

## Original Article

Evidence for multicontest eavesdropping  
in chickadeesCory A. Toth,<sup>a</sup> Daniel J. Mennill,<sup>b</sup> and Laurene M. Ratcliffe<sup>c</sup><sup>a</sup>Department of Biology, University of Auckland, 3A Symonds Street, Auckland 1010, New Zealand,<sup>b</sup>Department of Biological Sciences, University of Windsor, 401 Sunset Avenue, Windsor, Ontario N9B 3P4, Canada, and <sup>c</sup>Department of Biology, Queen's University, 116 Barrie Street, Kingston, Ontario K7L 3J9, Canada

Animals eavesdrop on dyadic interactions between other individuals to gather information for future mate choice and territory defense decisions. The capacity for eavesdroppers to combine information gathered from overhearing multiple two-way interactions is poorly studied. We tested whether inexperienced (second year) and older (after second year) male black-capped chickadees (*Poecile atricapillus*) eavesdrop on rivals' song contests to evaluate the relative threat levels of multiple unfamiliar territorial intruders. We used a multiple speaker playback experiment to simulate 3 male territorial intruders (A, B, and C) engaging in 2 successive dyadic song contests, presenting focal males with the information that A was more threatening than B, and B was more threatening than C. We then assayed the response of focal males when presented with simulated intruders A and C without relative information. We predicted that males would defend against the intruder perceived to be the greater threat. Focal males initially responded toward the more threatening intruder (A) significantly more than the less threatening intruder (C), consistent with our predictions. Older birds approached the more threatening intruder (A) significantly more than the less threatening intruder (C), whereas young males showed more variable responses. Our results suggest that male chickadees were able to acquire relative threat information from separate song contests that influenced their responses toward rivals paired in novel contests. These findings indicate that territorial songbirds in communication networks may be capable of integrating information gathered through eavesdropping on multiple interactions. *Key words*: black-capped chickadee, communication networks, eavesdropping, song contests. [*Behav Ecol*]

## INTRODUCTION

In species where dominance status, territory acquisition, or mate choice are mediated through competitive interactions, the ability to observe and remember relative relationships without direct interaction with the contestants would be very useful. Evidence from primate societies featuring large groups, such as baboons (e.g., *Papio anubis*; Nash 1976) or macaques (e.g., *Macaca fuscata*; Takasaki 1981), show that individuals change their behavior toward certain individuals or groups after viewing interactions between them and are able to recognize the dominance status of others (e.g., Cheney and Seyfarth 1990; Silk 1999; Bergman et al. 2003). However, in complex animal societies, it is unlikely that an individual can view all possible dyadic interactions between group members. Consequently, viewing only a small subset of the possible interactions and using that information to infer the remaining relationships would be beneficial.

Songbirds provide an interesting system for examining the use of social information provided by individuals to conspecific observers (e.g., "public information," reviewed by Hamblin et al. 2010). Many songbirds interact through long-range communication networks during the breeding season, where the broadcasting and receiving of information is not limited to dyadic exchanges but can extend to include multiple signalers

and receivers that repeatedly interact (McGregor 2005). Network communication, described in such varied taxa as crabs (Burford et al. 1998), frogs (Grafe 2005), and whales (Payne and Webb 1971), among others, has favored the development of complex strategies of signaling and information gathering, such as eavesdropping (reviewed in Peake 2005). For example, males can attend to interactions involving other males in order to inform their behavior during future encounters, such as determining the relative threat level of rivals (e.g., Naguib and Todt 1997; Naguib et al. 1999; Peake et al. 2001; Mennill and Ratcliffe 2004a; Amy and Leboucher 2009). Females may also extract information from male song contests to assess social mates (e.g., Kunc et al. 2006) and extrapair partners (e.g., Otter, McGregor, et al. 1999; Mennill et al. 2002). Eavesdropping therefore provides a natural context in which animals are exposed to interactions between multiple neighbors from which they can infer relative relationships.

Great tits (*Parus major*) provide 2 compelling examples of relative ranking through eavesdropping. Peake et al. (2002) used playback to demonstrate that territorial males were able to rank themselves relative to a previously unencountered intruder if they had heard that intruder interact with a male of known quality; these males reacted with increased song output toward simulated intruders they determined to be of high or ambiguous quality. Similarly, female great tits paired to males who lost a song contest to a simulated intruder were more likely to visit the territories of neighboring males who won against the same intruder (Otter, McGregor, et al. 1999). These females were seemingly able to determine the relative quality of both their mate and their neighbors, using their performances against another male as an intermediary.

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In this study, we ask whether territorial songbirds are capable of eavesdropping on multiple dyadic contests between rivals and using that information to assess the relative threat of contestants when presented in novel pairings. Acoustic communication networks, in theory, should provide focal individuals the opportunity to obtain relational information about others by indirect observation, due to long-distance transmission of acoustic signals. Whether songbirds possess the cognitive capacity to perform such relational tasks is presently unknown.

Black-capped chickadees (*Poecile atricapillus*) are an excellent candidate species for investigating the ability of animals to combine information from multiple sources. In winter, chickadees form mixed-sex flocks consisting of 3–12 individuals which forage and travel together (Smith 1991). These flocks are characterized by stable linear dominance hierarchies, in which males dominate females, and older birds dominate younger birds (Ratcliffe et al. 2007). Social rank is important in both the non-breeding and breeding seasons (reviewed in Ratcliffe et al. 2007), influencing many aspects of chickadee fitness; high-ranking birds have larger territories (Mennill et al. 2004), safer and more profitable feeding sites (Desrochers 1989), higher fledgling success (Otter, Ramsay, et al. 1999), and more mating opportunities (Smith 1991; Otter and Ratcliffe 1996). Flocks disband in the breeding season and pairs establish and defend territories, where territorial males engage in song contests with one another. Male chickadees sing a tonal two-note “fee-bee” song and vary their song by shifting this single song-type over a continuous range of approximately 860 Hz (Horn et al. 1992). Males also interact extensively in communication networks (Mennill and Otter 2007), where countersinging interactions often involve both frequency matching (where one male will shift his songs to within 50 Hz of another) and temporal overlapping (where one male will sing over the songs of another; Fitzsimmons et al. 2008a; Foote et al. 2010).

The combination of a linear dominance hierarchy in the nonbreeding season and a complex communication network during the breeding season makes black-capped chickadees an excellent system for exploring eavesdropping on multiple acoustic interactions and the ways that animals extract relational cues about nearby individuals. As Peake et al. (2002) point out, the benefits to individuals of participating in a network should be significantly greater when accurate information about the relative threat posed by multiple unfamiliar rivals (those beyond immediate neighbors) can be acquired with relatively low effort and risk (i.e., no direct interaction required). Testing these abilities can also help us understand the cognitive demands of network communication, as eavesdroppers would need to perceive signalers as separate individuals, internalize the relative threat of those signalers, and then subsequently recall and apply that information in a novel context.

To evaluate whether territorial male chickadees extract relative threat information from multiple song contests and subsequently use this information to evaluate the threat levels of unfamiliar individuals, we used a modified version of the multispeaker experiment developed by Mennill and Ratcliffe (2004a). We presented males with 2 sequential song contests between 3 simulated unfamiliar intruders (A, B, and C), providing them with the information that A was more threatening than B, and B was more threatening than C. We then tested the focal males' response to A and C when the 2 were presented with no relative aggression information provided. We predicted that if males can infer the relative threat of A and C, they would choose to defend against the intruder they perceive to be the greater threat: intruder A. We also examined behavioral differences between young males (second year [SY]) and older males (after second year [ASY]), as previous studies on chickadees have shown marked age effects in response to playbacks (e.g., Mennill and Ratcliffe 2004a).

## MATERIALS AND METHODS

Playback trials were conducted from 13 April to 4 May 2010 at the Queen's University Biological Station at Chaffey's Lock, Ontario, Canada (lat 44°34'N, long 76°19'W). All focal males were territorial and mated to females in either the nest-building or egg-laying stage (average first laying day in the population: May 2; average first incubation day: May 8). Adult birds had been captured during the previous winter between October 2009 and February 2010 using Potter traps and banded with a unique combination of 3 color bands and an aluminum Canadian Wildlife Service band. Individuals were aged as SY or ASY based on their outer tail feathers (Smith 1991). Rank data were not collected on the birds. In total, 29 focal males were tested, of which 15 were SY males and 14 were ASY males.

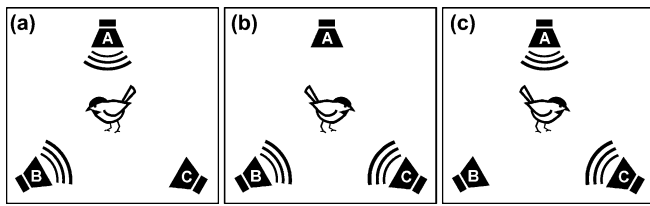
### Playback design

Playback experiments were carried out between 0800 and 1700 h each day, using a four-speaker setup (modified from the three-speaker setup described in Mennill and Ratcliffe 2004a; Figure 1). Prior to each trial, the territory of the focal bird was marked onto a detailed topographical map based on singing posts observed. We defined a bird's territory as the maximum extent of space occupied as observed over the preceding week. Three SONY SRS-77G active loudspeakers (A, B, and C) mounted on 1.8 m poles were then arranged 24 m apart in an equilateral triangle, connected in stereo (2 at a time) to a digital playback device (Apple iPod) located in the center of the triangle, where a seated observer operated the playback device. A fourth “lure” speaker (also a SONY SRS-77G mounted on a 1.8 m pole) was located in the center of the triangle. The observer was seated in the exact center of the triangle, to minimize the influence of observer position on the birds' responses. To avoid attracting males from neighboring territories during playback sessions, the speakers were positioned near the center of the focal male's territory, with the 3 outer speakers facing the center of the triangle. No trials attracted males from neighboring territories. The distances of 3, 6, and 12 m between each speaker were marked with flagging tape as reference points for estimating the approach distances of focal birds from the speaker.

Each playback trial consisted of 4 parts. 1) We lured the focal male to the center of the playback setup (lure phase). 2) We then exposed the focal male to song contests between simulated intruders A and B and then B and C (song contest phase) (Figure 1a,b). 3) We then tested his response toward speaker A versus C (response phase) (Figure 1c). 4) We then tested for possible speaker location effects (post-playback assay).

The lure phase consisted of looped playback of nonsong vocalizations (“chick-a-dee” calls) from the fourth speaker in the center of the triangle. Within 10 s of the focal male being attracted to within 5 m of the lure speaker, the song contest phase began.

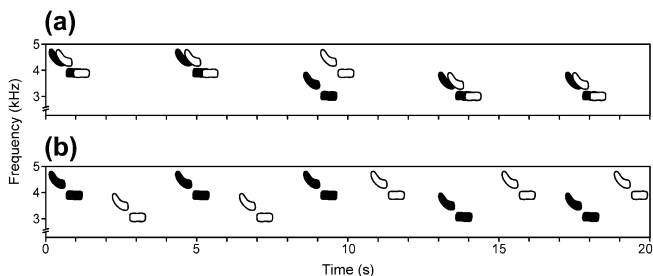
During the song contest phase, two-channel stimuli were broadcast from the A and B speakers, followed by the B and C speakers. Focal males were thus exposed to 2 simulated successive dyadic song contests involving 3 intruding males. In the first song contest, we simulated intruder B (A's songs were offset by 0.7 s, consistently overlapping the last 0.3 s of B's songs) and also frequency matching B's songs within  $23.7 \pm 3.4$  Hz (Figure 2a). In the second contest, which began approximately 10 s after the end of the first contest, we simulated intruder B overlapping and frequency matching the songs of simulated intruder C. In both contests, each of the simulated intruders sang 15 songs at a rate of 1 song every 4.0 s (Mennill and Ratcliffe



**Figure 1**

Schematic representation of the experimental setup used to test multiple-contest eavesdropping in black-capped chickadees. Three loudspeakers arranged in an equilateral triangle with sides of 24 m. After luring the focal male to the center using “chick-a-dee” calls, males heard 2 contests. (a) In the first song contest, speakers A and B broadcast two-channel stimuli simulating a countersinging interaction between 2 territorial intruders. (b) In the second song contest, speakers B and C simulated a second countersinging interaction. (c) The response phase consisted of two-channel stimuli being broadcast from speakers A and C, simulating alternating singing by 2 males (i.e., no relative information was provided), and the subject’s response to speaker A versus C was compared.

2004a), making each song contest approximately 60 s in length. Halfway through each contest, the overlapped bird switched to a lower frequency after 7 songs, and the other bird followed suit after 8 songs (i.e., the song following the frequency shift of the opponent), simulating a frequency-matching event (Figure 2a; following Fitzsimmons et al. 2008b). Previous playback studies have determined that both frequency matching (Horn et al. 1992; Otter et al. 2002; Mennill and Ratcliffe 2004a, 2004b) and song overlapping (Otter et al. 2002; Mennill and Ratcliffe 2004a) are directed, threatening signals in chickadee song contests, and the 2 commonly occur together in natural countersinging interactions (Fitzsimmons et al. 2008a). Using frequency matching and overlapping stimuli as a proxy for relative aggression levels, the song contest phase provided each focal male with information that simulated intruder A was more threatening than simulated intruder B and simulated intruder B was more threatening than simulated intruder C. In each contest, an equal number of songs were broadcast at high and low frequencies (15 songs each at  $3626 \pm 7.3$  and  $3225 \pm 9.4$  Hz, respectively); therefore,



**Figure 2**

Stylized spectrograms of stimuli consisting of “fee-bee” songs from 2 simulated male black-capped chickadees. One male denoted by black songs, the other with white. (a) Song contest phase simulating one male frequency matching and temporally overlapping the songs of another in a directed signal of aggression. One simulated male shifted from a higher to a lower frequency after 7 songs, whereas the other shifted after 8 to match the frequency of the first. (b) Response phase, in which no frequency matching or temporal overlapping occurred between the 2 males. One male began singing at a higher frequency, whereas one began at a lower frequency, with both switching after 8 songs. Each male sang at a rate of 1 song every 4.0 s in both phases, and both phases lasted approximately 60 s. The middle 10 songs are depicted from each phase (from a total of 30 songs each; 15 per male).

there were no absolute differences in song output, only relative information in the timing and patterning of the simulated males’ songs.

The response phase began approximately 10 s after the simulated song contests, and involved simulated intruders A and C singing alternating songs, providing no information from overlapping or frequency matching about which intruder (A or C) was more threatening. During this phase, simulated intruders A and C sang alternating songs with no overlapping (songs were offset by 2.0 s) or frequency matching (frequency difference:  $401 \pm 7.0$  Hz; Figure 2b). The order of which simulated intruder sang first during this phase was balanced across trials. Thus, focal males were exposed to a novel dyad (A and C) whose singing patterns provided no information about relative threat. As before, both simulated males sang at a rate of 1 song every 4.0 s for a total of 15 songs each, and both switched frequencies after 8 songs, for a total duration of 60 s (see Figure 2b).

During the response phase, the focal bird’s movements were described by an observer positioned outside of the area bounded by the 3 loudspeakers with a clear view of the setup, noting whether the subject approached speaker A or speaker C first. We also measured the number of flights of approximately 1 m or greater and the number of approaches to within 0.1 m (i.e., directly above) each speaker. In order to be categorized as making a directed response toward a speaker, the focal male needed to perform one of the following: 1) an approach to within 12 m of a speaker from a starting distance of greater than 12 m or (2) if a male was already positioned within 12 m of the A or C speakers at the beginning of the response phase (birds sometimes made small movements during the song contest phase), he was required to remain within 12 m of that speaker for one full repeat of the 60-s playback stimulus ( $n = 9$  of 29 subjects). If a male did not approach within 12 m of either speaker after 2 full repetitions of the playback ( $n = 2$  of 29 subjects), he was deemed as having made no response. Excluding the lure, the overall duration of trials (song contests and response phase) ranged from 198 to 274 s ( $213 \pm 4.3$  s), as a function of subjects requiring either 1 or 2 repetitions of response phase stimuli. The subjects’ singing behaviors were recorded during the song contests and response phase using a digital recorder (Marantz PMD670) and a directional microphone (Audiotechnica 815b).

A post-playback assay was started 10 s after the end of the response phase playback, to check both A and C speakers were placed within the focal male’s territory and that placement alone did not bias the focal male’s decision during the response phase (following Naguib and Todt 1997; Mennill and Ratcliffe 2004a). Solo songs were broadcast from whichever speaker the focal male did not approach during the response phase (e.g., if the focal male approached speaker A, solo songs of simulated intruder C were broadcast from speaker C during the post-playback assay). If the male approached both speakers during the response phase ( $n = 5$  of 29 subjects), the post-playback assay was not initiated.

### Playback stimuli

The chick-a-dee calls used in the lure phase were recorded in 2005 from males no longer present in the population by 2010. Chick-a-dee calls are used naturally in situations of mild alarm (Ficken et al. 1978) and have commonly been used as lures in other playback studies with chickadees (e.g., Mennill and Ratcliffe 2004a; Wilson and Mennill 2010). Nine individual calls (from different males) were isolated and played randomly throughout the lure phase at a rate of 1 call every 2.5 s (amplitude of 90 dB, measured at 1 m from the playback speaker using a Realistic 332050 sound-level meter).

Chickadee songs possess a number of individually distinctive structural characteristics, which conspecifics can use to discriminate between individuals in the field (Wilson and Mennill 2010) as well as in the laboratory, where no information about singer's territorial location is available (Phillimore et al. 2002). Therefore, playback stimuli (fee-bee songs) were created using recordings of 10 chickadees from the study population in 2000 (and no longer present in 2010) to create songs for 5 simulated intruders. Using CoolEdit 2000 (Syntrillium, Phoenix, AZ), the "fee" notes from 5 of the birds were combined with the "bee" notes of the other 5 at population-typical duration and frequency differences. The songs were further modified so that they were the same length, amplitude, and frequency. Using these stimuli, we created 5 stimulus sets with Audition (Adobe Systems, Mountain View, CA), each set consisting of 3 two-channel sound files: the 2 song contests (A/B and B/C) and the solo singing phase (A and C). Each treatment involved 3 of the 5 simulated males, and across the 5 treatments, each simulated male had the role of the most threatening (i.e., A) and least threatening (i.e., C) bird exactly once. For each experiment, a treatment was chosen randomly (random choice without replacement), and all songs were broadcast at the same amplitude (90 dB at 1 m). The role of each particular loudspeaker was also shifted with each playback trial (i.e., if a speaker broadcasts the A intruder for one playback, it broadcasts the B intruder for the next and the C after that).

### Statistical analyses

We analyzed which speaker focal males approached first during the response phase using binomial tests. Data on latency to first speaker approached and total time within 12 m of that speaker were log-transformed to meet the assumptions of normality for parametric analyses and tested using *t*-tests assuming unequal variances. In comparing responses of focal males by age (SY and ASY), data on latency to first approach to the more threatening speaker (speaker A) during the response phase were nonnormally distributed and could not be transformed, so were compared using a Wilcoxon rank-sum test. The total number of movements (of 1 m or greater) made by SY and ASY males during the song contests and response phase were compared using a multivariate analysis of variance. All tests are two-tailed ( $\alpha = 0.05$ ).

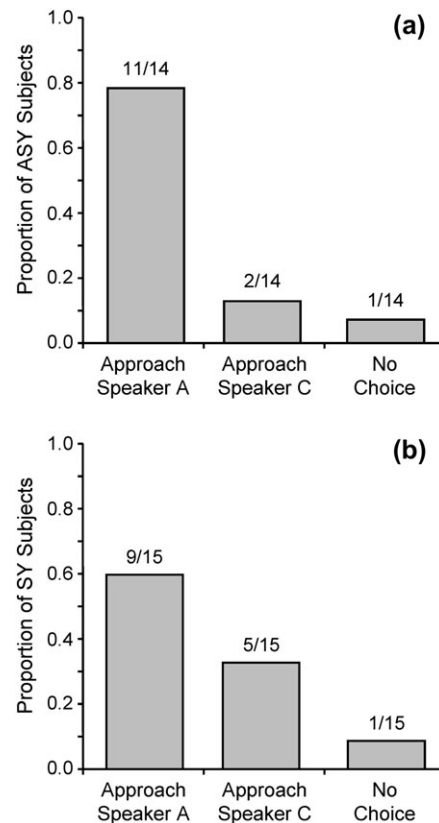
### RESULTS

Focal male chickadees were disproportionately attracted to the loudspeaker broadcasting songs of the more threatening male (loudspeaker A), as simulated by the combined information from the 2 earlier song contests. Of the 29 males tested, 27 males responded differently to the 2 speakers during the response phase (one male of each age class did not respond), with 20 making a directed response to speaker A (binomial test,  $P = 0.02$ ). The 2 males that did not respond were attracted during the lure phase but did not approach either speaker during the response phase through 2 full repetitions (120 s) of stimulus; one male remained attentive to the playback, remaining perched above the central lure speaker, whereas the other male steadily moved away from both speakers A and C. There was no effect of song stimulus version or individual loudspeaker on focal birds' behavior during playback (see Supplementary Data).

Behavior during the response phase varied with subject age. Of 13 ASY males that directed their response toward a speaker during the response phase, 11 responded toward the more threatening stimulus (speaker A: binomial test:  $P = 0.02$ ) (Figure 3a). Of the 14 SY males that approached a speaker,

9 responded toward the more threatening stimulus (speaker A: binomial test:  $P = 0.42$ ) (Figure 3b). Nine males (5 ASY and 4 SY) were already positioned—and remained within—12 m of either A or C at the beginning of the response phase, 7 of which moved closer to the speaker during the playback (3 ASY and 4 SY). For the males that approached the more threatening speaker from a distance of over 12 m, latency to approach was not associated with age (ASY males:  $37.3 \pm 9.1$  s,  $n = 7$ ; SY males:  $32.8 \pm 18.2$  s,  $n = 5$ ; Wilcoxon:  $W = 26$ ,  $P = 0.33$ ). Overall, neither latency to first approach (ASY males:  $36.8 \pm 8.4$  s,  $n = 8$ ; SY males:  $47.9 \pm 14.0$  s,  $n = 10$ ; *t*-test:  $t = 0.03$ ,  $P = 0.75$ ) nor time spent within 12 m of the speaker they responded to first (ASY males:  $40.4 \pm 4.9$  s,  $n = 13$ ; SY males:  $32.5 \pm 6.2$  s,  $n = 14$ ; *t*-test:  $t = -1.52$ ,  $P = 0.14$ ) were associated with age. The total number of movements made by males across the 2 song contests and response phase was not associated with age (multivariate analysis of variance:  $F_{1,25} = 0.31$ ,  $P = 0.58$ ).

We used a post-playback assay involving songs broadcast from the loudspeaker that they did not respond to, to ensure that both speakers were located within the subject's territory and that the subject would approach either loudspeaker, given the opportunity. Once males had approached a speaker during the response phase, most remained within 12 m of that speaker, however, 5 males approached both speakers before the end of the response phase. Of the remaining 22 males that approached a single speaker during the response phase, all approached the opposite speaker during the post-playback assay.



**Figure 3** Behavior of young (SY) and old (ASY) territorial males during the response phase of playback. (a) Old males (ASY) preferentially approached the A speaker, whereas (b) young males (SY) males showed no significant preference. Two males made no response toward either speaker.

## DISCUSSION

Our multispeaker playback design suggests that territorial male black-capped chickadees use information gathered from multiple song contests to infer the relative threat level of unfamiliar individuals. Our playback study provided wild territorial males with information that simulated intruder A was a greater threat than simulated intruder B and simulated intruder B was a greater threat than simulated intruder C. After witnessing these short (60 s) simulated song contests, focal male chickadees were preferentially attracted to A over C when the 2 were presented in a novel pairing with no relative information provided. We conclude from these results that chickadees can eavesdrop on multiple contests and extract relative information about the contestants. The cognitive basis underlying the differential response toward the more threatening intruder remains unclear. Given that chickadee songs possess individually distinctive characteristics (Christie et al. 2004; Wilson and Mennill 2010), it is reasonable to suggest that focal males perceived the stimuli as distinct individuals, internalized the relative threat of those individuals based on their singing behavior, and then subsequently recalled and applied that information in a novel situation.

The order of playback sessions in the song contest phase of our experiment was not randomized; the A versus B contest always preceded the B versus C contest, raising the possibility of sequence effects (Murdoch 1962) in explaining the behavior of subjects during the response phase (Fig. 1c). If a recency effect was at work, we would expect the C stimulus to be chosen more often than the A during the response phase, which was not the case. A primacy effect (wherein we would expect A to be chosen more often than C), on the other hand, cannot be so easily discounted for that same reason. It is possible that during the response phase (Fig. 1c), focal birds identified A as an aggressive male returning after being silent for an interval of 80 s, whereas C had just been encountered in the second part of the song contest phase (Fig. 1b). As pointed out in the RESULTS, song output and male movement did not vary significantly throughout the 3 playback phases (see Supplementary Data), suggesting that males were equally attentive throughout the entirety of trials and that any effects due to habituation or carryover were unlikely. Nevertheless, further experiments using a randomized order of playback design would be needed to conclusively demonstrate that the birds' responses arose from eavesdropping rather than a primacy effect. It should be noted that the order of which simulated intruder sang first during the response phase was varied across trials, and the order of playback did not affect male response. Of the 29 trials, 16 of the focal males heard simulated intruder A sing first during the choice phase (9 of which chose A), whereas 13 focal males heard simulated intruder C sing first (1 of which chose C).

Our results are consistent with the prediction that territorial males would choose to defend their territories against the intruder they perceive to be the greater threat. This is similar to the behavior shown in great tits (Peake et al. 2002), with focal males reacting with varying levels of aggression depending on the threat level of the intruder. The results of the current study have important implications for the evolution of eavesdropping, as the ability to infer threat levels by listening to separate vocal interactions could be an important tool for animals to assess individuals around them. For chickadees, inferences through eavesdropping could be useful in several natural situations, including the dawn chorus, where males interact extensively to mediate social relationships (Foote et al. 2008) or during attempts by floater males to insert themselves into territories (Smith 1991). Thus, males could eavesdrop on song contests as an early warning system to gauge the

threat posed by potential intruders (Eason and Stamps 1993). Females would also benefit from this ability to assess potential extrapair mates, as they have been shown to make reproductive decisions based on the outcomes of song contests (Mennill et al. 2002, 2003; Amy et al. 2008; Caro et al. 2010).

One possible mechanism that animals may use to gather relative information about others is transitive inference. Transitive inference is the ability to observe a series of linear relationships between objects (e.g.,  $A > B$ ,  $B > C$ ) and infer the relationship between objects not compared directly (i.e.,  $A > C$ ). Historically, this was thought to be an exclusively human ability (Vasconcelos 2008), however, laboratory-based evidence has slowly accumulated showing that some animals demonstrate transitive inference, including primates (e.g., McGonigle and Chalmers 1977; Gillan 1981; MacLean et al. 2008), rats (e.g., Davis 1992), fish (*Astatotilapia burtoni*; Grosenick et al. 2007), and birds (e.g., von Fersen et al. 1991; Paz-y-Miño et al. 2004; Weiss et al. 2010). Transitive inference is one possible mechanism that might explain the behavior of the chickadees in our experiment. However, conclusive evidence for transitive inference requires testing of at least 5, rather than 3, ordered stimuli (i.e., A, B, C, D, and E; Bryant and Trabasso 1971), a challenging task for field experiments involving wild animals. Our design differs from traditional transitive inference testing in that the playback consisted of only 3 ordered stimuli (A, B, and C). Thus, we cannot conclude that the birds in our study were using transitive inference because our results could be affected by an "end-anchor" effect (Bryant and Trabasso 1971). In operant tests, higher performance is expected on comparisons involving the end stimuli as one has always been rewarded, whereas the other has never been rewarded (Bryant and Trabasso 1971). In our experiment, focal males only heard simulated intruder A win and simulated intruder C lose and therefore could have been responding toward the winner of a previous contest. We chose to use a three-stimulus design because it provided an appropriate initial test of multicontest eavesdropping for wild chickadees and because it presented territorial chickadees with a simulation that matched the extent of contests normally encountered in the wild (daytime song contests often involve 2 or 3 individuals but rarely more; Foote et al. 2010). Future research extending our experimental design to include 5 contests, rather than 3, will be a challenging but interesting line of research.

There was a clear distinction between the behavior of young (SY) and old (ASY) males. Although they did not differ in any other behavior during the song contests and response phase, older males approached the A speaker significantly more than the C speaker, whereas the young males were more variable in which speaker they responded toward first. These results complement those of Mennill and Ratcliffe (2004a), who used a similar multispeaker design, and found that older males responded toward the overlapping speaker, whereas young males showed more variable responses. These age-related differences in response to playback in our study do not necessarily suggest that young males are unable to perform inferential tasks (although early social environment has been shown to affect transitive inference ability in a foraging context in geese; Weiss et al. 2010), but perhaps that experience plays an important role in the decision-making process of chickadees when defending their territories from unfamiliar intruders. It is possible that the young males were more cautious in responding to intruders because at the time of testing, they had only a few weeks' experience defending territories. Age-related variation in response to playback has been documented in other species (e.g., Cucco and Malacarne 1999; Rajala et al. 2003; Osiejuk et al. 2007), suggesting that as individuals accrue tactical experience with time, they can adjust their responses to various situations.

Previous studies revealed an important role of winter dominance status on male territorial behaviors (Mennill and Ratcliffe 2004a, 2004b). We did not collect dominance rank data in the present study, so we cannot compare the responses of high- versus low-ranking individuals in this task. However, age in chickadees is correlated with social rank (Smith 1991; Otter, Ramsay, et al. 1999; Schubert et al. 2007), so we would predict a similar pattern in results to that of age, that is, males of high rank more consistently approach the A speaker. Mennill and Ratcliffe (2004a) found this pattern with their multispeaker eavesdropping study; high-ranking male chickadees preferentially approached an overlapping speaker, whereas low-ranking males showed inconsistent responses. As social rank and experience are correlated with age, further studies will be necessary to disentangle why males of different age and rank might exhibit different responses to territorial intruders.

Ability to gather information by attending to interactions between conspecifics may be beneficial for animals living in complex social groups. Our multispeaker playback experiment confirms that wild free-living black-capped chickadees extract relative information from dyadic interactions between unfamiliar intruders and suggests they integrate information across multiple sessions. We conclude that social eavesdropping is an important cognitive mechanism for assessment of rivals.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>.

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