

## 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?

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Birds that nest in cavities may regulate nest microclimate by orienting their nest entrance relative to the sun or prevailing winds. Alternatively, birds may orient their nest entrance relative to conspecific individuals around them, especially if the acoustic properties of cavities permit nesting birds to better hear individuals in front of their nest. We measured the cavity entrance orientation of 132 nests and 234 excavations in a colour-banded population of black-capped chickadees *Poecile atricapillus* for which the reproductive behaviour of nesting females was known. Most chickadees excavated cavities in rotten birch *Betula papyrifera*, aspen *Populus tremuloides* and maple *Acer saccharum*. Nest cavities showed random compass orientation around 360° demonstrating that chickadees do not orient their cavities relative to the sun or prevailing winds. We also presented chickadees with nest boxes arranged in groups of four, oriented at 90° intervals around the same tree. Nests constructed in these nest box quartets also showed random compass orientation. To test the acoustic properties of nest cavities, we conducted a sound transmission experiment using a microphone mounted inside a chickadee nest. Re-recorded songs demonstrate that chickadee nest cavities have directional acoustic properties; songs recorded with the cavity entrance oriented towards the loudspeaker were louder than songs recorded with the cavity entrance oriented away from the loudspeaker. Thus, female chickadees, who roost inside their nest cavity in the early morning during their fertile period, should be better able to hear males singing the dawn chorus in front of their nest cavity. Using GIS analyses we tested for angular-angular correlation between actual nest cavity orientation and the azimuth from the nest tree to the territories and nest cavities of nearby males. In general, nest cavity entrances showed no angular-angular correlation with neighbourhood territory features. However, among birds who followed a mixed reproductive strategy and nested in the soft wood of birch and aspen trees, nest cavity entrances were oriented towards their extra-pair partners. We conclude that nest cavity orientation in birds may be influenced by both ecological and social factors.

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Birds that nest in cavities may benefit by orienting their nest entrance in a particular direction. Patterns of nest entrance orientation have been explored for primary cavity nesting birds (birds that excavate their own nest cavities; reviewed in Zwartjes and Nordell 1998) and secondary cavity nesting birds (birds that use cavities

excavated by others; reviewed in Rendell and Robertson 1994). These investigations typically conclude either (1) that there is no relationship between nest entrance orientation and compass orientation, or (2) that nest entrances are non-randomly oriented and individuals regulate nest microclimate by nesting in cavities oriented

relative to prevailing winds or solar radiation. To date, no study has investigated whether nest entrance orientation may be influenced by the acoustic properties of nest cavities or by the pressures of avian social behaviour and acoustic communication.

Black-capped chickadees *Poecile atricapillus* are non-migratory songbirds that excavate nest cavities in rotten wood. In winter, black-capped chickadees gather in small flocks where interactions between individuals follow stable linear dominance hierarchies (Smith 1991). Immediately prior to nesting in spring, flocks break apart and birds begin to defend all-purpose breeding territories against their former flockmates. Both males and females cooperate in excavating nest cavities, however females do the majority of excavation (Ramsay et al. 1999, Mennill et al. 2004) and the female alone constructs the nest in one of these cavities (Smith 1991). Chickadees follow a mixed reproductive strategy where females paired to low-ranking males often seek extra-pair copulations from high-ranking males in neighbouring territories (Smith 1988, Otter et al. 1998, Mennill et al. 2004). Females construct nests in cavities near territory edges (Ramsay et al. 1999) and females paired to low-ranking males frequently construct nests near a territory boundary with a high-ranking male (Mennill et al. 2004), suggesting that the nesting behaviour of chickadees may be influenced by conspecific attraction to preferred (high-ranking) males.

Male song plays an important role in the reproductive behaviour of black-capped chickadees. Previous research shows that dawn chorus singing performance reflects male quality (Otter et al. 1997, Christie et al. 2003) and that fertile females make reproductive decisions based on information contained in male-male song contests (Mennill et al. 2002, 2003). In the early morning, during their egg laying period, fertile females remain inside the nest cavity while males sing an extended dawn chorus (average egg-laying period  $6.7 \pm 0.1$  SE days; D. J. Mennill unpubl. data). Therefore, the acoustic properties of the nest cavity may mediate females' ability to evaluate male song performance and thus male quality. If fertile females can better hear males in front of their nest cavity, versus males behind their nest cavity, females may benefit by nesting in a cavity oriented towards males in nearby territories. In particular, given that females consistently nest near territory boundaries and seek extra-pair copulations from neighbouring males, females may benefit by orienting their nest cavity towards potential copulation partners to monitor the dawn singing of those males.

We measured the orientation of 132 nest cavities in a colour-banded population of black-capped chickadees where the reproductive patterns of breeding females was known (Mennill et al. 2004). If black-capped chickadees orient their nest entrances to regulate nest microclimate, we predicted that cavity entrances would show non-

random compass orientation. If, however, chickadees orient their nest entrances so that they may better monitor the vocal behaviour of neighbouring individuals, we predicted that cavity entrances would show random compass orientation, but would show angular-angular correlation with the azimuth from the nest tree to neighbouring males' territories. To test whether chickadee nest cavities have acoustically directional properties, we broadcast chickadee songs through the forest and re-recorded them with a microphone mounted inside a chickadee nest cavity. Using geographic information system (GIS) spatial analyses, we evaluate the acoustic properties of nest cavities relative to features of chickadee territories and neighbourhoods.

## Methods

We monitored chickadees at Queen's University Biological Station in eastern Ontario, Canada ( $44^{\circ}34'N$ ,  $76^{\circ}19'W$ ) from 1999 through 2001. After ringing birds in January of each year, we assessed flock dominance hierarchies according to established protocols (see Otter et al. 1998) to distinguish high-ranking males from low-ranking males. During the breeding season, from mid-April onwards, we visited each pair every two to four days to find nest cavities, map breeding territories and monitor breeding behaviour (see Mennill et al. 2004). We conducted microsatellite paternity analyses to determine which broods contained extra-pair young and to assign fathers to those extra-pair young (see Mennill et al. 2004).

During behavioural observations, we recorded all locations where pairs excavated a cavity (removed material from a tree or nest box). We defined a pair's "excavations" as all cavities from which a pair was observed removing material on two or more different occasions. We defined a pair's "nest" as the cavity in which the female placed nest lining material and laid eggs. Most pairs had several excavations (average  $2.2 \pm 0.1$  SE excavations per pair) but each pair had only one nest. For all excavations and nests, we recorded the tree species and the compass orientation of the cavity entrance.

## Transmission playback

To test the acoustic properties of black-capped chickadee nest cavities, we cut off a 1.0 m section of a tree which contained a recently abandoned nest cavity. This nest cavity had a typically-sized entrance hole and typical depth, and was in the most common nesting substrate for our population – a semi-rotten birch snag *Betula papyrifera*. We drilled a hole through the back of this nest cavity and inserted an omni-directional micro-

phone (model Sennheiser K6-C). The head of the microphone was positioned where a female would sit while incubating eggs, just above the bottom of the nest cavity. To prevent sound from “leaking” into the cavity through the hole we had drilled, we padded the area immediately around the microphone insertion point with a small amount of sound-proof foam. We connected the nest-mounted microphone to a cassette recorder (model Sony WM-D6C) through a preamplifier (model Saul-Mineroff BA3).

We played songs originally recorded from the dawn choruses of 12 different male chickadees (see Christie et al. 2003) from a cassette player (model Sony WM-D6C) connected to a loudspeaker (model Sony SRS-77G). Both the loudspeaker and the nest-mounted microphone were erected on poles at a height of 1.5 m, a height not atypical of chickadee song perch and nest heights. Songs were re-recorded at two distances along a transect through a chickadee’s territory, with 25 m and 50 m between the loudspeaker and nest-mounted microphone. At each distance, we re-recorded the 12 songs three times, rotating the nest-mounted microphone to achieve three cavity entrance orientations; (i) cavity entrance facing directly towards the loudspeaker ( $0^\circ$ ), (ii) cavity entrance facing at a right angle to the loudspeaker ( $90^\circ$ ), and (iii) cavity entrance facing directly away from the loudspeaker ( $180^\circ$ ). Across all recordings, we held the volume of the playback loudspeaker constant and the input to the recording device constant. We digitized the re-recorded songs using SyrinxPC software (J. Burt, Seattle WA), holding the input level constant. We measured the amplitude of each re-recorded song using the peak amplitude feature of CoolEdit 2000 software (Syntrillium, Phoenix AZ). These amplitude measurements are of little use for estimating the actual amplitude of the broadcast songs, however they are useful for comparing the relative amplitude of the broadcast songs for each of the orientations of the nest cavity entrance.

## GIS analyses

We obtained Universal Transverse Mercator (UTM) coordinates for all excavations and nests using a Trimble global positioning system (GPS) (accuracy  $\leq 1$  m). We analyzed cavity entrance orientations relative to nest locations and territorial boundaries (see Mennill et al. 2004) using ArcView GIS 3.2. We used the ‘Nearest Feature’ extension (v 3.6; J. Jenness, Flagstaff AZ) to calculate the azimuth from each female’s nest to the following features: (i) the nearest edge of her social partner’s territory, (ii) the nearest edge of the closest neighbour’s territory, (iii) the nearest edge of the closest high-ranking male’s territory, (iv) the nest tree of the closest neighbour, and (v) the nest tree of the closest high-ranking neighbour. Given that males often sing

much of their dawn chorus near their partner’s nest, measurements (iv) and (v) serve as a proxy for the dawn chorus singing location of the closest neighbouring male and the closest high-ranking male, respectively. For nests with mixed paternity, we also calculated the azimuth from the promiscuous female’s nest to the following features: (vi) the edge of her extra-pair partner’s territory and (vii) the nest tree of her extra-pair partner.

## Nest box quartets

A minority of chickadees in our study population use nest boxes made from PVC tubing and filled with sawdust (24 of 123 nests and 8 of 234 excavations were in boxes between 1999 and 2001). To offer chickadees free choice of the entrance orientation of nest boxes, we constructed 176 nest boxes and hung them in groups of four per tree ( $n=44$  “nest box quartets”) with the four boxes oriented at  $90^\circ$  intervals around the same tree. Occupancy of nest box quartets between 1999 and 2001 was low ( $n=12$ ), so we include nest box data from 2002 ( $n=9$  nest box quartets were occupied in 2002; total of  $n=21$  nest box quartets measured between 1999 and 2002) although we do not have paternity data or territory data for 2002.

## Statistical analyses

We measured a total of 132 nests (99 in natural cavities, 21 in nest box quartets, and 12 in single nest boxes) and 234 excavations (226 in natural cavities, 8 in nest boxes). We analyzed cavity entrance orientation using Raleigh’s test ( $z$ ; Zar 1999) to evaluate whether nest entrances were randomly distributed around  $360^\circ$ . We use angular-angular correlation ( $r_{aa}$ ; Zar 1999) as a nonparametric measure of correlation between actual cavity entrance orientations and azimuth measures (i) through (vii) (above). All results are reported as mean  $\pm$  SE. All tests are two-tailed. Statistical were calculated in JMP 4.0 (SAS institute, Cary, NC) and circular statistics were calculated in Oriana 2.0 (Kovach, Wales, UK).

## Results

### Nest trees

Of 93 nests in natural cavities where the tree species was known, the majority were in paper birch *Betula papyrifera* ( $n=49$ , 50%), trembling aspen *Populus tremuloides* ( $n=14$ , 14%), and sugar maple *Acer saccharum* ( $n=14$ , 14%; the remaining 22% of nests occurred in 9 other species of tree). Of 203 non-nest excavations where the tree species was known, the majority were in paper birch ( $n=80$ , 39%), trembling aspen ( $n=27$ , 13%), and sugar

maple ( $n=21$ , 10%; the remaining 36% of excavations occurred in 18 other species of tree). Nests in trees other than birch and aspen were often in knot holes or in cavities that appeared to have been excavated initially by another animal. Nests in birch and aspen, on the other hand, tended to be in rotten wood and not associated with knot holes or other cavities. Therefore, we analyze the subset of nest cavities in birch and aspen separately, because chickadees may have greater control over nest entrance orientation in these softer substrates.

### Nest orientation

Black-capped chickadee nest cavity entrances had random compass orientation (Fig. 1a;  $z=0.5$ ,  $n=132$ ,  $P=0.63$ ; Raleigh's test). The subset of these nests that were constructed in natural cavities had random compass orientation ( $z=1.4$ ,  $n=99$ ,  $P=0.25$ ). The subset of these nests that were excavated in softwood trees (birch and aspen) had random compass orientation ( $z=0.23$ ,  $n=59$ ,  $P=0.80$ ). The 21 nests in nest box quartets had random compass orientation (Fig. 1b;  $z=1.42$ ,  $n=21$ ,  $P=0.25$ ). Non-nest excavations also had random compass orientation ( $z=2.36$ ,  $n=199$ ,  $P=0.10$ ).

### Playback recordings

By broadcasting male songs through the forest and re-recording them using a microphone mounted in an abandoned nest cavity, we found that black-capped chickadee nests have directional acoustic properties (Fig. 2). When the cavity-mounted microphone was placed 25 m from a loudspeaker broadcasting chickadee songs, recordings had significantly higher amplitude when the cavity entrance was facing towards the speaker ( $-25.1 \pm 0.7$  dB) relative to recordings made when the cavity entrance was facing  $90^\circ$  away from the speaker ( $-29.1 \pm 0.4$  dB;  $0^\circ$  versus  $90^\circ$ :  $t=11.9$ ,  $n=12$  broadcast songs,  $P < 0.0001$ ; paired t-test) or when the cavity

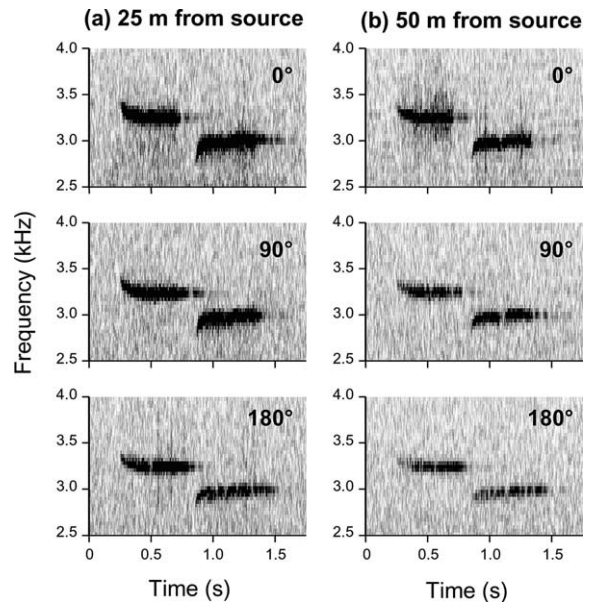


Fig. 2. Black-capped chickadee nest cavities have directional acoustic properties. Sound spectrograms depict the same male black-capped chickadee song broadcast and re-recorded using a microphone mounted inside an abandoned nest cavity. Songs were re-recorded with the nest-mounted microphone positioned (a) 25 m from the loudspeaker or (b) 50 m from the loudspeaker. Songs were re-recorded with the entrance to the cavity oriented directly towards the loudspeaker ( $0^\circ$ ; top), at a right angle to the loudspeaker ( $90^\circ$ ; middle), or directly away from the loudspeaker ( $180^\circ$ ; bottom). Volume of the loudspeaker and recording input level of the nest-mounted microphone were held constant and spectrograms were generated using identical settings.

was facing  $180^\circ$  away from the speaker ( $-31.3 \pm 0.6$  dB;  $0^\circ$  versus  $180^\circ$ :  $t=20.9$ ,  $n=12$ ,  $P < 0.0001$ ;  $90^\circ$  versus  $180^\circ$ :  $t=7.6$ ,  $n=12$ ,  $P < 0.0001$ ; Fig. 3a). When the cavity-mounted microphone was placed 50 m from the loudspeaker, again the recordings had significantly higher amplitude when the cavity entrance was facing towards the speaker ( $-27.7 \pm 0.8$  dB) relative to recordings made when the cavity entrance was facing  $90^\circ$  away from the speaker ( $-31.8 \pm 0.6$  dB;  $0^\circ$  versus  $90^\circ$ :  $t=7.8$ ,  $n=12$  broadcast songs,  $P < 0.0001$ ) and when the cavity entrance was facing  $180^\circ$  away from the speaker ( $-33.6 \pm 0.3$  dB;  $0^\circ$  versus  $180^\circ$ :  $t=9.6$ ,  $n=12$ ,  $P < 0.0001$ ;  $90^\circ$  versus  $180^\circ$ :  $t=4.3$ ,  $n=12$ ,  $P=0.001$ ; Fig. 3b).

### Entrance orientations relative to neighbours

Nest entrance orientation showed no correlation with the azimuth from the nest tree to the nearest edge of the social partner's territory ( $r_{aa}=0.01$ ,  $n=123$ ,  $P > 0.2$ ; angular-angular correlation), the nearest edge of the closest neighbour's territory ( $r_{aa}=0.003$ ,  $n=123$ ,  $P > 0.2$ ), the nearest edge of the closest high-ranking male's territory ( $r_{aa}=0.003$ ,  $n=123$ ,  $P > 0.2$ ),

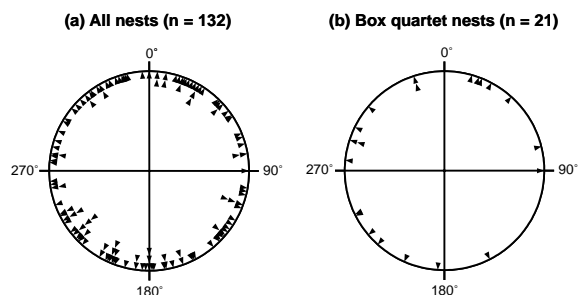


Fig. 1. Entrances to black-capped chickadee nest cavities were randomly distributed around  $360^\circ$ . This was true of (a) all nests in natural cavities and (b) all nests in nest box quartets (where females could choose one of four nest boxes oriented at  $90^\circ$  intervals around the same tree).

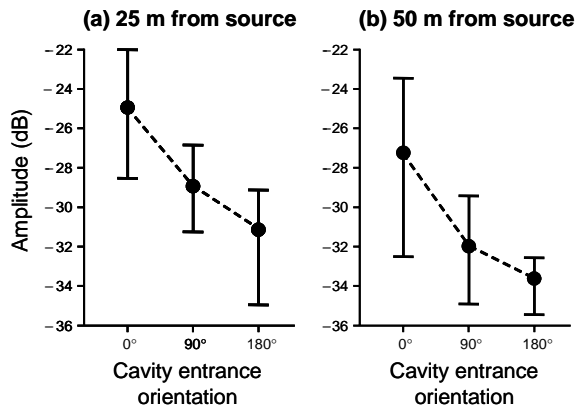


Fig. 3. Sound attenuation increases with the angle between the nest cavity entrance and the bearing to the sound source. Songs recorded using a microphone mounted inside an abandoned black-capped chickadee nest cavity were significantly louder when the entrance was oriented towards the loudspeaker (0°) than when the entrance was oriented at a right angle to the loudspeaker (90°) or directly away from the loudspeaker (180°). This pattern held true when the nest containing the microphone was positioned (a) 25 m from the loudspeaker or (b) 50 m from the loudspeaker (b). Circles show mean amplitude for at each cavity entrance orientation and vertical bars show the full range of data for broadcast songs of  $n=12$  males.

the nearest neighbour's nest ( $r_{aa} = 0.003$ ,  $n = 123$ ,  $P > 0.2$ ), or the nearest high-ranking male's nest ( $r_{aa} = 0.005$ ,  $n = 123$ ,  $P > 0.2$ ). For 34 females with mixed paternity broods, nest entrance orientation showed no correlation with the azimuth to the edge of the extra-pair male's territory ( $r_{aa} = 0.02$ ,  $n = 34$ ,  $P > 0.2$ ), or the extra-pair male's nest ( $r_{aa} = 0.02$ ,  $n = 34$ ,  $P > 0.2$ ).

Among females with extra-pair offspring nesting in the soft wood of birches and aspens, we found a significant correlation between nest entrance orientation and azimuth to the edge of the extra-pair partner's territory ( $r_{aa} = 0.23$ ,  $n = 17$ ,  $0.02 < P < 0.05$ ). On average, nest entrances were oriented within  $82.9 \pm 11.2^\circ$  of the azimuth to the nearest edge of the extra-pair male's territory. All other relationships were non-significant among the subset of females nesting in soft wood ( $r_{aa} < 0.03$ ,  $P > 0.10$ ). Among females who nested in nest box quartets, there were no significant correlations between nest orientation and any of the above measures ( $r_{aa} < 0.4$ ,  $P > 0.2$ ).

## Discussion

Black-capped chickadees nest in cavities with random compass orientation. The random dispersion of nest entrance orientations demonstrates that chickadees do not systematically excavate nest cavities oriented towards the sun or prevailing winds. Results from a sound-transmission experiment, involving a microphone mounted inside an abandoned nest, showed that chick-

adee nest cavities have directional acoustic properties; during the dawn chorus, a roosting female chickadee will be better able to hear males singing in front of her nest than males singing beside or behind her nest. Given that the singing performance of males during the dawn chorus contains cues to male quality (Otter et al. 1997, Christie et al. 2003) and that females make reproductive decisions based on male singing behaviour (Mennill et al. 2002, 2003), the directional acoustic properties of chickadee nest cavities could influence females' assessment of males and ensuing reproductive behaviour. GIS analyses revealed no significant relationships between the orientation of nest cavities and the azimuth from nest trees to nearby males. However, the cavities of promiscuous females who nested in soft substrates (birch and aspen trees) were oriented towards the territory of their extra-pair partner. We conclude that female chickadees may construct nest cavities to facilitate assessment of extra-pair males. When we considered all nests together, however, we found no relative orientation patterns, indicating that nest entrance orientation must be influenced by other factors as well.

Black-capped chickadees are considered weak cavity excavators (Aitken et al. 2002). With a small bill, chickadees lack the strong excavation abilities of many woodpeckers. Yet unlike secondary cavity nesting birds, chickadees excavate cavities "from scratch" or further excavate old holes before nesting in them (Smith 1991, D. J. Mennill pers. obs.). The majority of chickadee nests were constructed in birch and aspen trees and usually in rotten sections of these trees. Chickadees may target these tree species because they are the softest wood available and are easy to excavate. Birds excavating in birch and aspen trees may have greater control over cavity entrance orientation, since cavities in other tree species tend to occur in knot holes or old holes where cavity orientation is pre-determined. Chickadees' restricted capacity to excavate hard wood may contribute to the observed random dispersion among nest cavity entrances, where ease of excavation and the architecture of pre-existing holes may override preferences for cavities oriented in a particular direction.

Promiscuous female chickadees nesting in birch and aspen trees tended to construct nests oriented towards their extra-pair partners. This result begs the question: Do females excavate nests that will face potential extra-pair partners so they can better monitor the singing behaviour of those males? Or, do breeding females excavate nests at random and then choose extra-pair partners from the subset of males in the direction their nest cavity faces? Further investigations of the phenology of territory establishment, nest construction and extra-pair copulations may help to answer these questions. Between flock breakup and egg laying, chickadees spend several weeks excavating cavities and establishing territory boundaries. During this time period, females

have ample opportunity to assess the activities of their neighbours and to monitor the location of males whose quality they may have assessed throughout the previous winter. Given that chickadees excavate multiple cavities and that territories are established prior to the time when females build nests, we suggest that females may tactically choose cavities oriented towards potential extra-pair partners. Among females nesting in nest box quartets, who were presented with a choice of four nests oriented at 90° intervals around the same tree, we did not observe the pattern seen among promiscuous females nesting in birch and aspen, although the number of promiscuous females nesting in nest box quartets was low ( $n = 5$ ).

Despite many investigations of the absolute compass orientation of avian nest cavities, very few have evaluated relative cavity orientation. Notable exceptions are studies of the cactus nests of gilded flickers *Colaptes chrysoides* (Zwartjes and Nordell, 1998) and Gila woodpeckers *Melanerpes uropygialis* (Inouye et al. 1981), which demonstrated that birds orient their cavities relative to cactus structure to avoid obstructed nest entrances. We encourage others to consider both absolute compass orientation of nest cavities together with relative orientation of nest cavities and ecological and social factors. Many songbirds *Passeriformes* nest in cavities, follow mixed reproductive strategies, and have dynamic song systems which include extended dawn chorus performances. Recordings from microphones mounted in the nest boxes of great tits *Parus major* show that females incubating inside boxes can hear the dawn chorus performances of neighbouring males (Otter and Ratcliffe, in press). Given that male chickadee song maintains individually distinctive characteristics and rank distinctive characteristics over broadcast distances of at least 80 m (Christie et al. 2003, 2004), female chickadees may similarly monitor the dawn singing of their neighbours, especially those singing in the direction their nest cavity faces. Nest entrance orientation may be connected to the assessment behaviour of fertile females across many species, including both primary cavity nesters and secondary cavity nesters, whenever individuals have a choice over nest entrance orientation. In addition, many non-passerine cavity-nesting birds have long-distance vocal communication systems, including many species of *Piciformes*, *Coraciiformes*, *Trogoniformes*, *Strigiformes*, and *Psittaciformes*. Given that cavities have directional acoustic properties, and that individuals incubating or roosting within cavities receive information from individuals outside, the social consequences of nest orientation should be considered together with the ecological consequences of nest orientation.

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