



## Tied to the nest: male black-capped chickadees decrease dawn chorus movement behaviour when their mate is fertile

JENNIFER R. FOOTE\*, LAUREN P. FITZSIMMONS†, DANIEL J. MENNILL† & LAURENE M. RATCLIFFE\*

\*Biology Department, Queen's University, Kingston

†Department of Biological Sciences, University of Windsor

(Received 12 March 2008; initial acceptance 24 April 2008;  
final acceptance 26 May 2008; published online 17 July 2008; MS. number: A08-00171R)

Male songbirds typically mate-guard by closely following the female during her fertile period. At dawn, males may sing near the nest or roost to direct their chorus at mates. Recent evidence suggests males may also be involved in singing interactions with neighbours during the dawn chorus. We used a 16-channel acoustic location system to examine the movement behaviour of 37 male black-capped chickadees, *Poecile atricapillus*, during the dawn chorus to determine if male proximity to the nest is a function of breeding stage. Males with fertile females covered a significantly smaller area within their territory, made fewer long-distance movements and sang at a lower song rate compared to males with nonfertile females. Males with fertile mates remained significantly closer to their nest cavity than males with incubating mates. Males with nonfertile mates spent more time near their neighbours with fertile mates than near their neighbours with nonfertile mates. Neither social rank nor age had a significant effect on movement behaviour or song rate. Our results clearly show that female fertility influences dawn chorusing behaviour in male black-capped chickadees. Males may remain near their nest to minimize the risk of cuckoldry, but when their partner is not fertile males may increase movement behaviour to interact with neighbours and/or to advertise to potential extrapair mates.

© 2008 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

**Keywords:** acoustic location system; dawn chorus; mate guarding; movement; *Poecile atricapillus*; song rate

The dawn chorus of songbirds begins before sunrise and is characterized by high song rates and simultaneous singing by all males (Staicer et al. 1996). Due to the high volume of song and the difficulty of following individual males at dawn, the functions of dawn chorusing for intra- or intersexual communication are not well understood (Staicer et al. 1996). For example, in black-capped chickadees, *Poecile atricapillus*, three lines of evidence suggest that males direct their dawn chorus performance at females. First, males perform the chorus near their nests, often singing close to or even directly into the nest cavity where females typically roost (Otter & Ratcliffe 1993). Second, males usually stop chorusing when their female emerges

(Otter & Ratcliffe 1993; Gammon 2004). Third, dawn chorus start time, average length of song rate, and maximum song rate honestly indicate male quality (Otter et al. 1997). However, male chickadees also engage in interactive communication with neighbours during the dawn chorus (Foote et al., in press). Staicer et al. (1996) proposed that chorusing may function to mediate social relationships among territorial males and recent evidence supports this hypothesis (Liu 2004; Burt & Vehrencamp 2005; Foote et al., in press).

Singing behaviour of males often varies with their mate's breeding stage, and this variation may provide useful clues about dawn chorus function. Møller (1991) predicted that once paired, males would sing at a high rate during their mate's fertile period to announce their female's fertility and thereby guard their paternity. However, recent research shows that daytime song rate typically declines following pairing and may subsequently increase once females begin incubating (e.g. Hanski & Laurila 1993a; Nemeth 1996; Gil et al. 1999). In contrast, dawn chorus

Correspondence: J. R. Foote, Department of Biology, Queen's University, Kingston, ON K7L 3N6, Canada (email: [footej@biology.queensu.ca](mailto:footej@biology.queensu.ca)). L. P. Fitzsimmons is now at the Biology Department, Carleton University, Ottawa, ON, Canada. D. J. Mennill is at the Department of Biological Sciences, University of Windsor, Windsor, ON, Canada.

song rates typically remain high after males have paired and decline only once the young have hatched (Pärt 1991; Staicer et al. 1996; Amrhein et al. 2004a). During the female's fertile period, males may instead guard their paternity by physical mate guarding (Birkhead & Møller 1992). If females are stationary at dawn, males may be able to sing at a high rate during the fertile period by remaining near their nest, without the added task of physically following their mate to mate-guard (Slagsvold et al. 1994). The relative importance of male location and singing rate as paternity guards during the dawn chorus can be assessed by simultaneous measurement of male movements and vocal output. If male location acts as a paternity guard, and is related to female fertility, then males with fertile mates should sing their dawn chorus closer to their nest and move through a smaller area of their territory than males with nonfertile mates. If song acts as a paternity guard, males with fertile mates should sing at a higher rate than males with nonfertile mates.

Radiotracking is a useful technique for studying daily and/or seasonal movement patterns of birds such as home-range size (e.g. Elchuk & Wiebe 2003), dispersal (e.g. Anders et al. 1998), migration (e.g. Fuller et al. 1998) and extraterritorial behaviour (e.g. Stutchbury 1998; Naguib et al. 2001). Radiotracking has been used at dawn to examine movement behaviour of nonterritorial males (e.g. Amrhein et al. 2004b) and females (e.g. Double & Cockburn 2000). However, movement patterns of singing territory holders during the dawn chorus have received little attention. Otter & Ratcliffe (1993) found that male black-capped chickadees increased their movement behaviour when females were experimentally removed. Hansen et al. (2005) followed male chickadees during the dawn chorus and found that males in disturbed and undisturbed habitat covered similar areas within their territory. Whether breeding stage affects male movement during the dawn chorus has not been investigated, despite the fact that daytime mate guarding has been well studied (e.g. Johnsen & Lifjeld 1995; Chuang-Dobbs et al. 2001). Movement at dawn has not been studied in detail because of the lack of suitable technology; both radiotracking and physically following males are difficult in the low light levels at dawn. An acoustic location system (ALS) consists of an array of simultaneously recording microphones that record the content and timing of vocalizations as well as information on positions of singers that can be used to study movement patterns. An ALS triangulates the positions of singers using arrival time differences of sounds at multiple microphones (Mennill et al. 2006). We used an ALS to study the movement and singing behaviour of male black-capped chickadees during the dawn chorus.

To determine whether male position during the fertile period may function in mate guarding, we compared the dawn activity space and number of long-distance movements made by males whose mates were fertile with those of males whose mates were not fertile. We also determined whether males with fertile mates remained closer to their nest cavity than males whose mates had already begun incubation. We predicted that males with fertile mates would move less and sing closer to their nest cavity than males whose mates were not fertile. We also compared

song rates of males with fertile and with nonfertile mates to determine if males with fertile mates sing at a higher rate, as predicted by Møller (1991).

## METHODS

### Study Area, Population and Recording Methods

We studied a banded population of black-capped chickadees at Queen's University Biology Station, near Kingston, Ontario, Canada (44°34'N, 76°19'W) from January to July of 2005–2007. We captured adult birds ( $N = 149$  birds in 2005,  $N = 236$  in 2006,  $N = 61$  in 2007) in winter using treadle-traps baited with sunflower seeds and banded with a unique combination of three coloured bands and a numbered aluminium Canadian Wildlife Service band. We determined the dominance status of males in winter flocks by observing pairwise interactions at feeding stations ( $N = 2811$  interactions in 2005,  $N = 8423$  in 2006,  $N = 1100$  in 2007). Behaviours of dominant birds included supplanting or chasing subordinates, whereas behaviours of subordinate birds included waiting to feed and displaying submissive postures (details provided in Ratcliffe et al. 2007). Following Mennill et al. (2004), we classified males into three rank categories: (1) high-ranking males were the top two males in flocks of four or five males and the top male in flocks of two or three males; (2) midranking males were the middle male in flocks of three or five males; (3) low-ranking males were the bottom two males in flocks of four or five males and the bottom male in flocks of two and three males.

From 27 April to 15 May of 2005–2007, we recorded neighbourhoods encompassing 6–10 (average  $7.2 \pm 0.3$  males,  $N = 15$ ) black-capped chickadee territories using a 16-microphone ALS. A neighbourhood consisted of a cluster of breeding territories with males who were familiar with each other from their winter flocks and males from nearby flocks. Average territory size of males was  $18\,393 \pm 990$  m<sup>2</sup> (range 4637–28 957 m<sup>2</sup>,  $N = 37$  males). We recorded in 15 different neighbourhoods of up to 160 000 m<sup>2</sup>, five neighbourhoods in each of 2005, 2006, and 2007. The ALS consisted of 16 omnidirectional microphones housed in PVC tube rain covers and mounted on 3-m-long wooden poles that were elevated and attached to small trees using bungee cords. In each array, the average between-microphone distance was  $206.8 \pm 2.2$  m (calculated pairwise for all microphones in each array,  $N = 1800$ ), minimum distance was  $75.3 \pm 1.2$  m ( $N = 240$ ) and maximum distance was  $350.2 \pm 4.1$  m ( $N = 240$ ). We placed microphones as evenly as possible throughout the neighbourhood, to the extent permitted by vegetation and topography. Microphones were connected to a central computer using 2200 m of cable. Input from all microphones was digitized using a multichannel data acquisition card (National Instruments DAQ-6260) and recorded as 16-channel AIFF files using Chickadee version 1.9 recording software (J. Burt, Seattle, Washington, U.S.A.). This set-up was an extension of the eight-microphone system described by Mennill et al. (2006). We recorded from 0425 to 1130 hours Eastern Standard

Time (EST) on 2 to 4 consecutive days in each neighbourhood. During recording sessions, three or four observers transcribed the activities of individual birds within the recording area, including details of male singing locations and identities.

As winter flocks began to break up and breeding pairs began to defend territories (late March to early April), we visited each pair every 1–3 days. We recorded movements and territorial interactions of each pair on a detailed map using both landscape features and grid flags as landmarks to map breeding territories using the method of Bibby et al. (1992). We also recorded all pair locations during the array recordings, when we intensively followed the 6–10 pairs in the neighbourhood over a period of 2 to 4 days. A pair's territory was defined as the maximum extent of space exclusively occupied by the pair following the period of winter flock breakup but before the female's fertile period (Mennill et al. 2004). We calculated the area of the territory by plotting the boundaries from our field maps on the GPS map of the detailed landscape features using software (J. Burt) written in MatLab (Mathworks, Inc., Natick, Massachusetts, U.S.A.).

### Sound Recording Analysis

From the 49 mornings recorded with the ALS, we chose 14 for analysis (one dawn chorus from each of 14 of the 15 neighbourhoods; one neighbourhood in 2005 was not included because high winds and less than optimal microphone placement prevented analysis). We analyzed the first morning of recording for 10 neighbourhoods. For the remaining four, the second morning was analyzed, because weather or technical difficulties with the ALS on the first morning reduced the quality of those recordings.

For the 14 dawn chorus recordings, we annotated all songs sung by all males recorded ( $N = 92$  males,  $N = 41\,071$  songs) from the start of recording until approximately 0630 hours EST using the time and frequency cursors in the Syrinx PC sound analysis software (J. Burt). We used a combination of field notes, fine structural details of male songs and location information to confirm male identities. We used software (J. Burt) written in MatLab to localize male songs as described by Mennill et al. (2006). We determined the location of each male for every 20th consecutive song that he sang. When males moved long distances ( $>10$  m), we located the first song before and after each movement as well. We considered every 20th song appropriate given that chickadees sing from one perch for an extended period between movements (Otter & Ratcliffe 1993). Average song rate for the first 30 min of the chorus was  $11.58 \pm 0.62$  songs/min such that songs were located on average every 1.73 min. For songs that were not localized, we assigned the location of the previous localization to those songs.

### Statistical Analysis

To examine male movement behaviour while females were still roosting, we analysed the first 30 min of each

male's dawn chorus. Dawn chorus length in this study was  $38.8 \pm 1.6$  min ( $N = 45$ ). The end of the chorus was defined as the point at which a male stopped singing for at least 3 min after the first 30 min of the chorus. In keeping with previous studies (Otter & Ratcliffe 1993; Gammon 2004), our observations showed that during the first 30 min of the chorus, males were unaccompanied by their mate, who was either roosting in her nest cavity or outside the cavity in a tree. After 30 min, females often emerged and males continued to chorus for several minutes before stopping. We chose a 30-min period so that most females would still be roosting and, therefore, not influencing male movements. When females emerged and accompanied males before 30 min had elapsed ( $N = 2$  pairs), we examined male behaviour up to and including the time of emergence.

Of the 92 males recorded, we excluded 37 from the analysis either because we had difficulty triangulating their positions (e.g. male was at the periphery of the ALS or high winds precluded triangulation) or because they were unpaired ( $N = 6$ ) or because their mate's breeding stage could not be accurately determined. For individual males recorded in subsequent years, we included only the first year of recording ( $N = 18$  males) and excluded the second year from the analysis, giving a total sample size of 37 individuals. We distinguished three breeding stages: (1) prefertile ( $N = 11$ ): males who were paired but were still excavating a nest cavity; (2) fertile ( $N = 20$ ): determined by female 'broken-dee' vocalizations, or nest lining by females and pair copulations, or both (Smith 1991); (3) incubation ( $N = 6$ ). We located nests for 18 fertile females and six incubating females. We confirmed nesting stage based on behavioural observations by back-dating nests from the date of hatch for these pairs.

To analyse movement behaviour we calculated the area of the minimum convex polygon formed by each male's positions, which we call 'dawn activity space'. To control for variation in territory size, we used the residuals of the regression of dawn activity space on territory size ('residual dawn activity space'). For each male, we determined the number of movements of greater than 10 m (Otter & Ratcliffe 1993). Dawn activity space and territory size were square-root transformed to meet the assumptions of normality necessary for parametric statistical analyses. Average song rate was calculated as the total number of songs sung divided by 30 min. After establishing that dawn activity space and song rate of males with incubating and prefertile females did not significantly differ (dawn activity space:  $t_{15} = 0.57$ ,  $P = 0.58$ ; song rate:  $t_{15} = 0.15$ ,  $P = 0.88$ ), we combined these two groups into the 'nonfertile' category.

We used backwards stepwise regression ( $P$  enter = 0.25,  $P$  leave = 0.10) to determine if males with fertile mates had smaller residual dawn activity spaces and higher song rates than males with nonfertile mates. We examined the effects of date (expressed as day since April 28, the earliest recording date), year, male dominance rank in winter (high, mid, and low) and male age (second year or after second year). For nest distance we compared males with fertile mates to those with incubating mates because there is no expectation that prefertile birds roost near their excavations, and birds often have multiple excavations

(Ramsay et al. 1999; Mennill & Ratcliffe 2004). We categorized the positions of males with nonfertile females who had at least one fertile neighbour ( $N = 15$  males) as near boundaries with neighbours (closer to the boundary with a neighbour than to the centre of the territory), in the centre of the territory (closer to the centre of the territory than to a territory boundary) and near excavations or nests (within 25 m). We calculated the time spent at each location (determined by subtracting the end time of the last song sung at this location from the start time of the first song sung at this location). For males who had both fertile and nonfertile neighbours ( $N = 12$ ), we also compared the time spent near fertile and nonfertile neighbours. We used JMP 7 (SAS Institute, Cary, North Carolina, U.S.A.) for all statistical analysis at  $\alpha = 0.05$ . Results are presented as means  $\pm$  standard error. Effect sizes (ES) were calculated using Cohen's  $d$  (Cohen 1988).

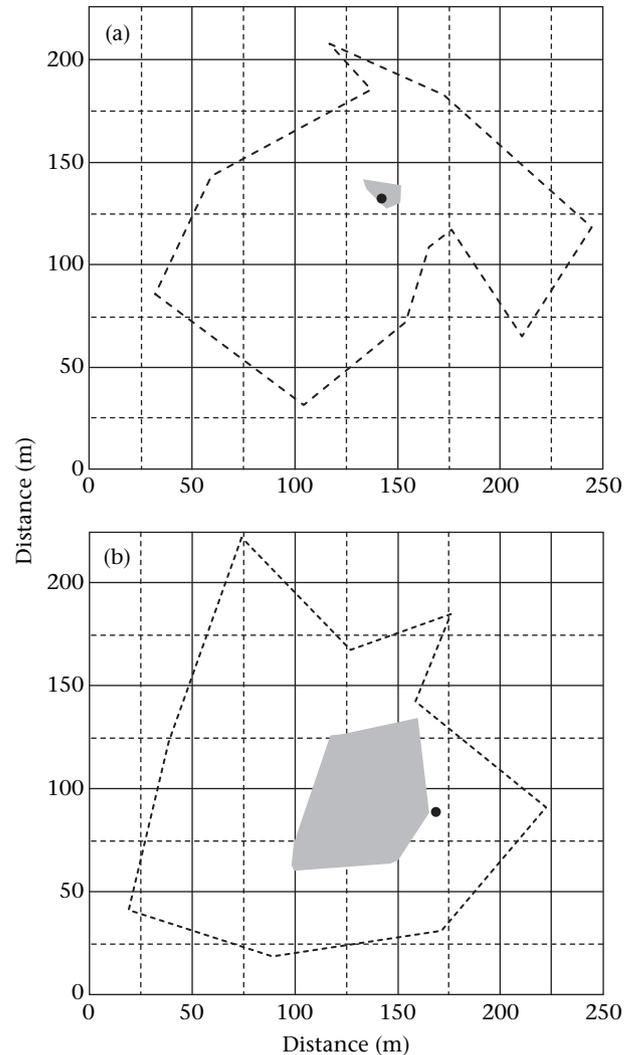
### Ethical Note

All aspects of this study were approved by the Queen's University Animal Care Committee (Foote-2004-052). Birds were captured and banded under Canadian Wildlife Service Banding (10766A) and Scientific Collection (CA 0146) permits issued to J. Foote.

### RESULTS

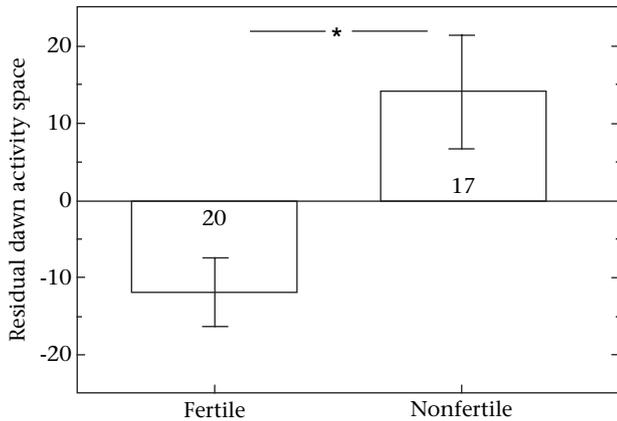
Breeding stage was the only factor significantly related to residual dawn activity space (backwards stepwise regression:  $F_{1,35} = 10.04$ ,  $P = 0.003$ ,  $r^2 = 0.22$ ,  $ES = 1.03$ ). Males with nonfertile mates had significantly larger residual dawn activity spaces than males with fertile mates (Figs. 1, 2). Date, year, male rank, and male age did not show a significant relationship with dawn activity space. When we excluded males with incubating mates and compared just the males with prefertile mates, residual dawn activity space was still significantly related to breeding stage (backwards stepwise regression:  $F_{1,29} = 8.94$ ,  $P = 0.006$ ,  $r^2 = 0.24$ ,  $ES = 1.03$ ). We conducted a pairwise comparison of males who were recorded in one year with a fertile mate and in another year with a nonfertile mate. Residual dawn activity space was significantly larger for males recorded when their mate was nonfertile (Wilcoxon matched-pairs signed-rank test:  $W_7 = 13.0$ ,  $P = 0.04$ ,  $ES = 0.58$ ). Males with fertile females made significantly fewer movements of greater than 10 m during the first 30 min of the chorus than males with nonfertile mates ( $t$  test:  $t_{34} = 2.26$ ,  $P = 0.03$ ,  $ES = 0.75$ ). Males with fertile mates made  $4.4 \pm 0.7$  movements greater than 10 m, whereas males with nonfertile mates made  $7.5 \pm 1.2$  movements greater than 10 m.

Males with fertile females stayed significantly closer to their nest cavity than males with incubating females for mean ( $t$  test:  $t_{22} = 3.83$ ,  $P < 0.001$ ,  $ES = 1.58$ ), maximum ( $t$  test:  $t_{22} = 2.98$ ,  $P = 0.007$ ,  $ES = 1.41$ ) and minimum ( $t$  test:  $t_{22} = 2.72$ ,  $P = 0.01$ ,  $ES = 1.01$ ) distance from the nest (Table 1). Males with nonfertile mates who had at least one fertile neighbour did not spend significantly more time near fertile neighbours than they did elsewhere in



**Figure 1.** Examples of dawn activity spaces of a male with (a) a fertile mate and (b) a nonfertile mate. The grey area represents dawn activity space, the black dashed line represents the territory boundary and the black circle represents the nest location. Dawn activity space was calculated as the residual of the regression of the area of the minimum convex polygon of dawn song posts versus territory size. Males with nonfertile mates moved over a larger area of their territory than males with fertile females. Each grid square marked with a solid grey line represents  $50 \times 50$  m.

their territory (paired  $t$  test:  $t_{14} = 1.40$ ,  $P = 0.18$ ,  $ES = 0.70$ ). These males spent 59.8% of their time near their boundaries (closer to boundary than to centre of territory) with neighbours who had fertile females and 40.2% of their time elsewhere in their territory (near nonfertile neighbours, central or near their excavation/nest). Comparing just the time spent near neighbours, however, males spent significantly more time near their neighbours who had fertile mates compared to their neighbours who had nonfertile mates (paired  $t$  test:  $t_{11} = 2.31$ ,  $P = 0.04$ ,  $ES = 1.17$ ). Males with neighbours in both fertile and nonfertile stages spent  $60.8 \pm 10.3\%$  of their chorus time near their fertile neighbours and  $21.6 \pm 8.5\%$  of their time near neighbours with nonfertile females.



**Figure 2.** Residual dawn activity space (residuals of regression of the area of a minimum convex polygon around dawn chorus song posts versus territory size) was smaller for males with mates who were fertile compared to males whose mates were not fertile. Error bars show standard error.

Song rate was significantly related to breeding stage and year (backwards stepwise regression:  $F_{2,34} = 7.22$ ,  $P = 0.002$ ,  $r^2 = 0.30$ ,  $ES = 0.88$ ). Males with fertile females had lower song rates than males with nonfertile females (Fig. 3). Song rates were slightly higher in 2005 than in 2006 and 2007, although comparing them directly, there was no significant difference between the years (ANOVA:  $F_{2,34} = 3.16$ ,  $P = 0.06$ ,  $r^2 = 0.16$ ). Date, male social rank and male age did not relate to dawn song rates in the first 30 min of the chorus. For males recorded over multiple years, chorus song rate was significantly lower for individuals recorded when their mate was fertile compared to the year that their mate was not fertile (Wilcoxon matched-pairs signed-rank test:  $W_7 = 15.0$ ,  $P = 0.04$ ,  $ES = 0.56$ ); seven of the eight males had lower song rates when their mate was fertile.

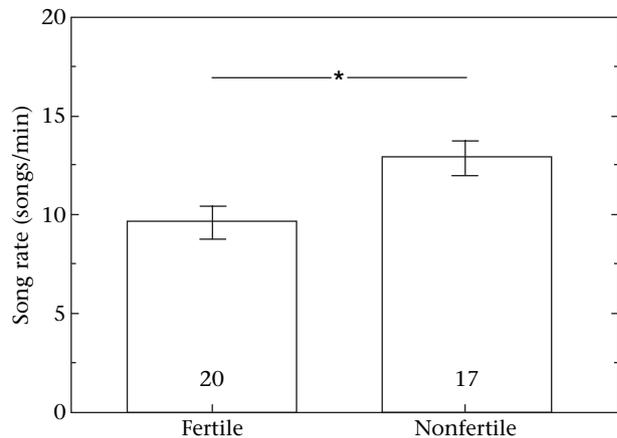
## DISCUSSION

Our spatial analysis of dawn chorus singing behaviour revealed that male black-capped chickadees with fertile mates had significantly smaller dawn activity spaces, made fewer long-distance movements and sang at lower song rates than males with mates who were not fertile. Males with fertile mates also remained closer to their nest cavity than males with incubating (nonfertile) mates. Movement behaviour was not influenced by either the social rank or the age of males. Males with nonfertile mates spent more time singing near neighbours with fertile

**Table 1.** Males with fertile females remain closer to the nest

	Mean	Maximum	Minimum
Fertile	29.7±5.3	56.3±8.1	15.0±3.9
Incubating	77.2±14.7	104.3±13.8	45.6±16.2

Mean, maximum and minimum distance (m) from nest cavities of males with fertile mates ( $N = 18$ ) and males with incubating mates ( $N = 6$ ). Values are means ± SE. Average territory size for males with fertile mates was  $19\,670 \pm 1338\text{ m}^2$  and for males with incubating mates was  $17\,906 \pm 1851\text{ m}^2$ .



**Figure 3.** Average song rate of males in the first 30 min of the dawn chorus was lower for males with fertile females than for males with nonfertile females. Error bars show standard error.

females than they did near neighbours without fertile females. We show that male chickadees remain close to the nest during their female's fertile period, suggesting that male location at dawn may function as a form of mate guarding. Moreover, our results, combined with those of others (Otter et al. 1997; Foote et al., in press) suggest that males have multiple audiences at dawn, including their mate as well as neighbouring males and females.

Males with fertile mates may minimize movement and remain close to their nests to minimize the risk of being cuckolded. Males may be particularly at risk of losing paternity at dawn. In some species, including chickadees, females may leave their territory at dawn to seek extrapair copulations (Smith 1988; Double & Cockburn 2000; Mennill et al. 2004). Female black-capped chickadees engage in extrapair copulations near territorial boundaries with extrapair sires or in the territories of extrapair sires, usually within an hour of dawn (Smith 1988; Mennill et al. 2004). Males may choose to stay near their nest at dawn when their mate is fertile to guard their paternity, and they may advertise themselves to neighbouring females when their mate is not fertile to gain extrapair paternity. Neither age nor rank significantly influenced movement behaviour during the dawn chorus. High-ranking chickadees are rarely cuckolded (Mennill et al. 2002) and sire young in the nests of lower ranked neighbours (Otter et al. 1998; Mennill et al. 2004), yet still remain near their nest at dawn. Less attractive males (Johnsen & Lifjeld 1995; Kempnaers et al. 1995) or younger males (Welling et al. 1995a; Johnsen et al. 2003) physically mate-guard more than attractive or older males in some species, suggesting that mate guarding in part may be a 'best of a bad job' strategy. Our results suggest that dawn chorus mate guarding is not a best of a bad job strategy because high-, mid- and low-ranked birds moved less and remained near their nest cavity when their mate was fertile. Evidence from other species suggests that mate guarding may be a successful strategy for males in general, reducing intrusion and preventing extrapair copulations (Komdeur et al. 1999; Chuang-Dobbs et al. 2001; Brylawski & Whittingham 2004). Similar patterns of lower levels of movement when females are fertile occur

in other species. Male great tits, *Parus major*, spend less time near their nest cavity when their mate is incubating than when she is fertile (Slagsvold et al. 1994), and male chaffinches, *Fringilla coelebs*, decrease their territory size when their mate is fertile (Hanski & Laurila 1993b).

Males whose mates are not fertile may shift the focus of their communication and displays from their own mate to neighbouring females by expanding the area from which they sing at dawn. Male chickadees with nonfertile mates approached their territory boundaries with neighbours and preferentially approached those that contained fertile females. Males may approach boundaries to advertise to neighbouring fertile females or to place themselves in a position in which females making extraterritorial forays can easily locate them. Female chickadees often place their nests near territory boundaries (Ramsay et al. 1999; Mennill et al. 2004) and those that follow a mixed reproductive strategy preferentially orient their cavity towards the territory of their extrapair sire (Mennill & Ratcliffe 2004). By moving closer to boundaries, males with nonfertile mates may be improving the transmission of their song to roosting female neighbours.

Male chickadees also approach boundaries with neighbours whose mates are nonfertile, supporting the hypothesis that one of the functions of the chorus is to adjust social dynamics among territorial neighbours (Staicer et al. 1996). Male chickadees interact with neighbours at dawn by matching the frequency of their song (Foote et al., in press). The amount of matching at dawn does not relate to the distance between neighbours (Foote et al., in press) which might be explained by the fact that some males remain close to their nest and do not move closer to individuals with whom they might be involved in intense interactions, whereas others approach rivals. Remaining close to fertile females may make it difficult for males simultaneously to interact with neighbours at close range, visit potential extrapair mates, and defend the entirety of their territories.

Male chickadees with fertile mates had lower song rates during the first 30 min of the dawn chorus than males with nonfertile mates. Consequently, our results do not support the hypothesis that males sing at a high rate to guard their paternity as predicted by Møller (1991). In some species, daytime postchorus song rate is lower when females are fertile and increases when females begin incubation (e.g. Hanski & Laurila 1993a; Nemeth 1996; Gil et al. 1999). Like black-capped chickadees, the dawn song rates of Eastern kingbirds, *Tyrannus tyrannus*, are also highest when their mates are not fertile (Sexton et al. 2007). However, male willow tits, *Parus montanus*, are less likely to perform in the dawn chorus when their mate is not fertile (Welling et al. 1995b), and male great tits have higher dawn song rates during the peak period of female fertility (Mace 1987). In contrast, male collared flycatchers, *Ficedula albicollis*, have similar dawn song rates in the fertile and nonfertile periods (Pärt 1991). Male chickadees may look into their nest cavities during the chorus or sing directly into them (Otter & Ratcliffe 1993). Lower song rates may result from males' checking to ensure the female has not left the cavity. Male chickadees with fertile mates often appeared agitated and interspersed their singing with gargle and 'chick-a-dee' vocalizations (J. Foote, personal observations), which may

also help to explain the lower song rates. Mixing calls with song during the chorus has been described for black-capped chickadees and related parid species (reviewed in Hailman & Ficken 1996). Female great tits interact vocally with their mate from inside the nest cavity after their mate approaches the cavity (Gorissen & Eens 2004). If female chickadees also produce vocalizations, males with fertile mates may sing at a lower song rate because they must listen for signals from their mate as well as from other males. Males may produce 'chick-a-dee' calls, which appear to have smaller transmission distances, to communicate with their mate without communicating information to rival males.

In summary, male black-capped chickadees with fertile females had smaller dawn activity spaces and remained closer to their nest than males with nonfertile females. This study is the first to examine movement patterns during the dawn chorus in detail and provides evidence that males may position themselves to minimize the risk of cuckoldry. We show that mate guarding at dawn may also be important in addition to mate guarding during the daytime. Our results do not support the fertility announcement hypothesis that males sing at a high rate when their mate is fertile to advertise their fertility (Møller 1991). When females are not fertile, males cover a larger area of their territory and approach neighbours. The dawn chorus may function both intrasexually, whereby males are involved in interactive communication with neighbours to mediate their social relationships, and intersexually, whereby males are honestly advertising their quality to their mate and perhaps also to potential extrapair females.

### Acknowledgments

We thank J. Baldock, T. Barran, R. Bull, S. Doucet, D. Gabriel, H. Hennin, R. Jamieson, S. Lippold, A. McKellar, A. Osmun, D. Potvin, C. Toth and K. Winger for field assistance. We thank the Curtis, Lundell, Warren, Weatherhead-Metz and Zink families for access to property and the staff of Queen's University Biological Station for logistical support. We thank J. Burt for software design. We thank Dustin Rubenstein and an anonymous referee for comments that improved the manuscript. We thank the Natural Sciences and Engineering Research Council of Canada, Canada Foundation for Innovation, Ontario Government, Society of Canadian Ornithologists, American Ornithologists' Union, American Museum of Natural History, University of Windsor and Queen's University for funding.

### References

- Amrhein, V., Kunc, H. P. & Naguib, M. 2004a. Seasonal patterns of singing activity vary with time of day in the nightingale (*Luscinia megarhynchos*). *Auk*, **121**, 110–117.
- Amrhein, V., Kunc, H. P. & Naguib, M. 2004b. Non-territorial nightingales prospect territories during the dawn chorus. *Proceedings of the Royal Society of London, Series B*, **271**, S167–169.
- Anders, A. D., Faaborg, J. & Thompson, F. R., III. 1998. Postfledging dispersal, habitat use, and home-range size of juvenile wood thrushes. *Auk*, **115**, 349–358.
- Bibby, C. J., Burgess, N. D. & Hill, D. A. 1992. *Bird Census Techniques*. London: Academic Press.

- Birkhead, T. R. & Møller, A. P. 1992. *Sperm Competition in Birds: Evolutionary Causes and Consequences*. London: Academic Press.
- Brylawski, A. M. Z. & Whittingham, L. A. 2004. An experimental study of mate guarding and paternity in house wrens. *Animal Behaviour*, **68**, 1417–1424.
- Burt, J. M. & Vehrencamp, S. L. 2005. Dawn chorus as an interactive communication network. In: *Animal Communication Networks* (Ed. by P. K. McGregor), pp. 320–343. Cambridge, U.K.: Cambridge University Press.
- Chuang-Dobbs, H. C., Webster, M. S. & Holmes, R. T. 2001. The effectiveness of mate guarding by male black-throated blue warblers. *Behavioral Ecology*, **12**, 541–546.
- Cohen, J. 1988. *Statistical Power Analysis for the Behavioral Sciences*. Hillsdale, New Jersey: L. Erlbaum.
- Double, M. & Cockburn, A. 2000. Pre-dawn infidelity: females control extra-pair mating in superb fairy-wrens. *Proceedings of the Royal Society of London, Series B*, **267**, 465–470.
- Elchuk, C. L. & Wiebe, K. L. 2003. Home-range size of northern flickers (*Colaptes auratus*) in relation to habitat and parental attributes. *Canadian Journal of Zoology*, **81**, 954–961.
- Foote, J. R., Fitzsimmons, L. P., Mennill, D. J. & Ratcliffe, L. M. In press. Male chickadees match neighbors interactively at dawn: support for the social dynamics hypothesis. *Behavioral Ecology*.
- Fuller, M. R., Seeger, W. S. & Schueck, L. S. 1998. Routes and travel rates of migrating peregrine falcons *Falco peregrinus* and Swainson's hawks *Buteo swainsoni* in the western hemisphere. *Journal of Avian Biology*, **29**, 433–440.
- Gammon, D. E. 2004. Black-capped chickadee dawn chorus and subsequent sexual activity. *Wilson Bulletin*, **116**, 252–256.
- Gil, D., Graves, J. A. & Slater, P. J. B. 1999. Seasonal patterns of singing in the willow warbler: evidence against the fertility announcement hypothesis. *Animal Behaviour*, **58**, 995–1000.
- Gorissen, L. & Eens, M. 2004. Interactive communication between male and female great tits (*Parus major*) during the dawn chorus. *Auk*, **121**, 184–191.
- Hailman, J. P. & Ficken, M. S. 1996. Comparative analysis of vocal repertoires, with reference to chickadees. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 136–159. Ithaca, New York: Cornell University Press.
- Hansen, I. J. K., Otter, K. A., van Oort, H. & Holschuh, C. I. 2005. Communication breakdown? Habitat influences on black-capped chickadee dawn choruses. *Acta Ethologica*, **8**, 111–120.
- Hanski, I. K. & Laurila, A. 1993a. Variation in song rate during the breeding cycle of the chaffinch, *Fringilla coelebs*. *Ethology*, **93**, 161–169.
- Hanski, I. K. & Laurila, A. 1993b. Male chaffinches do not enlarge their territory to prevent cuckoldry. *Animal Behaviour*, **46**, 1036–1038.
- Johnsen, A. & Lifjeld, J. T. 1995. Unattractive males guard their mates more closely: an experiment with bluethroats (Aves, Turdidae: *Luscinia s. svecica*). *Ethology*, **101**, 200–212.
- Johnsen, A., Lifjeld, J. T. & Krokene, C. 2003. Age-related variation in mate-guarding intensity in the bluethroat (*Luscinia s. svecica*). *Ethology*, **109**, 147–158.
- Kempnaers, B., Verheyen, G. R. & Dhondt, A. A. 1995. Mate guarding and copulation behaviour in monogamous and polygynous blue tits: do males follow a best-of-a-bad-job strategy? *Behavioral Ecology and Sociobiology*, **36**, 33–42.
- Komdeur, J., Kraaijeveld-Smit, F., Kraaijeveld, K. & Edelaar, P. 1999. Explicit experimental evidence for the role of mate guarding in minimizing loss of paternity in the Seychelles warbler. *Proceedings of the Royal Society of London, Series B*, **266**, 2075–2081.
- Liu, W.-C. 2004. The effect of neighbours and females on dawn and daytime singing behaviours by male chipping sparrows. *Animal Behaviour*, **68**, 39–44.
- Mace, R. 1987. The dawn chorus in the great tit *Parus major* is directly related to female fertility. *Nature*, **330**, 745–746.
- Mennill, D. J. & Ratcliffe, L. M. 2004. Nest cavity orientation in black-capped chickadees *Poecile atricapillus*: do the acoustic properties of cavities influence sound reception in the nest and extra-pair matings? *Journal of Avian Biology*, **35**, 477–482.
- Mennill, D. J., Ratcliffe, L. M. & Boag, P. T. 2002. Female eavesdropping on male song contests in songbirds. *Science*, **296**, 873.
- Mennill, D. J., Ramsay, S. M., Boag, P. T. & Ratcliffe, L. M. 2004. Patterns of extrapair mating in relation to male dominance status and female nest placement in black-capped chickadees. *Behavioral Ecology*, **15**, 757–765.
- Mennill, D. J., Burt, J. M., Frisrup, K. M. & Vehrencamp, S. L. 2006. Accuracy of an acoustic location system for monitoring the position of duetting songbirds in tropical forest. *Journal of the Acoustical Society of America*, **119**, 2832–2839.
- Møller, A. P. 1991. Why mated songbirds sing so much: mate guarding and male announcement of mate fertility status. *American Naturalist*, **138**, 994–1014.
- Naguib, M., Altenkamp, R. & Griessmann, B. 2001. Nightingales in space: song and extra-territorial forays of radio tagged song birds. *Journal für Ornithologie*, **142**, 306–312.
- Nemeth, E. 1996. Differential singing styles in mated and unmated reed buntings *Emberiza schoeniclus*. *Ibis*, **138**, 172–176.
- Otter, K. & Ratcliffe, L. 1993. Changes in singing behavior of male black-capped chickadees (*Parus atricapillus*) following mate removal. *Behavioral Ecology and Sociobiology*, **33**, 409–414.
- Otter, K., Chruszcz, B. & Ratcliffe, L. 1997. Honest advertisement and song output during the dawn chorus of black-capped chickadees. *Behavioral Ecology*, **8**, 167–173.
- Otter, K., Ratcliffe, L., Michaud, D. & Boag, P. T. 1998. Do female black-capped chickadees prefer high-ranking males as extra-pair partners? *Behavioral Ecology and Sociobiology*, **43**, 25–36.
- Pärt, T. 1991. Is dawn singing related to paternity insurance? The case of the collared flycatcher. *Animal Behaviour*, **41**, 451–456.
- Ramsay, S. M., Otter, K. & Ratcliffe, L. M. 1999. Nest-site selection by female black-capped chickadees: settlement based on conspecific attraction? *Auk*, **116**, 604–617.
- Ratcliffe, L., Mennill, D. J. & Schubert, K. 2007. Social dominance and fitness in black-capped chickadees. In: *Ecology and Behavior of Chickadees and Titmice* (Ed. by K. A. Otter), pp. 131–146. Oxford: Oxford University Press.
- Sexton, K., Murphy, M. T., Redmond, L. J. & Dolan, A. C. 2007. Dawn song of eastern kingbirds: intrapopulation variability and sociobiological correlates. *Behaviour*, **144**, 1273–1295.
- Slagsvold, T., Dale, S. & Sætre, G.-P. 1994. Dawn singing in the great tit (*Parus major*): mate attraction, mate guarding, or territorial defence? *Behaviour*, **131**, 115–138.
- Smith, S. M. 1988. Extra-pair copulations in black-capped chickadees: the role of the female. *Behaviour*, **107**, 15–23.
- Smith, S. M. 1991. *The Black-Capped Chickadee: Behavioral Ecology and Natural History*. New York: Comstock Publishing Associates.
- Staicer, C. A., Spector, D. A. & Horn, A. G. 1996. The dawn chorus and other diel patterns in acoustic signaling. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 426–453. Ithaca, New York: Cornell University Press.
- Stutchbury, B. J. M. 1998. Extra-pair mating effort of male hooded warblers, *Wilsonia citrina*. *Animal Behaviour*, **55**, 553–561.
- Welling, P., Koivula, K. & Rytkönen, S. 1995a. Differences in mate guarding between age classes in the willow tit, *Parus montanus*. *Animal Behaviour*, **49**, 852–854.
- Welling, P., Koivula, K. & Lahti, K. 1995b. The dawn chorus is linked with female fertility in the willow tit *Parus montanus*. *Journal of Avian Biology*, **26**, 241–246.