

# Patterns of extrapair mating in relation to male dominance status and female nest placement in black-capped chickadees

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In sexually promiscuous animals, females may benefit by nesting close to the edge of their partner's territory to facilitate extrapair copulations. In the present study, we describe the extrapair mating system of black-capped chickadees, *Poecile atricapillus*, and test whether nest locations are influenced by conspecific attraction to extrapair partners. We conducted a spatial analysis of female mating strategies by using microsatellite paternity analysis in conjunction with geographic information system (GIS) analysis of nest and territory locations. Extrapair offspring comprised 52 of 351 offspring (14.8%) and were present in 19 of 57 broods (33.3%). Females paired to males with low dominance status in the previous winter's flock hierarchy were more likely to engage in a mixed reproductive strategy than were females paired to males with high dominance status. Females had extrapair copulations and extrapair fertilizations with high-ranking males more often than with low-ranking males. Not all extrapair copulations resulted in extrapair fertilizations. Females constructed their nests within  $16.8 \pm 1.0$  m of the edge of their partner's territory, significantly closer to the edge of their nearest neighbor's territory than to the center of their own partner's territory. Extrapair males usually shared territory boundaries with cuckolded males. Females paired to low-ranking males constructed nests near the territory edges of neighboring high-ranking males. However, females did not have extrapair copulations with the neighbor nearest to their nest or even with the high-ranking neighbor nearest to their nest. We conclude that conspecific attraction to neighbors may influence nesting location in black-capped chickadees; however, it does not operate by facilitating extrapair copulations. *Key words*: black-capped chickadee, conspecific attraction, extrapair copulations, extrapair fertilizations, female choice, male dominance rank, nest location, *Poecile atricapillus*. [*Behav Ecol* 15:757–765 (2004)]

Many animals aggregate in response to environmental and social factors. Rather than distributing themselves evenly across available habitat, animals preferentially settle near conspecific individuals (Stamps, 1988). In other words, “birds of a feather gather together” (Burton, 1632). Conspecific attraction may be intimately related to social and genetic mating systems for both colonial and territorial animals (Allee, 1931; Danchin and Wagner, 1997; Wagner, 1997). In genetically promiscuous birds, for example, the proximity of neighbors influences extrapair mating strategies; high densities are generally associated with increased extrapair copulations (Birkhead and Møller, 1992) and extrapair fertilizations (Westneat and Sherman, 1997). Numerous studies have investigated how spatial relationships among males influence their success as extrapair partners (Wagner, 1997; Westneat and Sherman, 1997). In many species, however, females also actively pursue extrapair fertilizations (see Currie et al., 1998; Double and Cockburn, 2000; Gray, 1996; Kempenaers et al., 1992; Smith, 1988; Stutchbury and Neudorf, 1997), yet little attention has been given to the spatial distribution of females relative to their preferred extrapair partners.

In territorial birds, females usually have extrapair fertilizations with neighboring males (see Gibbs et al. 1990; Hasselquist et al., 1995; Kempenaers et al., 1997; Richardson and Burke, 2001; Westneat, 1993). In several species, females nest at the edges of their partner's territory (clay-colored

sparrow, *Spizella pallida*: Knapton, 1979; Swainson's warbler, *Limnothlypis swainsonii*: Griscom and Sprunt, 1979; black-capped chickadees, *Poecile atricapillus*: Ramsay et al., 1999). We propose that female nest location may be influenced by conspecific attraction: females may adjust their nest location to facilitate extrapair copulations with neighbors (Ramsay et al., 1999).

We investigate female reproductive decisions and nest locations in black-capped chickadees, socially monogamous, territorial songbirds that follow a mixed reproductive strategy. Chickadees spend the winter in small flocks, in which social interactions between individuals follow a stable linear dominance hierarchy (Smith, 1991). Patterns of extrapair copulations (Smith, 1988) and extrapair fertilizations (Otter et al., 1998) suggest that females prefer males with high dominance status as extrapair partners. Chickadees are primary cavity nesters, and females appear to control nest location; although both partners participate in the excavation of multiple nest cavities, females are responsible for the bulk of excavation (Mennill DJ, personal observation; Ramsay et al., 1999) and are exclusively responsible for lining their chosen nest (Smith, 1991). During their egg-laying period, females remain in their nest cavities while males perform their dawn chorus. Females copulate with males shortly after emerging from their nest. As such, nest location may be intimately related to female mate choice decisions. Previous research demonstrated that nest sites are not different from random locations in male territories with respect to both vegetation characteristics and food abundance (Ramsay et al., 1999). Instead, females construct nests near the edges of their partner's territory boundaries independent of habitat features (Ramsay et al., 1999).

We combined microsatellite analysis of paternity with geographic information system (GIS) analysis of nest and territory features in a 5-year study of black-capped chickadees.

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Our goal was twofold. First, we examined patterns of extrapair partner choice with respect to male dominance status and female nest location. Second, we evaluated the hypothesis that females choose nest sites to facilitate extrapair copulations (Ramsay et al., 1999). We tested four predictions of this hypothesis: (1) we predicted that females would nest close to the edge of their social partner's territory; (2) we predicted that females paired to low-quality males would nest close to preferred extrapair partners; (3) we predicted that extrapair copulations would occur near female nest sites; and (4) we predicted that extrapair young would be fathered by the neighboring male nearest a female's nest.

## METHODS

We monitored black-capped chickadees at Queen's University Biological Station near Chaffey's Lock, Ontario, Canada (44°34' N, 76°19' W), from January–June of 1997–2001. In January of each year, we captured birds by using Potter traps (average of  $152 \pm 13$  birds per year) and banded each bird with an individually distinctive combination of two or three plastic color bands and one Canadian Wildlife Service (CWS) aluminum band. We assessed the age of birds based on the shape of their outer tail feathers (second-year versus after-second-year; Pyle, 1997; Smith, 1991). We collected a small blood sample (10–80  $\mu$ l) from the brachial vein of each individual. Blood was stored in Queen's lysis buffer (Seutin et al., 1991) and frozen at  $-20^{\circ}\text{C}$ .

### Assigning dominance status

In February and March of each year, we assessed flock dominance hierarchies by tabulating pairwise dominance interactions between birds at winter feeding stations. We inferred dominance when an individual (1) supplanted or chased an opponent, (2) resisted a supplanting attack by an opponent, (3) elicited a submissive posture in an opponent, or (4) fed while an opponent waited to approach a feeder (Ficken et al., 1990; Otter et al., 1998). Between 1997 and 2001 we observed 17,413 dyadic interactions between birds in 101 flocks (average of  $3483 \pm 1029$  interactions per year;  $20.2 \pm 2.3$  flocks per year; mean  $\pm$  SE). Flock membership was confirmed by monitoring groups of birds as they traveled between feeding stations. Our observations matched previous research (Smith, 1991), in that dominance relationships were consistent within flocks across feeding sites.

We assigned each male to a nominal rank class: high, mid, or low. To do this, we entered male-male dominance interactions into a separate matrix for every flock and reordered each matrix to fit a linear hierarchy by using MatMan software (DeVries, 1998; Noldus Information Technology). We identified high-ranking males as the top-ranking male in flocks with two or three males, or the top two males in flocks with four or five males. We identified mid-ranking males as the middle-ranking male in flocks of three or five males. We identified low-ranking males as the bottom-ranking male in flocks with two or three males or the bottom two males in flocks with four or five males.

We also assigned each male a continuous rank score, which facilitated quantitative comparison between males across flocks. For each male we calculated the total number of interactions he won divided by the total number of interactions in which he was involved. Rank scores varied from zero (males who never won an interaction) to one (males who never lost an interaction). Rank scores were strongly related to nominal rank classes (high-ranking males:  $0.78 \pm 0.02$ ,  $n = 129$ ; mid-ranking males:  $0.55 \pm 0.03$ ,  $n = 40$ ; low-ranking males:  $0.26 \pm 0.02$ ,  $n = 125$ ; ANOVA  $F_{2,291} = 225$ ,  $p < .0001$ ).

## Monitoring breeding season behavior

In mid-April of each year, when flocks began to break up and pairs of individuals began to defend breeding territories against their former flockmates, we visited each pair every 2–4 days. We censused birds and mapped breeding territories according to the method of Bibby et al. (1992), recording the movements and territorial interactions of each pair on a detailed map by using fine-scale landscape features and grid flags as landmarks. We considered a pair's territory to be the maximum extent of space exclusively occupied by the male and the female after the period of flock breakup but before the female's fertile period.

We monitored the reproductive activities of 249 pairs (189 pairs in which the nest location was known and the female completed nest building). The onset of female fertility was judged by two cues: (1) the lining of the nest cavity by the female, followed by (2) "broken dee" vocalizations given by the female (Smith, 1991). The onset of these behaviors coincides with female-initiated copulations and precedes egg laying by 1–4 days (Mennill DJ, personal observation). We confirmed the onset of egg laying and incubation by visual inspection of all nest cavities that were low enough to check with a mirror and flashlight. For cavities that were too high to inspect directly, we inferred the onset of egg laying and incubation from female behavior. We confirmed all laying dates by back-dating from the nestlings' stage of development at time of banding. We calculated a synchrony index for all females according to the method of Kempnaers (1993).

Although within-pair copulations are commonly observed in black-capped chickadees, extrapair copulations are secretive and difficult to detect (Smith, 1988). Accordingly, we used radiotelemetry to follow females in an attempt to describe their extrapair copulation behavior. We attached Holohil LB-2 transmitters to six females by using a figure-eight leg harness made of beading-cord elastic. We radio tracked females by using a three-element Yagi antenna and a Wildlife Materials TRX 1000S receiver. In 1999 we radio tracked four females for 10 h each, early in the morning over multiple days early in their fertile periods. In 2000 we focused our efforts on two females and followed each female for 1 h per morning for 20 days surrounding their first egg dates. Whenever an extrapair copulation was observed, with the assistance of radiotelemetry or otherwise, we noted the individuals involved and the context and location of the copulation.

When nestlings reached approximately 7 days of age, we opened nest cavities, collected a small blood sample (5–40  $\mu$ l) from each bird's tarsal or brachial vein, and banded each nestling with a CWS aluminum band. We returned nestlings to their nests and repaired cavities with duct tape. No nests suffered structural failure owing to our modifications.

### Paternity assignments

DNA was extracted from blood samples by using an ammonium acetate-based extraction protocol (DeSousa L, personal communication). Paternity was analyzed by polymerase chain reaction (PCR) amplification using radioactively labeled primers for three highly variable microsatellite loci (Table 1). These three loci had a combined exclusionary power of 0.995.

To detect extrapair young and assign extrapair fathers, we visually assessed autoradiographs of polyacrylamide gels. Offspring were considered to be extrapair young if alleles were mismatched with either parent at two or more loci. (This conservative approach prevented us from mistakenly labeling an individual who appeared to have a null allele as an extrapair offspring—an apparently homozygous offspring

**Table 1**  
**Polymorphism among three microsatellite markers used to detect extrapair offspring and assign extrapair fathers in black-capped chickadees**

Marker	Reference	<i>n</i> <sup>a</sup>	Observed Heterozygosity	Alleles ( <i>n</i> )	Frequency of most common allele	<i>p</i> <sub>exclusion</sub> <sup>b</sup>
Pca8	Dawson et al., 2000	234	95.3	52	0.07	0.93
Pat14	Otter et al., 1998	234	77.8	26	0.40	0.59
Pat43	Otter et al., 1998	234	87.6	32	0.19	0.80

<sup>a</sup> Number of unrelated adults genotyped.

<sup>b</sup> Probability of exclusion calculated according to the method of Marshall et al. 1998.

with an apparently homozygous father at locus Pat43 matched his father at the remaining two loci and was therefore not considered an extrapair young.) Allele combinations for all individuals were scored relative to a standard that was run in two to four lanes distributed evenly across every gel. We compared the genotypes of extrapair offspring to all males in the study population. For all extrapair male assignments, only one extrapair male matched the extrapair offspring at all three loci. Extrapair assignments were confirmed by running putative extrapair fathers next to extrapair offspring for all three loci. All autoradiographs were scored by two independent observers, one of whom was blind to the individuals' social relationships; observer assignments agreed in all cases.

### Geographical Information System analyses

We obtained Universal Transverse Mercator (UTM) coordinates for all nests by using a Trimble global positioning system (GPS) unit with real-time correction (accuracy  $\leq 1$  m). From 1997–1999 we used a TSC1 datalogger connected to a ProXRS and RTCM receiver, and in 2000 and 2001 we used an MC-V datalogger connected to a ProXL and ProBeacon receiver. We obtained UTM coordinates for territory boundaries in 1997–1998 by using the GPS unit, recording the maximum extent of exclusively occupied space; lines representing territory boundaries were converted to a closed polygon for each territory in AutoCad 2002. To obtain coordinates for territory boundaries in 1999–2001, we transcribed all known locations from daily field maps directly into AutoCad 2002; we drew closed polygons around all locations where pairs had been observed independently of their flockmates after flock breakup (early April) but preceding the onset of egg laying (early May; average sightings per pair,  $n = 36.7 \pm 5.5$ ).

Analyses of map features were conducted in ArcView Geographical Information System (GIS) 3.2. We calculated the area of each territory to the nearest 1.0 m<sup>2</sup>. To evaluate nest location relative to territory features, we used the Nearest Feature extension (version 3.6; Jenness Enterprises) to calculate the distance between each female's nest and the following territory features: (1) the center of her partner's territory (calculated as the geometric centroid of the polygon representing the territory), (2) the nearest edge of her partner's territory, and (3) the nearest edge of the territories of the 16 closest neighbors. Owing to the presence of small but variably sized undefended areas between territories, the distance from a female's nest to the edge of her partner's territory was smaller than the distance to the edge of the nearest neighbor's territory. We used the Random Point Generator extension (version 1.1; Jenness Enterprises) to calculate 100 random points within each male's territory; we calculated measures 1 through 3 for all random points and compared nest sites against these 100 random points for each territory. Although random points do not exactly represent

nest sites available to females, they allowed us to compare actual nest sites against other sites within each bird's territory.

For all nests in which we knew the extrapair father, we calculated the distance from the nest to the nearest edge of the extrapair father's territory. We tabulated the number of males with closer territory edges than the extrapair father. We compared the distance between the nest containing extrapair young and the extrapair father's territory against the average distance between 100 random points and the extrapair father's territory.

### Statistical methods

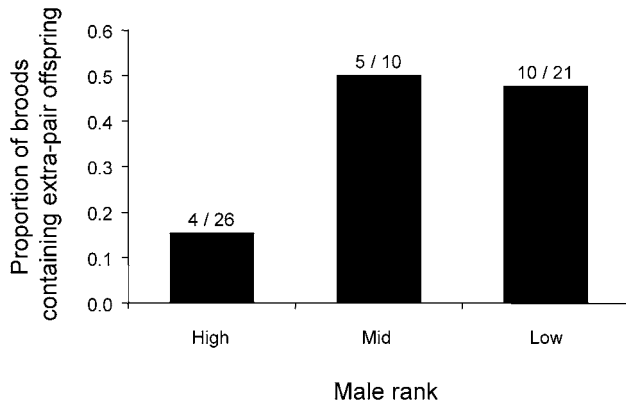
We collected blood from nestlings in 124 broods between 1997 and 2001. From 1999–2001 we conducted a playback experiment that influenced patterns of extrapair paternity (Mennill et al. 2002, 2003a). In the present study, we analyze paternity in 57 broods that were not manipulated in playback trials. Another 57 broods that were subject to experimental manipulation are included in GIS analyses but not paternity analyses (playback manipulations occurred after females had chosen and begun lining their nests). In addition, we classified 10 broods as unusual cases (three broods in which the female re-nested after initial nest predation; three broods in which the experimental playback protocol failed; three broods in which the parents had received experimental playback the previous year; and one brood in which two polygynous males attended the nest). As with the 57 experimental broods, these 10 unusual cases are included in GIS analyses of nest sites but not paternity analyses. Of 189 pairs included in nest site analyses, 28 pairs were represented in multiple years. We include nesting attempts in multiple years as independent events (only one female ever re-nested in the same cavity in consecutive years); however, statistical relationships did not change when only one nesting attempt per pair was considered.

Nonparametric statistics were used when data could not be normalized. Distances to territory edges and distances to neighbors were log transformed to achieve normality. Analyses were conducted in JMP 4.0. Values are reported as mean  $\pm$  SE. All tests are two-tailed.

## RESULTS

### Extrapair copulations

We observed six extrapair copulations between color-banded individuals (two with the assistance of radio telemetry). In four cases, females paired to low-ranking males had extrapair copulations with high-ranking neighbors. The fifth extrapair copulation involved an experimentally manipulated female (Mennill et al., 2002) who copulated with a low-ranking male. The sixth extrapair copulation was unusual: a recently widowed female, actively feeding eight 3-day-old nestlings,



**Figure 1**

The proportion of broods containing extra-pair offspring in relation to the dominance rank of the attending male. Females paired to low-ranking males and mid-ranking males frequently engaged in a mixed reproductive strategy, whereas females paired to high-ranking males did not ( $\chi^2_{2,55} = 6.9, p = .03$ ).

copulated with a low-ranking neighbor. On average, extra-pair copulations took place  $64.0 \pm 21.6$  m from the female's nest, either as the female moved to the boundary of the social and extra-pair males' territories ( $n = 5$  copulations at the boundary of the extra-pair male's territory and the cuckolded male's territory) or as the female forayed into the extra-pair male's territory ( $n = 1$ ). Three extra-pair copulations occurred in the twilight of dawn, shortly after the female emerged from her nest cavity (average time =  $0600 \pm 0014$  h), whereas the other three extra-pair copulations took place in mid-morning (average time =  $1040 \pm 0040$  h).

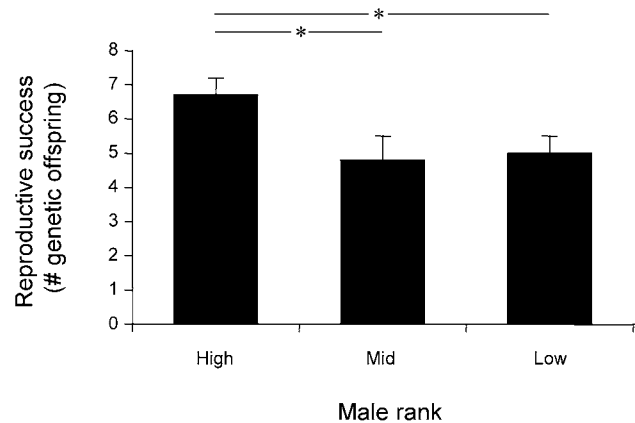
### Extra-pair paternity

Microsatellite paternity analysis revealed that 19 of 57 broods (33.3%) contained one or more extra-pair offspring. Of 351 offspring analyzed, 52 (14.8%) were unrelated to their social father. No offspring were unrelated to their social mother. Broods with mixed paternity contained an average of  $2.2 \pm 0.4$  extra-pair offspring (mode = 1; maximum = 6). Broods contained an average of  $6.2 \pm 0.2$  offspring. Broods with mixed paternity ( $6.1 \pm 0.4$  offspring,  $n = 19$ ) were not larger than were broods without mixed paternity ( $6.2 \pm 0.3$  offspring,  $n = 38; Z = -0.6, p = .58$ ).

Mixed paternity was common in the broods of low-ranking males and mid-ranking males, but rare in the broods of high-ranking males (Figure 1). Brood size did not vary with male rank (total number of offspring, high:  $6.3 \pm 0.4, n = 26$ ; mid:  $5.8 \pm 0.6, n = 10$ ; low:  $6.1 \pm 0.4, n = 21; F_{2,55} = 0.3, p = .74$ ). After deducting extra-pair young, high-ranking males tended to have greater within-pair reproductive success (number of within-pair offspring, high:  $6.1 \pm 0.4, n = 26$ ; mid:  $4.6 \pm 0.7, n = 10$ ; low:  $5.0 \pm 0.5, n = 21; F_{2,55} = 2.8, p = .07$ ), in agreement with previous genetic analyses of birds in this population (Otter et al., 1998). Male age had no influence on the presence of mixed paternity (fathers of broods with mixed paternity:  $2.5 \pm 0.4$  years,  $n = 19$ ; fathers of broods without mixed paternity:  $2.7 \pm 0.3$  years,  $n = 38; F_{2,55} = 0.2, p = .65$ ).

### Extra-pair males

We assigned paternity to 50 of 52 extra-pair young, identifying 21 extra-pair males who each fathered one to three extra-pair offspring (two males fathered extra-pair offspring in two broods, whereas the remaining 19 males fathered extra-pair



**Figure 2**

Mean  $\pm$  SE number of genetic offspring in relation to male dominance rank. High-ranking males ( $n = 26$ ) had higher reproductive success than did both mid-ranking males ( $n = 10$ ) and low-ranking males ( $n = 21$ ) (ANOVA  $F_{2,55} = 3.7, p = .03$ ). Asterisks show significant differences between groups (Tukey Kramer test  $p < .05$ ).

offspring in only one brood). Males with high dominance status were more likely to be extra-pair sires. We observed dominance interactions between the cuckolded male and the extra-pair male during the previous winter for 17 of the 21 extra-pair males; in 15 of 17 cases the extra-pair male was dominant to the cuckolded male (binomial test  $p = .001$ ). For 20 of the 21 extra-pair males with known rank class, 14 were high-ranking males, four were mid-ranking males, and two were low-ranking males. For 19 broods in which we knew the rank score of both males, extra-pair males had higher rank scores than did cuckolded males (extra-pair males:  $0.68 \pm 0.05$ ; cuckolded males:  $0.38 \pm 0.07$ ; paired  $t$  test  $t = 3.7, p = .002$ ). As a group, extra-pair males had a higher average rank score ( $0.68 \pm 0.05, n = 20$ ) than the average rank score of all other males in the population combined ( $0.47 \pm 0.02, n = 273; Z = 2.7, p < .01$ ). High-ranking males had higher reproductive success than did both mid-ranking males and low-ranking males (Figure 2).

Of 19 broods with mixed paternity, 15 broods had one extra-pair father and four broods had two extra-pair fathers. The social fathers of broods with one extra-pair father had higher rank scores ( $0.51 \pm 0.07, n = 15$ ) than did the social fathers of broods with two extra-pair fathers ( $0.18 \pm 0.12, n = 4; Z = 2.2, p = .03$ ). Furthermore, there were proportionately fewer extra-pair offspring in broods with one extra-pair father (average proportion of brood which was extra-pair  $0.33 \pm 0.07, n = 15$ ) than in broods with two extra-pair fathers ( $0.61 \pm 0.13, n = 4; Z = 2.0, p < .05$ ). Extra-pair males fathered fewer offspring in broods with a single extra-pair father ( $1.6 \pm 0.2$  extra-pair young per male) compared with broods with two extra-pair fathers ( $2.4 \pm 0.3$  extra-pair young per male;  $F_{1,22} = 4.9, p = .04$ ).

One of the six observed extra-pair copulations gave rise to an extra-pair fertilization. Two of the six females who were observed having extra-pair copulations had extra-pair young in their brood; however, they were not fathered by the observed extra-pair copulation partner. The remaining three females who were observed having extra-pair copulations did not have extra-pair young in their subsequent brood.

### Territory size

On average, territories were  $1.82 \pm 0.6$  ha ( $18205 \pm 593$  m<sup>2</sup>;  $n = 249$ ). Average territory size varied significantly across the

5 years of the study (ANOVA  $F_{4,244} = 10.8$ ,  $p < .0001$ ); territories tended to be smaller in years with higher population-wide densities ( $r = -.84$ ,  $p = .07$ ,  $n = 5$ ; annual population-wide density calculated based on the number of breeding and nonbreeding individuals present during the female fertile period). Across all years, territories of high-ranking males were significantly larger than were the territories of both mid-ranking males and low-ranking males (high:  $2.05 \pm 0.86$  ha,  $n = 116$ ; mid:  $1.67 \pm 1.61$  ha,  $n = 33$ ; low:  $1.64 \pm 0.96$  ha,  $n = 92$ ; ANOVA  $F_{2,238} = 5.7$ ,  $p < .005$ ). This pattern was evident in each year of the study, although only significantly so in 1999 and 2001 (ANOVA  $F$  values  $> 2.9$ ,  $p < .05$ ). There were no differences in average territory sizes across the regimes of the two principal investigators (S.M.R. in 1997–1998:  $1.98 \pm 1.07$  ha,  $n = 76$ ; D.J.M. in 1999–2001:  $1.75 \pm 0.71$  ha,  $n = 173$ ; ANOVA  $F_{1,247} = 3.1$ ,  $p = .08$ ).

### Nest location and mixed paternity

Females constructed nests close to the edge of their partner's territory (Figure 3A). Females nested closer to the edge than the center of their partner's territory (Figure 3A,B), whether rank classes were pooled (paired  $t$  test  $t = 17.7$ ,  $p < .0001$ ,  $n = 189$ ) or treated separately (paired  $t$  tests  $t > 5.4$ ,  $p < .0001$ ). Nests were located closer to territory edges than were points randomly drawn within territory boundaries (paired  $t$  test  $t = 5.0$ ,  $p < .0001$ ,  $n = 189$ ). Females nested closer to the edge of the nearest neighbor's territory than to the center of their social partner's territory (paired  $t$  test  $t = 9.3$ ,  $p < .0001$ ,  $n = 189$ ) (Figure 3B,C). For females paired to low-ranking males, the nearest neighbor to the nest was more likely to be a high-ranking male (44 nests in which nearest neighbor was a high-ranking male; 11 nests in which nearest neighbor was a low-ranking male; binomial test  $p < .0001$ ). For females paired to high-ranking males, the nearest neighbor to the nest was equally likely to be a high- or low-ranking male (39 nests in which nearest neighbor was a high-ranking male; 47 nests in which nearest neighbor was a low-ranking male; binomial test  $p = .4$ ). Females did not preferentially nest near flockmates; in only 71 of 189 cases, the nearest neighbor was a flockmate from the previous winter.

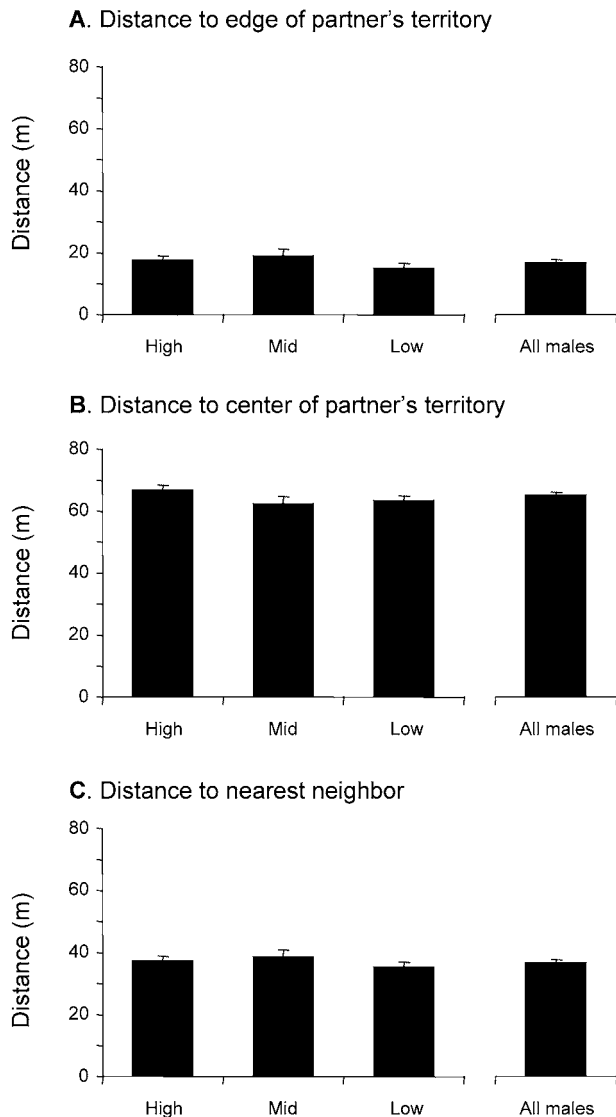
Female experience had no effect on nest location. Naïve females did not construct nests significantly closer to the edge of their partner's territory compared with nests of experienced females (second-year females:  $14.9 \pm 1.6$  m; after-second-year females:  $18.4 \pm 1.3$  m;  $F_{1,182} = 2.9$ ,  $p = .09$ ). Naïve and experienced females constructed their nests within proximity of a similar number of neighboring males' territories (Figure 4A) and a similar number of neighboring females' nests (Figure 4B).

### Territory density and breeding synchrony

Territory density had no influence on extrapair fertilizations (number of neighbors within 100 m; broods without mixed paternity:  $6.6 \pm 0.5$ ,  $n = 38$ ; broods with mixed paternity:  $7.2 \pm 0.7$ ,  $n = 19$ ;  $F_{1,56} = 0.5$ ,  $p = .5$ ). Breeding synchrony showed no relationship with female reproductive strategy (broods without mixed paternity:  $0.45 \pm 0.04$ ,  $n = 38$ ; broods with mixed paternity:  $0.40 \pm 0.05$  m,  $n = 19$ ;  $F_{1,56} = 0.6$ ,  $p = .4$ ).

### Nest location and extrapair partners

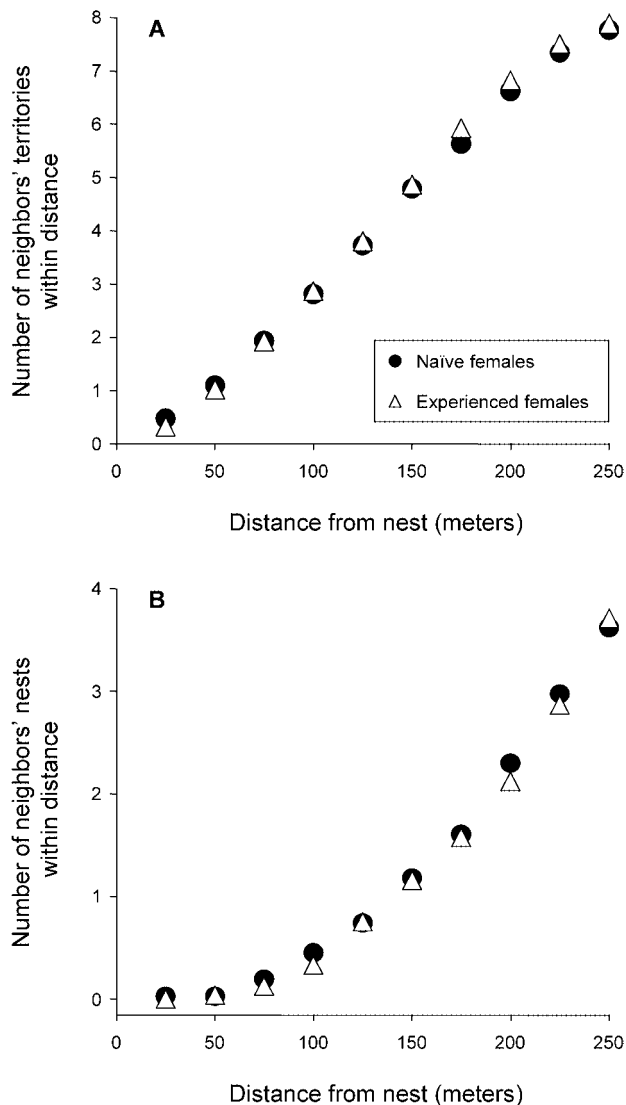
Females who followed a mixed reproductive strategy did not construct nests closer to the edge of their partner's territory (nests without mixed paternity:  $18.5 \pm 2.6$  m; nests with mixed paternity:  $19.3 \pm 3.7$  m;  $F_{1,55} = 0.0$ ,  $p = .86$ ), nor did they construct nests significantly closer to the edge of their



**Figure 3**  
Mean  $\pm$  SE distance between female nest sites and the territory features of social partners and neighbors. (A) Distance to the edge of the partner's territory did not vary with the partner's rank (ANOVA  $F_{2,187} = 1.2$ ,  $p = .3$ ). (B) Distance to the center of the partner's territory did not vary with the partner's rank (ANOVA  $F_{2,187} = 0.3$ ,  $p = .8$ ). (C) Distance to the nearest neighbor did not vary with partner's rank (ANOVA  $F_{2,187} = 0.1$ ,  $p = .9$ ). Females nested closer to the edge of their partner's territory and their nearest neighbor than to the center of their partner's territory.

nearest neighbor's territory (nests without mixed paternity:  $34.1 \pm 3.3$  m; nests with mixed paternity:  $31.6 \pm 4.7$  m;  $F_{1,55} = 0.2$ ,  $p = .66$ ).

Females chose extrapair partners who shared a territory boundary with their social partner in 16 of 21 cases. Extrapair young tended not to be fathered by the neighbor nearest the female's nest. On average, there were  $4.3 \pm 1.0$  neighboring males closer to the female's nest than was the chosen extrapair partner. Considering only the neighbors of high social rank, there were an average of  $1.9 \pm 0.5$  high-ranking males closer to the female's nest than was the chosen extrapair partner. In total, only the rank of a female's social partner, and no measured variables of nest location or



**Figure 4**

The number of neighboring territories (A) and the number of neighbor nests (B) in relation to distance from female nests. Naïve and experienced females showed no age-related differences in conspecific attraction. Naïve, second-year females (closed circles) did not build nests closer to neighbors than experienced, after-second-year females (open triangles) ( $n = 183$  females of known age).

breeding synchrony, showed a relationship with the presence of extrapair young in a female's nest (Table 2).

Females did not construct nests closer to their extrapair partner than expected by chance; on average, 51.7 % of random points within a male's territory were closer to the extrapair father than the female's nest ( $n = 21$ ). The distance between a female's nest and her extrapair partner ( $126 \pm 29$  m) was not significantly different from the average distance between 100 random points and the extrapair partner ( $96 \pm 19$  m; paired  $t$  test  $t = 1.5$ ,  $p = .15$ ,  $n = 21$ ).

## DISCUSSION

Female black-capped chickadees nested near the edge of their partner's breeding territory. Females paired to males with low dominance status had extrapair copulations and extrapair fertilizations with neighboring high-ranking males and built

**Table 2**

**Nominal logistic regression model of the influence of male rank, nest location features, and breeding synchrony on the presence of mixed paternity in the broods of black-capped chickadees**

Explanatory variable	Does brood have mixed paternity?	
	Wald $\chi^2$	$p$
Male rank	<b>5.9</b>	<b>.05</b>
Male age	1.5	.22
Distance from nest to edge of partner's territory	0.0	.89
Distance from nest to nearest neighbor	0.0	.95
Distance from nest to nearest high-ranking neighbor	0.8	.39
Distance from nest to nearest neighbor's nest	0.0	.84
Synchrony index	0.1	.73
Year	1.1	.89

Wald effect tests are shown for each variable. Significant effects are highlighted in bold. Whole model  $r^2 = .16$ ,  $df = 12,43$ ,  $n = 57$ .

nests so that their nearest neighbor was a high-ranking male. However, females did not target the neighbor nearest their nest, or even the high-ranking neighbor nearest their nest, as an extrapair partner. We conclude that conspecific attraction may influence nest location in black-capped chickadees, but nesting near territory edges does not benefit females by facilitating extrapair copulations or extrapair fertilizations.

Animal aggregations are expected to correspond to environmental features or social factors (Allee, 1931; Muller et al., 1997). Previous research demonstrated that black-capped chickadee nest sites are not significantly different from random locations within males' territories with respect to habitat characteristics (characteristics of live trees, snags, shrubs, and ground cover) or with respect to the distribution of prey (arthropod abundance; Ramsay et al., 1999). Given the absence of a relationship between nest sites and habitat features, we proposed a social explanation for nest site selection. Our results matched two predictions of the hypothesis that females choose nest sites to facilitate extrapair copulations: (1) females constructed nests close to the edge of their partner's territory. Indeed, females constructed nests closer to the nearest neighbor than to the center of their partner's territory. (2) Females paired to low-ranking males nested closer to high-ranking males, although females paired to low-ranking males did not nest closer to the edge of their partner's territory than did females paired to high-ranking males. However, our results did not support the remaining two predictions. (3) Extrapair copulations took place far away from the nest cavity, on average 64 m from the female's nest (almost half the diameter of the average breeding territory). Females often had extrapair copulations shortly after emerging from their nest cavity, yet they moved away from their nest site to pursue these copulations. (4) Although extrapair young were usually fathered by a neighboring male, they were not fathered by the neighbor nearest the female's nest. On average, there were 4.3 neighbors closer to the female's nest than was the chosen extrapair partner.

If the placement of nests at territory edges does not correspond to habitat features or the location of extrapair partners, why do female chickadees nest at territory edges? Neighbors may function as an "early warning system" to detect the presence of predators (Smith, 1986). Consequently,

females nesting at territory edges may benefit from enhanced predator protection because of an improved ability to monitor their neighbors (Smith, 1986; Stamps, 1988). In addition, individuals that nest near boundaries may be better able to recruit the assistance of neighbors in defending against nest predators. Anecdotal evidence supports this idea. We observed a black rat snake, *Elaphe obsoleta*, climbing an active nest tree. The resident birds gave emphatic mobbing calls that attracted the neighboring pair and the four adults actively drove the would-be predator from the area (Mennill DJ, personal observation).

Alternatively, nesting near territory edges may allow females to better monitor the quality of neighboring males. During the breeding season, male chickadees give dawn chorus song performances in the immediate vicinity of their nest while fertile females remain inside the nest cavity. The dawn chorus singing behavior of chickadees contains honest indicators of male quality in both the total song output (Otter et al., 1997) and in the fine structural features of male song (Christie et al., 2004b). Given the substantial territory sizes of chickadees (approximately 18000 m<sup>2</sup>; average diameter = 152 ± 27 m) and the fact that chickadee song maintains individually distinctive and rank-distinctive features over transmission distances of 80–100 m (Christie et al., 2004a; Fotheringham and Ratcliffe, 1995), females might better assess neighbors' dawn chorus performance by placing their nests at territory edges. A paired comparison of the number of neighbors' nests (and therefore the number of neighboring males within earshot during the dawn chorus) within 100 m of nest sites versus the number of neighbors' nests within 100 m of territory centers supports this idea; more neighbors' dawn chorus positions fell within 100 m of nest sites than within 100 m of territory centers (paired *t* test  $t_{189} = 2.9$ ,  $p < .005$ ). Females mated to low-ranking males may nest nearer to high-ranking males because they are more motivated to respond to opportunities for extrapair matings with high-ranking neighbors. Furthermore, we have previously shown that black-capped chickadees will readily divorce their partner if the opportunity arises to pair with a neighbor of higher social status (Ramsay et al., 2000). Nesting at territory edges may assist females monitoring higher-ranking neighbors for both extrapair mating opportunities and divorce opportunities.

Our results corroborate two other investigations of mixed mating strategies in black-capped chickadees. As in Smith's (1988) observational study, females had extrapair copulations with males of high dominance status. Although Smith (1988) found that most extrapair copulations took place during female forays into extrapair partners' territories, we found extrapair copulations typically took place at territory boundaries. Male territory sizes in our study were 34–42% smaller than were territories in Smith's and others' studies (Odum, 1941; Smith, 1991; but see Brewer, 1963, in which territories were smaller than in the present study), suggesting that females may not need to move beyond the edge of their partner's territory for an extrapair copulation when male territory sizes are small. In a previous investigation of our study population, Otter et al. (1998) also found that females had extrapair fertilizations with high-ranking males; in 58 families monitored between 1992 and 1995, females paired to low-ranking males had extrapair fertilizations by higher-ranking males. The cumulative results show that the mating system of black-capped chickadees is driven by discriminating promiscuous females, in which high-ranking males gain fitness benefits by siring young in the nests of neighboring females.

Paternity analyses suggested that promiscuous females may pursue multiple mixed mating strategies. In 79% of cases, females had extrapair fertilizations with only one extrapair

partner, who sired an average of 1.6 extrapair offspring. In the remaining 21% of cases, females had extrapair fertilizations with two extrapair partners, each of which sired an average of 2.4 extrapair offspring. These especially promiscuous females were paired to males with very low rank scores. Thus, female chickadees appear to use a two-tiered mixed mating strategy; when paired to a very low quality partner, females devote a significantly greater proportion of their brood to extrapair fertilizations and seek paternity from multiple extrapair partners. Therefore, beyond simply bearing the cost of female promiscuity, low-quality males may suffer greatly diminished reproductive success if their relative quality is substantially below that of their neighbors.

Females had extrapair copulations and fertilizations with males in neighboring territories. This pattern has been detected in many birds with mixed mating systems (see Gibbs et al., 1990; Hasselquist et al., 1995; Kempenaers et al., 1997; Richardson and Burke, 2001; Westneat, 1993). Why do females have extrapair copulations with neighbors? This widespread pattern may be driven by at least two factors. First, access to extrapair males may be constrained in animals with territorial breeding systems. In particular, if females seek extrapair copulations from distant males during long extraterritorial forays, they may risk harassment by unwanted copulation partners (Birkhead and Møller, 1992), or they may face aggression from neighboring males and females as they move through their territories. The latter risk seems especially relevant to black-capped chickadees, in which extrapair copulations are often followed by aggressive interactions between the neighboring pairs and in which resident females engage in aggressive interactions with intruding females early in the breeding season (Mennill DJ, personal observation). Under this explanation for neighbor preference, females must settle with local extrapair partners because their capacity to reach distant males is constrained. If this is the case for chickadees, females make adaptive decisions in the face of such a constraint; females chose the best of the available males (neighbors with high dominance status) as extrapair partners.

In addition, females may favor neighbors as extrapair partners because they have better opportunities to assess the quality of nearby males. Male-male song contests are particularly important for females making mate choice decisions (Mennill et al. 2002, 2003a; Otter et al., 1999), and the song contests of neighbors will be most easily assessed. Furthermore, indicators of male quality available through visual inspection of male ornaments or male behavior will be most readily available from neighbors. Therefore, females may prefer neighbors as extrapair partners because they have opportunities to assess neighbors but lack adequate opportunities to assess more distant males. Indeed, all known indicators of male quality in black-capped chickadees, including male performance in song contests (Mennill and Ratcliffe 2004; Mennill et al. 2002), dawn chorus singing performance (Christie et al. 2004b; Otter et al. 1997), and male plumage features (Mennill et al., 2003b), are available from neighbors but not from distant individuals. In addition, territorial neighbors tend to be flockmates or birds from neighboring flocks (Smith, 1991), such that females may have direct experience with their neighbors from the previous winter but may lack such information for more distant males.

Spatial analysis improves our understanding of the mating systems of animals that follow mixed reproductive strategies. GIS analysis shows that female chickadees construct nests asymmetrically within their partners' territories, near territory edges, although females do not choose the neighbors nearest their nests as extrapair partners. Spatial analyses reveal that females choose extrapair partners from a small pool of

candidate males who share territory boundaries with the female's social partner. Given the fitness consequences of extrapair copulations, our results support the view that a male songbird's worst enemies may be his territorial neighbors.

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