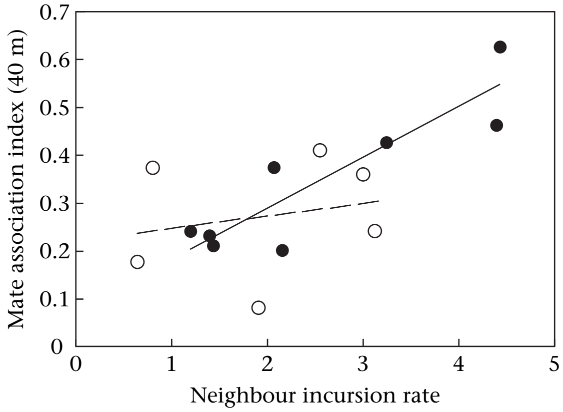

Figure 4. Mate association index as a function of neighbour incursion rate. In a general linear model, the interaction between treatment type and neighbour incursion rate was significant (Table 5). Therefore, two regression lines are shown, representing T-males (-●-) and C-males (- -○- -).

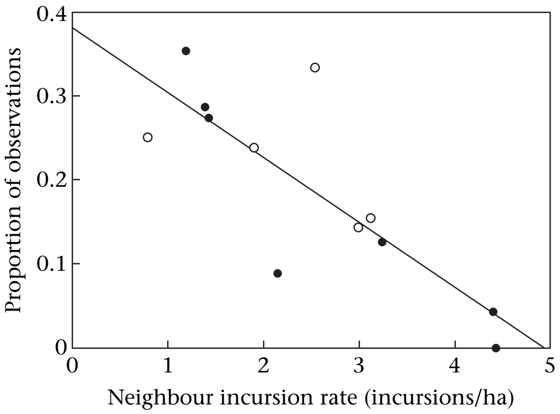

Figure 5. The proportion of focal observations during which female woodpeckers were seen within 40 m of a nonmate male as a function of the neighbour incursion rate experienced by each female's mate. ●: T-females; ○: C-females.

hypotheses, and then provide an alternative hypothesis that is more consistent with our results.

Resource Defence

Some of our data were clearly inconsistent with the resource defence hypothesis. With sufficiently high statistical power, we found that T-males did not have larger home ranges than did C-males, at least at the 95% activity level. Power was lower for the other home range analyses, but data from a group of males studied in successive years showed that T-treatment in the second year did not consistently increase the size of core-use areas over those used in the first year when no T-implants were given. We also found with marginally high power that the proportion of a male's home range not overlapping with neighbouring males was the same regardless of T-treatment. This result suggests that T-males were no more exclusive of home range space than were C-males. Indeed, the rate of neighbour incursions into a T-male's 75% use area was no different from the rate of incursions into a C-male's use area.

T-males used space within their home ranges differently than did C-males. Specifically, the ratio of the 75% use area to the 35% use area ('range ratio') was significantly higher in T-males. This result indicates that T-males had a more dispersed activity pattern, on average straying further from their home range centre than controls. This might be interpreted as territorial patrolling, particularly because males with relatively high range ratios appeared to have 75% use areas geographically centred in a direction away from their mate. However, T-males were proximate to other males less often than were C-males; similarly, T-males spent a smaller proportion of time in male-directed aggressive displays than did C-males. This result was opposite of what would be expected if T increased territory-centred aggressive conflicts between males, as has been found in other species (Wingfield 1984; Wingfield & Ramenofsky 1985).

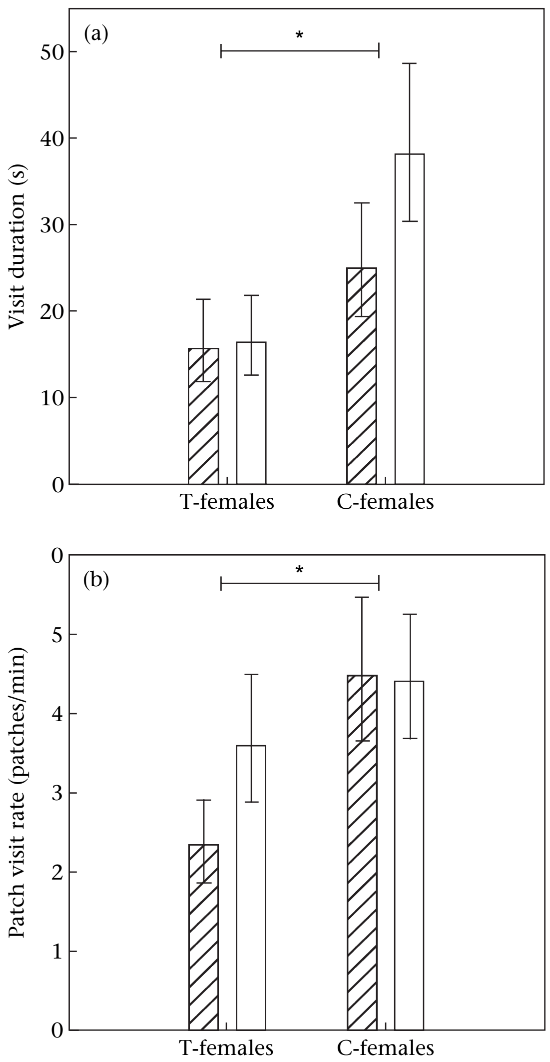

Figure 6. (a) Patch visit duration and (b) patch visit rate of female downy woodpeckers when the mate was within 40 m (▨) and when the mate was more distant (☐). Presented are least-squares means with standard errors generated from a repeated measures model. Values are back-transformed from original analysis. *$P < 0.05$.

We offer three possible reasons for the reduced male–male interactions found between T-implanted male woodpeckers. First, the challenge hypothesis states that male aggression and T are only correlated during periods of social instability (Wingfield 1988). Thus, when T-males first received implants, rates of male–male displays may have increased. Within days, however, the social relationships between neighbouring males should have stabilized, and male–male display rates would have diminished to normal levels (Wingfield et al. 1987). However, the challenge hypothesis would not predict that elevated T would cause reduced male–male interaction, as we found.

A second possible reason for reduced male display among T-males is that the T-implants could have increased dominance status, reducing the likelihood that other males would approach and interact with T-males. Beletsky (1992) found this kind of hormone effect by giving free-living male red-winged blackbirds, *Agelaius phoeniceus*, anti-androgen treatments. He found that males with artificially reduced T levels experienced many more territorial challenges than males with normal T levels. However, there are significant differences in natural history between *A. phoeniceus* and *P. pubescens*, and several studies of captive birds show administration of T does not necessarily change male dominance status, despite an increased level of T-male aggression (Wingfield et al. 1987; Wiley et al. 1999; Collias et al. 2002).

A third reason for reduced male display among T-males is that testosterone simply increases overall male activity rate (Gwinner & Gwinner 1994). This could proximately explain the higher range ratios. However, T-males in our study also appeared to be more responsive to the incursions of other males. This observation suggests that, if T-males detected a relatively high number of neighbour male incursions, instead of confronting the intruding males, the T-males flew towards their mate and maintained shorter intrapair distances (e.g. Eason & Hannon 2003). Thus, although T-implants could have increased overall activity rates, they clearly affected mate association patterns in the presence of male competitors.

Pair Bond Maintenance

The second hypothesis that we proposed to explain the function of male T in winter was the pair bond hypothesis. We based this hypothesis on several observations. First, nonbreeding male T correlates in some species with male sexual behaviour (Paulke & Haase 1978; Lincoln et al. 1980; Dawson 1983; Bluhm 1988). Second, females in laboratory and aviary experiments spent more time with T-implanted males than with controls (Domjan 1987; Enstrom et al. 1997). Third, when pairs are together, males in some species increase female foraging success by increasing antipredator vigilance and alarm calling (Sullivan 1985; Rohwer & Anderson 1988; Hannon & Martin 1996), and at least one study showed that these male behaviours were mediated by T (Fusani et al. 1997). Lastly, experimental increases in female reproductive steroids during autumn and winter seem to hasten reproductive behaviour between mates (Moore 1983; Wingfield & Monk 1994), so T could have a similar effect.

Based on these findings, we predicted that T-pairs would have greater home range overlap and higher frequencies of mate association than C-pairs. Neither prediction was consistently true, indicating that T-implants did not affect females in the ways predicted by the pair bond hypothesis. For instance, the T-implants did not appear to result in more cohesive pair relationships that could promote an early coordination of pair members' reproductive cycles. If this were the case, all T-males would have had high values of mate association, because this potential benefit of pair bond maintenance should apply to all males and not just ones with relatively high neighbour incursion rates. The same reasoning applies to benefits males and females incur from mate investment behaviour. If exogenous T increased male mate investment in female survivorship and condition (i.e. Hogstad 1995), T-females should have experienced improved foraging efficiency as a result. Our results are contrary to this prediction, because the food patch visit rates of T-females and the average duration of their visits were significantly below those of control females. The mechanism responsible for these declines is unknown, but the results suggest that if T-males were investing in mate survivorship and condition, their efforts were grossly ineffective.

Mate Guarding

We conclude that any effect of T on pair bond maintenance appears to be male centred; that is, females do not benefit from T-mediated changes in the pair bond. Instead, female foraging efficiency may be hindered, and their opportunity to assess other males as future reproductive partners appears to be diminished as a result of elevated testosterone in their mate. This conclusion is supported by the finding that as neighbour incursion rate increased, the rate at which females associated with nonmate males decreased. This pattern is opposite of what would be expected if females associated with nonmate males in proportion to the rate at which they frequented the area.

Given these findings, we reject both a priori hypotheses and propose a third hypothesis for the effect of exogenous T on male behaviour in the nonbreeding season: competition-dependent mate guarding. Mate guarding is most typically described in a variety of animals as a behaviour in which males closely follow their mates to prevent cuckoldry during a female's fertile period (Gowaty 1996), and its expression in the breeding season is mediated by T (Moore 1984). However, females do not have to be fertile for mate guarding to be selectively advantageous (Härdling et al. 2004). Even in the nonbreeding season, mate guarding can function to increase a male's assurance of paternity (Artiss & Martin 1995; Guillemain et al. 2003). For example, complete loss of future paternity is possible when the female mate (either the former mate or prospective future mate) deserts the male before the start of the breeding season and begins associating with one of his male neighbours (e.g. Swenson & Boag 1993). This 'mate switching' has been observed in our population (although not during the present study), and the deserted individuals did not always find 'replacement' mates before the start of the breeding season (Kellam et al. 2004).

The mate-guarding hypothesis is similar to the pair bond hypothesis because both involve male behaviours that function to prevent mate loss. The results of this study do not rule out the possibility that male downy woodpeckers invest in their mate's health and survivorship through mate investment, but results do indicate that T either has no net effect on this behaviour, or the effect is negative. In contrast, our findings suggest that T facilitates mate guarding, a second mechanism by which males can reduce the risk of mate loss. The presence of mate guarding might be indicated in both treatment groups, where increased frequencies of mate association corresponded with a decreased frequency of female interactions with nonmate males. If such nonmate interactions aid a female in making future mate choice decisions, a reduction in this behaviour would benefit the male by lowering the probability of future cuckoldry or prebreeding desertion by the female. Mate association frequencies of males covaried with the frequencies at which they experienced incursions onto their home range by other males, and the relationship was strongest among T-males. Although we cannot be sure of the cause for this pattern, we suggest that males were responding to increased male–male competition by guarding their mate. Testosterone may have enhanced the response but not initiated it.

Together, our findings show that the strength and nature of pair bond relationships during winter probably depend upon a variety of mechanisms, both hormonal and social. More work should be done on pair bond maintenance outside of the breeding season, because it may be an important way that individuals retain, protect and assess potential mating partners. Furthermore, from this study, it is clear that the role of T in prebreeding pair bond and other social behaviours could be important. The function of T and its consequences on fitness should be further investigated in winter birds.

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Appendix: Explanation of Power Analyses

Table 1 and nonmate female associations

We hypothesized that if male home range size increased, males would have the opportunity to meet and interact with more nonmate females. However, we found no significant treatment effect on the number of nonmate females that males associated with per focal. We also found no significant difference between the home range sizes of T-males and C-males. To calculate power for each set of tests, we derived an effect size based on the findings of Chandler et al. (1994). In their study of dark-eyed juncos, *Junco hyemalis*, during the incubation phase, T-implanted males maintained home ranges more than three times the area of C-males. No studies of home range size have been conducted on T-implanted male birds during the nonbreeding period. Nevertheless, because female woodpeckers were not fertile during our study period, we felt a three-fold treatment effect would be unreasonably high. Thus, we chose an effect size based on a 1.5-fold increase in home range from C- to T-males. In the same way, we expected T-males to associate with nonmate females 50% more frequently than C-males.

Table 3

T- and C-males did not differ significantly in the proportion of the 75% core-use area not overlapped with the home ranges of other males. Likewise, T-treatment appeared to have no effect on the number of neighbouring male incursions onto a focal male's home range, corrected for its overall size. It was logical to expect that if T-males were more aggressive and defensive of home range space, they would be able to reduce the number of other males using nearby resources. This is true in numerous studies documenting the more aggressive responses of T-implanted males to simulated territorial intrusions relative to controls. The T-males' responses to these intrusions were more than 70% greater than that of controls in most studies (Moore 1984; Wingfield 1984; Gwinner & Gwinner 1994), including those conducted during nonbreeding periods (Wingfield 1994; Soma et al. 2000). Therefore, we assumed C-males would have 70% more incursions onto their home range than C-males. To calculate an effect size for power to detect a treatment difference in the proportion of male home range overlapped by neighbouring males, we formulated an expectation for C-males based on the T-male average (expected C-male mean $= 0.39$, actual T-male mean $= 0.66$; a 1.7-fold difference).

Pair interactions

We found no significant differences between treatment groups with respect to mate association index (using a 40-m threshold distance) and the proportion of male home range overlapped by the mate's home range (using the 75% core-use area). To find an appropriate effect size while calculating power for these tests, we assumed in both cases that T-pairs would be more spatially and temporally proximate than C-pairs by a factor of 1.7. This is based on two laboratory studies that showed that infertile female birds spent more time with T-implanted males than with controls by a factor of 1.7–2.7 (Domjan 1987; Enstrom et al. 1997). We used the average values of T-male mate association and home range overlap to compute the expected values for C-males. Note that the power of these tests was lower when we used a threshold male association distance less than 40 m or when we considered core-use areas less than 75%.

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