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# Heterospecific alarm call eavesdropping in nonvocal, white-bellied copper-striped skinks, *Emoia cyanura*



Holly Fuong, Kathryn N. Keeley, Yasemin Bulut, Daniel T. Blumstein\*

Department of Ecology and Evolutionary Biology, University of California Los Angeles, U.S.A.

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Keywords: alarm call antipredator behaviour Emoia cyanura heterospecific eavesdropping nonvocal species predator vocalization Many species benefit from listening to the vocalizations of their predators as well as the alarm vocalizations of other species. This eavesdropping is an important way to acquire information regarding predator location and threat magnitude. Previous studies have investigated lizards eavesdropping on predators, while others have studied lizards eavesdropping on alarm calls. Studies that examine lizard responses to playbacks of both predatory calls and heterospecific alarm calls are absent, even though eavesdropping may be especially important in nonvocal species. By comparing both types of calls, we can assess their relative importance to skinks and understand how skinks discriminate between these calls. We broadcast sympatric predator vocalizations and both alarm call and nonalarm social vocalizations from a nonpredatory bird (red-vented bulbul, Pycnonotus cafer) to determine whether nonvocal, whitebellied copper-striped skinks could discriminate among them. Upon hearing red-vented bulbul alarm calls, white-bellied copper-striped skinks reduced their rate of looking and increased their rate of bloating compared to a baseline period. However, they did not respond significantly to red-vented bulbul social calls or to vocalizations from potential predators. Our study is the first to look at the relative magnitude of response to playbacks of predator and heterospecific vocalizations in lizards. White-bellied copper-striped skinks most likely depend on heterospecific vocalizations for predator information because they are nonvocal and found low on the forest floor, making it harder for them to identify predators directly than through alarm calls of avian heterospecifics.

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Because predation has profound influences on future fitness (Lima & Dill, 1990), prey that can best identify and evade their predators will be favoured by natural selection. Antipredator behaviour can ameliorate the effect of predation, and includes alarm calls, which are produced in response to potential danger (Caro, 2005). Caro (2005) suggested that calls have several putative targets. They could deter attacks by letting predators know that they have been sighted or that their prey is in good physical condition to escape. They may also serve to redirect predator attention, warn kin or conspecifics, increase dilution effects through group formation, induce mobbing, or reduce future predator attacks (Caro, 2005). Receivers can gain specific information on the predator type and location from the calls. For instance, vervet monkeys

E-mail address: marmots@ucla.edu (D. T. Blumstein).

(Chlorocebus pygerythrus) give different alarm calls based on the predator, and receivers respond accordingly: they look up for alarm calls about birds, they look down for alarm calls about snakes, and they climb into trees for alarm calls about leopards (Seyfarth, Cheney, & Marler, 1980). Alarm calls may also encode information about the magnitude of threat. For example, Leavesley and Magrath (2005) found that birds increase the pitch and number of elements in their calls when predators are closer.

Both conspecifics and heterospecifics can benefit by hearing calls. Such heterospecific eavesdropping occurs when an unintended individual acquires sensory information to enhance its own fitness (Peake, 2005). By doing so, eavesdroppers reduce their risk of predation by detecting predators before an encounter (Ito & Mori, 2010). Listening to heterospecifics could also decrease time allocated to vigilance and increase energy allocated to foraging and breeding (Ridley, Wiley, & Thompson, 2014). Eavesdropping may be learned, as has been reported in golden-mantled ground squirrels, *Callospermophilus lateralis* (Shriner, 1999), or be innate, as has been reported in common cuckoos, *Cuculus canorus* (Davies, Madden, Butchart, & Rutila, 2006). Responses to heterospecific alarm calls

<sup>\*</sup> Correspondence: D. T. Blumstein, Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90095-1606, U.S.A. breeding (Ric learned, as h Callospermor reported in

have been observed in a variety of mammals and birds (Caro, 2005), but have rarely been reported in lizards (Ito & Mori, 2010; Vitousek, Adelman, Gregory, & St Clair, 2007). Interestingly, day geckos, *Phelsuma kochi*, respond with antipredator responses to heterospecific alarm calls but not to heterospecific songs (Ito, Ikeuchi, & Mori, 2012).

In addition to alarm calls, songs may provide valuable information to some species. For example, the sound of singing birds may suggest safety if birds stop singing when predators are around (Møller, 1992). Wild dwarf mongooses, *Helogale parvula*, eavesdrop on avian contact calls as an alternative to constant predator vigilance while foraging (Sharpe, Joustra, & Cherry, 2010). Male tungara frogs, *Physalaemus pustulosus*, eavesdrop on courtship calls of another species of frog and may use these to assess predation risk and mate competition (Phelps, Rand, & Ryan, 2006). Heterospecific songs and social calls can indirectly provide information similar to that gleaned from heterospecific alarm calls.

Prey may not only eavesdrop on alarm and social calls, but also on predator vocalizations. In fact, a number of mammals and birds not only listen to their predators, but also discriminate among them (Hettena, Munoz, & Blumstein, 2014). For instance, MacLean and Bonter (2013) found that black-backed gulls, Larus marinus, respond to different types of playbacks. They are most sensitive to predator vocalizations, responding more to human voice playbacks than to predatory eagle vocalizations. They also respond to conspecific alarm calls and heterospecific calls, but their responses are less pronounced. Similarly, predator discrimination has been reported in African elephants, Loxodonta africana, which respond to the more threatening voices of adult male humans, but not to the voices of adult females and juvenile males (McComb, Shannon, Sayialel, & Moss, 2014). Separately, Cantwell and Forrest (2013) suggested that response to predator vocalizations (but not to nonpredatory calls) leads to efficient antipredator responses.

Taken together, eavesdropping on heterospecifics' vocalizations, whether they are social calls, alarm calls or predator vocalizations, may provide valuable information about predation. Thus, prey may benefit from identifying and discriminating such vocalizations from other sounds.

In lizards, predator discrimination is usually studied by observing the lizards' reactions to chemical and visual stimuli (Amo, Lopez, & Martin, 2006; van Damme & Castilla, 1996). Auditory cues are less extensively studied (but see: Cantwell & Forrest, 2013; Elmasri, Moreno, Neumann, & Blumstein, 2012; Huang, Lubarsky, Teng, & Blumstein, 2011; Ito & Mori, 2010; Jones & Jayne, 2012; Vitousek et al., 2007). Despite this, a sense of hearing is important when identifying and avoiding predators (Cantwell & Forrest, 2013; Jones & Jayne, 2012), especially avian predators, which are not always visually or chemically detectable. In their study with Gunther's dik-diks, *Madoqua guentheri*, Lea, Barrera, Tom, and Blumstein (2008) suggested that less vocal species may benefit more from responding to heterospecific alarm calls than more vocal species.

White-bellied copper-striped skinks living on Moorea, French Polynesia are an ideal subject in which to study auditory discrimination because they are nonvocal and have relatively few but imminent predators on the island. On Moorea, skinks may be preyed upon by swamp harriers, *Circus approximans* (Pratt, Bruner, & Berrett, 1987), chattering kingfishers, *Halcyon tuta* (Freeman, 1997), Pacific reef herons, *Egretta sacra* (Bruna, Fisher, & Case, 1996), common mynas, *Acridotheres tristis* (Bruna et al., 1996), and tree rats, *Rattus rattus* (Case & Bolger, 1991). In New Zealand, swamp harriers predominantly eat rabbits but switch to skinks when rabbits (*Oryctolagus cuniculus*) are scarce (Pierce & Maloney, 1989). However, chattering kingfishers include skinks as a major part of their diet and hunt at varying levels of the forest, including

the ground where skinks exist (Rowe & Empson, 1996). In addition, there are several other bird species that are not likely to prey on skinks but that utter alarm calls. For instance, red-vented bulbuls, *Pycnonotus cafer*, are mainly frugivores in the South Pacific, with a small percentage of their diet consisting of arthropods, flowers and vegetation (Spotswood, Meyer, & Bartolome, 2012). Bulbuls also fall prey to harriers (Watling, 1978) and utter alarm calls in response to them. To understand better the communication network between skinks and their heterospecifics (McGregor & Dabelsteen, 1996), we conducted playback experiments on skinks. We documented skinks' responses to playback of vocalizations from two avian predators and one nonpredatory bird.

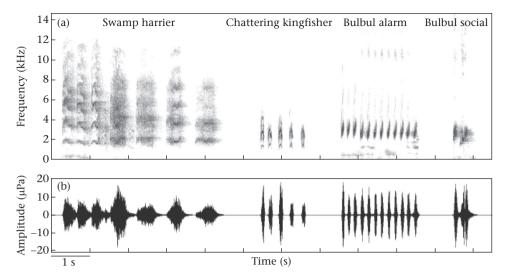
#### **METHODS**

Three observers conducted playback experiments on white-bellied copper-striped skinks from 24 January to 11 February 2014 between 0700 and 1700 hours Tahiti Time (THAT) on the island of Moorea, French Polynesia. Experiments were conducted at either the University of California Berkeley Richard Gump Research Station (17°29′32″S, 149°49′39″W) or a nearby small, local dump (17°29′12″S, 149°49′54W). Skinks were identified based on Zug (2013).

We examined the response of skinks to four playback treatments: two predatory bird calls, one nonpredatory bird alarm call and one nonpredatory bird, nonthreatening social call. For the predatory bird calls, we chose swamp harriers and chattering kingfishers based on their reported diets of lizards (see above). They face some risk of swamp harrier predation and may utter alarm calls in response to the presence of harriers (Watling, 1978). Therefore, we used red-vented bulbul alarm calls as the nonpredatory bird alarm call and red-vented bulbul social calls as the nonthreatening call. Social calls of red-vented bulbuls are common contact calls that do not appear to communicate the presence of a threat, because bulbuls do not respond to these calls in an alarmed manner. Swamp harriers and chattering kingfishers do not appear to utter calls while hunting, so we used representative exemplars of calls uttered by these birds when flying or communicating to potential mates. Over the span of 3 weeks, we observed swamp harriers on three occasions and heard them multiple times, observed chattering kingfishers on two occasions and heard them once and observed bulbuls daily and heard them throughout the day.

We obtained all vocalizations online (Fig. 1, Appendix Table A1). All of these calls appeared distinct in frequency from each other (Fig. 1). Despite the fact that the calls we used were not recorded in Moorea, calls were fairly similar to those heard on site (H. Fuong, personal observation), and no research has demonstrated pronounced dialect differences in these three bird species. Audacity 2.0.5 (Audacity Team, 2013) was used to remove background noise and adjust amplitude. Sounds were calibrated for each set of Tivoli Audio iPal speakers (Tivoli Audio LLC, Boston, MA, U.S.A.) and Apple iPods (Apple Inc., Cupertino, CA, U.S.A.) using a sound level meter (Sper Scientific digital sound meter model number 840029). Calls were calibrated for broadcast at 85 dB (±1 dB SPL measured 1 m from speaker, peak response, weighting A), which is the approximate sound level of natural calls.

For each call, we had multiple exemplars: two for the chattering kingfisher call, six for the swamp harrier call, two for the bulbul alarm call and six for the bulbul social call. As previously stated, there were few recordings available. These vocalizations were chosen from as many different individual recordings as possible in order to provide some replication and variation. However, during playback trials, treatments and subsequent exemplars were systematically rotated throughout the entire experiment to ensure a balanced design and distribution of treatment replicates.



**Figure 1.** Examples of acoustic stimuli used in skink playback experiments. Spectrogram parameters: 1024 point, Boxy spectrogram, Hamming filter, 87.5% overlap, with 2.902 ms temporal resolution, 43.07 Hz frequency resolution.

Skinks were found in and around the foliage alongside roads, either on top of or immediately next to cover. They were 17-70 mm in body length and identified by their bluish-green tails and three dorsal stripes. Identification was confirmed by dorsal scale configuration (Zug. 2013). We searched for skinks by walking slowly and quietly in suitable habitat. When we found a skink, we pointed speakers directly at them, 3 m away (Huang et al., 2011; Ito & Mori, 2010) and 1 m off the ground. We allowed skinks to acclimate for 30 s. Then, we started a 30 s baseline focal observation. This baseline observation was immediately followed by a 2-5 s stimulus playback and then 55-58 s of silence, with focal observations recorded throughout. To conduct focal observations. we dictated behavioural transitions (Table 1) into a voice recorder. Our ethogram included a set of general mutually exclusive lizard behaviours: stand and look, walk, run, tail wag, hop, bloat, other, and out-of-sight (Table 1). Each behavioural duration spanned the time interval between its onset and the onset of another (mutually exclusive) behaviour. A priori predictions as to how skinks would respond to playbacks could not be made because animals may vary in their responses to potential danger (e.g. freezing and escape are both potential responses to a threat).

Following the experiment, we recorded information on the skink's tail colour and body length (estimated visually as the distance between a skink's snout and the base of its tail). Data on group size within 1 m, cloud cover, wind speed (based on the

**Table 1**Ethogram of white-bellied copper-striped skink antipredatory or vigilant behaviours (modified from Elmasri et al., 2012)

| Abbreviation | Behaviour      | Definition                                   |
|--------------|----------------|--|
| 1            | Stand and look | Body still, head fixed in position. Scored   |
|              |                | every time head moved                        |
| W            | Walk           | Locomotion from initial position using all   |
|              |                | four legs                                    |
| Γ            | Run            | Rapid locomotion from initial position using |
|              |                | all four legs                                |
| t            | Tail wag       | Move tail                                    |
| h            | Нор            | Jumping                                      |
| b            | Bloat          | Standing motionless and expanding body.      |
|              |                | Scored every time body expanded              |
| Z            | Other          | Other behaviour not listed                   |
| 0            | Out of sight   | Not in view of observer                      |

Beaufort scale), rain and temperature were also recorded. All of these variables could affect how skinks perceive predators and assess risk. Because skinks maintain thermal homeostasis based on the external temperature, their antipredator behaviour could vary with temperature (Shine, Olsson, Lemaster, Moore, & Mason, 2000). We measured tail colour based on the proportion of blue in the tail because previous studies have suggested that individuals with more conspicuous tails may compensate for this conspicuousness with increased vigilance (Husak, Macedonia, Fox, & Sauceda, 2005) or increased responsiveness to predator vocalizations (Journey, Drury, Haymer, Rose, & Blumstein, 2013). These findings suggest that increased predation risk may increase antipredator behaviour in prey (Cabido, Galán, López, & Martín, 2009; Losos, Schoener, & Spiller, 2004).

Body size could also affect predation risk and antipredator behaviour (Shine et al., 2000). To obtain estimates of skink body length and blue tail proportion, the three observers were first trained to estimate the variable lengths of imitation lizards at a distance of 3 m away (overall mean error  $\pm$  SD = 1.4  $\pm$  0.14% error, N = 105). Using JMP 11.1 (SAS Institute Inc., Cary, NC, U.S.A.), we found that there was no significant difference in error estimates among these three observers (ANOVA:  $F_{2,33}$  = 0.773, P = 0.464).

After conducting a playback, we looked for the next skink and repeated the process with different playback exemplars. Each observer conducted experiments independently. To minimize both the likelihood of sampling the same individuals and carryover effects from playbacks, each observer studied skinks at least 25 m apart within a given playback area. Distances between tested skinks were regularly greater than this, typically reaching 40–80 m. At a distance of 25 m, vocalizations sounded natural and were not distorted. Potential carryover effects were controlled for with systematic treatment and exemplar rotation. Experiments were not conducted during rain. Furthermore, results from playback trials were discarded if a human, car or other distraction interrupted the experiment, or if the subject was autotomized.

## Statistical Analysis

We analysed focal animal samples using JWatcher 1.0 (Blumstein & Daniel, 2007) and calculated the change in rate of looking, total locomotion (hop, walk, run) and bloating between the 30 s baseline and the first 30 s following playback. Rates were

calculated as the number of times that the behaviour occurred divided by the total time the skink was in sight. The rate of each postplayback behaviour was then subtracted from the rate of each preplayback (baseline) behaviour in order to obtain a sensitive measure of responses to the playback. From this, a positive change value reflected an increase in the behaviour rate, while a negative change value reflected a decrease in the behaviour rate. We used the first 30 s following the playback to increase reliability of the information obtained because the response in the first 30 s is less likely to be influenced by other stimuli.

Because variances between treatments were not homogeneous and could not be transformed to be homogeneous, we fitted generalized linear models with an identity function to explain variation in our dependent variables after controlling for treatment and observer effects. Given the variety of potentially confounding variables that we measured, we tested for possible confounds by determining whether each independent variable was homogeneously distributed among treatments by fitting a series of general linear models. Of the tested variables (proportion of blue tail colour, body size, group size, cloud cover, wind speed, rain, temperature), only one varied significantly by treatment (P values ranged from P = 0.21 (number of heterospecifics within 1 m) to P = 0.86 (distance from speaker), except P = 0.01 (temperature)). Thus, most of these variables could not be viewed as confounding, only obscuring. To avoid overfitting our model, we only included temperature and observer in our generalized linear model. These models were fitted in R 3.0.2 (R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org) using Deducer (Fellows, 2012).

Our main models were fitted in IBM SPSS Statistics 21.0 (IBM, Armonk, NY, U.S.A.). We used general linear models to examine covariate effects and fitted generalized linear models for behavioural analyses. We calculated the marginal means and 95% confidence intervals to determine whether skinks responded to playbacks. If the 95% confidence intervals did not contain zero, then skinks responded to playbacks. Pairwise comparisons were calculated using Tukey tests that were uncorrected for multiple comparisons. We calculated Cohen's *d* (a measure of effect size) from marginal mean values to compare red-vented bulbul alarm calls to the other vocalizations.

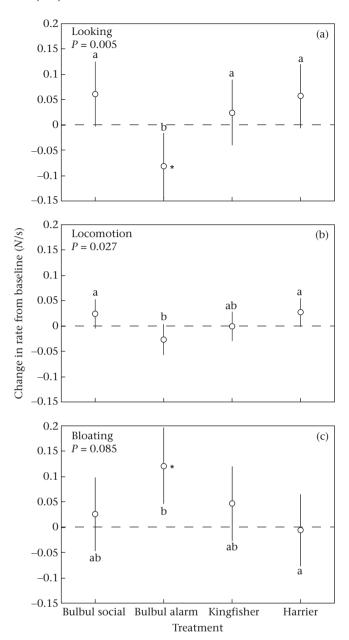
There were no significant exemplar effects. Using R and Deducer, we tested for exemplar effects by fitting a general linear model for each treatment and behaviour, by exemplar, to see whether there was a significant difference between each exemplar (Appendix Table A2). There were no significant exemplar effects for any treatment.

### Ethical Note

Skinks were studied under University of California Los Angeles Institutional Animal Care and Use protocol 2000-147-42 (issued on 7 June 2013), and under permission of the Government of French Polynesia (issued 6 June 2013). Skinks were neither handled nor captured during the course of this experiment. By design, our experiments caused only minimal distractions, and skinks resumed prior behaviour soon after we completed an experiment and moved away from them.

## **RESULTS**

Our final data set contained 87 focal observations of different white-bellied copper-striped skinks. Skinks decreased their rates of looking from baseline in response to red-vented bulbul alarm calls but not in response to red-vented bulbul social calls, chattering kingfisher calls or swamp harrier calls (Fig. 2a). Skinks increased



**Figure 2.** Marginal means ( $\pm$ 95% CI) for change in rate from baseline of (a) looking, (b) total locomotion and (c) bloating. *P* values for the generalized linear model. \*Illustrates treatments that differed from baseline (i.e. 95% CI does not include 0). Letters illustrate significantly different responses.

their rates of bloating from baseline in response to bulbul alarm calls but not in response to bulbul social calls, chattering kingfisher calls or swamp harrier calls (Fig. 2c). Skinks did not change their rate of total locomotion from baseline in response to any of our playback treatments (Fig. 2b).

Pairwise analyses showed that skinks responded significantly differently to bulbul alarm calls when compared to either bulbul social calls (Tukey test: P = 0.002, d = 1.443), chattering kingfisher calls (P = 0.023, d = 0.632) or swamp harrier calls (P = 0.002, d = 0.943) in terms of changes in the rate of looking from baseline (Fig. 2a). In addition, skinks were able to discriminate between bulbul alarm calls and bulbul social calls (Tukey test: P = 0.013, d = 0.701) and between bulbul alarm calls and swamp harrier calls (P = 0.009, P = 0.008) with respect to changes in the rate of total

locomotion from baseline (Fig. 2b). They also discriminated between bulbul alarm calls and swamp harrier calls (Tukey test: P = 0.013, d = 0.626) with respect to changes in the rate of bloating from baseline (Fig. 2c). However, skinks did not discriminate between both predator vocalizations and red-vented bulbul social calls (Tukey test: P > 0.183, d < 0.419).

#### DISCUSSION

This study demonstrated that white-bellied copper-striped skinks reduced their rate of looking and increased their rate of bloating when red-vented bulbul alarm calls were experimentally broadcast but not when predator vocalizations or bulbul social calls were broadcast. This finding is contrary to previous studies that have suggested that predators are more informative than nonpredatory heterospecifics. For instance, Rainey, Zuberbühler, and Slater (2004b) found black-casqued hornbills, Ceratogymna atrata, react more to avian predator vocalizations than to a heterospecific's alarm calls. They also introduced the information precision hypothesis, which suggests that direct spatial information can be acquired from predator vocalizations, while indirect information is acquired from alarm calls. Based on this hypothesis, predator vocalizations should be more useful in detecting the presence of immediate danger. Similar results have been reported in zenaida doves, Zenaida aurita (Barrera, Chong, Judy, & Blumstein, 2011), although a previous literature review suggested that indirect predator cues may be more valuable than direct predator information (Barrera et al., 2011).

Our results suggest that heterospecific vocalizations may provide more important information to skinks than predator vocalizations. There are three possible explanations for this: (1) predator vocalizations do not provide reliable information about potential danger; (2) skink alarm calls are more informative than predator vocalizations; (3) skink alarm calls are less informative than predator vocalizations and make skinks more wary.

Predators often do not vocalize while hunting (Blumstein, Cooley, Winternitz, & Daniel, 2008; Brown & Amadon, 1968). Furthermore, Steer (2010) suggested that swamp harriers generally vocalize irregularly. Thus, to skinks, there may be less information about the extent of threat in predator vocalizations than in alarm calls, which are produced when actual danger may be present (Caro, 2005).

In addition, for nonvocal skinks, heterospecific alarm calls may be more informative than predator vocalizations because they are produced by a species that can better detect predators. Goodale, Beauchamp, Magrath, Nieh, and Ruxton (2010) suggested that this could be because of heterospecifics' general morphology, sensory physiology, foraging technique and group size. Red-vented bulbuls are arboreal (Bhatt & Kumar, 2001) and feed higher in the trees than skinks, so they may be better at detecting avian predators. Thus, alarm call eavesdropping allows the recipient to acquire more information than they could otherwise obtain from conspecifics (Goodale et al., 2010). In a nonvocal species such as the whitebellied copper-striped skink, eavesdropping on heterospecific alarm calls may be especially important.

Another possible explanation for the decrease in the rate of looking in response to heterospecific alarm calls is that these calls are actually less informative, forcing skinks to become more alert when they hear them. Because heterospecific alarm calls do not accurately inform the eavesdropper of the exact position of predators (Rainey, Zuberbühler, & Slater, 2004a), they may make eavesdroppers more wary (Rainey et al., 2004b). Skinks may decrease their rate of looking to reduce the chance of being detected by predators. For example, yellowhammers, *Emberiza citronella*, vary their antipredator behaviour depending on the

amount of information received (van der Veen, 2002). Yellow-hammers that only hear conspecific alarm calls are much more cautious and alert than those that can see a predator. van der Veen (2002) attributed this to the completeness of information hypothesis, suggesting that the more information an individual has, the less fitness opportunities are lost. A decade before, Sih (1992) modelled this idea and suggested that uncertain prey should stay in refuges longer than those that know their predator's location. Thus, heterospecific alarm calls may reduce certainty about predators. However, we found that while skinks decreased their rate of looking, they increased their rate of bloating. Importantly, bloating may make the skink more obvious, which suggests that alarm calls are not less informative. Furthermore, effect size estimates (Appendix Table A3) suggest that heterospecific alarm calls are more informative to skinks than predator calls.

Red-vented bulbuls have two types of alarm calls: one that is uttered upon detection of a predator (the one used in this experiment) and one that is uttered when predators are in close proximity to their nests and fledglings (Kumar, 2004). Because these alarm calls are uttered under different levels of threat, skinks could potentially extract additional information from them. Future studies could examine skink responses to the different types of alarm calls.

Despite being in contact with red-vented bulbuls for only a few decades (they were introduced in late 1970s to Moorea; Monnet, Thibault, & Varney, 1993), skinks are able to respond to bulbul alarm calls. Given this short period, it is unknown whether their responses are learned or can be correctly performed without experience. Skinks could respond simply because of the acoustic properties of red-vented bulbul alarm calls. The swamp harrier, chattering kingfisher and red-vented bulbul alarm calls all include downshift tones, which are usually associated with threatening sounds. The red-vented bulbul social call includes an upshift tone, which has been reported to be a less threatening sound (Blesdoe & Blumstein, 2014). This is because some calls produced when animals are stressed may include certain nonlinear, acoustic phenomena such as deterministic chaos, subharmonics and abrupt frequency shifts (Fitch, Neubauer, & Herzel, 2002). These acoustic properties may be generally arousing (Blesdoe & Blumstein, 2014; Blumstein & Récapet, 2009; Slaughter, Berlin, Bower, & Blumstein, 2013). Therefore, particular calls may elicit fear responses. However, experience often hones antipredator responses, and many species seemingly learn to respond to heterospecific vocalizations (Magrath & Bennett, 2012). Substantial experience may not be required. For instance, Shriner (1999) demonstrated that goldenmantled ground squirrels could learn to respond to novel sounds paired with predator models after 57 presentations over 7 days.

To our knowledge, this is the first paper to contrast lizard responses to predator and heterospecific alarm calls simultaneously. Our results suggest that heterospecific alarm calls may be more informative than predator vocalizations for skink risk assessment. Because nonvocal, ground-dwelling animals are at a disadvantage when it comes to detecting aerial predators, it may be generally important for them to eavesdrop on vocalizations made by heterospecifics to avoid predation.

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## APPENDIX

**Table A1**Source of each vocalization and exemplar

| Treatment             | Exemplar no. | Stimulus<br>duration<br>(min:s) | Web site       | URL  | Location of recording |
|-----------------------|--------------|---------------------------------|----------------|--|-----------------------|
| Chattering kingfisher | 1            | 0:03                            | Xeno-Canto     | http://www.xeno-canto.org/species/Todiramphus-tutus  | New Zealand           |
| Chattering kingfisher | 2            | 0:05                            | Xeno-Canto     | http://www.xeno-canto.org/species/Todiramphus-tutus  | New Zealand           |
| Swamp harrier         | 1            | 0:02                            | Xeno-Canto     | http://www.xeno-canto.org/browse.php?query=Swamp%20Harrier   | New Zealand           |
| Swamp harrier         | 2            | 0:02                            | Xeno-Canto     | http://www.xeno-canto.org/browse.php?query=Swamp%20Harrier   | New Zealand           |
| Swamp harrier         | 3            | 0:02                            | Xeno-Canto     | http://www.xeno-canto.org/browse.php?query=Swamp%20Harrier   | New Zealand           |
| Swamp harrier         | 4            | 0:02                            | Xeno-Canto     | http://www.xeno-canto.org/browse.php?query=Swamp%20Harrier   | New Zealand           |
| Swamp harrier         | 5            | 0:02                            | Xeno-Canto     | http://www.xeno-canto.org/browse.php?query=Swamp%20Harrier   | New Zealand           |
| Swamp harrier         | 6            | 0:02                            | Xeno-Canto     | http://www.xeno-canto.org/browse.php?query=Swamp%20Harrier   | New Zealand           |
| Bulbul alarm call     | 1            | 0:03                            | Xeno-Canto     | http://www.xeno-canto.org/sounds/uploaded/UUXSJGNURV/XC157864-Bulbul %20Red-vented%20%28Pycnonotus%20cafer%29%20alarm%20Mahatma%20RNP.                             | India                 |
| Bulbul alarm call     | 2            | 0:02                            | Xeno-Canto     | mp3<br>http://www.xeno-canto.org/sounds/uploaded/UUXSJGNURV/XC157864-Bulbul<br>%20Red-vented%20%28Pycnonotus%20cafer%29%20alarm%20Mahatma%20RNP.<br>mp3            | India                 |
| Bulbul social call    | 1            | 0:02                            | NZ Biosecurity | http://www.biosecurity.govt.nz/files/pests/red-vented-bulbul/red-vented-bulbul-soundv2.mp3   | New Zealand           |
| Bulbul social call    | 2            | 0:02                            | Xeno-Canto     | http://www.xeno-canto.org/sounds/uploaded/VKGELLURFO/XC161254-Red% 20Vented%20Bulbul%20-Goncoi%2C%20ALdona%2C%20Goa%20_May%2019% 202012%204.28%20pm.mp3            | India                 |
| Bulbul social call    | 3            | 0:02                            | Xeno-Canto     | http://www.xeno-canto.org/sounds/uploaded/VKGELLURFO/XC161471-goa% 20goncoi%20aldona%20red-vented%20bulbul%2012%20sept%202012%206.33% 20pm%20CP.mp3                | India                 |
| Bulbul social call    | 4            | 0:02                            | Xeno-Canto     | http://www.xeno-canto.org/sounds/uploaded/YTUXOCTUEM/XC149692-<br>Pycnonotus_cafer-FL%20song%20calls%20%5Bcom%20tailorb%5D%20Gir%20NP%<br>2028Jan13%20LS113400.mp3 | India                 |
| Bulbul social call    | 5            | 0:02                            | Xeno-Canto     | http://www.xeno-canto.org/sounds/uploaded/EHGWCIGILC/XC146251-red-vented-bulbul.mp3  | Nepal                 |
| Bulbul social call    | 6            | 0:02                            | Xeno-Canto     | http://www.biosecurity.govt.nz/files/pests/red-vented-bulbul/red-vented-bulbul-soundv2.mp3   | India                 |

**Table A2**Exemplars for each treatment and behaviour were fitted to a general linear model to test for exemplar effects

| Vocalization             | F     | df    | P     |  |  |
|--------------------------|-------|-------|-------|--|--|
| Rate of looking          |       |       |       |  |  |
| Swamp harrier            | 1.634 | 5, 16 | 0.208 |  |  |
| Chattering kingfisher    | 0.362 | 1, 19 | 0.555 |  |  |
| Red-vented bulbul alarm  | 0.147 | 1, 19 | 0.706 |  |  |
| Red-vented bulbul social | 0.980 | 5, 17 | 0.458 |  |  |
| Rate of total locomotion |       |       |       |  |  |
| Swamp harrier            | 0.910 | 5, 16 | 0.500 |  |  |
| Chattering kingfisher    | 0.335 | 1, 19 | 0.570 |  |  |
| Red-vented bulbul alarm  | 0.645 | 1, 19 | 0.432 |  |  |
| Red-vented bulbul social | 1.054 | 5, 17 | 0.419 |  |  |
| Rate of bloating         |       |       |       |  |  |
| Swamp harrier            | 1.258 | 5, 16 | 0.329 |  |  |
| Chattering kingfisher    | 0.874 | 1, 19 | 0.362 |  |  |
| Red-vented bulbul alarm  | 2.605 | 1, 19 | 0.123 |  |  |
| Red-vented bulbul social | 0.581 | 5, 17 | 0.715 |  |  |

No exemplar effects were found.

**Table A3** Cohen's effect size calculations

| Interaction              | Cohen's effect size, d |  |  |  |  |
|--------------------------|------------------------|--|--|--|--|
| Rate of looking          |                        |  |  |  |  |
| SC – AC                  | 1.443                  |  |  |  |  |
| SC - KF                  | 0.234                  |  |  |  |  |
| KF - AC                  | 0.632                  |  |  |  |  |
| SH - SC                  | 0.026                  |  |  |  |  |
| SH – AC                  | 0.943                  |  |  |  |  |
| Rate of total locomotion |                        |  |  |  |  |
| SC - AC                  | 0.701                  |  |  |  |  |
| SC - KF                  | 0.419                  |  |  |  |  |
| KF - AC                  | 0.044                  |  |  |  |  |
| SH - SC                  | 0.423                  |  |  |  |  |
| SH – AC                  | 0.688                  |  |  |  |  |
| Rate of bloating         |                        |  |  |  |  |
| SC – SH                  | 0.179                  |  |  |  |  |
| AC - SC                  | 0.602                  |  |  |  |  |
| AC - KF                  | 0.428                  |  |  |  |  |
| AC - SH                  | 0.626                  |  |  |  |  |
| KF - SC                  | 0.178                  |  |  |  |  |

SC: bulbul social call; AC: bulbul alarm call; KF: chattering kingfisher call; SH: swamp harrier call.