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RESEARCH PAPER

Shift down, look up: A test of the non-linearity and fear hypothesis in a non-vocal skink

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Abstract

The non-linearity and fear hypothesis predicts that certain non-linear sounds are one way to evoke antipredator responses in both birds and mammals. This hypothesis, however, has not been studied in non-vocal species or in reptiles. Such a study would be important because if non-linear sounds are evocative even in a species that does not produce sounds, then there may be generally salient cues of risk in these sounds. We asked whether non-vocal lizards, white-bellied copper-striped skinks (*Emoia cyanura*), respond to experimentally broadcast non-linearities. This species is ideal to ask the question in because prior research has shown that they respond to predator sounds and alarm calls of other species even though they are not vocal. We conducted playback experiments with three computer-generated simulated non-linearities to assess whether or not skinks increased antipredator behavior after hearing them. We controlled for novelty by broadcasting a 3-kHz, 500-ms pure tone and tropical kingbird (*Tyrannus melancholicus*) song. Our treatments consisted of a 3-kHz, 400-ms pure tone followed by a frequency shift up to 5-kHz for 100-ms, a 3-kHz, 400-ms pure tone to frequency shift down to 1-kHz for 100-ms, and a pure tone followed by 100-ms of white noise. Following a total of 222 playbacks, we categorized responses into looking, locomotion, and high locomotion, focusing on how skinks changed their rates of time allocation from baseline. We examined 95% confidence intervals to identify whether skinks responded to playbacks and fitted general linear models followed by pairwise comparisons to ask whether skinks discriminated between broadcast stimuli. We found that skinks were especially responsive to frequency downshifts: They significantly increased looking and locomotion, consistent with our predictions based on the non-linearity and fear hypothesis. Surprisingly, they decreased rates of looking behavior after hearing frequency upshifts, possibly suggesting an increase in relaxed behavior. While skinks responded to noise by increasing their rate of locomotion, this response was not significantly different from controls. We conclude that skinks increase antipredator behavior after hearing downshifts more than any other type of non-linearity. This provides some support for the non-linearity and fear hypothesis; even non-vocal species may respond fearfully to specific types of non-linear sounds.

KEYWORDS
antipredator behavior, *Emoia cyanura*, motivation-structural rule hypothesis

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1 | INTRODUCTION

Animals should use any available information to assess the risk of predation, and many species have evolved the ability to respond to sounds that are associated with risk. Such information may come directly from the sounds that predators produce (e.g., Hettena, Munoz, & Blumstein, 2014), indirectly from alarm calls produced by conspecifics (e.g., Klump & Shalter, 1984), or indirectly from alarm calls produced by similarly vulnerable members of other species (Magrath, Haff, Fallow, & Radford, 2015). Taken together this literature has shown that many species capitalize on available acoustic information to improve their assessments of risk, and that even species that do not produce sounds are able to respond to acoustic cues of risk (Huang, Lubarsky, Teng, & Blumstein, 2011; Vitousek, Adelman, Gregory, & St. Clair, 2007). What is lacking is a foundational understanding of whether there are specific acoustic features that may "universally" encode risk to a variety of different taxa.

Darwin's (1872) principle of antithesis describes a relationship between the structure and function of ritualized displays; specifically, those associated with appeasement contrasted with those associated with aggression. Expanding on Darwin's ideas, Morton (1977) focused on vocal communication and proposed a formal motivation-structural rule hypothesis, which predicted a relationship between the specific structure of animal vocalizations and the contexts under which they are used. Morton (1977) made a distinction between high-frequency vocalizations, which are usually fearful or appeasing, and low-frequency vocalizations, which are usually aggressive or hostile. For example, guinea pigs' (*Cavia porcellus*) (Eisenberg, 1974) vocalizations consist of a low-frequency grunt or snort when aggressive, but a high-frequency squeak when appeasing. Chaffinches (*Fringilla coelebs*) (Marler, 1956) modify the structure of their calls between coarse, shrill, and ringing to convey aggression, escape, and conflict, respectively. However, comparative tests of the motivation-structural rule are equivocal. In primates, Gouzoules and Gouzoules (1999) compared the screams of four different species of macaques (*Macaca mulatta*, *Macaca nemestrina*, *Macaca nigra*, *Macaca arctoides*) and found a general relationship between acoustic structure and the vocalizer's state, but no strict support for Morton's motivation-structural rule hypothesis.

An alternative hypothesis focusing primarily on acoustic cues of fear is the non-linearity and fear hypothesis. First proposed by Blumstein and Récapet (2009), this hypothesis focuses on the non-linearities produced when a vocal system is overblown, for instance when an individual screams. These non-linear sounds are predictably unpredictable because they are a product of a non-linear sound production system (Fitch, Neubauer, & Herzen, 2002). The hypothesis suggests that the unpredictability and noisiness of these vocalizations should be generally evocative, and they should be harder to habituate to (Blumstein & Récapet, 2009; Karp, Manser, Wiley, & Townsend, 2013).

Predictions from the non-linearity and fear hypothesis have been tested in marmots (*Marmota flaviventer*) (Blumstein & Récapet, 2009), meerkats (*Suricata suricatta*) (Townsend & Manser, 2011), and birds (Blesdoe & Blumstein, 2014; Slaughter, Berlin, Bower, & Blumstein, 2013). The addition of white noise to simulate deterministic chaos (Blumstein, Whitaker, Kennen, & Bryant, 2017) to marmot alarm calls resulted in decreased foraging time, which was suggested to represent increased responsiveness to playback (Blumstein & Récapet, 2009). In meerkats, alarm calls with non-linearities were harder to habituate to than calls without them (Karp et al., 2013). White-crowned sparrows (*Zonotrichia leucophrys*) were significantly less relaxed after hearing frequency downshifts, but not after hearing pure tones or frequency upshifts (Blesdoe & Blumstein, 2014). Great-tailed grackles (*Quiscalus mexicanus*) presented with various non-linear sounds responded most evocatively to frequency downshifts, particularly those with more abrupt frequency changes (Slaughter et al., 2013). The non-linearity and fear hypothesis has also been tested in humans: Novel music clips incorporating synthesized non-linearities have been shown to elicit increased perceptions of arousal (Blumstein, Bryant, & Kaye, 2012). Additionally, there is a relationship between a film's genre and the frequency of use of specific non-linear sounds (horror films had more noisy screams than would be expected by chance while sad dramatic films had less noisy sounds–Blumstein, Davitian, & Kaye, 2010). Taken together, we can hypothesize that noise and other non-linearities are specifically evocative to a range of species.

The non-linearity and fear hypothesis has been tested exclusively on species which produce sounds and presumably include non-linear sounds in their repertoire. It remains an open question as to whether or not species that do not produce sounds may still respond in similar ways to non-linearities. There is reason to suspect that they might, because even reptiles that do not produce alarm vocalizations respond to the sounds of potential predators (Fuong, Keeley, Bulut, & Blumstein, 2014; Huang et al., 2011; Vitousek et al., 2007). For example, Galapagos marine iguanas (*Amblyrhynchus cristatus*), non-vocal lizards, increased antipredator and vigilance behaviors in response to heterospecific alarm calls. Previous research on skinks and lizards also showed that they can eavesdrop on heterospecific alarm calls (Fuong et al., 2014) and respond to predator vocalizations from kestrels (*Falco sparverius*) as well as camera shutter clicks (Huang et al., 2011).

Fuong et al. (2014) found specifically that white-bellied copper-striped skinks (*Emoia cyanura*) increased antipredator behavior in response to the alarm calls of red-vented bulbuls (*Pycnonotus cafer*), a heterospecific that may share predators with skinks. Following from this understanding that skinks respond fearfully upon hearing heterospecific alarm calls, we ask whether skinks respond fearfully upon hearing synthetic, non-linear sounds. If non-linearities were generally evocative, even in non-vocal species, then we predicted that skinks would have heightened responses after hearing non-linear sounds compared to a variety of control sounds.

2 | METHODS

2.1 | Study site and species

We studied the response of white-bellied copper-striped skinks (Family Scincidae) to playback in and around the University of California Berkeley Richard Gump Research Station in Mo'orea, French Polynesia (17°29′32′′S, 149°49′39′′W) from 18 Jan. to 1 Feb. 2018. Skinks are approximately 8–12 cm body length and identified to species by their distinct three light-colored dorsal stripes and greenish-brown tails (Zug, 2013). Three researchers worked independently between 0700 and 1500 hr at different study sites every other day throughout the study period. We avoided visiting the same site on consecutive study days to prevent habituation. We used two controls: a pure tone and five exemplars of tropical kingbird (*Tyrannus melancholicus*) song. Our nonlinearities included a rapid frequency shift up, a rapid frequency shift down, and noise. We conducted a total of 222 playbacks to white-bellied copper-striped skinks: 44 frequency shifts down, 45 frequency shifts up, 44 tropical kingbird exemplars, 45 frequency shifts to noise, and 44 pure tones. The pure tone, shift up, shift down, and noise sounds were computer-generated and were the same sounds used by Slaughter et al. (2013), while the tropical kingbird exemplars (also used by Slaughter et al.) were taken from a commercially produced CD (Oberle, 2008). Tropical kingbirds are neither a predator, nor are the skinks at our French Polynesian study site familiar with them, so they served as a biologically novel control stimulus. Although some individuals may have inadvertently been resampled, skinks were locally abundant, and this substantially decreases the likelihood of inadvertently re-testing the same individuals. Each observer used a Latin Square Design for playback stimuli to ensure a balanced distribution of treatments, resulting in no potentially confounding carryover effect.

2.2 | Behavioral observations

We broadcast exemplars of acoustic stimuli (saved as uncompressed AIF files) obtained from Slaughter et al. (2013). The computer-generated stimuli were 500 ms, and the five distinct tropical kingbird exemplars were approximately 1 s long, but stimulus length varied slightly by exemplar. Sounds were broadcast with Apple iPhones (Apple Inc., Cupertino, CA, USA) through Tivoli Audio iPal speakers (Tivoli Audio LLC, Boston, MA, USA). We calibrated our speakers using a sound level meter (Radio Shack model 33-2055 Digital Sound Level Meter, Fort Worth, TX, USA) so that all were broadcast at 85 dB (±1 dB SPL, level A, fast response, measured 1 m from speaker), which is similar to the amplitude of natural bird sounds that skinks heard in their habitat.

Skinks were abundant and were found primarily near foliage and brown leaf debris along paths, mostly concentrated near denser vegetative cover. Observers trained together several times at the start of the study until behaviors were scored consistently. Working independently thereafter, we searched for skinks by slowly and quietly walking along trails in their habitat. Once a skink was identified, we positioned speakers directly toward them, 1 m above the ground and 3 m away (Fuong et al., 2014; Huang et al., 2011). We allowed them to acclimate to our presence, shown by slowly walking and low rates of looking. Once the skink was relaxed, we began a 30-s baseline focal observation. Immediately following this we broadcast the acoustic treatment and continued our focal observation for the next 60 s. Behavioral transitions were dictated and later scored using JWatcher 1.0 (Blumstein, & Daniel, 2007). Following the playback, we recorded observer, date, time, number of conspecifics within 1 m, exact distance from speaker (m), wind speed (Beaufort scale), and additional comments. After conducting one trial, we moved 10 m and continued looking for the next skink to repeat the process with a different playback stimulus. This distance decreased the likelihood that the next skink had heard a playback, and by rotating playback stimuli using a Latin Square design we further ensured that treatments were not repeated for a considerable geographic distance (often more than 50 m). Experiments were not conducted in high wind (Beaufort scale >4; the vast majority were conducted in Beaufort scale 0–2) or during rain. Moreover, if distracting ambient noise such as adjacent humans, dogs, or motor vehicles occurred during the playback, we removed these trials from further analyses.

2.3 | Statistical analyses

We used JWatcher 1.0 (Blumstein, Richardson, Cooley, Winternitz, & Daniel, 2008) to analyze focal animal samples. Our ethogram followed Fuong et al. (2014) and included look, walk, run, tail wag, jump, bloat, other, and out of sight (Table 1). We focused on the change in rates of looking, total locomotion (walk, run, jump), and high locomotion (run and jump only—which we inferred represented a higher risk response) between the 30 s baseline and the first 30 s following the playback sound (Table 1). We did not include bloating in our analyses because we did not observe much bloating behavior, and thus, we cannot compare that specific response with the results of bloating in Fuong et al. (2014). We calculated rates as the numbers of times the behavior occurred divided by the total time the individual was in sight. We subtracted the rate of each pre-playback (baseline) behavior from the post-playback response to standardize behavioral changes for each individual observed. From these calculated values, a negative change value indicated a decrease in the rate of behavior, while a positive change value indicated an increase in the rate of behavior. Following Fuong et al. (2014), we analyzed the difference from baseline for the first 30 s after the playback. By expressing responses as difference from baseline, and calculating 95% confidence intervals, we are able to determine if skinks responded to the playback (CI's that did not include zero indicate a response).

Formally, to determine if there was a response to playback, we examined the mean and 95% confidence interval for each change in rate of behavior with respect to treatment. We then fitted the responses to a series of general linear models in SPSS v.24 (IBM, Armonk, NY, USA) to explain variation in response to playback.

TABLE 1 Ethogram of copper-striped skinks behavior (modified from Fuong et al., 2014)

Behavior	Definition
Stand and look[a]	Fixed body and head position. Scored with each visible head movement (which is interpreted as a shift in gaze)
Walk[b]	Locomotion (any number of steps) using all four legs
Run[b,c]	Fast locomotion (any number of steps) using all four legs
Jump[b,c]	Movement off the ground
Tail wag	Tail movement
Bloat	No change in position with expanding body. Scored with each body expansion
Other	Other behaviors not listed
Out of sight	Skink was not in sight either because it disappeared into the litter or view was obstructed by vegetation

[a]Analyzed as looking. [b]Analyzed as locomotion. [c]Analyzed as high locomotion.

Our independent variables included treatment, number of conspecifics within 1 m, observer, and distance to observer. We set our alpha to 0.05. Pairwise comparisons (not adjusted for multiple comparisons) asked if skinks were able to significantly differentiate between two different stimuli. We tested the homogeneity of variance across treatments using Levene's test. Looking and locomotion had non-significant Levene's tests ($p > 0.05$; high locomotion was significant ($p = 0.046$). Transformation failed to homogenize variation and the results were not influenced by transformation so we report the untransformed results. Plots of predicted versus standardized residuals did not have obvious relationships, and a visual examination of residuals did not reveal substantial deviation from normality.

Skinks were studied under UCLA Animal Use Protocol 2000-147 (11 Jan. 2018) and under permission of the Government of French Polynesia (permit approved on 9 Nov. 2017). By design, playbacks led to only brief responses. Animals were neither captured nor marked as part of this study.

3 | RESULTS

Skinks increased their rate of looking after hearing shift down and decreased their rate of looking after hearing shift up playbacks (Figure 1). Skinks increased locomotion in response to noise and increased high locomotion in response to shift down playbacks (Figure 1). There was a significant overall treatment effect on rate of looking ($F_{4,213} = 3.145$, $p = 0.015$) but not for locomotion ($F_{4,213} = 1.343$, $p = 0.255$) or high locomotion ($F_{4,213} = 1.363$, $p = 0.248$). Pairwise comparisons revealed that after hearing a shift down stimulus, skinks increased their rate of looking compared to pure tone ($p = 0.006$) (Figure 1A), tropical kingbird ($p = 0.023$), and shift up ($p = 0.001$). Skinks also increased their rate of total locomotion (but not high locomotion) after hearing a shift down stimulus compared to a pure tone ($p = 0.041$) (Figure 1B). For rates of looking, only the number of conspecifics ($F_{1,213} = 4.731$, $p = 0.031$) was a significant covariate; observer ($F_{2,213} = 1.918$, $p = 0.149$) and distance to speaker ($F_{1,213} = 0.986$, $p = 0.322$) did not explain significant variation. For rates of locomotion and high locomotion, no covariates significantly explained variation in rates (all p-values >0.173).

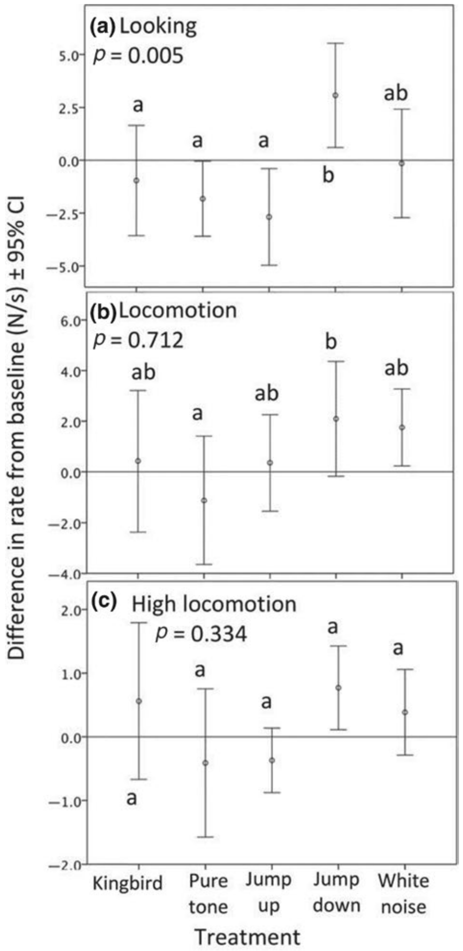

FIGURE 1 Means (±95% CI) for change in rate from baseline of (A) looking, (B) total locomotion, (C) high locomotion in white-bellied copper-striped skinks (*Emoia cyanura*) after playbacks of different sounds with and without simulated non-linearities. p-values were obtained from general linear models. Different letters indicate significant differences in behavioral responses ("a" is significantly different from "b," while "ab" is not significantly different from "a" or "b")

4 | DISCUSSION

White-bellied copper-striped skinks responded fearfully to two out of three of the non-linear sounds we broadcast; they did not respond to either of the two controls. After hearing frequency downshifts, skinks increased their rate of looking. Additionally, as skinks had more conspecifics within 1 m, rates of looking decreased, a finding consistent with the increased security of being in a larger group (Beauchamp, 2014; Roberts, 1996). Thus, increased rates of looking can be interpreted as fearful responses to threatening situations. In addition, skinks hearing our noise playback increased total locomotion compared to baseline levels, but this increase was not significantly different from controls.

Rapid frequency upshifts resulted in less looking, indicating more relaxed behavior and supporting Morton's (1977) conclusion that frequency shifts up are generally produced in appeasing contexts. Rapid frequency downshifts resulted in increased looking and high locomotion, which is consistent with Morton's (1977) complementary conclusion that frequency shifts down are produced in aggressive or hostile interactions.

Surprisingly, we found no consistent antipredator responses to white noise. Previous experiments found that noise and frequency shifts down were the most evocative stimuli in sparrows (Blesdoe & Blumstein, 2014), abrupt frequency shifts were most evocative in grackles (Slaughter et al., 2013), noise elicited the greatest responses in marmots (Blumstein & Recapet, 2009), and meerkats responded by decreasing foraging after hearing alarm calls with subharmonic non-linearities (Townsend & Manser, 2011). Non-vocal skinks responded more strongly to only rapid frequency downshifts. Thus, our results indicate that not all non-linearities have the same valence since downshifts are only one type of non-linearity. The difference in response questions whether it is any non-linearity or only specific ones that may evoke fearful responses.

Regardless of which specific non-linearities skinks respond to, skinks must obtain some benefit from having the ability to respond to rapid downshifts, and these results provide strong support for Morton's (1977) motivation-structural rule hypothesis. Skinks increased vigilance after exposure to downshifts, which can be explained by the associations Morton made between downshifts and aggression. In addition, skinks decreased vigilance after hearing upshifts, which is consistent with Morton's prediction that these sorts of sounds are used in appeasing contexts.

Can we explain this difference in response between rapid upshifts and rapid downshifts? Error management theory predicts specific biases when there are potential negative consequences associated with making a decision (Johnson, Blumstein, Fowler, & Haselton, 2013). Avoiding risky decisions maximizes an individual's chance of survival, and there is a bias toward making the least costly error where consequences differ (Johnson et al., 2013). Thus, individuals tend to err on the side of caution (Haselton & Nettle, 2006). The logic of error management theory may explain why skinks tend to respond to the rapid downshift: It is more likely associated with threats.

How do animals acquire this ability to respond to non-linearities? Responses to conspecific alarm calls have been previously suggested to not necessarily require experience with conspecific alarm vocalizations, while learning is usually invoked to explain the responses to heterospecific alarms (Fallow, Gardner, & Magrath, 2011; Herzog & Hopf, 1984; Magrath & Bennett, 2012). We know that skinks presumably learn to respond to heterospecific alarm calls and predator sounds (Fuong et al., 2014). Importantly, skinks are naturally exposed to sounds that contain both frequency shifts up and down. At our study site skinks routinely heard bulbul alarm calls (Fuong et al., 2014) and rooster's crows (a species that could eat them; Muyshondt, Claes, Aerts, & Dirckx, 2017) which contain rapid frequency changes both up and down. Skinks seemingly biased what they learned toward downshifts. Marler (1970) suggested that animals are programmed to learn biologically important things. Thus, programmed learning, combined with the logic of error management theory, may explain why skinks show a bias toward rapid frequency downshifts but not upshifts: Downshifts are more likely to be associated with threatening or alarming situations.

We conclude that skinks increase antipredator behavior after hearing downshifts more than any other type of non-linearity. This provides some support for the non-linearity and fear hypothesis; non-vocal species may respond fearfully to specific types of non-linear sounds. Being able to produce vocal alarm signals may not be essential for being able to associate biologically relevant sounds with threats.

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