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THE EFFECTS OF FOREST GAPS ON ANIMAL COMMUNICATION NETWORKS

By

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Thesis

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The Effects of Forest Gaps on Animal Communication Networks

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To avoid predation, many animals have evolved complex systems of anti-predator communication. Alarm calls are a key component of anti-predator behavior in many birds, and can provide detailed information about predators. Additionally, many birds and mammals produce and respond to each other's alarm calls, creating a complex communication network. Furthermore, individuals may give alarm calls in response to the alarm calls of others nearby, without actually seeing a predator. This makes possible the spatial spread of alarm information, which can result in complex communication networks extending over a large area. However, this requires suitable habitat in which birds will be present to detect and produce alarm calls. Gaps in habitat may preclude the functioning of these networks if they do not contain birds.

To quantify the extent of alarm networks and assess the impact of forest gaps, I conducted a series of playback experiments wherein I broadcast alarm calls to forest bird communities and monitored alarm responses at a distance away, either across a gap or same-size tract of continuous forest. I predicted that alarm responses would be lower across gaps than through forest, and that regardless of the presence of a gap, response will also decrease with increasing distance from the site of alarm call playback. Birds did respond over large distances through continuous forest, but contrary to my predictions, responses across gaps were actually greater than through continuous forest. This implies that, rather than impeding communication through networks, gaps may actually facilitate the spatial spread of information. To my knowledge, this study is the first to explicitly investigate space or habitat structure as a component of communication networks. My results suggest that communication networks allow for a kind of indirect communication, whereby individuals are able to share information over great distances through intermediary signalers.

## **Introduction**

Wild animals must respond appropriately to danger to survive. Many animals produce distinctive vocalizations, known as alarm calls, when they detect a predator or other threat. Alarm calling is an especially important anti-predator strategy because it provides advance warning to other animals about the presence of a predator (Marler, 1957). Alarm calls may also contain detailed information about predators, including the type (Seyfarth, Cheney, & Marler, 1980; Templeton, Greene, & Davis, 2005), degree of threat (Blumstein, 1997), and/or behavior (Griesser, 2008) of a predator, and listeners may use this information to respond appropriately to the specifics of an encounter (Goodale, Beauchamp, Magrath, Nieh, & Ruxton, 2010). In birds, two types of alarm call seem to be especially common in a wide range of species: aerial threat or “seet” calls, and mobbing calls. Seet calls (sometimes referred to as “seeet” (Vanderhoff & Eason, 2009), “zee” (M. S. Ficken, 1990), or flee alarm calls (Cunningham & Magrath, 2017)) are typically given to raptors in flight or other high-threat situations, and are characteristically high-frequency, narrow-band calls (Marler, 1957). In response to seet calls, potential prey will generally increase vigilance, perform cryptic behaviors such as fleeing to cover or freezing, and sometimes produce seet or other alarm calls themselves (M. S. Ficken & Witkin, 1977; Marler, 1955; 1957). Mobbing calls, on the other hand, are given in response to perched or terrestrial predators, and are typically broad-band and produced repeatedly through the duration of an encounter (Curio, 1978; Marler, 1957). In response to mobbing calls, prey will approach a predator, often producing mobbing calls themselves and performing conspicuous, stereotyped behaviors which may include diving

at or striking the predator (Curio, 1978; Hurd, 1996; Marler, 1955; 1957). In response to being mobbed, predators will often leave the immediate area (Bildstein, 1982; Curio, 1978; Flasskamp, 1994; Pavey & Smyth, 1998; Pettifor, 1990).

When several species are vulnerable to the same predators, it may be advantageous to attend to heterospecific alarm calls. Indeed, interspecific responses to alarm calls have been observed in a wide range of taxa, including many birds (e.g., scrubwrens and fairywrens in Australia (Fallow & Magrath, 2010; Flower, 2011; Templeton & Greene, 2007)) and mammals (e.g., marmots and ground squirrels in California (Carrasco & Blumstein, 2012; Russ, Jones, Mackie, & Racey, 2004; Shriner, 1998; Zuberbuhler, 2000; Zuberbühler, 2002)), as well as between birds and other taxa, including mammals (e.g., monkeys (Rainey, Zuberbühler, & Slater, 2004; Randler, 2006; Schmidt, Lee, Ostfeld, & Sieving, 2008; Seyfarth & Cheney, 1990)) and even lizards (Fuong, Keeley, Bulut, & Blumstein, 2014; Ito & Mori, 2010; Vitousek, Adelman, Gregory, & Clair, 2007). In many cases, detailed information about predators can be reliably decoded by heterospecifics (Templeton & Greene, 2007; Zuberbuhler, 2000). In systems such as these, communities of alarm-calling animals disseminate information within multi-species communication networks, where individuals produce information which can be used by other members of the network (Magrath, Pitcher, & Gardner, 2009).

While studies of animal communication have historically focused on simple dyadic interactions between signaler and recipient, the past two decades have seen increased interest in the context of communication within networks of directly and indirectly interacting individuals (McGregor, 2005b). When signals produced by one

individual are perceptible to multiple receivers, communication occurs within a network (McGregor, 2005a). We are beginning to understand that communication networks are extremely common (McGregor & Peake, 2000). Indeed, eavesdropping, in which unintended receivers attend to the signals and signaling interactions of others, appears to be quite common (Peake, 2005), and allows for the widespread phenomenon of heterospecific use of alarm signals (Magrath, Haff, Fallow, & Radford, 2015).

It appears that conspecifics are able to extract a great deal of information from interactions occurring within these networks, especially those related to territoriality, dominance, and sexual signaling. In the handful of systems where these types of interactions have been explored, individuals have been shown to compare and assess potential mates by eavesdropping on sequential encounters (Mennill, Ratcliffe, & Boag, 2002; Otter et al., 1999), to infer a rival's competitive ability in relation to one's own (Peake, 2005), and even to infer and integrate the relative competitive abilities of two unknown rivals (Toth, Mennill, & Ratcliffe, 2012). Thus, it would seem that communication networks provide a great amount and variety of information, especially for the social species in which they have been investigated in depth.

The existence of communication networks also presents the possibility for information to spread beyond the immediate vicinity of a signaler. For long-range signals, this is obvious: loud sounds are broadcast over great distances, and thus are likely to reach multiple receivers (McGregor, 2005). However, in communication networks it might also be possible for the information encoded in signals to spread further than the audible range of the signal, even for those intended primarily for close-range communication. If receivers change their signaling behavior in response to a signal,

additional receivers might attend to this change, and perhaps change their signaling behavior as well. Thus, it may be possible for information to spread over substantial distances, as animals further and further from the initial stimulus respond by producing signals of their own. Few studies have explicitly addressed space as a component in communication networks (Sprau, Roth, Amrhein, & Naguib, 2012), and, to my knowledge, no published study has considered the spatial reach of information through a communication network.

However, some work on communication networks has hinted at the possibility of indirect information exchange occurring through communication networks; that is, information received not directly from an initial signaler but through one or more intermediary signalers. In one aquarium study, parent convict cichlids (*Cichlasoma nigrofasciatum*) observing another adult performing a fin-flicking alarm display responded by performing the same warning display to their young (Shennan, Waas, & Lavery, 1994). Here, information from an initial signaler is transmitted indirectly to unrelated young, via the intermediary of an observant parent. This may or may not increase the spatial range of the information in a signal, but it certainly makes this information available to individuals that would not have collected it themselves. In this way, this behavior has the potential to increase the numerical and spatial reach of alarm information.

Studies of singing interactions during the dawn chorus have suggested a similar pattern on a much larger scale. Fitzsimmons et al. describe a “ripple effect” on singing behavior in territorial neighborhoods of Black-capped Chickadees (*Poecile atricapillus*) (Fitzsimmons, Foote, Ratcliffe, & Mennill, 2008). In their study, researchers simulated

dyadic counter-singing interactions, which signaled either aggression or submission between the two simulated rivals. Paired with an extensive microphone array that recorded chickadee vocalizations well outside the audible range of the experimental playback, the authors showed that differences in the aggressiveness of the simulated interactions elicited differences in the level of song output of the entire neighborhood analyzed as a whole. In this case, information present in an interaction may have affected behavior well beyond the audible range of the initial stimulus. However, because the authors did not consider the specific locations of singers in this analysis, it is unclear whether this pattern may have simply resulted from increased singing by birds within earshot of the playback stimulus.

Preliminary research on alarm signaling in communication networks has suggested that information in alarm signals might also move substantial distances, presumably through a similar “ripple”-like phenomenon (Greene et al., 2017). Information about the presence of a predator should be valuable even if the predator is some distance away, especially since some predators, such as raptors, move quickly and can be stealthy (Bildstein & Meyer, 2000). If alarm calls are propagated through communication networks, then the information they contain might travel far beyond the audible range of the initial caller. However, these hypotheses have not been rigorously tested, and it thus remains unknown whether this phenomenon does in fact occur at large spatial scales, to what types of stimuli, or how common it might be. Furthermore, questions regarding the effects of distance or habitat characteristics on communication networks have received very little attention.



Habitat loss and fragmentation are widely recognized as being among the most extreme anthropogenic changes to global ecosystems (Brooks et al., 2002; Wilson et al., 2015; Wu, 2013). The impacts of these changes are widespread, and together are considered to be the greatest threats to biodiversity (Hanski, 2011; Wilson et al., 2015). While studies of habitat loss and fragmentation have investigated large-scale effects on plant and animal communities (Robinson et al., 1992), such as effects on predation (Andrén, Angelstam, Lindström, & Widén, 1985) and changes in species abundance or richness (Debinski & Holt, 2000), we know very little about how loss and fragmentation might affect communication. A few studies suggest that fragmentation may affect animal communication over long time scales, causing cultural loss of song types (Laiolo & Tella, 2007), decreased song complexity (Hart et al., 2018), and reduced repertoire size and song type similarity (Rivera-Gutierrez, Matthysen, Adriaensen, & Slabbekoorn, 2010) in fragmented populations. Anti-predator strategies may also be affected (Banks, Piggott, Stow, & Taylor, 2007). For example, fragments may support smaller groups, requiring each individual to spend more time vigilant to achieve the same level of vigilance as larger groups (Tellería, Virgós, Carbonell, Pérez-Tris, & Santos, 2001). Additionally, fragmentation may cause historical predators to disappear from some habitat patches, resulting in the loss of appropriate alarm-calling responses by prey species (Saborse & Renne, 2012).

Breaks in habitat can also affect animal behavior and communication at small temporal and spatial scales. For instance, forest bird species are less likely to respond aggressively to territorial intruders when they are separated even by short (40-100 m) gaps (Rail, Darveau, Desrochers, & Huot, 1997). Similarly, many bird species are

reluctant to cross gaps when provoked with mobbing calls (C. S. Clair, Bélisle, & Desrochers, 1998; Shimazaki et al., 2016). Habitat gaps might similarly affect behavioral responses to alarm calls by impeding the flow of information. While animals able to detect an alarm signal from across a gap would likely respond to it, a wide enough gap would prevent a signal from being detected on the other side. For the information in an alarm call to spread over distance, animals must hear the call and propagate it. If a gap in habitat is wide and there are no animals within the gap to call in response, that information will not be transmitted across the gap. Thus, gaps in habitat may interrupt communication networks, making it more difficult for prey to detect and avoid predators.

We know very little about how communication networks work. In particular, we know very little about how far information travels, or what environmental features might affect the movement of this information. In this study, I first attempt to experimentally demonstrate the indirect transmission of alarm information in a multi-species communication network of forest birds. To do so, I conducted playback experiments to elicit alarm responses in forest bird communities. I tracked the acoustic responses of birds using an extensive microphone array, and conducted behavioral observations to quantify non-vocal alarm responses. I hypothesized that alarm information would spread through communication networks, and that this would be detectable in the responses of birds outside of the audible range of the playback stimulus.

Next, I attempt to elucidate the effects of forest gaps on this alarm network. I hypothesized that the transmission of alarm information through communication networks would be impeded by forest gaps, and that responses of birds across gaps would be lower than responses of birds across the same length of continuous forest.

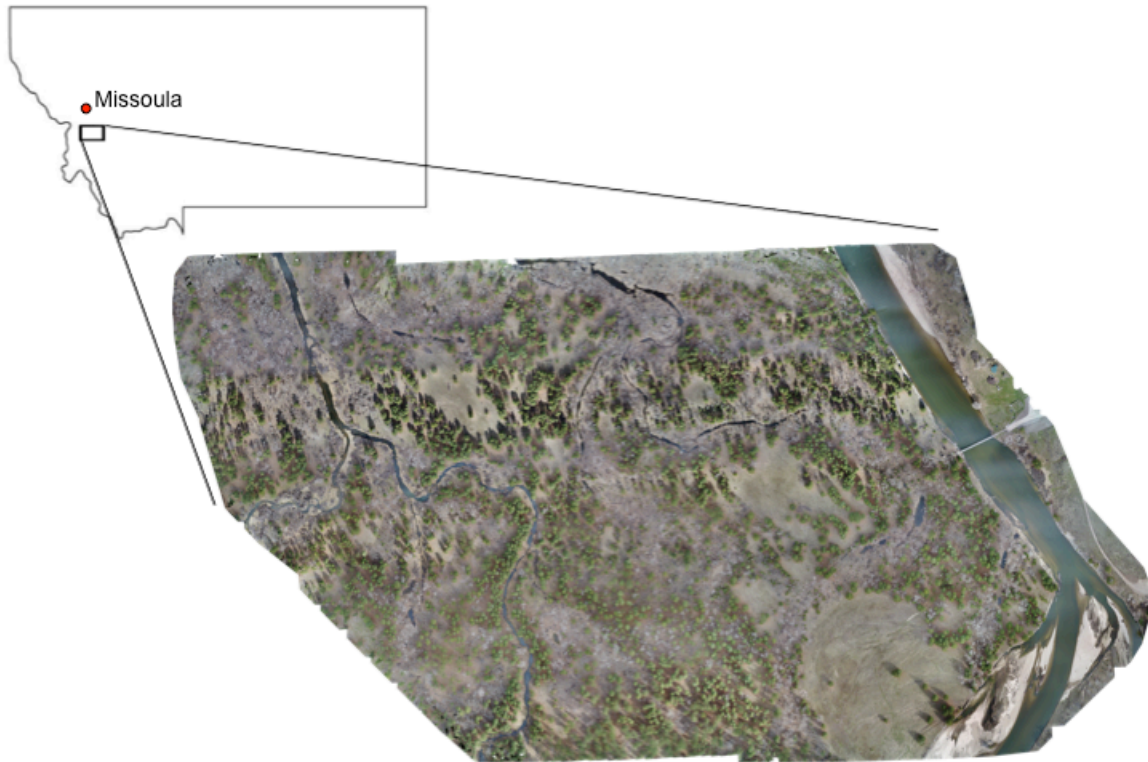
Furthermore, I predicted that, while birds further from the playback stimulus would respond more weakly than birds that were closer, this would be more extreme across forest gaps than through continuous forest. To test these predictions, I conducted identical playback experiments across gaps of varying widths, and compared these with playback experiments in matched lengths of continuous forest. Using the acoustic location and behavioral observation techniques described above, I attempt to determine the effects of different sized forest gaps on alarm responses in birds, and compare these to the effects of distance alone in continuous forest.

## **Methods**

### *Study site and species*

I conducted my experiments at a large ranch in the Bitterroot Valley, MT, USA (Figure 1; 114° 3' 15.955" W, 46° 43' 12.23" N). This location has been established as a long-term research site for studying communication networks, and contains uninterrupted woods intermixed with clearings of different sizes. The habitat at this location is primarily riparian forest, with mixed ponderosa pine (*Pinus ponderosa*), black cottonwood (*Populus balsamifera trichocarpa*), and quaking aspen (*Populus tremuloides*). This site supports a high abundance of Black-capped Chickadees (*Poecile atricapillus*) and other species that attend and respond to chickadee alarm calls, including Red-breasted and White-breasted Nuthatches (*Sitta canadensis* and *S. carolinensis*) (Hurd, 1996; Templeton & Greene, 2007), and Downy Woodpeckers (*Picoides*

*pubescens*) (Sullivan, 1984). To ensure birds were present for experiments, I set out bird feeders filled with black oil sunflower seeds at desired locations. I conducted experiments in winter to take advantage of mixed-species flocks, and to ensure that these flocks were attracted to feeders.

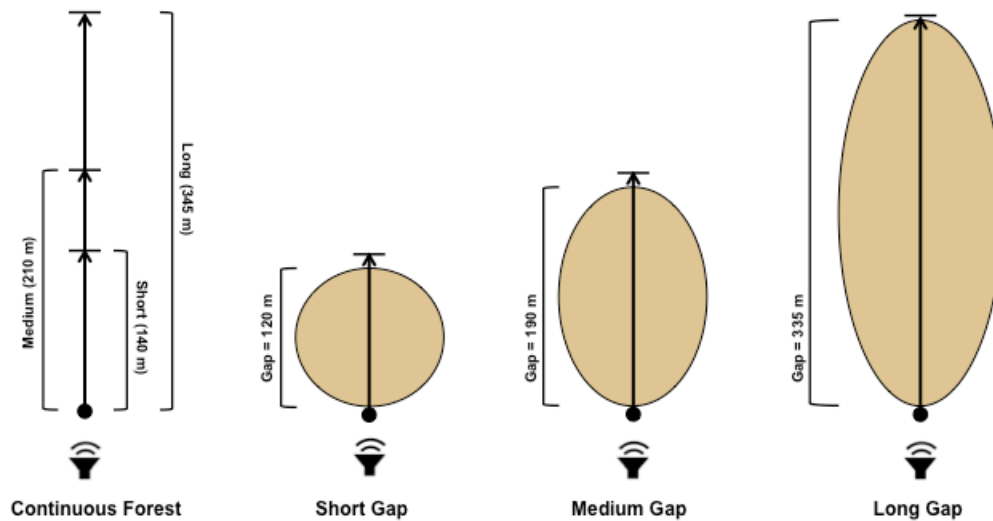


**Figure 1:** Location map and composite drone orthomosaic image of the field site in the Bitterroot Valley, MT. Note the presence of both continuous forest (deciduous trees have defoliated) and gaps of different sizes

### *Field procedures*

To test my hypotheses about the spread of alarm information through communication networks, I conducted a series of playback experiments where I broadcast alarm calls of Black-capped Chickadees to forest bird communities. I conducted experiments in continuous forest, and across forest gaps of different sizes. Continuous

forest controls took place in large unbroken forest patches, while gaps at my study site are old clear-cut sections of forest that have become open fields. Some research has shown that mobbing flocks, especially those which include members of the family Paridae such as chickadees, can facilitate forest birds in crossing forest boundaries and entering open habitat (Sieving, Contreras, & Maute, 2004). However, I observed no forest birds of any species flying into or crossing these gaps below canopy height. Occasionally non-focal birds such as ducks or geese would fly across my gaps high over the canopy, but I did not consider these flyovers to be relevant to my study. This is in agreement with previous work demonstrating that forest birds are reluctant to cross small gaps, even when stimulated with territorial song (Rail et al., 1997) or mobbing calls (C. S. Clair et al., 1998; Shimazaki et al., 2016). I conducted experiments across gaps of 120 m, 190 m, and 335 m (hereafter short, medium, and long gaps, respectively) in width. In addition, I had two control areas in continuous forest. Distance treatments in continuous forest were paired with gaps of approximately equal length (Figure 2). Thus, I had short, medium, and long distance treatments as well (140 m, 210 m, and 345 m, respectively).



**Figure 2:** Schematic illustrating the three distance treatments for continuous forest and gaps. Gap lengths and distance treatments are to scale.

Playback experiments consisted of three treatments: Black-capped Chickadee mobbing calls, Black-capped Chickadee seet calls, and neutral Red Crossbill song (*Loxia curvirostra*), with order of treatments randomized for each experiment. To avoid pseudoreplication, I used three different exemplars for each type of playback stimulus, which I cycled through in random order for successive experiments at each site. Recordings of crossbill song were from the Stokes Field Guide to Bird Songs: Western Region (Stokes, 1999), The Peterson Field Guide to Western Bird Songs (Cornell Lab of Ornithology, 1992), and the Macaulay Library at the Cornell Lab of Ornithology (*Loxia curvirostra* [ML106640](#)). Chickadee mobbing and seet calls were recorded locally around Missoula, MT. All stimuli were played using a Roland R-26 connected to a PigNose Legendary 7-100 field speaker, which produces a frequency response curve that is flat between 500 Hz and 17,000 Hz (PigNose, Las Vegas, NV, U.S.A.). The auditory range of

chickadees lies well within this scope (Henry & Lucas, 2010; Wong & Gall, 2015), as do the frequency ranges of my playback stimuli.

Consecutive trials at a given site were always conducted at least 30 minutes apart, or longer if necessary to allow birds to return to normal behavior and baseline rates of feeding. Each trial consisted of three stages: 1) pre-playback (two minutes of data collection before playback began, to gather baseline feeding, behavioral, and vocal data); 2) playback (two minutes of playback of a treatment stimulus); 3) post-playback (five minutes of data collection after playback ceased, to determine the length of vocal and behavioral responses to playback, and delay to resume foraging).

For each experiment, several trained observers collected data on a specified set of behavioral responses. I had two observation sites for each experiment, one at the site of playback and one at a site a designated distance away. Depending on the experimental treatment, the intervening distance between observation sites consisted of either continuous forest, or included a gap. Bird feeders were placed at each observation site (10-20 m from a gap edge, if applicable) to ensure that birds were present during experiments, and to provide a standardized focal point for measuring feeding behavior. I did not start an experiment until there were birds feeding at both feeders, and remaining consistently in the area such that they were visible to observers. Observers noted the numbers and species of birds in the area, duration and species of each feeding trip, and tallies of several alarm behaviors – scanning, wing-flicking, rapid upward flights (hereafter “up-flights”), and flying over the playback speaker. Tallies of feeding trips and all alarm behaviors were measured only for the most common species at my feeders – Black-capped Chickadees and Red- and White-breasted Nuthatches. Measurements of

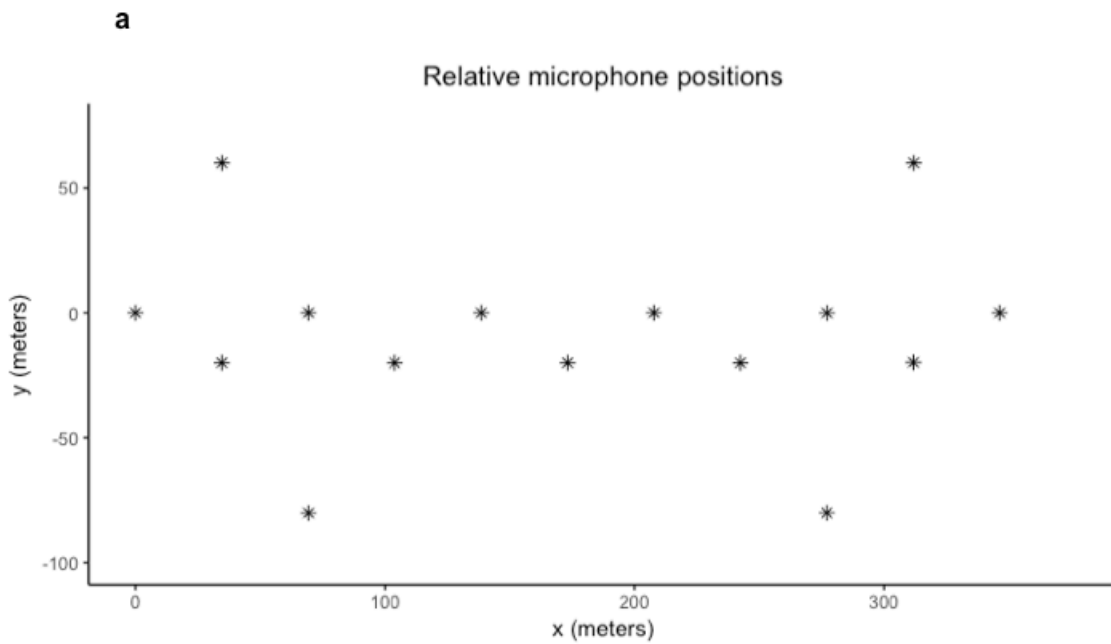
alarm behavior were taken together for each species and intended to represent the flock as a whole. Durations of each scan and wing-flicking bout were timed and marked as they occurred when an observer noted any individual of a given species performing one of these behaviors. Up-flights and speaker over-flights typically lasted only 1 second or less, so these were taken as a tally for each species over the course of each experiment.

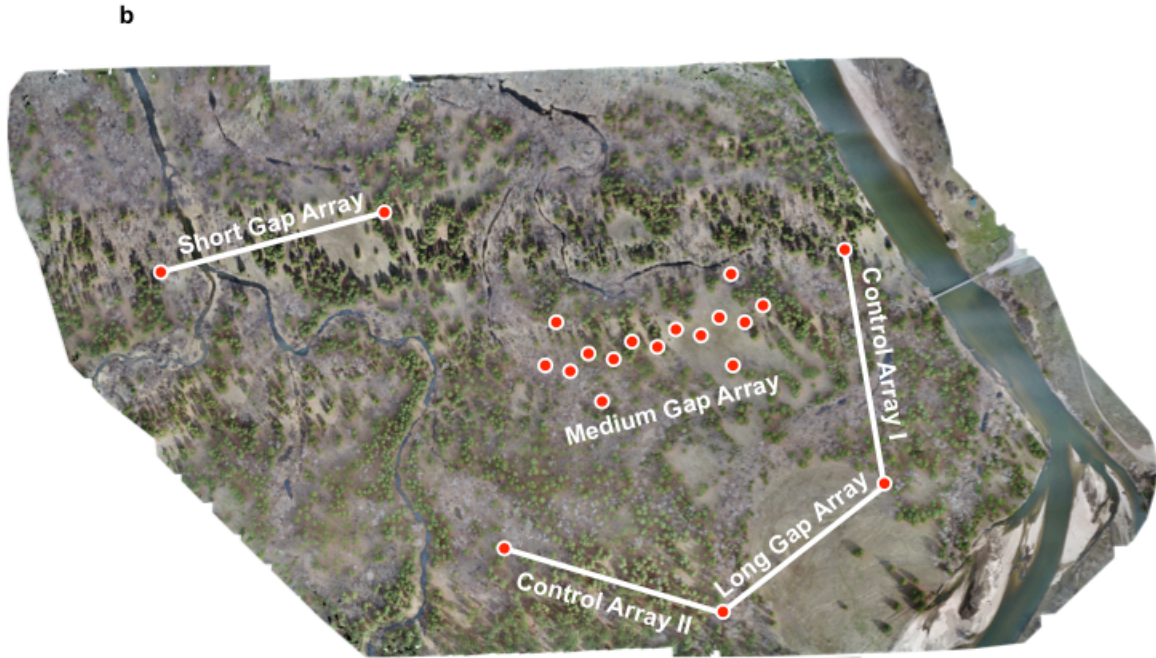
### *Microphone Arrays*

I recorded vocal responses of birds using synchronized arrays of 15 microphones. These microphone arrays were 346.41 m long by 140 m wide, covering an area of 48,497.4m<sup>2</sup> (Figure 3). Microphone arrays provide a powerful method of creating acoustic maps, and have been used to determine the locations in space and time of a wide variety of animals, especially whales (C. W. Clark, Charif, Mitchell, & Colby, 1996; Frankel, Clark, Herman, & Gabriele, 1995) and birds (Bower & Clark, 2005; Foote, Ratcliffe, Fitzsimmons, & Mennill, 2010), but also including elephants, marmots, and bats (Blumstein et al., 2011). I used a zigzag design to prevent the left-right ambiguity which can be problematic in straight line arrays (Boyle & Grant, 2001). I placed adjacent microphones on the zigzag line 40 m apart, at alternating angles of 30° and 150°. To increase my range of detection at either end of each array, I added two off-line microphones on either side of the array at each end, orthogonal to the orientation of the zigzag and 70 m from the nearest zigzag microphone points. Preliminary transmission experiments indicated that calls of interest could travel at least 80 m through the densest habitat I was working in, so my design never placed adjacent microphones more than 80 m apart. This was to ensure that calls would be recorded from multiple locations, thus



allowing us to later localize calls using triangulation based on differences in arrival time (see *Acoustical Analysis*, below). This design allowed us to determine the location of most vocalizing birds and mammals at any position within at least 50 m of any point along the zigzag line. I used the same array design for all experiments, covering the same distance regardless of the locations of the two observation points.





**Figure 3:** (a) Relative microphone positions for each of the seven arrays. Note central zigzag line and two off-line microphones at each end of array. (b) Aerial image of field site showing all microphone arrays. For simplicity, microphone points are represented for the medium gap array only; all other arrays are represented by a white line connecting microphones at endpoints.

Based on the auditory sensitivity thresholds of Black-capped Chickadees (Wong & Gall, 2015), I conservatively estimated that the lowest minimum frequencies of seet calls (7 kHz) could be heard from a maximum distance of about 18 meters away.

Mobbing calls have a minimum frequency of 2.5 kHz, so chickadees should be able to perceive these calls from no more than 300 meters away. I calculated these values by subtracting transmission loss from an estimated maximum source level for each call type (70 dB SPL at 1 m for seet calls, 80 dB SPL at 1 m for mobbing calls).

$$\textit{Received level} = \textit{source level} - \textit{transmission loss}$$

I calculated transmission loss using the inverse square law,

$$\text{Transmission loss} = 20 * \log (d)$$

where  $d$  is distance in meters. This assumes spherical spreading and no excess attenuation. Thus, the actual range of these calls *in situ* is likely to be substantially lower, especially in areas with vegetation.

To estimate the locations of sounds I used a time-difference of arrival (TDOA) algorithm. These algorithms use the difference in arrival times of a sound at different microphones in the array to derive the location of the sound source. The mathematics underlying the TDOA method are well-established, and involve solving for a set of nonlinear hyperbolic equations (Li, Deng, Rauchenstein, & Carlson, 2016). Since sound travels fast (330 m/s at 0 °C in dry air), the differences in arrival times at different microphones are very small. Thus there are two requirements for accurately localizing sounds in recording arrays: 1) the spatial relationships of the microphones to each other must be known, and 2) all the recorders must be working with the same clock.



**Figure 4:** Microphone locations setup for each point on arrays. From left to right: Omni-directional microphone, solid-state digital recorder, and GPS clock synchronizer.

I paid special attention to both of these requirements to maximize the accuracy of localizing sounds. I worked with a professional surveyor to determine the precise locations of the microphones relative to each other. I used a Sokkia SET6 Total Station and Spectra Precision Ranger data collector, which gave us extremely accurate point locations for my microphones ( $\pm < 1$  cm). I inserted fence posts into the ground at each microphone location, to which I attached the microphones and recording gear. Each array point included a sensitive omnidirectional microphone connected to a digital recorder

(Figure 4). I recorded audio data with Roland R-26 digital stereo recorders. All recordings were made as two-channel WAV files, recorded at a sampling rate of 48 kHz/s with 24-bit depth. For each recorder, the left channel received audio input from a Sennheiser ME 62 omnidirectional microphone with a K6 power module. To reduce extraneous sources of noise, the microphones were stabilized with Rycote shock mounts and covered with Rycote windscreens. The right stereo channel received the timing information from a time synchronizing unit (hereafter, “synchronizer”).

To ensure that all the recorders were using the same reference clock, I used custom-built synchronizers with each recorder. These synchronizers are solar-powered devices that have a satellite GPS receiver (GlobalTop FGPMOPA6H). Once each second, the synchronizers receive data from GPS satellites, including extremely accurate time signals from a cesium atom clocks. These once-per-second signals served as extremely accurate “metronome” pulses from the synchronizers, which are recorded as digital audio data. In addition, the synchronizers produced a timing pulse each minute, followed by a longer string of serial data that labeled the exact time for the pulse. In addition, this longer data pulse included the internal and external temperatures ( $^{\circ}\text{C}$ ), the battery voltage, and the synchronizer unit ID.

To localize sounds within the recording array I needed to create a multichannel recording in which all of the data from each recorder was time-aligned. This was because each recorder was turned on at a different time before the start of the experiments. To accomplish this, I used a custom-designed a “synch and merge” program in MATLAB (2016b). The program searched the timing signals in the synchronizer channels of each unsynchronized stereo recording, and then used the common timing signals to align the

audio channels. Once the timing alignment was done, the timing channels were stripped out, producing one synchronized, multi-channel audio recording.

Tests showed that these synchronizer systems are accurate within a few billionths of a second (ns). During several tests of over an hour (far longer than my experiments), the outputs of synchronizers remained within one recording sample of each other. This is an error rate of less than  $10^{-9}$ , and thus my recorders were synchronized to the same clock with essentially no error.

### *Acoustical analysis*

For each experiment I combined recordings from each location into a single multi-channel sound file, with all channels synchronized in time. To understand how information encoded in alarm calls moved through the environment during my experiments, I analyzed these files in XBAT, a MATLAB platform for acoustical analysis that allows for two-dimensional localization of recorded sounds (Figuroa & Robbins, 2008). For the 19 species recorded, I categorized vocalizations into discrete call types (Table 1). These types were based on available literature, Birds of North America Online species accounts and associated recordings, and recordings from the *Cornell Guide to Bird Sounds: Master Set for North America* (2013). Despite the range of species recorded, I focused my efforts on the three most common species: Black-capped Chickadees, and Red- and White-breasted Nuthatches.

I conducted my analysis in sequential ten-second segments through the entirety of each experiment. Within each segment, I attempted to localize one call of each type for each individual of each species that vocalized. Individuals were differentiated by overlap

with others and apparent location, based on the locations of microphones that recorded a given call, and relative amplitude and arrival time if multiple individuals were recorded from the same microphone location(s). Estimates of the number of individuals were conservative, and tended to underestimate the actual number of individuals present (unpublished data). This methodology gave us a snapshot of the overall vocal activity for each consecutive ten-second segment of each experiment. Sounds that could not be confidently identified to species were not localized, including all non-vocal sounds such as pecking and wing beats.

I selected calls for localization in XBAT by drawing boxes around the spectrograms, then allowing XBAT to attempt to derive a location. XBAT locates a recorded sound event by triangulation, using differences in arrival time between recordings of a given sound from different locations (Figueroa & Robbins, 2008). If XBAT could find at least three channels that had recorded a given call, a location was estimated. These locations were proofed to ensure that only recordings of the selected call were used (i.e., that XBAT didn't "mistakenly" use another sound in its calculation), and that derived locations were plausible based on obvious cues from the recording such as relative arrival times, relative amplitudes, and the locations of microphones that did and did not record that call. If a location did not meet these criteria, it was excluded from further analysis. To test the accuracy of my location system, I derived locations for playback of Black-capped Chickadee seet and Red Crossbill song from experiments at four of my arrays. I then compared the locations calculated in XBAT to the actual known locations of the playback speakers. I found that my location system was reasonably

accurate, with an error of about 10 m for a given location (median = 15.25 m, 1<sup>st</sup> quartile = 9.83 m, 3<sup>rd</sup> quartile = 25.75 m).

### *Statistical analysis*

To investigate the relationships between bird behavior and my different treatments, I relied largely on non-parametric permutation tests. Permutation methods test for differences between groups by resampling the data in a manner consistent with the null hypothesis. If the null hypothesis is that both groups come from the same population (i.e., no difference between groups), then the data are randomly assigned to each group, maintaining the original sample sizes. A test statistic (often the mean) is then calculated from this new permutation of the data. This process of permutation and calculation of the test statistic is repeated thousands of times to generate a permutation distribution. Finally, the test statistic for the real data is located on the permutation distribution to generate a p-value. Because permutation tests create a distribution from the sample data, they do not rely on assumptions of normality or sample size (Oden & Wedel, 1975), and so can be used on small samples. Permutation tests have been used to address a wide range of biological questions, e.g. (Ghalambor et al., 2015; Laiolo & Tella, 2005; Mates, Tarter, Ha, Clark, & McGowan, 2014).

In addition to running permutation tests for each comparison, for each of these tests that produced a p-value < 0.1, I also ran a t-test. In all instances, these were for paired responses (either seet compared with crossbill song in the same treatment series at a given array, or pre-playback compared with experimental period for a given experiment). I considered t-tests appropriate because they are robust to deviations from



normality, and though my sample sizes were small, response values did appear to be normally distributed. Furthermore, t procedures tend to be conservative, so I did not consider Type I errors to be very likely (Yuen & Technometrics, 1974). All statistical analyses were conducted in R (version 3.3.0).

For this study, I focus on set and Red Crossbill control experiments. For behavioral analyses, I first calculated the overall rate of various flock behaviors for chickadees and both nuthatch species per time for both the 2-minute pre-playback and 7-minute experimental period (combined 2-minute playback and 5-minute post-playback periods). Thus, responses measure the overall rate at which a behavior was performed during each period of an experiment. For most analyses, I used the difference between these rates as my response. I considered behaviors at the level of the flock (i.e., chickadees and the two nuthatch species were lumped). In addition, I examined behaviors separately for Black-capped Chickadees and Red-breasted Nuthatches. Because White-breasted Nuthatches were relatively uncommon, I excluded their behavioral responses from species-level analyses. I analyzed the following behaviors: feeding, scanning, up-flights, alarm and non-alarm vocalizations for chickadees, and wing-flicking by nuthatches. Because I was primarily interested in the responses of birds at a distance from playback, I restricted my analysis of vocalizations to birds that called from within 70 m of the treatment distance for a given experiment – short (140 m), medium (210 m), or long (345 m). I conducted a separate statistical test for each response variable. Because speaker over-flights were not possible at observation sites away from the playback speaker, this response variable was excluded from analysis.

To test whether my seet playback had any effect on birds at my selected distances, I used permutation tests to run paired comparisons of my playback periods (“symmetry\_test” function of “coin” package in R). These tests preserve the pairing of response values, but randomize their grouping. Thus, for each permutation, the response values in each pair were randomly assigned to either the pre-playback or experimental period group. For vocal responses, I also tested the ratio of alarm calls to non-alarm vocalizations.

I used the same method to determine whether playback of seet calls affected my birds differently than crossbill song. For these tests, my response variable was the difference in response between periods (pre-playback response subtracted from experimental response) in the rate of a given behavior. I ran a separate test for each distance category for both gap and continuous forest arrays. Because these experiments were conducted consecutively at each array, typically on the same day, I paired them by date or date range (no more than 2 days apart).

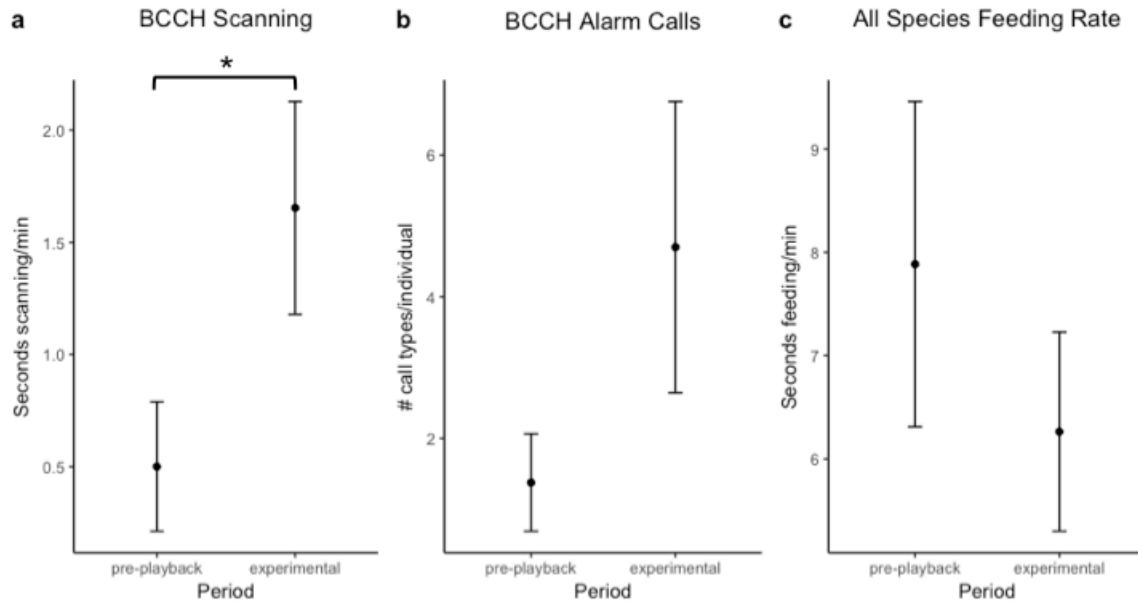
To test whether responses differed between matched-distance gap and control arrays, I conducted permutation tests (“independence\_test” function in the “coin” package), as well as custom-coded permutation tests (100,000 permutations) on the difference of means. I conducted separate tests for each distance category.

These were very ambitious experiments with large recording arrays and 6 treatment blocks. Each experiment took a great deal of time and effort, which limited my sample sizes. Given this, I had little statistical power to determine significance at  $\alpha = 0.05$ . Indeed, for many of my permutation tests, the lowest mathematically possible p-value was  $> 0.05$ . With only a few exceptions, T-tests produced larger p-values than my

permutation tests. In these cases, I do not report results. In the few cases where T procedures produced a lower p-value than my permutation tests, I report results from both. Of the 184 tests conducted, I report all results where  $p < 0.1$ .

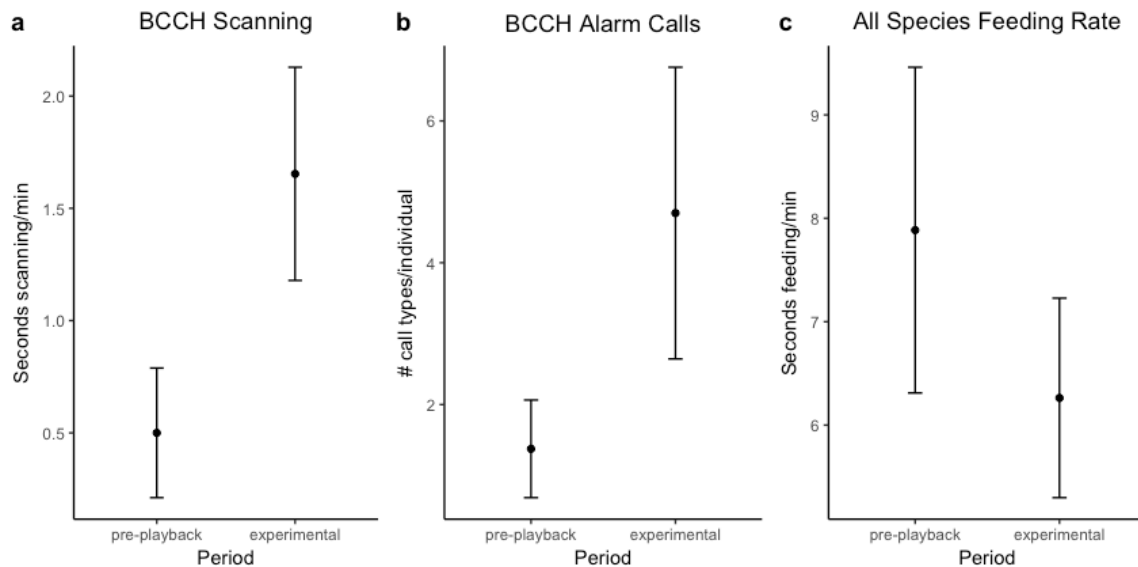
## Results

I conducted 36 field playback experiments of Black-capped Chickadee seet calls and 36 of Red Crossbill songs, split across the six treatment blocks (short, medium, and long distance treatments each for gap and continuous forest arrays). My analyses suggested that seet playback affected bird behavior at each distance from playback through continuous forest. At 140 m, chickadees gave significantly more up-flights per minute after playback than before (mean before playback: 0, mean after: 0.086;  $Z = 1.8472$ ,  $p = 0.03236$ ; Figure 5a). Similarly, Red-breasted Nuthatches gave more wing-flicks per minute (mean before: 0, mean after: 0.04;  $Z = 1.5705$ ,  $p = 0.05815$ ; Figure 5b), and chickadees gave more alarm calls (mean before: 6.125, mean after: 8.571429;  $Z = -1.3057$ ,  $p = 0.09583$ ; Figure 5c) and the ratio of chickadee alarm to non-alarm vocalizations increased (mean ratio before: 0.583, mean after: 0.732;  $\max T = 1.7162$ ,  $p = 0.0804$ ).



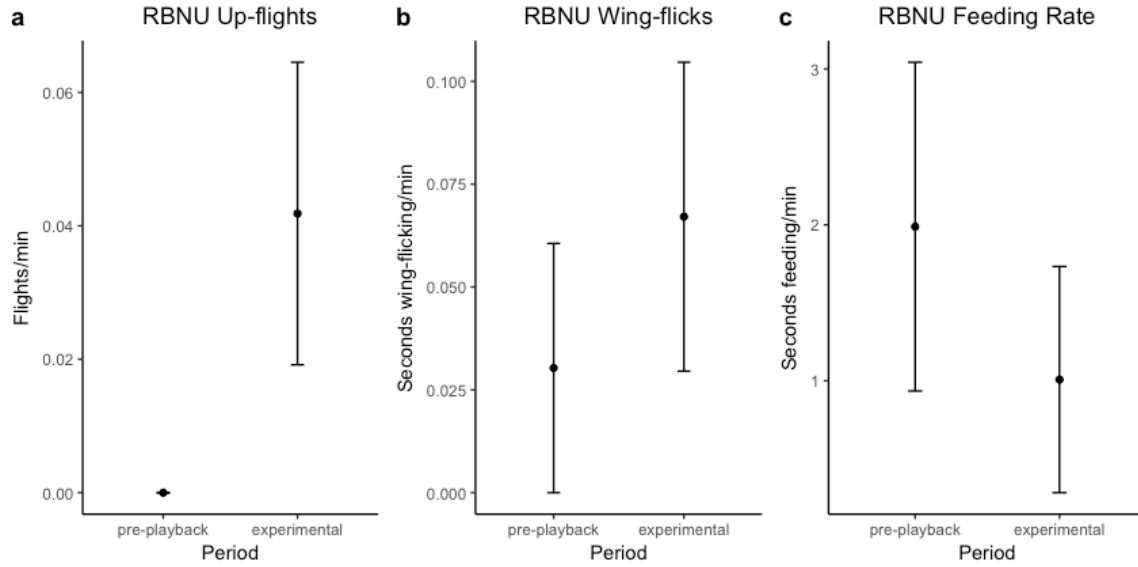
**Figure 5:** Changes in behavior between pre-playback and experimental periods in response to playback of Black-capped Chickadee set alarm calls, at the 140 m continuous forest array. Asterisk (\*) indicates significance at alpha = 0.05.

At 210 m in continuous forest, some comparisons suggested a change in behavior in response to set playback. Chickadees scanned more (mean before: 0.5, mean after: 1.654;  $Z = 1.4551$ ,  $p = 0.07283$ ; Figure 6a) and gave more alarm call types per individual per 10 seconds (mean before: 1.375 mean after: 4.7;  $Z = -1.4929$ ,  $p = 0.06773$ ; Figure 6b) after playback, while all three species considered together decreased feeding rate after playback (mean before: 7.885, mean after: 6.263; one-sided symmetry test:  $Z = -1.3689$ ,  $p = 0.08551$ ; Figure 6c). This pattern appears to have been driven by Red-breasted Nuthatches (mean feeding rate before: 6.146, mean after: 4.202; one-sided symmetry test:  $Z = -1.2929$ ,  $p = 0.09802$ ), as chickadees did not show any suggestion of a change in feeding rate (mean before: 1.775, mean after: 1.74; one-sided symmetry test:  $Z = 0.0823$ ,  $p = 0.5328$ ).



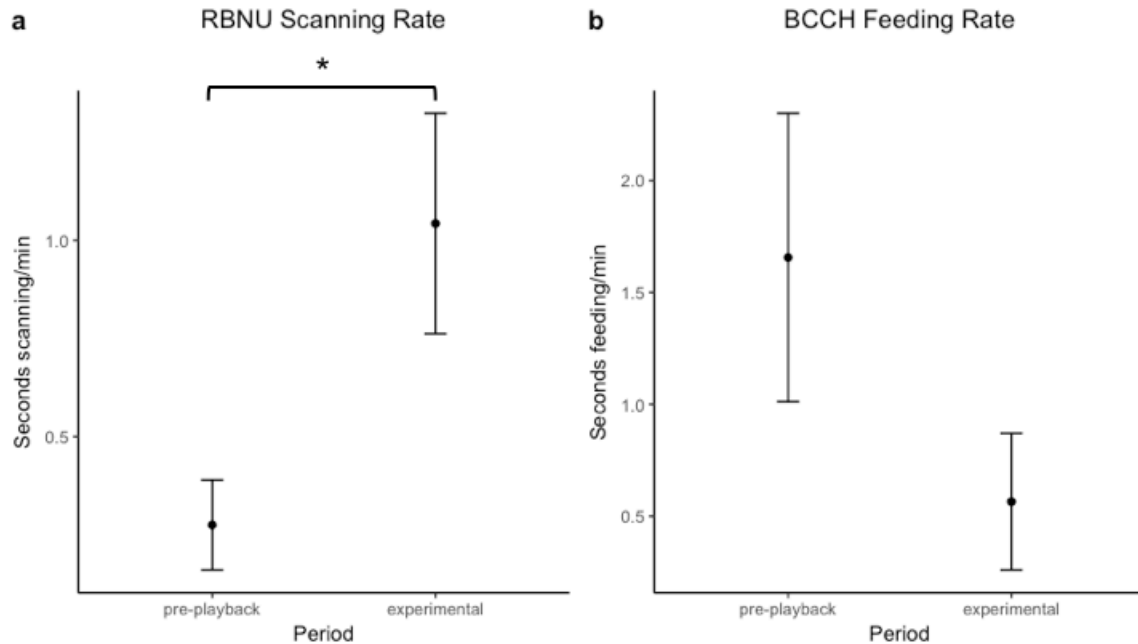
**Figure 6:** Changes in behavior between pre-playback and experimental periods in response to playback of Black-capped Chickadee seet alarm calls, at the 210 m continuous forest array. No comparisons were statistically significant at  $\alpha = 0.05$ .

At 345 m in continuous forest, only Red-breasted Nuthatches may have responded to seet playback. Nuthatches performed more up-flights (mean before: 0, mean after: 0.042;  $Z = 1.3747$ ,  $p = 0.08461$ ; Figure 7a) and increased their wing-flicking rates (mean before: 0.03, mean after: 0.067;  $Z = -1.3567$ ,  $p = 0.08743$ ; Figure 7b), while feeding rates decreased (mean before: 1.989, mean after: 1.008; one-sided symmetry test:  $Z = -1.3864$ ,  $p = 0.08281$ ; Figure 7c).



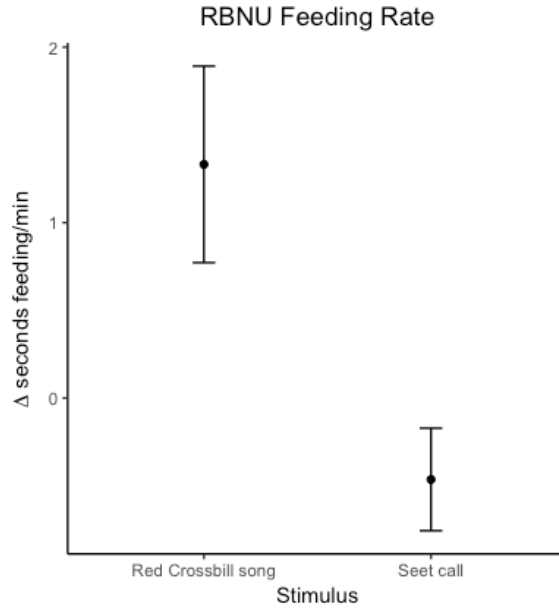
**Figure 7:** Changes in behavior between pre-playback and experimental periods in response to playback of Black-capped Chickadee seet alarm calls, at the 345 m continuous forest array. No comparisons were statistically significant at  $\alpha = 0.05$ .

For 140 m and 345 m gap arrays, I did not obtain enough samples for comparison (2 experiments each). However, at my 210 m gap array, I did detect some significant responses. After playback of seet calls, Red-breasted Nuthatches increased their scanning rates (mean before: 0.275, mean after: 1.043; Paired t-test:  $t = 4.5566$ ,  $p = 0.04494$ ; symmetry test:  $Z = 1.6542$ ,  $p = 0.04904$ ; Figure 8a). In addition, chickadees showed a trend toward reducing their feeding rate (mean before: 1.656, mean after: 0.565; one-sided symmetry test:  $Z = -1.4155$ ,  $p = 0.07846$ ; Figure 8b).

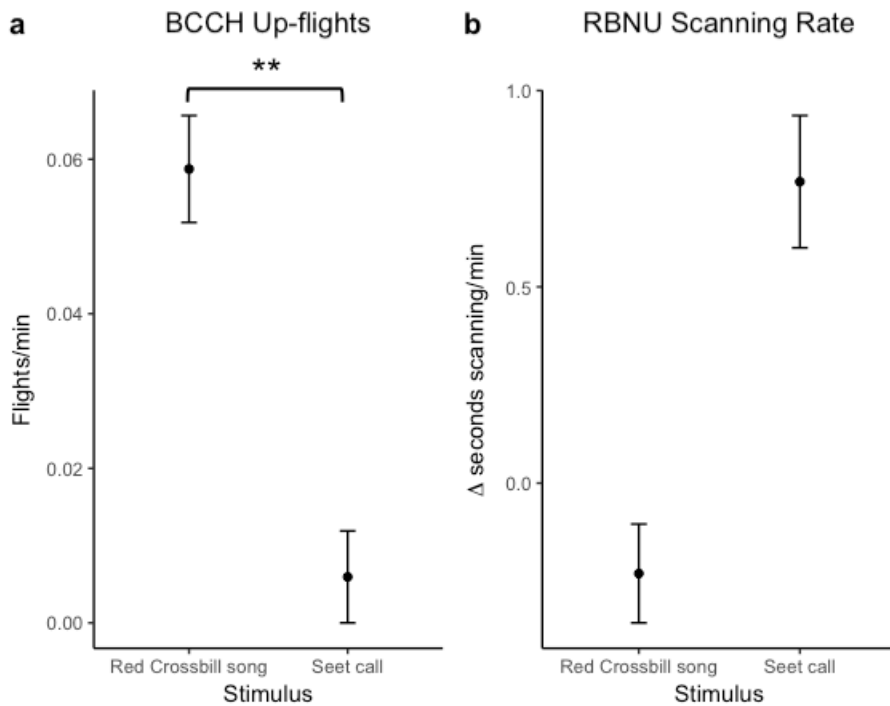


**Figure 8:** Changes in behavior between pre-playback and experimental periods in response to playback of Black-capped Chickadee seet alarm calls, at the 210 m gap array. Asterisk (\*) indicates significance at alpha = 0.05.

I also found differences in response to playback of crossbill song and seet calls. Across my 140 m-long continuous forest arrays, the difference in feeding rate between pre-playback and experimental periods for Red-breasted Nuthatches was significantly lower after seet playback (crossbill difference: 1.332, seet difference: -0.464; Paired t-test:  $t = 3.8975$ ,  $p = 0.02997$ ; symmetry test:  $Z = 1.8277$ ,  $p = 0.0676$ ; Figure 9). Contrary to my expectations, birds also responded to playback across my 210 m gap array. Surprisingly, chickadee up-flight rate was higher after crossbill playback (crossbill difference: 0.059, seet difference: 0.006; paired t-test:  $t = 19$ ,  $p = 0.002759$ ; symmetry test:  $Z = 1.7273$ ,  $p = 0.08412$ ; Figure 10a), while Red-breasted Nuthatch scanning rate was higher after playback of seet calls (crossbill difference: -0.23, seet difference: 0.768; paired t-test:  $t = -3.4705$ ,  $p = 0.07394$ ; symmetry test:  $Z = -1.6046$ ,  $p = 0.1086$ ; Figure 10b).



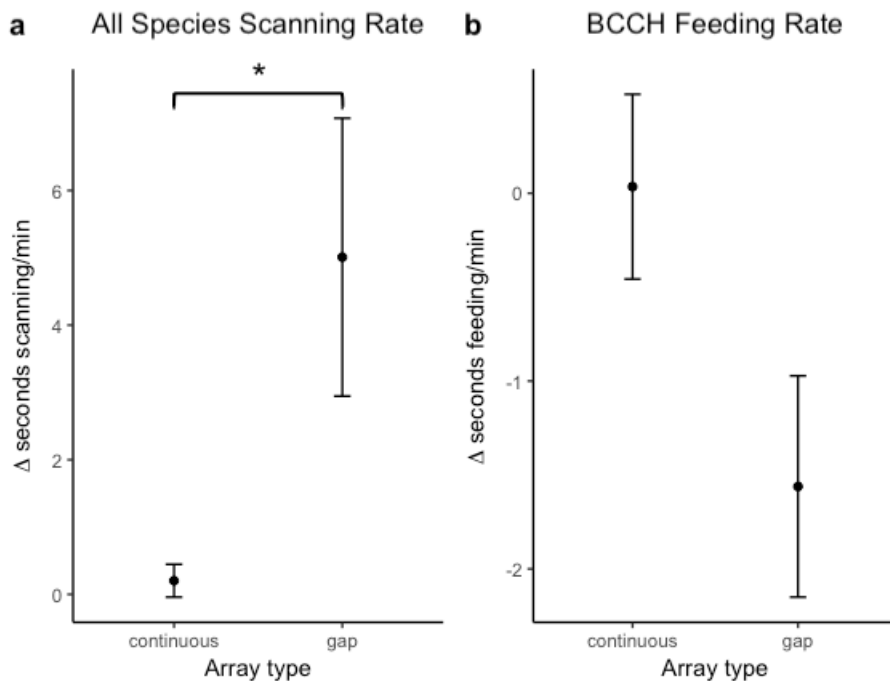
**Figure 9:** Difference in Red-breasted Nuthatch (RBNU) feeding rate between playback of Red Crossbill song and Black-capped Chickadee seet alarm calls at the 140 m continuous array. No comparisons were statistically significant at  $\alpha = 0.05$ .



**Figure 10:** Differences in behavior between playback of Red Crossbill song and Black-capped Chickadee seet alarm calls at the 210 m gap array. Double asterisk (\*\*) indicates significance at  $\alpha = 0.01$ .



Finally, my comparisons of gap and continuous forest arrays showed some differences as well. However, these were not in the direction expected. At 140 m, all species together scanned significantly more across the gap than the continuous forest array (gap mean: 4.084, continuous mean: 0.083; difference-of-means permutation test,  $p = 0.02872$ ; Figure 11a). Similarly, at 210 m, the change in chickadee feeding rate was less extreme during seet experiments at gap arrays than in continuous forest (gap mean: -1.562, continuous mean: 0.035;  $Z = 1.6742$ ,  $p = 0.09409$ ; Figure 11b).



**Figure 11:** Differences in behavior between continuous forest and gap arrays in response to playback of Black-capped Chickadee seet alarm calls, at (a) 140 m and (b) 210 m. Asterisk (\*) indicates significance at  $\alpha = 0.05$ .

## Discussion

My results provide the first experimental evidence that the information encoded in non-human signals may spread over distances greater than the audible range of the signal itself. Furthermore, I provide the first empirical evidence that the information encoded in alarm calls may be passed over such distances, even when the acoustic structure of seet calls (high frequency, narrow bandwidth) is not well-suited for long-distance transmission (Marler, 1955; Marten & Marler, 1977). Taken as a whole, my results from experiments in continuous forest suggest that, while alarm information might travel quite far (perhaps up to 345 m), this seems to be uncommon, especially at greater distances.

Birds also responded across wide forest gaps. Across species, scanning rate was significantly higher across the short compared with the same distance through continuous forest. Similarly, the reduction in the feeding rate of Black-capped Chickadees was more extreme across the medium gap as compared with continuous forest. Similarly, chickadee up-flights and Red-breasted Nuthatch scanning rates changed in response to different playback stimuli across my medium gap. These results suggest that, contrary to my predictions, gaps may in fact facilitate the spread of information. Intuitively, this makes sense for shorter distances such as my short gap; sound transmission is hindered by intervening objects such as tree trunks and understory vegetation, especially for higher frequency sounds (Aylor, 1972b; Marten & Marler, 1977). My gaps are mostly flat and almost completely devoid of vegetation, an environment which should facilitate sound transmission at all frequencies (Aylor, 1972a). However, all sounds should fall below the threshold of perceptibility at some distance due to attenuation, and this distance should be shorter for high-frequency sounds such as seet calls (Forrest, 1994). By my calculations

based on the source level and frequency range of seet calls, and the auditory thresholds of chickadees at these frequencies, these calls should not be perceptible by chickadees beyond about 50 m. For my shortest gap distance, this is almost certainly explained by the responses of birds at the feeder nearest the playback speaker. Birds always responded to seet call playback with a variety of alarm calls, mostly consisting of chickas and what I term “high-frequency” calls (Table 1). These calls contain lower frequencies than seet calls (~4 kHz), and as such, should be perceptible at greater distances (up to ~200 m). This explanation seems less likely for my medium gap. An alternative might be that the information may have circumvented my gap. Gaps at my site are all essentially ovoid and surrounded by forest. Thus, it is possible that birds around the perimeter of the medium gap passed information around to birds on the other side. My arrays could have easily missed vocalizations as far away as the gap edges, so unfortunately I cannot confirm this possibility. However, by whatever explanation, these communication networks seem to be robust to substantial gaps in habitat.

In addition, Red-breasted Nuthatches and Black-capped Chickadees responded differently to different experimental treatments. Chickadees seemed to respond most strongly across gaps, while nuthatches seemed to respond more strongly over greater distances. Typical predators of chickadees, such as *Accipiter* hawks and Northern Pygmy-Owls (*Glaucidium californicum*), rely primarily on surprise attacks (e.g., (D. W. Holt & Leroux, 1996); Bildstein & Meyer, 2000). It would seem that gaps would hinder this strategy because they offer less cover than uninterrupted forest. Additionally, the dozen or so naturally occurring attacks I observed over the course of my field season were by *Accipiter* hawks approaching through continuous forest and not from the

direction of forest gaps (personal observation). Thus, I do not consider this to be an adaptive response to forest gaps. A more likely explanation might be that chickadees respond more strongly across gaps simply because the threat stimulus is stronger due to reduced attenuation from vegetation.

Nuthatches, on the other hand, seemed to respond more strongly at greater distances, where the alarm stimulus strength may have been weaker. Chickadees are known to respond strongly to alarm situations at close range (Billings, Greene, & La Lucia Jensen, 2015; Hurd, 1996), and are considered information producers (Magrath et al., 2015), because they produce public information that may be used by many other species (C. S. Clair et al., 1998; Sullivan, 1984; Templeton & Greene, 2007). When producers such as chickadees are present at alarm events, so-called information-scroungers are generally less likely to respond (Bartmess-LeVasseur, Branch, Browning, Owens, & Freeberg, 2010; Sullivan, 1984). Conversely, in the absence of producers, scroungers may be more likely to produce appropriate alarm behaviors (Bartmess-LeVasseur et al., 2010). It is unclear why chickadees responded less strongly at greater distances, but this may contribute to nuthatches' propensity to respond more strongly in these situations.

In summary, I have provided evidence that the information encoded in alarm calls may travel substantial distances, both in continuous forest and in the presence of forest gaps. Birds responded by changing their rates of feeding, scanning, alarm calling, and other alarm-related behaviors, and these responses seem to be robust to or even facilitated by the presence of forest gaps. My results suggest that the presence of communication

networks can greatly expand the audible range of information encoded in alarm calls, far beyond the audible range of the individual calls themselves.

## **Acknowledgements**

This work would not have been possible without the help of many. Pat Little designed and built the synchronizers, and developed much of the code necessary for using them. Yu Shiu, Nhan Nguyen, and Eli Bayat were all crucial to finalizing the “synch and merge” code to produce the sound files for analysis. Great thanks are due to Mark Reiling, Bart Morris, and Libby Maclay for access to the land where I conducted this study. Rob Morgan surveyed all the arrays, and was a blast in the field. Jon Graham provided valuable input and advice with statistical issues. Charlie Katerba advised on mathematical issues large and small. Russ Charif and Karl Fitzke provided useful advice on the physics of sound propagation. And of course, none of the field experiments would have been possible without a great crew of field assistants. In the 2016-17 pilot season, Ian Anderson, Isaac VanDiest, and Joel Weltzien were indispensable, while necessary additional assistance came from Ty Harrison, Cole Sander, Blake Hoffman, Jonathan Gore, Cayla Daily, Kadie Heinle, Kelsey Donnelly, Kathryn Jaquet, Noah Booth. In the final 2017-18 field season, I had the help of another fantastic field crew. Great thanks to Kelsey Donnelly, Josiah Simmons, Blake Hoffman, Jenna Brendler, Cassidy Ruge, Hannah Cassidy, Mikayla Duvenick, Connor Hakala, Benin Laliberte, Emily Hamant, Skye Adcox, Kaitlyn Strickfaden, Juan Alvarez, Serena Nozawa, Jacob Arrington, and Kirk Booi. I am incredibly grateful as well to those who helped me in the final stages of this project, analyzing recordings in XBAT: Benin Laliberte, Jonathan Gore, Kelsey Donnelly, Josiah Simmons, Skye Adcox, Rebecca Ballard, and Abigail Borden.

**Table 1: Call type classifications**

<b>Species</b>	<b>Call type</b>	<b>Definition</b>	<b>Reference(s)</b>
Black-capped Chickadee	“chicka”	Any combination of A, B, or C notes that includes at least one of either B or C	(Billings et al., 2015; M. S. Ficken, Ficken, & Witkin, 1978; Odum, 1942)
	“dee”	D notes only	{Odum:1942dd}
	“chick-a-dee”	At least one “chicka” note followed by at least one “dee” note	(M. S. Ficken et al., 1978; Odum, 1942)
	“high frequency”	A notes only	(Billings et al., 2015)
	contact call	Resembles A note but given singly	{Odum:1942dd}
	Seet (aka “High zee”)	One or more high frequency notes, longer than “high frequency” A notes and without rapid terminal frequency drop	(M. S. Ficken et al., 1978; Odum, 1942)
	song	Two extended whistles given on separate pitches	(M. S. Ficken et al., 1978; Odum, 1942)
	“gargle”	Complex series of short notes at varying frequencies followed by a single long note at lower frequency	(M. S. Ficken et al., 1978; Odum, 1942)
Red-breasted Nuthatch	“yank”	Brief, low frequency notes given quickly and repeatedly	(Kilham, 1973) (Ghalambor & Martin 1999)
	song	Similar to “yank” but	(Kilham, 1973)

		louder, longer, and rising in pitch	
	interaction calls	Any of varied chitters, trills, and snarls given softly in interspecific context	(Kilham, 1973) (Ghalambor & Martin 1999)
White-breasted Nuthatch	“quank”	Lower frequency trills given in short bursts (<0.4s)	(Ritchison, 1983)
	rapid “quank”	Higher frequency trills given in longer bursts (>0.5 seconds)	(Ritchison, 1983)
	song		(Ritchison, 1983)
Pygmy Nuthatch	Piping call	Only call recorded	(Kingery & Ghalambor 2001)
Golden-crowned Kinglet	“ti” / “tse”	Short (<0.1s), high frequency notes given singly or in groups of 2-5, rising slightly in frequency	(B. Galati & Galati, 1985; Naugler, 1993)
	“zeet”	Longer (>0.1s), rapidly frequency- modulated call	(Naugler, 1993)
Pine Siskin	“zhree”		(Dawson 2014)
	Other calls not differentiated		
American Goldfinch	Flight call		(Coutlee, 1971)
	Other calls not differentiated		
Red Crossbill	flight call		(Groth, 1993)
	song		(Groth, 1993)
	Other calls not differentiated		
Hairy Woodpecker	“peak”	Short	(de Kiriline Lawrence, 1967; Kilham, 1966)
Downy	“pik”		(Kilham, 1962)



Woodpecker			
Northern Flicker	“kleer”		(de Kiriline Lawrence, 1967; Short & Sandström, 1982)
	Long call		(de Kiriline Lawrence, 1967; Short & Sandström, 1982)
	“whortle”		(de Kiriline Lawrence, 1967; Short & Sandström, 1982)
Pileated Woodpecker	Long call		(Short & Sandström, 1982)
	“wuk”		(Short & Sandström, 1982)
American Robin	“cuck”		(Howell, 1942)
Red-winged Blackbird	Song		(Yasukawa, Blank, & Patterson, 1980)
	“chick”		(Beletsky, Higgins, & Orians, 1986)
	“chee-dee-dee”		(Yasukawa, Boley, & Simon, 1987)
Common Raven	Calls not differentiated		
Black-billed Magpie	Calls not differentiated		
Clark’s Nutcracker	“kraa”		(Mewaldt, 1956)
Belted Kingfisher	Rattle		(W. M. J. Davis, 1988)
Canada Goose	Calls not differentiated		
Red Squirrel	Rattle / “rolled R call”	Long (>2 seconds), rapid trill	(Embry, 1970)
	Bark / “beta” call	Single or series of harmonically rich bursts	(Digweed & Rendall, 2010; Embry, 1970; Greene & Meagher, 1998)
	Seet / “alpha” call	Single or series of high-frequency notes, similar to Chickadee seet	(Digweed & Rendall, 2010; Embry, 1970; Greene & Meagher, 1998)
	Seet-bark	Bark preceded by a single short seet note	(Digweed & Rendall, 2010; Embry, 1970; Greene & Meagher, 1998)

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