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Blue jays (*Cyanocitta cristata*) do not spontaneously eavesdrop on red squirrel (*Tamiasciurus hudsonicus*) squeals to locate food

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Abstract

Organisms often eavesdrop on the cues and signals produced by other species to obtain information about their environment. Blue jays have dietary overlap with red squirrels, and learn to associate novel stimuli with food rewards in an experimental setting. Red squirrels produce "squeals" when contesting food resources with conspecifics. We tested whether blue jays eavesdrop on red squirrels by playing back red squirrel squeals, red squirrel rattles, white noise, and chick-a-dee calls to blue jays in Winnipeg, Manitoba. Additionally we examined the response of passerine birds in general to the playbacks, and attempted to condition free-living blue jays to respond to the playback of the squeal treatments. Results of the playbacks suggested that neither blue jays nor other passerines eavesdrop on vocalizations emitted in the context of red squirrel disputes over food. Conditioning trials did not produce any conditioned responses from blue jays; however, the limited number of trials performed does not constitute a robust test of the possible acquisition of a classically-conditioned response. Blue jays may also refrain from eavesdropping on red squirrel squeals as they are not reliable indicators of food resources, or because in an urban environment, blue jays readily learn the locations of bird feeders or other reliable food sources without eavesdropping on red squirrels.

Keywords: eavesdropping, blue jays, *Cyanocitta cristata*, reliable cues, foraging

1. Introduction

Eavesdropping is the use of public information when the information is either not intended for the eavesdropper, or when the information is inadvertently generated by another organism's behaviour (Peake, 2005). By eavesdropping on public information, animals can accrue information about both the location and quality of resource patches without sampling the resource patches themselves (Danchin et al., 2004). Via eavesdropping, animals have been reported to gather information about predators (Rainey et al., 2004), prey (Jones et al., 2011), potential mates (Bierbach et al., 2013), and other information important to their survival and fitness (Dall et al., 2005). The ability to gather information about the environment without directly experiencing it has benefits for an animal, such as decreasing exposure to predators and search times when foraging for food (Valone, 2007; Dall et al., 2005).

Eavesdropping on alarm calls is commonly reported, but eavesdropping is not limited to auditory stimuli alone (Templeton and Greene, 2007). Any signal, or cue, which is conspicuous in the environment, and is reliably associated with events or resources relevant to an animal, is vulnerable to eavesdropping (McGregor, 1993). For example, stingless bee (*Melipona rufiventris*) workers avoid foraging markers deposited by *Trigona spinipes*, a more aggressive stingless bee that attacks and harasses *M. ru-*

fiventris at flowers (Nieh et al., 2004). Visual stimuli, such as the presence or behaviour of organisms, are also subject to eavesdropping.

A common example of eavesdropping on visual stimuli is local enhancement, where individuals gain information about food patch quality by observing the feeding success of other organisms (Thorpe, 1956). A cue can be defined as information inadvertently generated by an organism's behaviour or presence. Cues are distinct from signals, which are traits that have undergone selection to convey information (Bradbury and Vehrencamp, 2011; Danchin et al., 2004). Information, in turn, can be considered anything that reduces uncertainty in an animal's knowledge of its environment (Danchin et al., 2004; Rendall et al., 2009).

The cues and signals of conspecifics often provide individuals with salient information about their environment. However, species commonly expand their eavesdropping networks to heterospecifics that share similar resource requirements or are faced with common predators (Goodale et al., 2010; Shriner, 1998). In any system where two species share a common predator, and one produces a reliable warning signal detectable by the other species, eavesdropping should arise (Shriner, 1998; Hauser, 1988). Similarly, we would expect organisms to be selected to respond to the signals or cues of heterospecifics that are associated with resources relevant to an animal's fitness.

Eavesdropping on heterospecifics has been reported throughout the animal kingdom in both invertebrates (e.g. Bees; Nieh et al., 2004; Slaa et al., 2003) and vertebrates (Hurd, 1996; Jones et al., 2011; Koda, 2012). Plants also eavesdrop on alarm chemicals of other plants (Kessler et al., 2006). Furthermore, eavesdropping can occur among diverse taxa. For example, yellow-casqued hornbills (*Ceratogymna elata*) eavesdrop on the alarm calls of Diana monkeys (*Cercopithecus diana*; Rainey et al., 2004) and also distinguish between the monkey's alarm calls for leopards (*Panthera pardus*; an unshared predator) and crowned eagles (*Stephanoaetus coronatus*; a shared predator; Rainey et al., 2004).

While examples of eavesdropping on alarm signals and conspecific local enhancement are well documented, the use of signals and cues of heterospecifics to locate shared food resources is less well studied (Koda, 2012). If an animal produces detectable signals, either when disputing food resources with conspecifics, or when recruiting conspecifics to an area to feed, they produce an opportunity for heterospecifics that share the food resource to eavesdrop. Japanese sika deer (*Cervus nippon*), for instance, have been reported to eavesdrop on the food calls of Japanese macaques (*Macaca fucuscata yauki*; Koda, 2012).

Organisms can also eavesdrop on non-feeding behaviours to assess the quality of environmental resources. For example, hermit crabs (*Coenobita compressus*) target areas with higher levels of conspecific activity (Laidre, 2013). Hermit crabs have cryptic feeding behaviours, which make it difficult for conspecifics to observe feeding behaviour past the feeding crab's shell (Dunham and Gilchrist, 1988). Hermit crabs instead cue in on the far more visible competitive interactions between conspecifics, such as jockeying for position at a resource patch, and are attracted to areas that have relatively higher levels of these competitive interactions (Laidre, 2013)

Red squirrels (*Tamiasciurus hudsonicus*) produce "squeal" calls upon discovering conspecifics raiding caches of stored food (Lair, 1990). Squeal calls are often produced in the context of aggressive interactions between red squirrels over food resources (C. Smith, 1978). These squeals may provide nearby blue jays (*Cyanocitta cristata*) with both the general location of food, and information that the resident squirrel is likely distracted by an intruding squirrel.

Red squirrels also produce "rattle" calls. Rattles serve as territorial calls, but are also produced in aggressive interactions between squirrels. Unlike squeal calls, rattles are often produced by red squirrels in the absence of another squirrel in their territory (Lair, 1990).

Thus rattles are presumably a less reliable indicator of available food. Squeals and rattles are quite conspicuous in the environment, and satisfy McGregor's (1993) stipulation that any signal broadcast in a detectable manner is vulnerable to eavesdropping.

McLinn and Stephens (2006) reported that blue jays learn to use novel, reliable signals to locate food rewards in uncertain environments in a laboratory setting. Both red squirrels and blue jays are seed predators with considerable dietary overlap, and blue jays have been observed pilfering food caches of red squirrels (Schmidt and Ostfeld, 2008). Given that red squirrels produce detectable signals while disputing food resources and blue jays learn to utilize reliable signals to locate food resources, suggests that blue jays may eavesdrop on the aggressive interactions of red squirrels over food. The calls of red squirrels may act as a reliable signal regarding the presence of a shared food resource. Blue jays eavesdropping on red squirrels would provide an example of heterospecific eavesdropping on non-feeding behaviours for information about food resources.

An anecdotal report of blue jays eavesdropping on the aggressive interactions of red squirrels in the city of Winnipeg suggested the presence of an eavesdropping system between red squirrels and blue jays. In the summer of 2013, the authors observed blue jays recruiting to the area when red squirrels vocalized during contests over peanuts offered in a backyard. In this incident, the vast majority of peanuts were ultimately taken by the blue jays instead of the squirrels, which had initially located the peanuts offered.

If blue jays eavesdrop on red squirrel calls for information about food location, then blue jays should respond to the playback of squeals by investigating the location of the broadcast. If blue jays are eavesdropping, then they should differentiate between red squirrel calls to reduce the cost of responding to calls that are not indicative of food. Blue jays should therefore respond more often to the playback of red squirrel squeals than to the playback of red squirrel rattles. Many passerine bird species are seed predators, and thus likely have some dietary overlap with red squirrels. If passerine species are eavesdropping to gain information about these shared food resources, then we might expect them to respond similarly to blue jays to the playback of red squirrel vocalizations.

In this study we investigate whether blue jays eavesdrop on the vocalizations produced by red squirrels to locate food resources. Secondarily, we examine if other passerine species are similarly eavesdropping on the aggressive interactions of red squirrels. If they do, this eavesdropping system would be a rare example of organisms eavesdropping on the vocalizations of others to locate common food resources (Koda, 2012).

2. MATERIALS AND METHODS

We used a playback experiment to evaluate the efficacy of acoustic stimuli independent of other cues (Bradbury and Vehrencamp, 2011) in attracting blue jays to an area. All playback treatments were broadcast from a Genexxa Pro LX5 loudspeaker (InterTan Ltd., Barrie, ON, Canada), using a SONY XM-2025 amplifier (SONY Corporation, Tokyo, Japan) and a SONY MZ-N707 MiniDisc player. Sound pressure levels were measured with a General Radio 1988 sound-level meter (GenRad, West Concord, MA, U.S.A). The playback area was recorded by two SONY DCR-TRV110 camcorders mounted so as to record an approximately 180° field of view on a Manfrotto 055NAT tripod (Lino Manfrotto + Co. Spa, Cassola, Italy) using a Vanguard Multi-Mount 6 Tripod Utility Bar (Vanguard, Markham, ON, Canada) positioned over the loudspeaker. A Tupperware container lid (Tupperware Corporation, Orlando, FL, U.S.A.) was used to hold 20 "no name" brand unsalted roasted peanuts (Loblaws Company Limited, Brampton, ON, Canada) in a single layer on the tray.

Squeal and rattle treatments were constructed by alternating the calls of two different red squirrels to mimic the back and forth exchange characteristic of an aggressive interaction. Treatments were constructed, standardized, and normalized in Avisoft-SASLab Pro (Sound Analysis and Synthesis Laboratory © Avisoft Bioacoustics, Berlin, Germany). Three different squeal and rattle treatments were broadcast during the experiment. Red squirrel squeals and rattles were recorded by Dr. S. Digweed from squirrels observed in Kananaskis Provincial Park, Alberta, Canada (50.39° N, 114.39° W; Digweed et al., 2012). The red squirrel vocalizations recorded in Alberta did not differ to the human ear from the vocalizations made by local red squirrels. There is evidence of regional differences in bark calls of red squirrels (Yamamoto et al., 2001). Bark calls, however, are the most variable of the red squirrel calls (C. Smith, 1978). Furthermore, C. Smith (1978) reports that other red squirrel calls were structurally very similar to each other. However, all the vocalizations compared came from squirrels in the same area, so regional differences cannot be ruled out entirely. The white noise control was generated in Avisoft-SASLab Pro over the frequency range of red squirrel squeals in nature (1-8 kHz; C. Smith, 1978). The chickadee (*Poecile atricapillus*) "chick-a-dee" mobbing call was downloaded from: http://www.learner.org/jnorth/tm/spring/ChickadeeDictionary.html.

Four playback treatment types were broadcast at each playback site during the experiment, including red squirrel squeals, red squirrel rattles, a white noise control, and chick-a-dee calls. Each treatment consisted of four fifteen-second presentations of a single playback stimulus type, each a minute apart. Four separate call bouts in a treatment were used to mimic red squirrel contests. Length of the treatment was chosen to reflect our own observations of aggressive interactions of red squirrels in nature. All playbacks were presented at 68-75 dB SPL (A-weighting) when measured two meters from the source, which parallels the amplitude of red squirrel vocalizations in nature (C. Smith, 1978; Shonfield et al., 2012). The four treatment types were broadcast at the same sound pressure level to avoid differential blue jay response based on louder playbacks reaching a larger number of blue jays.

Each treatment was preceded by a pre-playback observation period. Pre-playback observation periods began after a blue jay was seen or heard from the site, and lasted for five minutes. The criterion that a blue jay be observed or heard before the beginning of pre-playback observation ensured that blue jays would be within the range of each playback stimulus, and thus that null responses to playback stimuli would be interpretable. Blue jay response was observed for twenty minutes from the beginning of the playback.

A site was the general area at which a playback was performed. Within a site, the playback area consisted of a 10 m radius about the playback speaker. A single treatment consisted of four fifteen-second playbacks of a single stimulus type. Each fifteen second playback within a treatment was separated by a minute. A single trial includes all the treatments performed at a single site. Treatments at each site were separated from each other by 48-74 hours to ensure that playbacks were independent from each other. The temporal separation of treatments also reduced the probability of blue jays learning the location of the food resource (peanuts) present in the experimental set up, as well as minimizing potential carry-over effects among treatment types. The chick-a-dee mobbing call treatment was added halfway through the experiment due to the apparent lack of blue jay response to other treatment types. Sites 1 through 6 received the playback of three treatment types, while sites 7 through 12 received the playback of four treatment types.

The playback of red squirrel squeals may act as a reliable signal of a food resource as squeals are emitted in the context of contests for access to food resources (C. Smith, 1978). The playback of red squirrel territorial rattles should be a less reliable signal of the presence of food for blue jays as they are often produced in the absence of food resources (Lair, 1990). If blue jays show an equal response to the playback of squeals and rattles then it is less likely they are attracted specifically to food resources.

If blue jays show a greater response to squeals than rattles then it is likely that they are targeting information relevant to food resources. The playback of white noise acted as a positive control for blue jay attraction to noise. The playback of a chick-a-dee mobbing call acted as another positive control. We expected the playback of chick-a-dee mobbing calls to attract blue jays as ten other bird species have been reported to respond to chick-a-dee mobbing calls with a mobbing response (Hurd, 1996). Lastly, the pre-playback observation period served to quantify blue jay attraction to the observer and equipment used in the experiment, independent of the playback treatments broadcast.

During each pre-playback period and treatment playback twenty peanuts were put out to measure blue jay foraging success. If blue jays are attracted to an area looking for food (i.e. when attracted to the area by squeal treatment) we would expect blue jays to remove more peanuts than when they are attracted to an area looking for a predator (i.e. when attracted to the area by chick-a-dee mobbing call playback). If blue jays removed more peanuts to the playback of squeals than other treatment types, then that would be consistent with the proposed eavesdropping system.

The order of treatments at each site was determined randomly by pulling labelled pieces of paper from a hat. Three different playback exemplars were constructed using the calls of two red squirrels for both rattle and squeal treatments to reduce pseudoreplication at the treatment level (Kroodsma et al., 2001). The playback exemplars within a playback treatment type used was determined randomly by drawing numbers from a hat after treatment type had been selected.

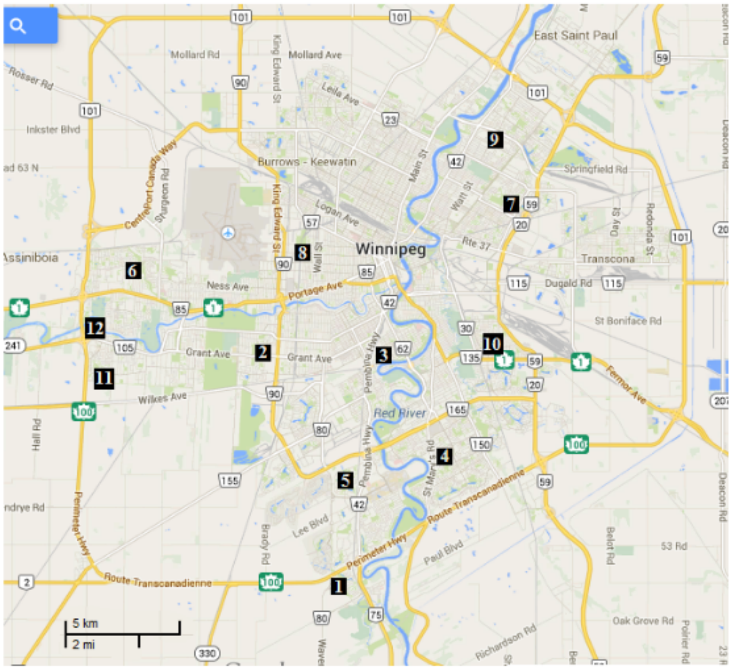


Figure 1: *Map of Winnipeg, MB from Google Maps (Google, California, USA), modified with playback site locations.*

Playbacks were performed in eleven parks and one residential yard within 500 m of locations where blue jays were observed in preliminary observations in 2013 (Fig. 1). Passerine birds, along with a few other urban wildlife species, were commonly observed foraging in these areas. All playback sites were within the city of Winnipeg, Manitoba, Canada (49.88° N, 97.15° W). Playbacks occurred from 10 June to 10 August 2013.

While we aimed to have playback sites roughly 5 km apart so that each site could be considered independent (in that blue jays' home ranges rarely exceed a 5 km radius (Johnson and Adkisson, 1985)), sites did not always meet this criterion owing to the geography of the city, locations where blue jays occurred, and where playback trials could be performed. We thus treated sites 2 to 6 km apart as independent since non-breeding individuals could move among even more distant sites.

The number of peanuts in the tray was counted at the end of the pre-playback observation period, after which the tray was refilled to twenty peanuts. Following the playback observation, the number of peanuts was counted again. When, and which, animal species removed peanuts from the tray was recorded during the observation periods as other species besides blue jays were free to remove peanuts from the tray. At one site a grey squirrel (*Sciurus carolinensis*) removed a few peanuts, while at another site grackles (*Quiscalus quiscula*) removed a few peanuts as well. As these were the only two instances of peanuts being removed by other species we do not consider this any further.

The playback area was defined as ten meters from the playback speaker. Playbacks were observed by a single person (the same observer was used at all playback sites) seated on a small tarp directly outside the playback area. The size of the playback area was chosen to allow the playback area to be easily observed by one person, and to reflect recruitment of individuals to the stimulus source (Mennill and Ratcliffe, 2004; Radford and Ridley, 2006). The location of the observer relative to the equipment changed among sites, but was kept constant among treatments within a site.

A positive response was defined as a blue jay entering the playback area. For blue jays already within the playback area at the beginning of a pre-playback observation period or a playback treatment, a positive response was defined as moving at least one meter closer to the playback speaker. In rare cases where a single blue jay entered, left, and then re-entered the playback area multiple times during an observation period, it was counted as a single positive response. However, if a blue jay left the observable area and then returned, it was considered a new bird, as we were unable to differentiate between individual birds.

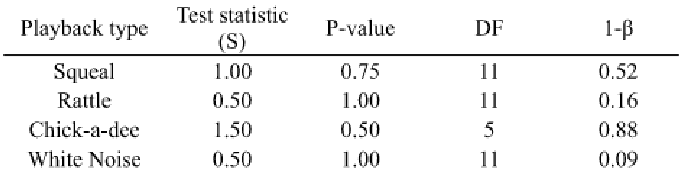
The camcorders were used as sampling frames for general passerine response to treatment type. As the original purpose of the camcorders was to aid in detection of blue jays, they were pointed at regions of the playback area that were difficult to view. The camcorders were left at the widest angle possible for all trials. In situations where the observer was confident in their ability to view the entire playback area, the cameras were pointed to places where blue jays were thought likely to appear. A positive response for passerines was any time a passerine bird entered the view of a camera. We used the full five minutes of pre-playback response for passerine response, but only the first ten of the twenty minutes of the playback observation period was used. Ten minutes is likely long enough for passerines to resume their regular behaviour, and to minimize repeated sampling of the same individuals. Of 42 possible playback trials, 9.5 percent were lost due to equipment malfunction. One site was excluded from the passerine response analysis due to the presence of a bird feeder, which were not present at any other site. Lastly, one playback treatment from site 7 was excluded due to a passerine response being inflated by a single bird repeatedly exiting and entering the recording frame.

Conditioning trials were conducted by playing back a squeal treatment as a blue jay dived for the peanut tray. The squeal treatment used at a site was determined by pulling labelled pieces of paper from a hat without replacement until each of the three squeal exemplars had been used. After ten presentations of the conditioned stimulus (the squeal playback) coincident with the unconditioned stimulus (the peanuts), the conditioned stimulus was presented alone to a blue jay to see if the blue jay then performed a conditioned response of orienting to the peanut tray. We defined a successful conditioned response as approaching the peanut tray for blue jays already in the playback area, and entering the playback site for blue jays outside the playback area.

Nineteen pairings of the unconditioned stimulus and conditioned stimulus were achieved. Preceding the pairings, the conditioned stimulus was presented alone, and blue jay response was recorded. After ten pairings the conditioned stimulus was presented alone again, and blue jay response was recorded. Statistical analyses were performed in JMP 10.0.0 (SAS Institute Inc.). As pre-playback and post-playback observation periods differed in length, positive responses were converted to mean blue jay response per minute. The distribution of response rates of blue jays was not normal (Shapiro-Wilk test; $W = 0.41$, $P < 0.0001$; Shapiro and Wilk, 1965), but variances were considered equal as a Levene's test failed to detect a statistically significant difference among the variance in response rate for the treatment types ($W7,4 = 2.23$, $P = 0.08$; Levene, 1960). As such, a Kruskal-Wallis test was used to compare mean blue jay response per minute among treatments (Zar, 1999; Kruskal and Wallis, 1952). Test results were considered significant for p-values below a significance level of 0.05 for all tests. A Kruskal-Wallis test was also used to compare the rate of blue jay positive responses among sites.

Similar to the blue jay positive response data, pre-playback and post-playback observation periods quantifying passerine response differed in length. To correct for this, passerine positive response was converted into passerine response per minute. The distribution of response rate of passerines was not normally distributed (Shapiro-Wilk test; $W = 0.44$, $P < 0.0001$). Levene's test, however, failed to reject that variances were equal among treatment types ($W7,4 = 2.02$, $P = 0.10$). Given the departure from normality, a Kruskal-Wallis test was used to compare mean passerine response among treatment types. As the distributions of differences were not normal, Wilcoxon signed-rank tests were conducted to compare each playback treatment type to pre-playback observation periods for both jay and passerine positive response (Zar, 1999; Wilcoxon, 1945). Post-hoc power analyses were performed using the power calculator available at http://www.statstodo.com. The calculator for power estimation for paired t-tests was used. Power $(1-\beta)$ is the probability of rejecting the null hypothesis when the null hypothesis is false (Cohen, 1992). A power of 0.80 will be considered sufficient, as is the convention (Cohen, 1992). A peanut was removed only once by a blue jay during the experiment. Therefore, no statistical analyses were performed on the number of peanuts removed.

Table 1. Results of Wilcoxon signed-rank test and power analysis on blue jay positive response during pre-playback observation period and during treatment.



Playback type	Test statistic (S)	P-value	DF	1-β
Squeal	1.00	0.75	11	0.52
Rattle	0.50	1.00	11	0.16
Chick-a-dee	1.50	0.50	5	0.88
White Noise	0.50	1.00	11	0.09

Table 2. Results of Wilcoxon signed-rank tests and power analysis on passerine positive response during the pre-playback observation period and during treatment.

Playback type	Test statistic	P-value	DF	1-β
Squeal	6.00	0.19	10	1.00
Rattle	1.50	0.81	8	0.25
Chick-a-dee	1.00	0.75	4	0.50
White Noise	1.00	0.88	8	0.06

3. Results

The mean number of blue jay positive responses did not differ significantly among treatments (Fig. 2; H4 = 2.97, P = 0.56). Further, blue jay response rates did not differ significantly among sites (Fig. 3; H11=12.34, P = 0.32). Wilcoxon signed-rank tests did not reveal a significant difference in blue jay positive response between the pre-playback and playback periods for any playback treatment type (Table 1). The mean response rate of passerines did not differ among the treatment groups (Fig. 4; H4 = 1.11, P = 0.89). However, mean rate of passerine response varied significantly among the playback sites (Fig. 5; H10 = 20.62, P = 0.02). Wilcoxon signed-rank tests did not reveal a significant difference in passerine response between the pre-playback and playback periods for any playback treatment type (Table 2). Blue jays did not demonstrate a conditioned response to the conditioned stimulus alone after ten pairings.

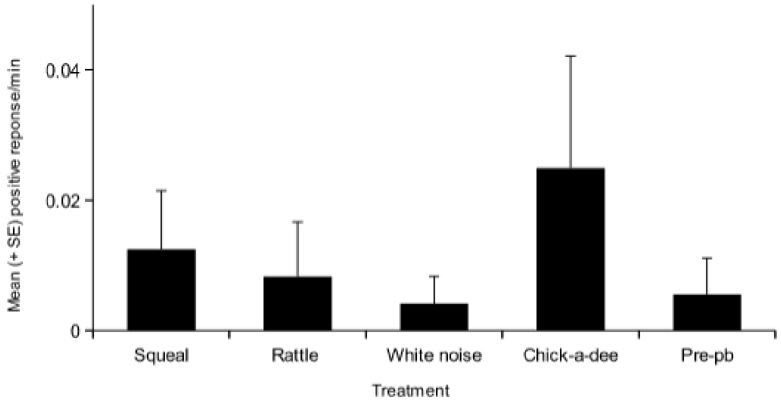


Figure 2: *The mean rate of positive responses of blue jays (positive responses/minute + SE; Cyanocitta cristata) to playback treatments (red squirrel (Tamiasciurus hudsonicus) squeals, red squirrel rattles, white-noise control, chick-a-dee (Poecile atricapillus) calls, and pre-playback observation period) in Winnipeg, MB during the summer of 2013. N = 12 for squeal, rattle, and white-noise control pre-playback observation period, N = 6 for chick-a-dee.*

4. Discussion

Our study revealed no evidence that blue jays spontaneously eavesdrop on the aggressive interactions of red squirrels over food resources. Blue jay response did not differ significantly among treatment types, or between pre-playback and post-playback. Koda (2012) demonstrated animals eavesdropping on heterospecific calls to locate food resources. However, the Japanese sika deer and Japanese macaques in Koda's (2012) experiment were not competing for the same fruit. The deer were feeding on fruit that was knocked to the ground by the macaques feeding in trees (Koda, 2012). As blue jays would compete for the food resource contested by the red squirrels themselves, we would not expect a call that reveals the location of the food resource to persist through evolutionary time. That is, selection would favour attenuation of a signal that imposes a cost on the signaler (Hasson et al., 1992). A call that reliably indicates the presence of contested resources would persist only if it creates a benefit for the signaler that outweighs the cost of attracting eavesdropping animals.

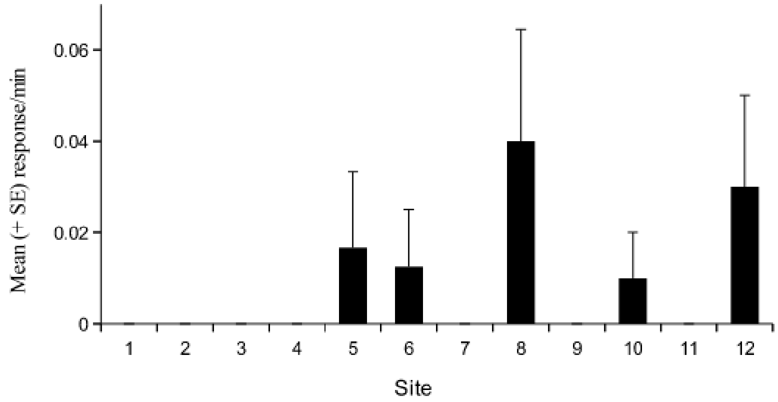


Figure 3: *The mean rate of positive responses of blue jays (positive responses/minute + SE; Cyanocitta cristata) to playbacks by site in Winnipeg, MB during the summer of 2013. N = 4 for sites 1 – 6, N = 5 for sites 7 – 12.*

Playbacks of the squeal treatment at the site where eavesdropping by blue jays was reported anecdotally did produce a positive response. The responses at this site are probably best explained by associative learning. Peanuts have routinely been placed at this site for several years (and subsequently contested by squirrels). The regular placement of peanuts, and absence of further evidence of blue jay eavesdropping, suggests that the blue jay response observed was likely a conditioned response. Blue jays might not have responded to red squirrel squeals during other experimental playbacks because, under normal conditions, squeals are not as strong an indicator of food resources as we initially believed. Supporting a classical conditioning paradigm, McLinn and Stephens (2006) demonstrated that blue jays utilize novel signals when they are reliably associated with a food reward.

We unsuccessfully attempted to demonstrate learning by training free-living blue jays to associate the playback of red squirrel squeals with the presence of peanuts. The lack of a conditioned response may have been due to the short-term nature of the association of peanuts and red squirrel squeals. Peanuts had been placed at the site which produced the positive response for many years, giving ample time for an association between red squirrel contests over food resources and the peanuts to develop. Perhaps longer-term pairings are necessary for a blue jay conditioned response to arise. Further confounding our conditioning trials, we were unable to identify individual blue jays and therefore had no way to know

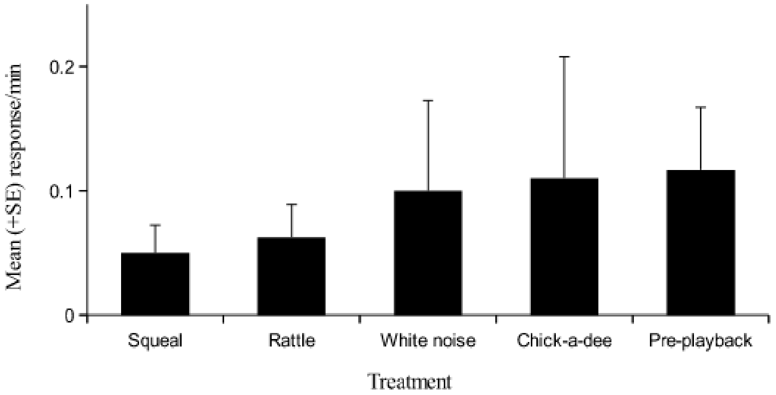


Figure 4: *The mean response rate of passerines (positive responses/minute + SE) to playback treatments (red squirrel (Tamiasciurus hudsonicus) squeals, red squirrel rattles, white-noise control, chick-a-dee (Poecile atricapillus) calls, and pre-playback observation period) in Winnipeg, MB during the summer of 2013. N = 5 for chick-a-dee, N = 8 for rattle, N = 9 for white noise, N = 10 for squeal, N = 11 for pre-playback observation period.*

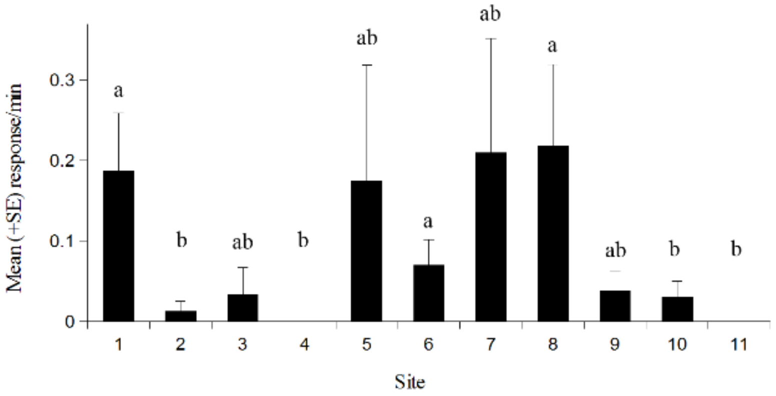


Figure 5: *The mean response rate of passerines (positive responses/minute + SE) among playback sites in Winnipeg, MB during the summer of 2013. Lowercase letters indicate which sites differ from each other based on pairwise contrasts using Mann-Whitney U Tests with the Bonferroni Correction (α = 0.009). N = 3 for sites 3, 4, 7, N = 4 for sites 1, 2, 5, 6, 7, 8, 9, N = 5 for site 10, 11*

how many unconditioned stimulus (peanuts) or conditioned stimulus (squirrel squeals) presentations an individual blue jay received. As such, we lacked a reliable measure to gauge whether learning occurred. In future experiments, blue jays should be marked so that individuals can readily be discerned.

As seed predators, blue jays and red squirrels have dietary overlap, but that overlap may not peak during the summer. During the summer, blue jays may preferentially forage on insects to provide their hatchlings with the energy and protein they require to grow. Other bird species have been reported to shift their diets after chicks hatch (Annett and Pierotti, 1989). In autumn or early spring, blue jays may show a greater response to red squirrel squeals. This could apply particularly well to areas where blue jays overwinter, as nuts can be cached as a winter food supply. Blue jays cache food, which they rely on as a readily monopolizable source of protein, fat, and calories during winter (Vander Wall and Jenkins, 2003). Blue jays are also known raiders of gray squirrel food caches, and likely pilfer from red squirrel food caches as well (Schmidt and Ostfeld, 2008). Blue jays are such prevalent cache pilferers that gray squirrels devalue their food caches when they perceive blue jays to be in the area (Schmidt and Ostfeld, 2008). This propensity to steal from squirrel food caches, and the importance of cached food for overwintering, suggests that blue jays may eavesdrop on red squirrels in winter.

Another possible reason that blue jays showed no apparent response to red squirrel squeals is that the urban environment is not unreliable enough in terms of food availability to warrant eavesdropping on aggressive contests between squirrels to locate food resources (K. Smith, 1978; Taylor et al., 2013). Bird feeders, and perhaps garbage cans, may represent high quality food patches that are routinely present in the same area. Stable food patches would reduce the need of blue jays to search for new food sources. For both blue jays and passerines, no statistical difference was found between the playback trials of chick-a-dee calls and other treatments. Both Hurd (1996) and Templeton et al. (2005) reported passerine birds responding to the playback of chick-a-dee mobbing calls. Thus, while the apparent lack of response of blue jays and passerines to the playback of the chick-a-dee mobbing call has troubling implications for the validity of our experiment, our statistical tests may have failed to detect a difference between chick-a-dee mobbing calls and other treatments due to the low sample size for chick-a-dee playbacks (N = 6 for jays, 5 for passerines). Power analysis, however, suggests the sample size was large enough to detect a difference in blue jay response to the chick-a-dee treatment versus their response during pre-playback observation (Table 1). For passerines, however, power analysis suggests that sample size was inadequate to detect a response difference between chick-a-dee playbacks and the pre-playback period (Table 2). While not statistically significant, playback of the chick-a-dee mobbing call did appear to elicit greater numbers of blue jay responses than any of the other treatments (Fig. 3), suggesting that the failure of our red squirrel playbacks in general to attract blue jays is not attributable to blue jays not detecting the playback stimuli.

While eavesdropping occurs in many species, and organisms gather a variety of information, it should not arise, or persist, in all circumstances. As potentially demonstrated by blue jays in this study, eavesdropping should not occur where the signal or cue is not reliably associated with salient information. The energetic cost of investigating areas without food, or fleeing absent predators, would select against such a response. Where eavesdropping has a negative effect on the fitness of the signaller, we would expect selection favouring either removal of the signal, or changes to the signal that make it less detectable to eavesdroppers (Marler, 1955; Witkin and Ficken, 1979; Klump and Shalter, 1984).

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