DO MALE BLACK-CAPPED CHICKADEES EAVESDROP ON SONG CONTESTS? A MULTI-SPEAKER PLAYBACK EXPERIMENT

by

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Summary

Within a network of communicating individuals, animals may gather information about the relative quality of conspecifics by eavesdropping on their signalling interactions. For territorial male songbirds, eavesdropping may be a low-cost, low-risk method for assessing the relative quality of the males around them. We used a three-speaker playback design to evaluate whether male black-capped chickadees (*Poecile atricapillus*) respond differently to two simulated countersinging intruders who differ only in relative features of their singing performance. We arranged three loudspeakers in an equilateral triangle at the center of playback subjects' territories. After luring males to the first loudspeaker by broadcasting non-song vocalizations, we played songs from the remaining loudspeakers to simulate a countersinging

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interaction between two male intruders. During the interactions, one simulated intruder consistently overlapped the songs of the other, a behaviour thought to be a signal of directed aggression in songbirds. Territorial male chickadees discriminated between the simulated intruders by preferentially approaching the loudspeaker broadcasting the overlapping signal, suggesting that males eavesdrop on other males' countersinging interactions. Male responses to playback support the idea that overlapping is a more threatening signal than being overlapped. Responses varied with the dominance status of the subject. High-ranking males approached the overlapping loudspeaker in 15 of 16 cases whereas low-ranking males approached the overlapping speaker in only 5 of 10 cases, suggesting that males of different quality may use different tactics for territorial defense.

Keywords: communication, eavesdropping, multi-channel playback, black-capped chickadee, *Poecile atricapillus*.

Introduction

Many models of animal communication are based on the principle of dyadic information exchange between one signaller and one receiver. However, animals typically live in close proximity to multiple conspecific individuals and many animal signals travel very far relative to the average spacing between individuals (McGregor, 1993). Consequently, models that account for a network involving multiple signallers and receivers may be more appropriate for describing some aspects of animal communication (McGregor & Dabelsteen, 1996; McGregor & Peake, 2000). As part of a communication network, animals may listen to the signalling interactions between others and extract relative information about those individuals. This behaviour is called 'eavesdropping' (McGregor, 1993; McGregor & Dabelsteen, 1996). Within the traditional dyadic model of information exchange, evaluating the quality of a competitor was assumed to be a costly behaviour because assessments involved direct encounters (Huntingford & Turner, 1987). Within a communication network model, on the other hand, evaluating competitors' quality by eavesdropping on their signalling interactions is assumed to be a low-cost and low-risk behaviour (McGregor & Dabelsteen, 1996).

Evidence from several taxa and multiple signalling modalities suggest that males eavesdrop on the signalling interactions of conspecific males to assess their relative quality. For visual signals, aquarium-based experiments involving fighting fish (*Betta splendens*; Oliveira *et al.*, 1998; McGregor *et al.*, 2001) and green swordtails (*Xiphophorus helleri*; Earley & Dugatkin, 2002) demonstrate that males differentiate between the winners and losers of observed interactions, showing reluctance to act aggressively towards observed contest winners (although see McGregor *et al.*, 2001). For acoustic signals, multi-speaker playback experiments show that territorial males differentiate between the winners and losers of overheard vocal interactions in two species of songbird. In multi-speaker playback experiments to great tits (*Parus major*), territorial males show less aggressive responses to loudspeakers broadcasting the songs of males who have recently lost a countersinging interaction to an overlapping opponent (Peake *et al.*, 2001, 2002). In two-speaker playback experiments to European nightingales (*Luscinia megarhynchos*), males preferentially approach the loudspeaker broadcasting the more aggressive signals (overlapping signals: Naguib & Todt, 1997; leading signals: Naguib *et al.*, 1999). Here, we test whether male black-capped chickadees (*Poecile atricapillus*) eavesdrop on the song contests of other males and whether this behaviour varies with the dominance status of the eavesdropping male.

Black-capped chickadees are socially monogamous territorial songbirds found throughout much of North America. Chickadees live in small, stable flocks throughout the winter, where social interactions are mediated by flock-specific, linear dominance hierarchies (Smith, 1991). High-ranking birds have preferential access to food during the winter (Ficken *et al.*, 1990) and increased reproductive success during the breeding season (Otter *et al.*, 1998, 1999; Ramsay *et al.*, 2000; Mennill *et al.*, in press). High and low-ranking males show status-related differences in singing behaviour, both during the dawn chorus (Otter *et al.*, 1997) and during dyadic song contests (Mennill & Ratcliffe, in press). Chickadee song contests often include asymmetrical exchanges where one individual repeatedly overlaps the songs of his opponent (Shackleton & Ratcliffe, 1994).

We evaluated male eavesdropping behaviour in black-capped chickadees using a three-speaker playback design. We began playback by attracting territorial males to the first speaker, located equidistantly from the other two speakers. After the subject approached the first speaker, we broadcast a stereo stimulus through the remaining speakers, simulating a countersinging interaction between two male intruders. The two simulated intruders sang nearly identical songs except that one consistently overlapped the other, a behaviour thought to be a signal of directed aggression in black-capped chickadees (Shackleton & Ratcliffe, 1994; Mennill & Ratcliffe, in press) and in territorial songbirds in general (Todt & Naguib, 2000). If males eavesdrop on other males' interactions to extract relative information about the relative quality of those males, we predicted that playback subjects would differentiate between loudspeakers simulating overlapping versus overlapped intruders. If males do not extract relative information from such countersinging contests, we predicted that males would respond to the simulated countersinging intruders with equal intensity. If high- and low-ranking males use information gained through eavesdropping to inform rank-specific decisions about territory defense, we predicted that male response to the simulated intruders would vary with the subject's dominance status.

Methods

We conducted 26 playback trials between 0800 and 1400 h, April 17 to May 10, 2001 and 2002, at Queen's University Biological Station at Chaffey's Lock, Ontario, Canada (44°34′N, 76°19′W). All playback subjects were territorial, paired males whose females had not yet finished egg-laying on the day of playback. In January of each year we colour-banded all adult black-capped chickadees in the 2.0 km^2 study site ($N = 183$ individuals in 2001, 140 individuals in 2002). During winter banding, we evaluated birds' outer tail feathers to distinguish hatch-year from after-hatch-year birds (Smith, 1991). Throughout February and March, we tabulated pairwise interactions between birds at winter feeding stations to establish each bird's position within its own winter flock dominance hierarchy ($N = 4000$ interactions in 2001, 2300 interactions in 2002). We inferred dominance when an individual (i) supplanted or chased an opponent, (ii) resisted a supplanting attack by an opponent, (iii) elicited a submissive posture in an opponent, or (iv) fed while an opponent waited to approach a feeder (Ficken *et al.*, 1990; Otter *et al.*, 1998). We confirmed flock membership by following groups as they traveled between feeding stations. Flock sizes ranged from 4 to 12 birds. We used MatMan software (DeVries, 1998; Noldus Information Technology) to reorder dominance interaction matrices to fit a linear hierarchy for the males in each flock. We identified 'high-ranking males' as the top-ranking male in flocks containing two or three males, or the top two males in flocks containing four or five males. We identified 'low-ranking males' as the bottom-ranking male in flocks containing two or three males or the bottom two males in flocks containing four or five males.

Playback design

The playback apparatus consisted of three loudspeakers arranged in an equilateral triangle, with exactly 24 m between each speaker. We mounted loudspeakers (Sony SRS-77G active loudspeakers) on 1.8 m poles and connected each speaker to playback devices located 18 m behind speaker #1. Each playback trial consisted of three phases; a lure phase, a choice phase, and a post-playback assay. During the lure phase (Fig. 1a), we attracted a territorial male subject to speaker #1 by broadcasting loop playback of non-song vocalizations. As soon as the subject perched within 5 m of speaker #1 we stopped lure playback and proceeded with the next phase of the experiment.

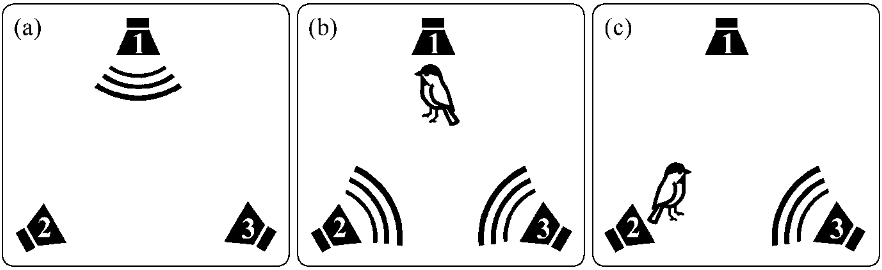

Fig. 1. Schematic representation of multi-speaker playback trials. Three loudspeakers were arranged in an equilateral triangle in the center of a breeding male chickadee's territory. (a) Lure phase — Loop playback of '*chick-a-dee*' calls were broadcast from speaker #1 in order to attract a territorial male subject. The lure phase ended when the subject perched within 5 m of speaker #1. (b) Choice phase — We observed the subject's behaviour while speakers #2 and #3 broadcast a two-channel stimulus that simulated a countersinging contest between two intruders. One simulated intruder consistently overlapped the other intruder for 128 s of playback (32 exchanges between the simulated intruders). (c) Post-playback assay — Intruder songs were broadcast from the speaker that the subject did not initially approach.

During the choice phase of playback experiments (Fig. 1b), we broadcast two-channel stimuli through speakers #2 and #3 to simulate two male intruders engaged in a countersinging contest. Both of the simulated intruders sang the same number of songs (32 songs per simulated intruder), at the same song rate (1 song every 4.00 s), the same song frequency (3202 Hz at the frequency of maximum amplitude of the second syllable of the song), and the same song amplitude (90 dB, measured at 1 m from playback speakers using a Realistic 33-2050 sound level meter). However, the songs of one simulated intruder consistently overlapped the songs of the other. During the choice phase, we described the subject's behaviour into a dictaphone, paying particular attention to whether the subject first approached the simulated intruder at speaker #2 or the simulated intruder at speaker #3. As a reference point, we compared the subject's location to a flag hung exactly halfway between speakers #2 and #3. If the subject made no movement towards either speaker #2 or #3 ($N = 3$ of 26 subjects), we repeated the choice phase stimulus up to a maximum of two repeats.

During the post-playback assay (Fig. 1c), we broadcast solo songs from whichever speaker was not initially approached by the subject in the choice phase (*e.g.* if the subject approached speaker #2 during the choice phase, we broadcast simulated intruder songs from speaker #3 during the post-playback assay). This assay allowed us to test whether both speakers were placed in appropriate locations to stimulate a territorial response (Naguib & Todt, 1997).

Playback stimuli

Stimuli for the lure phase of playback were '*chick-a-dee*' calls taken from the Peterson Audio Guide to Bird Songs of North America. This call is an attractive flock-rallying call and mobbing vocalization (Smith, 1991) ideally suited to the purpose of luring subjects to the playback site because it is acoustically and behaviourally distinct from the male's '*fee-bee*' song. Nine calls were isolated in separate sound files and broadcast in a random sequence at a rate of one call every 2.5 s.

Stimuli for the choice phase and post-playback assay were '*fee-bee*' songs created by modifying six songs recorded from six different chickadees in our study population in 1987, ensuring that the simulated intruders were unknown to playback subjects. We created three different simulated intruder songs by pairing the first syllable of three songs with the second syllable of the other three songs at population-typical frequency and duration differences (Horn *et al.*, 1992). Although we selected songs with similar frequency characteristics to create these stimuli, we used CoolEdit 2000 software (Syntrillium) to subtly modify the three recordings so that they were of the same length (time stretch transformation; length measured to the nearest millisecond), the same amplitude (amplify transformation; maximum amplitude of the '*bee*' note measured to the nearest dB) and the same frequency (pitch shift transformation; frequency measure to the nearest Hz by the frequency of maximum amplitude of the '*bee*' note).

To create two-channel stimuli for the choice phase of playback, we used Cool Edit 2000 to cut and paste songs into the left or right channel of stereo sound files. With separate signals in the left and right channels we could easily simulate countersinging opponents by broadcasting these two-channel sound files through stereo speakers (*i.e.* speakers #2 and #3 in Fig. 1b). Each sound file involved only two of the three simulated intruders, one in the left channel and another in the right channel. Although both simulated intruders sang 32 songs at a constant rate of one song every 4.00 s, songs in either the right or left channel were offset by 0.70 s, such that the songs in one channel consistently overlapped the last 0.30 s of all songs in the other channel (Fig. 2). We created 12 two-channel sound files which included all possible combinations of interactions between the three simulated intruders. Overlapping and non-overlapping signals were counterbalanced so that each of the three simulated intruders had the role of overlapping intruder and overlapped intruder an equal number of times. Further, each simulated intruder was represented in the left and right channel an equal number of times. We burned the 12 stimulus tracks to 12 different recordable compact discs. We shuffled these discs and then labeled them '1' through '12'. After setting up the playback apparatus in each subject's territory, we chose one of the 12 discs for playback (random choice without replacement until all 12 were played) so that we did not know which speaker would broadcast the overlapping opponent when setting up the apparatus. To avoid the confounding influence of neighbours' responses to playback, we placed loudspeakers centrally in subjects' territories (territory boundaries determined by focal watches on the morning preceding playback). Nevertheless, multiple males sometimes responded to playback and we aborted four trials where males other than the resident territorial male approached the playback apparatus.

Results

Male black-capped chickadees preferentially approached the overlapping loudspeaker. Of 23 subjects that approached one of the playback loudspeakers during the choice phase, 20 approached the overlapping speaker while only 3 approached the overlapped speaker (binomial test, $p < 0.0005$). Subjects did not show a significant tendency to approach the speaker broadcasting the left channel (speaker #2, $N = 9$ approaches) *versus* the speaker broadcasting the right channel (speaker #3, $N = 14$ approaches; binomial

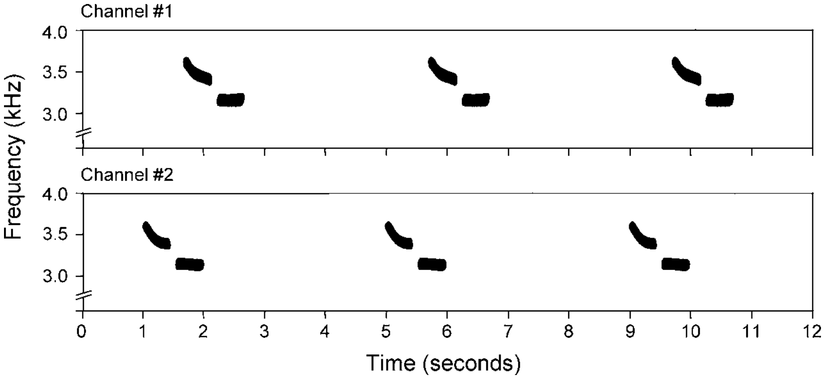

Fig. 2. Sound spectrogram of a portion of a two-channel playback stimulus that simulated a countersinging contest between two male black-capped chickadees. When broadcast through stereo speakers, the simulated male in channel #1 overlaps the songs of the simulated male in channel #2.

test, $p = 0.30$). Subjects did not show a significant tendency to approach one of the three recordings more often than the others (Pearson $\chi^2 = 4.5$, $p > 0.10$, $N = 23$). During the choice phase, three subjects remained perched above the lure speaker (speaker #1) at a position equidistant from both simulated intruders. Two of these 'no choice' subjects sat at their perch for two full repeats of the playback stimulus (384 s of stimulus), attentive to the simulated countersinging contest but approaching neither loudspeaker, while the other 'no choice' subject left the playback apparatus after 120 s of stimulus, retreating in the opposite direction from both speakers #2 and #3.

The preference for approaching the overlapping speaker was driven by the behaviour of males with high dominance status (Fig. 3). High-ranking males approached the speaker broadcasting overlapping songs in 15 of 16 cases. Only half the low-ranking males (5 of 10) approached the overlapping loudspeaker, two approached the overlapped loudspeaker and three approach neither, remaining instead at the lure speaker. Male rank did not influence the latency from the beginning of the choice phase stimulus to the time the subject first approached one of the simulated intruders (high-ranking males: 41.9 ± 7.7 s; low-ranking males: 61.4 ± 11.6 s; $F_{1,22} = 2.0$, $p = 0.17$). Male rank did not influence the amount of time subjects spent at the chosen loudspeaker during the playback trial (high-ranking males: 86.1 ± 7.7 s; low-ranking males: 66.6 ± 11.6 s; $F_{1,22} = 2.0$, $p = 0.17$). Male playback

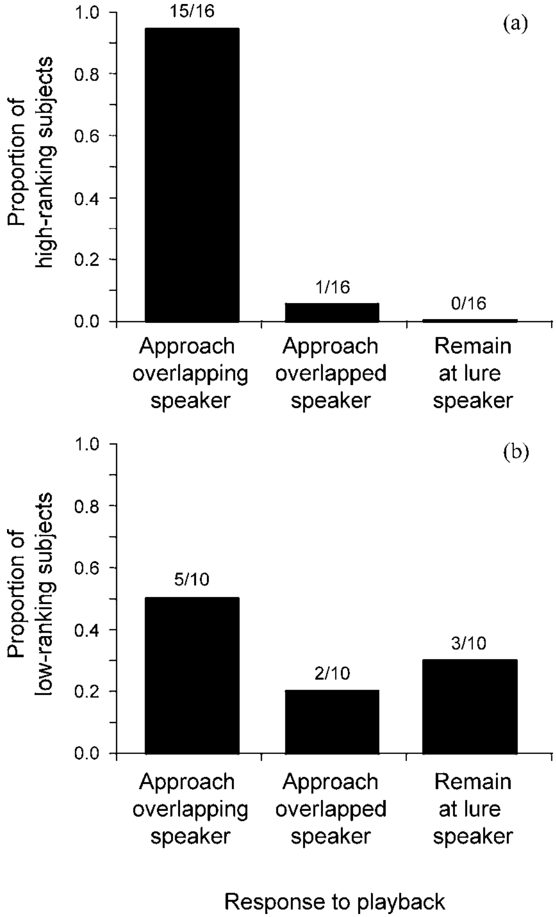

Fig. 3. The approach responses of high-ranking males and low-ranking males to multi-speaker playback. (a) High-ranking males preferentially approached the speaker simulating an overlapping intruder. (b) Low-ranking males approached the speaker simulating the overlapping intruder more often than the speaker simulating the overlapped intruder, but approached neither speaker in three cases.

response also varied with male age: among 16 after-hatch-year birds, all 16 approached the overlapping intruder ($N = 15$ high-ranking males and 1 low-ranking male), whereas among seven hatch-year birds, four approached the overlapping intruder and three approached the overlapped intruder ($N = 1$ high-ranking male and 6 low-ranking males).

All but four males sang during the choice phase of playback. On average, subjects gave their first song 35 ± 10 s after the start of the choice phase. Ten of 23 birds sang one or more songs before approaching one of the choice speakers; of the remaining 13 birds, ten approached the overlapping speaker and three approached the overlapped speaker (binomial test, $p < 0.05$). High-ranking males spent more time singing during the choice phase of playback trials than low-ranking males (high-ranking males: 80.1 ± 9.8 s; low-ranking males: 43.1 ± 14.9 s; $F_{1,22} = 4.3$, $p = 0.05$; time singing measured by the number of four-second intervals where the subject was heard singing).

After approaching one of the two loudspeakers during the choice phase, playback subjects typically stayed near this speaker for the duration of the choice phase, although four males also approached the opposite speaker before the choice phase was complete. All 23 subjects who approached one of the speakers in the choice phase readily approached the opposite speaker during the post-playback assay. There were no differences in latency to approach the opposite speaker during the post-playback assay between high and low-ranking males (high-ranking males: 40.2 ± 16.3 s; low-ranking: 52.7 ± 24.6 s; $F_{1,22} = 0.2$, $p = 0.68$) nor between males who initially approached the overlapping speaker versus those who initially approached the overlapped speaker (overlapping speaker: 46.6 ± 14.6 s; overlapped speaker: 27.0 ± 37.6 s; $F_{1,22} = 0.2$, $p = 0.63$).

Discussion

Territorial male black-capped chickadees discriminated between two simulated intruders engaged in an asymmetrical countersinging contest, preferentially approaching the loudspeaker broadcasting the overlapping signal. Subjects showed no preferential response to a particular recording, nor to a particular playback channel, and a post-playback assay confirmed that speaker location did not drive subject responses. McGregor & Dabelsteen (1996) define eavesdropping as extracting information from the interaction between other individuals that could not be gained from one signal alone. In our playback design, the vocalizations broadcast from each stereo channel revealed no information about the simulated intruders independently of the other channel; only the exchange of relative information between the simulated intruders differed between the simulated intruders. Therefore, the discrimination between overlapping and overlapped vocalizations demonstrated by territorial male black-capped chickadees is consistent with the hypothesis that males eavesdrop on the vocal interactions of other males.

An alternative explanation for our findings is that subjects did not eavesdrop on the simulated intruders as such, but instead responded to other perceived cues. For example, because we could not control subjects' vocal behaviour, it was impossible to prevent subjects from attempting to engage vocally with the simulated intruders. However, although most of the subjects sang during the choice phase, the majority began singing after they had approached the chosen speaker; moreover, because of the experimental design, subjects could not interact vocally with the loudspeakers to derive useful information for discrimination. It is also possible that subjects preferentially approached the overlapping speaker because the second stimulus (the overlapping song) was easier to detect or localize. Our experimental design did not control for stimulus order because overlapping songs, by definition, must come second. However, we think this explanation is also unlikely because in other two-speaker experiments, without overlapping, birds preferentially approach the first speaker that plays (Naguib *et al.*, 1999).

Our results mirror those of Naguib & Todt's (1997) two-speaker experiment with nightingales, where playback subjects preferentially approached simulated overlapping intruders, and Peake *et al.*'s (2001, 2002) multi-speaker experiments with great tits, where subjects showed lower-intensity responses to simulated intruders who had been overlapped. While chickadees have just a single song type (Horn *et al.*, 1992), great tits have multiple song types (Krebs *et al.*, 1981) and nightingales have repertoires of hundreds of song types (Hultsch & Todt, 1981). Despite dramatic differences in their song systems, territorial males show intense responses to overlapping intruders across all three species. This similarity suggests that overlapping may be a signal that is widely used by eavesdroppers to gauge the relative threat of conspecific males.

Subjects' intense responses to overlapping signals are consistent with the hypothesis that overlapping is a more threatening signal than being overlapped (Todt, 1981). Other experiments support the position that overlapping is a threatening signal in songbirds. In black-capped chickadees, males who are overlapped by a countersinging opponent shorten their songs and increase the variability in their song timing, in an apparent attempt to avoid consecutive overlaps (Mennill & Ratcliffe, in press). European robins (*Erithacus rubecula*) and blackbirds (*Turdus merula*) decrease their song output when overlapped by a countersinging opponent (Brindley, 1991; Dabelsteen *et al.*, 1997). Great tits and European nightingales increase the variation in their singing behaviour when overlapped by a countersinging opponent (Hultsch & Todt, 1982; Dabelsteen *et al.*, 1996; Naguib, 1999). Overlapping is thus understood to be a directed agonistic signal (Todt & Naguib, 2000). We suggest that the tendency of our playback subjects to approach the overlapping signal is a tactical decision; because overlapping is a more threatening singing strategy than being overlapped, the simulated overlapping intruder was perceived by territorial males as a greater threat than the simulated overlapped intruder.

Male response to playback intruders varied with male dominance status. High-ranking males showed clear discrimination, preferentially approaching the overlapping intruder. Low-ranking males, however, showed a mixed response and in several cases approached neither simulated intruder. Furthermore, high-ranking males had high song output during playback trials, whereas low-ranking males approached simulated intruders more quietly. These may be adaptive behaviours where male response to an intruder varies with male quality. Throughout the winter, high-ranking males dominate most individuals they encounter in physical confrontations at feeding sites (Ficken *et al.*, 1990). As such, high-ranking males face a low risk by engaging intruders with a strong territorial response. Low-ranking males, on the other hand, may benefit by quietly approaching intruders to gather more information about their relative quality. The observation that some low-ranking males approached neither speaker suggests that low-ranking males are reluctant to engage intruders. Taken together, differential playback responses by high and low-ranking males suggest that male dominance status influences male territorial behaviour.

Male dominance rank serves as a useful proxy for male fitness and female preference (Otter *et al.*, 1998, 1999; Ramsay *et al.*, 2000; Mennill *et al.*, in press). However, the black-capped chickadee dominance system presents interpretive challenges because male dominance status is related to male age (Smith, 1991) and is consequently related to male experience. In the present experiment, male age was also a predictor of male playback response; all after-hatch year birds approached the simulated overlapping intruder whereas only four of seven hatch-year birds approached the simulated overlapped intruder. Simultaneous territorial intrusion by two countersinging males is a relatively uncommon event (Mennill, pers. obs.). Older, experienced males may be better equipped to make a tactical decision about the relative threat of simultaneous intruders, whereas younger males may have never encountered such a situation. The relationship between male dominance and male age may be disentangled by testing territorial males with this playback design across multiple years. Our results emphasize the need to consider variation in subject age, experience, and quality when conducting playback experiments.

Multi-speaker playback designs present novel opportunities for testing network-based communication in free-living animals. Multi-speaker experiments are commonly used to study insect and anuran behaviour (Wagner, 1998), where subjects are placed halfway between two loudspeakers, pairs of stimuli are broadcast through the two channels, and subjects' responses to the two loudspeakers are compared (*e.g.* Grafe, 1996; Bosch & Marquez, 2000; Guerra & Morris, 2002). Such experiments are difficult to perform with other taxa, especially free-living birds, because individuals cannot easily be positioned between two loudspeakers. We included an additional speaker to act as a lure (as in Nelson & Stoddard, 1998 and Molles & Vehrencamp, 2001) to bring subjects to a standard location, equidistant from two other speakers which subsequently broadcast two-channel stimuli. By bringing subjects to a standard location prior to playback, this design prevents subjects from showing preferential responses to one of the loudspeakers based on their direction of approach, thereby allowing us to unequivocally test discrimination between two-channel stimuli. Multi-speaker playback may be used in discrimination tests where separate channels broadcast signals that vary only in relative information content, such as overlapping signals (*e.g.* Naguib & Todt, 1997; present study), alternating signals (*e.g.* Naguib *et al.*, 1999), or exchanges which convey other leader/follower roles. Degrees of overlapping and alternating may be explored in detail by varying the timing of exchanges between pairs of loudspeakers from complete overlap to perfect alternation. Furthermore, multi-speaker playback may be used in perception tests or preference tests, involving channels broadcasting different song-types, differentially-degraded signals, or even male and female duet contributions in duetting animals. In all cases, lure stimuli must be chosen carefully to ensure that lure playback does not differentially influence the subject's propensity to approach any of the choice speakers. Appropriate lure stimuli might be drawn from other conspecific vocalizations or even heterospecific vocalizations, such as an alarm call or mobbing call, that selectively incite approach by the desired subject.

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