



## RESEARCH PAPER

# Does Gray Squirrel (*Sciurus carolinensis*) Response to Heterospecific Alarm Calls Depend on Familiarity or Acoustic Similarity?

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**Abstract**

In habitats in which multiple species are prey to the same predators, individuals can greatly benefit from recognizing information regarding predators that is provided by other species. Past studies have demonstrated that various mammals respond to familiar heterospecific alarm calls, but whether acoustic similarity to a familiar call can prompt a mammal's recognition of an unfamiliar call has yet to be shown. We presented alarm calls to free-ranging eastern gray squirrels (*Sciurus carolinensis*) and recorded behavioral changes in vigilance and antipredatory response. Playbacks included alarm calls of a sympatric bird (American robin, *Turdus migratorius*), an allopatric bird with a call structure similar to that of the robin (common blackbird, *Turdus merula*), and an allopatric bird with a distinct call structure (New Holland honeyeater, *Phylidonyris novaehollandiae*). Squirrels responded significantly more frequently to squirrel alarm calls (positive control) than to robin song (negative control) or honeyeater calls. Squirrel response to robin and blackbird alarm calls was statistically similar to their response to squirrel alarm calls, indicating that squirrels responded to those alarm calls as if they provided information about the presence of predators. However, squirrel response to robin song was not statistically different from response to any of the other avian calls, including the robin and blackbird alarms, suggesting that squirrels neither respond to blackbird alarms as if they clearly signify danger, nor as if they clearly do not signify danger, perhaps reflecting some ambiguity in interpretation of the calls. These results suggest that squirrel responses to alarm calls are generally based on call familiarity, but that acoustic similarity of an unfamiliar allopatric call to a familiar call also can elicit antipredator behavior. The lack of response to honeyeater alarm calls also supports the hypothesis that call recognition by gray squirrels is dependent on familiarity, rather than simply detection of an acoustic feature common to alarm calls across a variety of avian species.

**Introduction**

An alarm call is an auditory signal produced by a prey organism in response to perceived predator threat. Although alarm calls are thought to be directed toward predators or members of the sender's own species, the information they contain may be intercepted and utilized by a third-party species within earshot. Responses to heterospecific alarm calls could be

beneficial due to the potentially high costs of not responding to signals of increased predation risk (Searcy & Nowicki 2005). However, detecting and assessing the alarm calls of heterospecifics may be more difficult than detecting and assessing conspecific calls due to interspecific differences in call structure and because heterospecific calls may convey somewhat different information than conspecific calls. Therefore, the information provided by heterospecific

calls may be less valuable or reliable than information provided by conspecifics and the opportunity costs of responding too indiscriminately to heterospecific calls may be substantial (Lima & Dill 1990; Searcy & Nowicki 2005). Whether and under what conditions individuals respond to heterospecific alarm calls has become a topic of great interest among behavioral ecologists (e.g. Bshary & Noë 1997; Shriner 1998; Randler 2006; Vitousek et al. 2007; Goodale & Kotagama 2008; Fallow & Magrath 2010; Carrasco & Blumstein 2012; Magrath & Bennett 2012).

Recognition of heterospecific alarm calls has been demonstrated in several species of birds (Magrath et al. 2007; Goodale & Kotagama 2008; Fallow & Magrath 2010), mammals (Shriner 1998; Trefry & Hik 2009; Aschemeier & Maher 2011), and even non-vocal reptiles (Vitousek et al. 2007; Ito & Mori 2010). Most of these studies have examined eavesdropping relationships between two bird species or between two mammal species, but several studies have demonstrated alarm call recognition across much greater phylogenetic distances (Randler 2006; Vitousek et al. 2007; Lea et al. 2008; Müller & Manser 2008; Schmidt et al. 2008; Ito & Mori 2010). How individuals acquire the ability to recognize heterospecific alarm calls is poorly understood. Some recent studies of predator–prey interactions have suggested that individual prey may learn or have the innate capacity to generalize predator cues from a familiar to a similar but unfamiliar predator species (Griffin et al. 2001; Ferrari et al. 2007; Stankowich & Coss 2007; Brown et al. 2011; Davis et al. 2012) and that the tendency to generalize appears to correlate with phylogenetic distance between the familiar and unfamiliar predator (Ferrari et al. 2007; Brown et al. 2011). However, alarm call systems differ from these sorts of predator–prey interactions because in alarm-calling situations, receivers must rely on information that is more disconnected from the actual predator itself and is interpreted by a third-party prey individual, rather than detecting information that is generated directly from the predator or from a captured prey as a direct consequence of the predation event.

Some recent studies have attempted to determine whether similarity of call structure is either necessary or sufficient to lead to recognition of a heterospecific alarm call. For example, Magrath and colleagues found that superb fairy-wrens (*Malurus cyaneus*) responded to alarm calls of sympatric scrubwrens (*Sericornis frontalis*) but not to the structurally similar calls of conspecific, yet allopatric scrubwrens (Magrath et al. 2009a). That study also found that the fairy-wrens could recognize an alarm call structurally

different from their own, that of the sympatric New Holland honeyeater (*Phylidonyris novaehollandiae*), concluding that similar call structure was neither necessary nor sufficient for recognition of heterospecific alarm calls, and that learning is the primary mechanism of this recognition (Magrath et al. 2009a). Similarly, Ramakrishnan & Coss (2000) found that bonnet macaques (*Macaca radiata*) not only responded to familiar alarm calls that were dissimilar to conspecific calls, but also that unfamiliar alarm calls were ignored, even though they were similar to conspecific calls. This evidence, along with the finding that juveniles were less discriminating in their responses to sudden sounds than adults were, supports the conclusion that recognition of heterospecific alarm calls relies heavily on learning the specific calls of sympatric species. However, in a subsequent study, Magrath's group found that superb fairy-wrens respond more strongly to heterospecific allopatric fairy-wren congeners that had alarm calls that were more acoustically similar to their own than to allopatric species outside their genus, therefore leading to the conclusion that acoustic similarity can prompt recognition of heterospecific alarm calls, regardless of experiential learning (Fallow et al. 2011). More recently, Magrath & Bennett (2012) provided strong evidence that some birds depend on experiential learning rather than innate recognition when it comes to recognizing alarm calls of other species. They found that superb fairy-wrens only respond to noisy miner (*Manorina melanocephala*) alarm calls in microgeographical areas in which the two species overlap. Despite these findings, the relative importance of call structure and call similarity to heterospecific alarm call recognition in non-primate mammals remains unclear. To our knowledge, no studies have investigated the possibility that a non-primate mammal might respond to an avian alarm call it had never encountered before, especially if the allopatric species' call structure was similar to a familiar call. Such responses might be expected if receivers attend to the structure of alarm calls and if alarm call structure tends to be convergent or homologous across species.

In this study, we aimed to determine whether the eastern gray squirrel (*Sciurus carolinensis*) increases its antipredator behavior in response to unfamiliar alarm calls of the common blackbird (*Turdus merula*), a species that is allopatric with eastern gray squirrels but emits alarm calls that are similar to those of the congeneric American robin (*Turdus migratorius*), a species that is sympatric with the gray squirrel throughout most of its range. We hypothesized that the similarity of the acoustic structure of this foreign call to a familiar call might elicit similar responses to both calls.

We also used playbacks of allopatric New Holland honeyeater (*Phylidonyris novaehollandiae*) alarm calls to determine whether squirrels respond to some 'alarm-like' element common to phylogenetically distant taxa of birds. For example, Marler (1955) showed that 'seeet' alarm calls have a convergent call structure across a variety of bird species, due to the fact that the high pitch and narrow bandwidth make such alarm calls difficult for hawks to locate, and Fallow et al. (2013) showed that fairy-wrens respond to synthetic calls containing structural elements that were similar to elements within fairy-wren alarm calls, even when other elements of the synthetic calls were dissimilar to fairy-wren calls. We did not use 'seeet' alarm calls in our experiment, and the honeyeater's call is acoustically distinct from those of the other species used in our study. Nonetheless, our use of honeyeater calls tests for response to features of avian alarm calls (for example, structural elements, bandwidth, or patterns of repetition or call rate) that may be convergent across a wide array of species and detectable by squirrels, but as yet unidentified by us. Including the honeyeater calls also allows us to control for the playback of novel calls.

## Methods

### Study Species and Overview of Experimental Design

The eastern gray squirrel is a widespread arboreal rodent occupying forests and suburban neighborhoods throughout the eastern half of North America (Barkalow & Shorten 1973), as far west as eastern Texas (Thorington & Hoffman 2005). Gray squirrels are known to have been preyed upon by a variety of predators that occur on our study site, including Cooper's hawks (*Accipiter cooperii*), red-tailed hawks (*Buteo jamaicensis*), red-shouldered hawks (*B. lineatus*), great horned owls (*Bubo virginianus*), barred owls (*Strix varia*), domestic cats (*Felis domesticus*) and dogs (*Canis familiaris*), and black rat snakes (*Elaphe obsoleta*) (Koprowski 1994). The eastern gray squirrel's species-specific alarm call, its readily observable behavioral responses to conspecific alarm calls, and its sympatry with other alarm-calling species make the gray squirrel an excellent model organism for studying recognition of heterospecific alarm calls. Gray squirrels are diurnal and do not hibernate at any point in the year (Thorington & Ferrell 2006), so daylight hours in late fall and winter, after trees have lost their leaves, are optimal times to observe squirrel behavior.

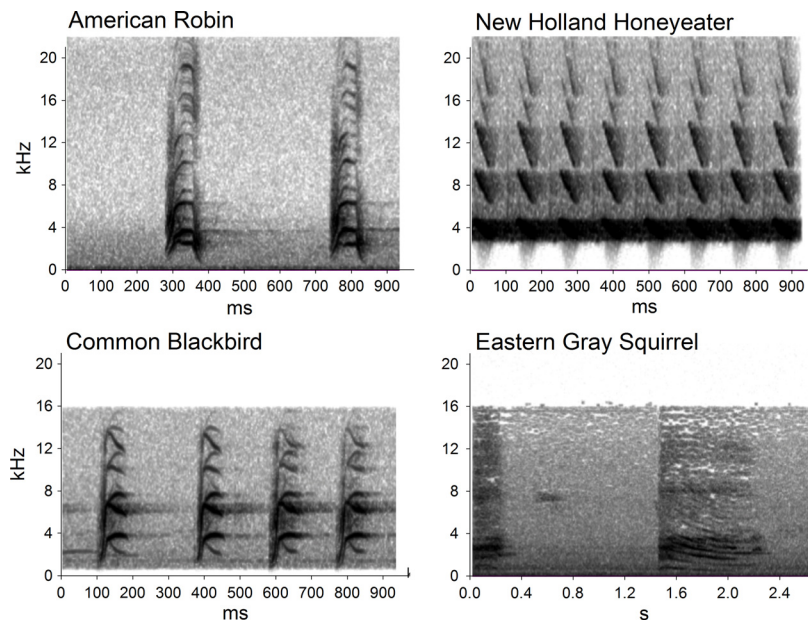
In order to assess squirrels' recognition of a sympatric bird's alarm call, we observed changes in

squirrels' behavior during playbacks of American robin alarm calls. American robins are common passerines that range throughout nearly all of North America (Sallabanks & James 1999). Their alarm calls ('chirps' for aerial predators, and 'chirps' and 'chucks' for terrestrial predators) are often combined with mobbing behavior as a means of predator deterrence (Shedd 1982; Gottfried et al. 1985). Similar to squirrels, adult robins are prey to Cooper's hawks, northern goshawks (Kennedy 1991), various snakes, and domestic cats (Sallabanks & James 1999). Because squirrels share predators with robins, a squirrel could enhance its fitness by responding to robin signals that indicate one of these predators is in the vicinity.

Common blackbirds range across Europe, from Ireland to the Ukraine (Collar 2005). As such, these birds are allopatric and unfamiliar to all North American populations of eastern gray squirrels. As expected given their close phylogenetic relationship (Nylander et al. 2008), the alarm calls of congeneric common blackbirds and American robins are structurally similar. The frequency range of the common blackbird's alarm call fits entirely within the range of the American robin's alarm call, although the robin's peak frequency is higher (22 vs. 15 kHz, Fig. 1). The 'chirps' of both calls also share a ladder-like appearance in a spectrogram (Fig 1).

To test whether squirrels respond to an unidentified but convergent feature of avian alarm calls, we used recordings of New Holland honeyeater alarm calls. Native to the southern coast of Australia, this species is allopatric to the others used in this study and does not share any recent ancestors or ecological history; in other words, it is phylogenetically and geographically distant from the other two bird species (Barker et al. 2004). Honeyeater alarm calls have been well-studied (Magrath et al. 2009a,b), and they are acoustically distinct from those of gray squirrels, robins, and blackbirds. In particular, call rate is much greater in honeyeaters than in robins and blackbirds, and visual inspection of spectrograms reveals that its structure is unlike the others (Fig. 1). Based on our stimulus recordings, honeyeaters call at a mean rate of 9.3 notes/s, while robins (1.84 notes/s) and blackbirds (2.83 notes/s) are more similar to one another than to the honeyeater.

In addition to avian alarm call playbacks, a number of control sounds were used: a gray squirrel alarm call to ensure that the playback methods worked as expected (i.e. a positive control), a robin non-alarm song to control for responses to loud playbacks in general (or to the presence of robins; i.e. a negative con-



**Fig. 1:** Spectrogram of American robin alarm call (Macaulay no. 93743), common blackbird alarm call (Xeno-Canto no. 64734), New Holland honeyeater alarm call (Magrath laboratory 01.1.NHHE), and eastern gray squirrel alarm call (Youtube, 'Grey Squirrel Alarm Call'). Note: squirrel call spectrogram is on a longer time scale than the avian calls.

trol), and a honeyeater contact call to control for responses to novel sounds.

### Playbacks and Materials

We obtained audio-recordings from digital repositories, online resources, and other researchers (Table 1). Because some birds and mammals are known to give different calls in response to terrestrial predators vs. aerial predators (e.g. Melchior 1971; Gottfried *et al.* 1985), we only used alarm call recordings with accompanying comments noting that the call was given in the context of a predator, and we gave preference to calls recorded in association with an avian predator. We used three exemplars of each call type to avoid pseudoreplication in the experimental design (Kroodsma 1989). However, due to scarcity of recordings with the context indicated, two exemplars of alarm calls in response to domestic cats were used: one squirrel alarm and one blackbird alarm. Analysis of squirrel responses to squirrel and blackbird alarm calls showed that neither of these exemplars was perceived as significantly different from the other two exemplars of its respective call type (see the section 'Field Observations' below for a description of behaviors used to assess responses to playbacks): the proportion of cat-evoked squirrel calls that elicited increased vigilance in the focal squirrels ( $N = 7$ ; proportion responding with increased vigilance =  $0.71 \pm 0.18$ ) did not differ from that of avian-evoked squirrel calls ( $N = 12$ ; proportion responding with increased vigi-

lance =  $0.83 \pm 0.11$ ; generalized linear model with binomial probability distribution and logit link function: likelihood  $\chi^2 = 0.368$ ,  $df = 1$ ,  $p = 0.544$ ); likewise, blackbird alarm to cat ( $N = 6$ ; proportion responding with increased vigilance =  $0.33 \pm 0.21$ ) was not different from blackbird alarm calls to birds of prey ( $N = 14$ ; proportion responding with increased vigilance =  $0.43 \pm 0.14$ ; generalized linear model with binomial probability distribution and logit link function: likelihood  $\chi^2 = 0.161$ ,  $df = 1$ ,  $p = 0.688$ ).

Where more than three suitable recordings were found, the three recordings with the least background noise were chosen for each call type. We used the sound editing program Raven (Cornell Lab of Ornithology, Bioacoustics Research Program, Cornell, NY, USA) to set recordings at a maximum peak amplitude of 25 kU and removed as much background noise as possible. Each final sound sample consisted of 15 s of alarm call or control vocalization. Two blackbird alarm call recordings were edited with a 1000–10 000 Hz band pass filter to remove wind noise; squirrels responded similarly to these as they did to the unfiltered blackbird exemplar (filtered:  $N = 12$ , mean  $\pm$  SE =  $0.33 \pm 0.14$ ; unfiltered:  $N = 8$ , mean  $\pm$  SE =  $0.50 \pm 0.19$ ; generalized linear model with binomial probability distribution and logit link function: likelihood  $\chi^2 = 0.554$ ,  $df = 1$ ,  $p = 0.457$ ).

The 18 final playback recordings (three exemplars of each of six call types) were assigned random numbers and saved as WAV files to an Olympus LS-10 Linear PCM recorder, with the numbers as their



**Table 1:** Origins of playback recordings used as stimuli

Playback type	Source	Catalog no. title	Predator context
Squirrel alarm	Borror Lab	No. 2741	Red-shouldered hawk
	Macaulay Library	No. 20431	Screech owl
	Youtube	'Grey Squirrel Alarm Call'	Domestic cat
		<a href="http://www.youtube.com/watch?v=8b-2TFrx3_fg">http://www.youtube.com/watch?v=8b-2TFrx3_fg</a>	
Robin song	Xeno-Canto	No. 13650	
	Xeno-Canto	No. 14442	
	Xeno-Canto	No. 22032	
Robin alarm	Xeno-Canto	No. 57382	Red-shouldered hawk
	Macaulay Library	No. 63026	Pygmy owl
	Macaulay Library	No. 93743	<i>Accipiter</i> (sp. unknown)
Blackbird alarm	Xeno-Canto	No. 42018 <sup>a</sup>	Scops owl
	Xeno-Canto	No. 64734	Pygmy owl
	Xeno-Canto	No. 64733 <sup>a</sup>	Domestic cat
Honeyeater song	R.D. Magrath	No. 1	
	R.D. Magrath	No. 2	
	R.D. Magrath	No. 5	
Honeyeater alarm	R.D. Magrath	01.1	Flying sparrowhawk model
	R.D. Magrath	02.1	Flying sparrowhawk model
	R.D. Magrath	03.1	Flying sparrowhawk model

<sup>a</sup>Recordings edited with a 1000–10 000 Hz band pass filter to remove wind noise.

titles. This provided some degree of experimenter blindness; however, complete blindness was not possible due to the nature of the experiment (experimenters could easily distinguish squirrel calls from bird calls, for example, and could hear the playbacks during trials).

### Study Site

We conducted field observations of gray squirrels within a 2.5 km radius of Oberlin College Science Center in Oberlin, OH (41°17'34.59" N, 82°13'01.68" W; elevation 247 m) between January 06 and March 05, 2012. Observers found squirrels along neighborhood streets and paths, in parks, and other human-modified habitats such as the local cemetery and golf course. Sampling from these environments ensured that squirrels were generally habituated to the presence of humans. We presented the playbacks in random order over a period of 2 mo (January 06–March 05, 2012). Trials were not conducted during rain or when wind noise seemed likely to interfere with playbacks.

Study sites visited within the same week were separated by at least 164 m to avoid habituation of squirrels in the immediate area. We selected this separation distance because the home range of male gray squirrels, which is larger than that of females, averages approximately 0.53 ha (Doebel & McGinnes 1974); this translates to a circle with a diameter of 82 m. To prevent resampling individual squirrels, a

given playback was not used more than once at any given site.

### Field Observations

Observer groups consisted of two or three people. When they located a gray squirrel, observers approached the squirrel within 15–30 m. Microhabitat (i.e. on ground or in tree) of the focal animal was recorded to control for variation in vulnerability and thus propensity to respond to an alarm call. After setting up the equipment, the observers moved at least 5 m away from the speakers. Observers broadcast recordings in the field from the Olympus recorder and portable RadioShack speakers with 500 Hz–12 kHz frequency response, 600  $\Omega$  amplifier input impedance, and 0.75 W power output per channel. Speakers were elevated 38 cm off the ground on an inverted plastic bucket to reduce sound attenuation. They observed the baseline activity of the squirrel for 1 min using a digital stopwatch that marked seconds, and in the final 2 s of this minute, the pre-playback behavior was recorded as a 'vigilance level' as follows (modified from Blumstein & Arnold 1995 and Houtman 2003): (1) preen or forage with head down/covered: squirrel's head was in a position such that it appeared to have limited visibility of surroundings beyond its immediate foraging or preening space; (2) preen or forage with head exposed: squirrel was foraging or preening with its head in a position such that it appeared to have extensive visibility; (3) look around

without standing: squirrel appeared to be assessing the surroundings beyond its immediate foraging or preening space; (4) stand up and look around: squirrel stood on its hind legs and appeared to survey the surroundings beyond its immediate foraging or preening space; (5) freeze: squirrel immediately ceased all movement and remained immobile for at least 5 s; (6) call: squirrel began vocalizing; (7) flee: squirrel ran to cover. Higher values on this scale are assumed to correspond with higher levels of vigilance or antipredatory response. If a naturally evoked squirrel alarm call (from the focal squirrel or others within earshot) occurred during set-up or during the pre-playback minute, observers waited at least 5 min following the conclusion of that alarm call before beginning or restarting the pre-playback minute (Randler 2006; Magrath *et al.* 2007).

At the expiration of the pre-playback minute, the playback began and automatically played for 15 s. Observers recorded the amount of time, in seconds, between playback onset and the squirrel's first change in behavior from one vigilance level to another, as well as the vigilance level of the squirrel's first response. If the squirrel's behavior remained the same for the entire duration of the playback, observers assigned it the same vigilance code it received during the pre-playback. At the conclusion of the playback, post-playback behavior was observed for an additional minute, and another vigilance code was recorded for the squirrel's behavior during the last 2 s of this period (i.e. the latent response). Distance from the speakers to the squirrel's position at playback onset was then measured with a tape measure to the nearest decimeter to control for variation in playback attenuation over distance. We excluded from the analysis any trials during which a physical interruption occurred, such as a car or human passing close enough to the squirrel to startle it.

### Data Analysis

We conducted 18–25 trials per playback type and included 126 trials in the dataset. We tested whether or not squirrels increased their vigilance in response to playbacks by coding the data binomially ('1' for changes in vigilance  $\geq 1$  and '0' for changes  $\leq 0$ , that is, increase or no increase) and fitted the data to a generalized linear model with a binomial probability distribution and logit link function. We used change in vigilance as the dependent variable, with playback type and microhabitat as fixed factors and distance as a covariate. We included microhabitat as a fixed factor because a preliminary test indicated that squirrels

were significantly more likely to respond to a playback when they were on the ground (mean  $\pm$  SE proportion increasing vigilance =  $0.80 \pm 0.11$ ;  $N = 15$ ) than when situated in a tree (mean  $\pm$  SE =  $0.37 \pm 0.04$ ;  $N = 111$ ; generalized linear model with binomial probability distribution and logit link function: likelihood  $\chi^2 = 10.26$ ,  $df = 1$ ,  $p = 0.001$ ), presumably due to their heightened vulnerability.

### Results

The binomial generalized linear model accounted for a significant amount of variation in the tendency of squirrels to respond to playbacks (likelihood ratio  $\chi^2 = 30.85$ ;  $df = 7$ ;  $p < 0.0001$ ). Playback type ( $\chi^2 = 19.68$ ;  $df = 5$ ;  $p = 0.0014$ ) and microhabitat ( $\chi^2 = 6.10$ ;  $df = 1$ ;  $p = 0.0135$ ) accounted for a significant amount of variation in the tendency of squirrels to respond to playback, while distance from speaker ( $\chi^2 = 2.53$ ;  $df = 1$ ;  $p = 0.1120$ ) did not. Bonferroni-corrected post hoc comparisons of playback responses showed that squirrels were significantly more likely to respond with increased vigilance to squirrel alarm playback than to robin song and honeyeater alarm and contact calls, but their tendency to respond to squirrel alarms did not differ from their tendency to respond to robin or blackbird alarms (Table 2). The proportion of squirrels responding to robin song was not significantly different from the proportion responding to any of the other avian calls (Table 2). A direct comparison of squirrel responses to robin and blackbird alarms revealed no difference (likelihood  $\chi^2 = 2.43$ ,  $df = 1$ ,  $p = 0.1193$ ).

The time span from onset of playback to first response did not vary among playback types (generalized linear model with linear probability distribution and identity link function based only on positive responses;  $\chi^2 = 3.23$ ,  $df = 5$ ,  $p = 0.6644$ ), microhabitat types ( $\chi^2 = 1.90$ ,  $df = 1$ ,  $p = 0.1685$ ), or with distance ( $\chi^2 = 0.12$ ,  $df = 1$ ,  $p = 0.7252$ ). The latent response, measured at the end of the 1-min playback/observation period, did not vary with playback type (generalized linear model with binomial response distribution and logit link function;  $\chi^2 = 3.48$ ,  $df = 5$ ,  $p = 0.6262$ ) or distance ( $\chi^2 = 0.04$ ,  $df = 1$ ,  $p = 0.8409$ ), but squirrels remained more vigilant when they were on the ground than when in trees ( $\chi^2 = 8.00$ ,  $df = 1$ ,  $p = 0.0047$ ).

### Discussion

This playback experiment aimed to elucidate whether acoustic similarity to a familiar heterospecific alarm

**Table 2:** Differences in proportion of experimental playbacks in which gray squirrels increased vigilance in response to recordings. Positive differences mean that the playback type in the left column elicited an increase in vigilance more frequently than the playback type in the right column

Playback type	Relative to	Mean difference in proportion of positive responses	95% Wald confidence interval for difference	df	p
Squirrel alarm	Robin song	0.40	0.13 to 0.68	1	<b>0.0043</b>
Squirrel alarm	Robin alarm	0.11	−0.10 to 0.31	1	0.3122
Squirrel alarm	Blackbird alarm	0.35	0.07 to 0.62	1	0.0138
Squirrel alarm	Honeyeater alarm	0.54	0.25 to 0.83	1	<b>0.0002</b>
Squirrel alarm	Honeyeater contact call	0.46	0.20 to 0.73	1	<b>0.0005</b>
Robin song	Robin alarm	−0.30	−0.59 to −0.01	1	0.0457
Robin song	Blackbird alarm	−0.06	−0.39 to 0.27	1	0.7341
Robin song	Honeyeater alarm	0.14	−0.20 to 0.48	1	0.4247
Robin song	Honeyeater contact call	0.06	−0.27 to 0.38	1	0.7200

Significant p-values after Bonferroni correction for multiple comparisons ( $\alpha = 0.0056$ ) are shown in bold.

call would prompt gray squirrels' recognition of heterospecific alarm calls given by an allopatric species. The tendency of squirrels to respond to robin and blackbird alarm calls was statistically similar to their tendency to respond to conspecific alarm calls, even though the squirrels were unfamiliar with blackbird alarm calls. In contrast, squirrel responses to both the alarm and contact calls of the New Holland honeyeater, an allopatric species with a call structure quite different from that of the robin and blackbird, were significantly different from responses to squirrel calls, but not different from their responses to non-threatening robin song. These findings are consistent with the hypothesis that squirrels attend to heterospecific alarm calls with which they are familiar and to similar calls from unfamiliar species, because of the adaptive significance of responding to sounds associated with presence of a predator (Bshary & Noë 1997; Caro 2005; Schmidt *et al.* 2008). Sharing habitat and predators with another species may allow an individual squirrel to learn the correlation between particular heterospecific sounds and the presence of a predator. However, discriminating between familiar calls and unfamiliar calls may be risky if the calls are similar enough to potentially contain reliable information about the threat of predation. Another possibility, which may work in combination with the first, is that individuals that respond to their heterospecific neighbors' alarm calls are favored by selection, and therefore, the recognition ability becomes innate over evolutionary time (Ferrari *et al.* 2007). Studies of other species suggest that learning is the primary mechanism in heterospecific alarm call recognition, but further research is necessary to demonstrate whether this is true of tree squirrels (Shriner 1999; Ramakrishnan & Coss 2000; Magrath *et al.* 2009a; Magrath & Bennett 2012).

Although squirrel responses to the American robin and common blackbird alarm calls were statistically similar to their responses to conspecific alarm calls, responses to these two calls did not differ statistically from responses to non-threatening robin song. This ambiguity may imply that squirrels neither respond to blackbird alarms as if they clearly signify danger nor as if they clearly do not signify danger and that similarity of call structure between familiar robin and unfamiliar blackbird alarm calls may play a subtle role in recognition. We find the lack of a strong distinction between robin alarm and robin song puzzling, as it seems that indiscriminate responses to uninformative sounds like robin song would be selected against. However, robin alarm calls may be less reliable or informative to squirrels than squirrel calls, and the patterns we observed may have arisen because squirrel responses to robin alarms are not as strong as they are to their own calls. Robins give chirps and chucks in a variety of contexts, including in the presence of predatory threat. Subtle variation in the intonation or call rate of these vocalizations may provide information to robins that squirrels are unable to decipher. Hence, squirrels may not always respond to all renditions of robin alarm calls as if they are providing clear information about a true threat. Another possible explanation for our ambiguous results, consistent with findings in a study of macaques by Ramakrishnan & Coss (2000), is that younger squirrels may have responded more indiscriminately to the avian calls because they had not yet developed the ability to discriminate between alarm calls and song; this could have raised the mean response to non-threatening song relative to a purely adult sample of squirrels. We were not able to identify relative ages of the squirrels and therefore cannot rule out this possibility.

Alternatively, because alarm calls vary among and within the individuals that produce them (Blumstein & Munos 2005; Leavesley & Magrath 2005; Templeton et al. 2005), a strategy in which receivers generalize to some degree from a model signal may be the most adaptive approach (see also Ferrari et al. 2007). Because the frequencies of squirrels reacting to robin alarms vs. blackbird alarms were similar, however, perhaps squirrels implement a strategy of 'playing it safe' to minimize risk when hearing an unfamiliar, but robin-like alarm call (Ferrari et al. 2007). The fact that squirrel behavior 1 min after the onset of the playbacks did not differ among any of the playback types, and that squirrels' response times also did not vary with playback type, supports this idea, as it appears that squirrels both responded quickly and returned to pre-playback behavior fairly quickly regardless of playback type.

Our study has furthermore rejected the possibility that squirrels perceive a common, convergent 'alarm-like' element in all avian alarm calls that is not present in other animal sounds or mechanical noises. When squirrels heard the honeyeater's alarm call, which presumably is unlike any alarm sounds they ordinarily experience, they behaved similarly to control conditions, rather than with predator avoidance behaviors. We do not yet know whether squirrels can recognize more structurally convergent avian alarm calls given by allopatric species, such as 'seeet' calls (Marler 1955).

This research adds to a growing body of evidence that individuals have much to gain by extracting information from heterospecific signals about shared predators (Griffin et al. 2001; Ferrari et al. 2007; Brown et al. 2011; Davis et al. 2012). It also raises new questions regarding which elements of the signal are most important to the information contained within an alarm call: how different from a known call can an alarm call be before the individual no longer responds with antipredator behavior?

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work complies with the laws of the United States of America and was approved by the Oberlin College Institutional Animal Care and Use Committee, protocol #F11RBKT-2. The authors declare no conflicts of interest.

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