

Human vocalizations impact skink risk assessment depending on human exposure

Carla Bruebach^{a,**}, Lauren Harper^{a,**}, David Jen^{a,*}, Amanda Leyel^{a,*}, Sean O’Fallon^a, Daniel T. Blumstein^{a,*}

^a Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90095-1606, USA

** denotes equal contribution listed alphabetically

*Corresponding Author

*Address correspondence to Daniel T. Blumstein. E-mail: marmots@ucla.edu

Handling editor: Zu-Shi Huang

David Jen ORCID ID: 0009-0004-7537-6237

Amanda Leyel ORCID ID: 0009-0001-5285-3545

Sean O’Fallon ORCID ID: 0000-0002-0169-3692

Daniel T. Blumstein ORCID ID: 0000-0001-5793-9244



© The Author(s) 2025. Published by Oxford University Press on behalf of Editorial Office, Current Zoology.

This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial License (<https://creativecommons.org/licenses/by-nc/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited. For commercial re-use, please contact reprints@oup.com for reprints and translation rights for reprints. All other permissions can be obtained through our RightsLink service via the Permissions link on the article page on our site—for further information please contact journals.permissions@oup.com.

Abstract

Sounds, like screams, which contain acoustic nonlinearities can elicit fearful, emotional responses in animals. In humans, screams activate the amygdala and are perceived as less positive than spoken words. We conducted a playback experiment to see if two skink species (one of which is known to negatively respond to nonlinearities) responded differently to human spoken word and screams. We broadcast short phrases of humans screaming, humans speaking, or a control, a novel bird song. We studied the immediate response by quantifying the change in rates of vigilance and locomotion. We also studied a slightly delayed response in risk assessments by measuring skink flight initiation distance after the playback. Furthermore, we conducted experiments in non-residential and residential areas to understand how human exposure may influence human discrimination and potentially valence perception (i.e., how sound is emotionally perceived). Blue-tailed skinks (*Emoia impar*) altered both immediate behavior and their delayed risk assessment when human screaming was broadcast, but only in residential areas. By contrast, white-bellied copper-striped skinks (*Emoia cyanura*) only altered their delayed risk assessment when human stimuli were broadcast in residential areas. These results indicate that skinks respond differently to human vocalizations depending on their exposure to humans and based on species-specific behaviors. Our results suggest the importance of considering many variables when studying cognition in nature. The amount of human exposure and the acoustic cues contained in auditory stimuli may affect an individual's risk assessment and behavioral responses.

Key words: blue-tailed skink, white-bellied copper-striped skink, flight initiation distance, human exposure, nonlinearity, valence.

Graphical abstract

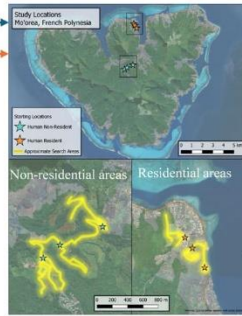
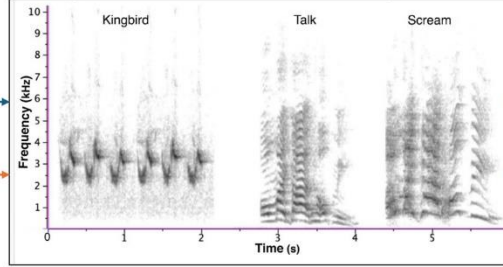
Blue-tailed Skink
(*Emoia impar*)



Copper-tailed Skink
(*Emoia cyanura*)



Grouped by playback treatments (1 playback per unique skink) and residential and non-residential locations to measuring short term behavior and delayed risk assessment



Human screams broadcast in residential areas altered short-term behavior (vigilance) and delayed risk assessment (flight initiation distance)

Human sounds (talking and screams) broadcast in residential areas altered only delayed risk assessment (flight initiation distance)

Species differ in their responses to human vocalizations as a function of human exposure

Accepted Manuscript

Risk assessment is vital for survival. Animals must weigh the costs and benefits of every decision. Many of these assessments rely on stimuli produced by both conspecifics and heterospecifics, with many using acoustic cues to evaluate predation risk (Fallow et al. 2011; Hettena et al. 2014; Ito et al. 2009; Vitousek et al. 2007). Such cues vary in their acoustic structure and may depend on the context in which they are used (Morton 1977). Morton's motivation-structural rule hypothesis categorizes high-frequency vocalizations as more appeasing or fearful, whereas low frequency vocalizations as aggressive or hostile. Similarly, nonlinearities—unpredictable and jarring frequency fluctuations—are also found within vocalizations that typically signal distress (Anikin et al. 2020; Blumstein 2025). Due to the sudden and discordant frequency changes, nonlinearities are effective at capturing attention and harder to habituate to, giving them an evocative nature that can modify a listener's behavior (Blumstein & Récapet 2009; Karp et al. 2013; Reby & Charlton 2012; Ruiz-Monachesi & Lubra 2020). For instance, in meerkat (*Suricata suricatta*) alarm calls, calls containing nonlinearities elicited stronger responses in conspecifics (as measured by a reduction in foraging time (Townsend & Manser 2011)). Non-vocal marine iguanas (*Amblyrhynchus cristatus*) respond to Galápagos mockingbird (*Nesomimus parvulus*) alarm calls and exhibit antipredator responses when alarm calls are played (Vitousek et al. 2007).

Recent research has suggested that humans occupy the niche of “super predator”, where other top predators are affected by human presence (Clinchy et al. 2016; Crawford et al. 2022; Zanette et al. 2023). Pumas (*Puma concolor*) living closer to humans had higher kill rates of mule deer (*Odocoileus hemionus*) than those living further from people possibly due to a fear of humans driving them to spend less time at each kill site and thus consume less of each kill (Smith et al. 2015). Similarly, pumas that heard human playbacks spent less time feeding and took longer to

return to the site (Smith et al. 2017). Yet another playback study found that animals on higher trophic levels reduced their foraging activity and acted more cautiously in response to human voices, while animals on lower trophic levels were emboldened to use their habitat more (Suraci et al. 2019). Urban herring gulls (*Larus argentatus*) reacted to a man's shouting in a similar way they would to a conspecific alarm call (Di Giovanni et al. 2022). Thus, animals can and do respond to the presence of humans in their environment and may generally perceive them as risky (Frid and Dill 2002).

However, other studies have found that risk assessment may differ based on the amount of human exposure and coexistence with humans. Previous literature suggests that some animals that live closer to humans are able to better discriminate alarm calls (Carrasco & Blumstein 2012; Coleman et al. 2008) and alter their foraging and antipredator behavior (Coleman et al. 2008). The influence of human presence has also been studied in blue-tailed skinks (*Emoia impar*). McGowan et al. (2014) and Williams et al. (2020) found that human density affected skink risk assessment as quantified by flight initiation distance (FID). FID is defined as the distance at which an animal escapes an approaching threat where a greater FID suggests a greater perceived risk (Ydenberg & Dill 1986).

Although prior studies assessed how human presence affects risk assessment, there has been little research conducted specifically on the effect of human vocalizations on risk assessment, especially with non-vocal species. Some non-vocal species respond to threatening sounds. For instance, white-bellied copper-striped skinks (*Emoia cyanura*) reduced the rate at which they moved their heads (which was interpreted as a reduction in the rate of looking) following the playback of an alarm call from a sympatric non-predatory bird compared to controls (Fuong et al.

2014). White-bellied copper-striped skinks also increased rates of looking after hearing playbacks of synthetic nonlinearities (Yan et al. 2019).

We wished to know whether skinks responded to human voices and whether this varied based on their exposure to humans. Prior work found that skinks altered their antipredator behavior in response to human presence (McGowan et al. 2014; Williams et al. 2020) as well as responded specifically to sounds containing nonlinearities (Yan et al. 2019). Thus, this system seemed well-suited to study the interaction of these two factors on skink behavior.

To assess the immediate and slightly delayed response of human vocalizations on blue-tailed and white-bellied copper-striped skinks' risk assessment, we conducted a playback experiment where we broadcast human speaking simple phrases, humans screaming the same phrases, and a novel kingbird call and quantified their responses on two time scales. We defined immediate responses as the behavioral response within 30 s of playback and delayed responses occurring after that. Following the playback we studied whether skink's assessment of risk was modified by the playback by walking towards them until they escape. So that we could understand whether frequent exposure to humans affected these responses, we conducted the experiments in residential locations and locations where humans were only intermittent visitors in that they walked, drove, or bicycled through the areas but there were not permanent residences in them.

We had two hypotheses. First, we hypothesized that both skink species found in residential areas would be better able to respond to differences in human valence than skinks in areas with less human presence because they were more accustomed to human vocalizations. Second, we hypothesized that both skink species would have greater changes in immediate behavior and later risk assessment after hearing human screams compared to human talking or the novel kingbird

specifically because the human screams contained nonlinearities which made them more evocative (Anikin et al. 2020).

Materials and Methods

Study area and system

We studied blue-tailed and white-bellied copper-striped skinks on the island of Mo'orea, French Polynesia (17°32'19.8"S 149°49'46.3"W). Blue-tailed skinks (Fig. 1a) were identified by a vibrant blue tail and white-bellied copper-striped skinks (Fig. 1b) were identified by copper or cream colored tails. To avoid misidentification, we did not conduct experiments on juveniles, due to their tail color not being fully developed, and skinks without tails.

We conducted the study every other day from 25 January 2024 to 2 February 2024 during the time of day where skink activity was at its peak (08:00-12:00) on multiple locations (Fig.2) chosen because they were studied before (McGowan et al. 2014). We had three locations near permanent human residences: Richard B. Gump South Beach Research Station (17°29'22.1"S 149°49'34.7"W), the Te Pu 'Atiti'a cultural center (17°29'34.8"S 149°49'35.9"W), the area surrounding the Manutea–Tahiti Rotui Juice Factory and Distillery (17°29'23.5"S 149°49'44.4"W) where human presence and exposure was frequent and in areas where humans lived. We also sampled three locations far from permanent residences: Agricultural College Opunohu (17°31'41.0"S 149°50'14.0"W), a cross-island trail (17°31'19.6"S 149°49'47.5"W), and the dirt road and area near Ranch Opunohu (17°31'35.3"S 149°50'06.3"W). These “non-residential areas” were at a higher elevation and more than five kilometers from any busy

residential area. Given the way the locations were situated on the island, we were unable to remove this potential confound between elevation and human impact.

Both species were abundant so sampling the same individual was unlikely. However, we still took precautions to avoid this. The same location was not revisited on the same day and observers at the same location were given different paths to sample from. To minimize carry-over effects of skinks influenced by a previous trial we ensured that skinks were at least 10 meters apart between experiments (*sensu* Williams et al. 2020); most were substantially farther apart. Due to the sporadic nature of skink habitats, we did not set a time constraint before proceeding with a new trial, but trials were at least five minutes apart. Furthermore, using a predetermined list, we alternated which stimulus was played in succession so that each stimulus and exemplar was played an equal amount of times and never consecutively.

Playback creation

We used three different auditory stimuli: kingbird (*Tyrannus tyrannus*) calls, human talking, and human screaming (Fig. 3). The kingbird call was used as a non-threatening sound that controlled for novelty since it was not found in Mo'orea. For our human vocalizations, we selected a subset of the sounds used by Arnal et al. (2015), which investigated how acoustic qualities in human screams affected perception and detection. These samples varied in their roughness, a type of nonlinearity that results from extremely rapid amplitude fluctuations (Arnal et al. 2015) as well as possessing other nonlinearities (Anikin et al. 2020). The screams in this study specifically differed from the spoken phrases (all were spoken or screamed in English; French is the official language in Mo'orea) in their negative valence as perceived by humans and were shown, by an

fMRI study, to differentially activate the human amygdala (Arnal et al. 2015). We used the software SoundStudio (Felt Tip 2022) to construct playback tracks. Each playback consisted of 30 s of silence, 2 s of stimuli, and then 60 s of silence. All of these stimuli were 2 s (*contra* Yan et al. 2019; which used 1 s stimuli). To avoid pseudoreplication, we had four different exemplars of each acoustic stimulus (kingbird calls, talking, screaming) that contained different phrases vocalized by different individuals. We normalized all stimuli to the same peak amplitude and then broadcast them at 85 ± 1 dB measured at 1 m (A weighting). While 85 dB is relatively loud for human talking, we needed to control amplitude since we focused on interpreting changes in valence perception, not loudness.

Data collection

At the start of the study, four observers trained together to ensure scoring and procedures were consistent. For subsequent playbacks and FIDs, all observers worked independently, but followed the same protocol. Once a skink was identified, the observer stopped and then slowly placed themselves an estimated 3 meters away from the skink. We then set up an Ultimate Ears - BOOM 2 speaker (Ultimate Ears, Irvine, CA; frequency response: 90-20,000 Hz) 1 m off the ground and started the playback audio within 30 seconds of skink identification. Throughout the 90 second playback, the observer quietly dictated the behavior of the individual into an audio recording device (Cappsu 64GB Digital Voice Recorder, model: V01, Shenzhen).

Our ethogram, based on the work of Fuong et al. (2014), contained several behaviors that are all indicative of the skink's vigilance as seen and defined in Table 1. We discarded observations if the skink disappeared before the stimulus was played.

For those individuals that remained in sight after we conducted the playback, we measured FID immediately after the 90 second playback. The observer first dropped a weighted flag made to mark the starting distance (SD) of FID. This distance was included as it is important as FID varies based on the starting distance of the approaching person (Blumstein 2003). The observer then directly approached the individual while looking at them at a constant (trained) speed of 0.5 m/s. If we could detect it, the observer marked the location with a second flag where the skink first responded to the approaching human by moving its head (alert distance). The observer marked the skink's location when it fled (FID) with a third flag. Then the observer measured the distance between each flag with a measuring tape to the nearest centimeter. For those individuals that fled before or directly after the playback ended, FID was not conducted.

We recorded wind speed, measured on the Beaufort scale; all were conducted when Beaufort was less than 3. We did not conduct the trial if potential predators (dogs, cats, raptors, and chickens) were in sight. We did not conduct (or terminated) experiments when a car or all-terrain vehicle drove by within 2 m. Conspecifics and heterospecifics (such as dogs, cats, chickens, and raptors), were recorded only if they were within a 1 m of the skink being observed. Finally, we estimated the skink's body size (measured as snout to tail length; average error: ± 0.55 cm based on the estimation of known-sized sticks in the same habitat).

Statistical analysis

We scored our focal observations using JWatcher v. 1.0 (Blumstein & Daniel 2007), an event recording program which codes behavioral transitions and quantifies time allocation. We conducted our statistical analyses in R (version 4.3.2; R Core Team, 2023). We used the

following statistical packages: dplyr (Wickham et al. 2023), ggplot2 (Wickham 2016), and performance (Lüdecke et al. 2023). We grouped behaviors as in Yan et al. (2019), with walking, running and jumping classified as total locomotion and looking was not grouped and was analyzed as its own category. While we aimed to examine bloating and tail wagging, these behaviors were too rare to use in our analysis. Following Yan et al. (2019), we focused on comparing the first 30 s after the stimulus to the 30 s interval before the stimulus was broadcast. To do so, we calculated the change in the rates of behavior (N events divided by the time the skink was in sight) and, using these rates, calculated the change in rates of behavior (N/s) before and after playback. Following Yan et al. (2019), we interpreted increased looking rate and locomotion rate along with greater FIDs as reflecting enhanced perceptions of risk because these are antipredator behaviors commonly found in lizards (Martín et al. 2009). Conversely, we interpreted lower FIDs and decreased looking rate and locomotion rate as more relaxed responses.

We fitted three linear models for both species: one for total locomotion, one for looking and one for FID. In each model, we fit our dependent variable as a function of treatment, location (residential or non-residential areas), the interaction of treatment and location. The total locomotion model for blue-tailed skinks was log transformed to meet model assumptions. To this we then added skink size and observer iteratively. Skink size, and number of conspecifics and heterospecifics were not significant, and so we omitted it from our models. Observer effects were significant within total locomotion and look models so they were included as covariates. Due to a broad range of SDs for our FID estimates, we tested if restricting the data to a limited range of SDs (2.5-4.5 m) would qualitatively alter our results. It did not (see Supplementary Material) and thus we report the results based on the full data set with the complete range of SDs.

We used the R package performance to evaluate assumptions of our models. We found that, despite trying a variety of transformations, we were unable to meet the normality assumptions of linear models because our data for locomotion and looking rates in both skink species was zero-inflated. Thus, we used a permutation test (with 1000 random permutations) to study the effects of treatment on behavioral responses for these four data sets. Given individuals were randomly assigned to treatments, we feel confident in assuming ‘exchangeability’ that is required for permutation tests. We report the estimates from the linear models, but we report the p-values from the permutation tests. In all cases, we set our alpha to 0.05 and interpret $0.05 < p < 0.10$ as moderately significant.

Results

Our final data set contained playback results from a total of 119 blue-tailed skinks and 93 white-bellied copper-striped skinks. Of the 119 playbacks for blue-tailed skinks, 41 were kingbird calls, 40 were human screaming, and 38 were human talking. A total of 24 of 41 of the kingbird playbacks, 17 of 40 of the screaming playbacks, and 22 of 38 of the talking playbacks were conducted in non-residential areas, with the rest being conducted in residential areas. Of the 119 blue-tailed skinks, 55 were found near residential areas with 41 FID trials and 64 were found in non-residential areas with 47 FID trials. After controlling for significant variation of the observer by including it as a factor in our linear models and permutation tests, we found significant interactions between treatment and location for both locomotion rate and looking rate (Table 2a, Table 2b). When compared to kingbird playbacks, blue-tailed skinks exhibited a 56% decrease in locomotion in non-resident areas but a 424% increase in locomotion in residential areas after hearing screams (Table 2a, Figure 4a). Skinks in non-residential areas decreased their rate of

looking by 44% after hearing screams but did not significantly change their rate of looking after hearing talking playbacks. After hearing a scream, skinks in residential areas decreased their rate of looking by 205%, and after hearing the talking playback, their rate of looking decreased by 338% (Table 2b, Figure 4b). There was a significant negative main effect of scream playback on FID (Table 2c, Figure 4c), but more notably, we found a significant interaction between scream playback and human residential status. Blue-tailed skinks in residential areas who were primed with the scream playback fled at larger distances than those not in residential areas, when compared to being primed with the control bird calls (Table 2c, Figure 4c).

Of the 93 playbacks for white-bellied copper-striped skinks, 29 were kingbird calls, 31 were human screaming, and 33 were human talking. A total of 7 of 29 of the kingbird playbacks, 14 of 31 of the screaming playbacks, and 10 of 33 of the talking playbacks, were conducted in non-residential areas, with the rest being conducted in residential areas. We acknowledge that our random sampling protocol resulted in relatively few non-residential playbacks of kingbirds. Of the 62 residential playback trials, we were able to collect 42 FID trials. For the 31 non-resident playback trials, we were able to collect 25 FID trials. After controlling for significant variation of observer, there were no significant effects nor interactions of any playback in either area on total locomotion rates or looking rates (Table 2a, Table 2b, Figure 4d, Figure 4e). White-bellied copper-striped skinks did not alter their short-term behavioral responses to either playback in either residential status, when compared to the control bird call.

However, white-bellied copper-striped skinks had different FID responses according to playback. Compared to the control, these skinks tolerated closer approaches after hearing talking or screaming by 110% and 129% respectively. White-bellied copper-striped skinks in residential areas also tolerated closer approaches and there was a significant positive interaction between

treatment and human residence (Table 2c, Figure 4f)). Compared to responses to the control sound, white-bellied copper-striped skinks primed with either human vocalization playback fled at larger distances in residential areas than in nonresidential areas (Table 2c, Figure 4f). These significant interactions explaining variation in FID continue to show that location can influence response to playbacks.

Discussion

We have shown that human exposure influences risk assessment and the ability of non-vocal blue-tailed and white-bellied copper-striped skinks to discern human sounds. Both species have been shown to respond to acoustic playbacks (e.g., Fuong et al. 2014; Yan et al. 2019), but this is the first experiment asking about their specific ability to respond to playbacks of human vocalizations. Blue-tailed skinks had immediate responses, as illustrated by their behavioral response to playback, and slightly delayed responses, as illustrated by their FID following playback, but only in residential areas where humans were consistently around. White-bellied copper-striped skinks did not respond differently in their immediate behavioral response to any of the playbacks, but did have an FID response. Following the talk and scream playbacks in residential areas, white-bellied copper-striped skinks had higher FIDs compared to their FID following the kingbird calls.

These results further confirm that nonvocal species can discern and respond to acoustic cues. Blue-tailed skinks responses were consistent with other reptile species, such as the non-vocal marine iguanas that display anti-predator responses upon hearing Galápagos mockingbird alarm calls (Vitousek et al. 2007) and Madagascan spiny-tailed iguana (*Oplurus cuvieri cuvieri*) that

heighten antipredator vigilance in response to hearing Madagascar paradise flycatcher (*Terpsiphone mutata*) alarm calls (Ito et al. 2009). However, the white-bellied copper-striped skinks did not have an immediate behavioral response to screams; rather, screams modified their delayed risk perception as seen by the increase in their FID after hearing screams. These responses were somewhat inconsistent with Yan et al. (2019) who found that white-bellied copper-striped skinks had an immediate behavioral response after hearing synthetic nonlinear playbacks. Perhaps human screams are not immediately evocative to this species, but nonetheless do modify delayed risk perception.

It is plausible that the different responses by these two close relatives may be due to the difference in coloration between the two species. The blue-tailed skinks are much more vivid and conspicuous than the white-bellied copper-striped skinks and this conspicuousness may be associated with how they manage threatening situations. Previous research has found that more vivid birds tend to exhibit increased rates of locomotion following predator call playbacks and are more wary than their less vivid counterparts (Journey et al. 2013). Yet, another study found that more vivid birds did not have significantly different FIDs than less vivid birds (Hensley et al. 2015). Our findings support both these previous studies as the more vivid blue-tailed skink had an immediate behavioral response in the form of higher rates of locomotion and looking than the less vivid white-bellied copper-striped skinks. Both species still had delayed responses indicated by higher FIDs. Future research on the association between detectability and response to a threat are needed to better understand whether and how increased vulnerability explains variation in response to threats.

Even though these two species are sympatric, they responded not only in different ways, but also to different stimuli. This could reflect how different species perceive acoustic cues. The

blue-tailed skinks only discerned human screaming playbacks from control playbacks, which suggests that they do not ‘recognize’ humans. Rather, they may instead respond to the different valence and nonlinear characteristics associated with a scream. This result is consistent with the sound of fear hypothesis in which nonlinearities cause calls to be more unpredictable and thus more evocative (Blumstein & Récapet 2009; Karp et al. 2013). These results indicate that it may be an illusion that some species seem to respond to humans by identifying them as humans; rather they may be responding to the acoustic cues contained in human vocalizations. Of course, results where animals are responding to spoken words (Huber et al. 2017; Maigrot et al. 2022; Zanette et al. 2023), particularly if they do not contain non-linearities, are consistent with the hypothesis that animals may identify people based on their sounds alone.

White-bellied copper-striped skinks, on the other hand, responded to both talking and screaming stimuli in their delayed response. This may indicate that they are able to recognize humans, but do not differentially respond to valence. Prior studies have shown that wild animals may respond even more fearfully to human sounds than to their apex predators. For instance, Zanette et al. (2023) showed that a guild of African savannah mammals had enhanced fear responses to playbacks of humans compared to lions (*Panthera leo*). Future research is needed to tease apart the exact reasons these two species of skinks respond in the way they do. Future research could also examine other sounds that naturally contain a variety of nonlinearities to see whether and how they affect antipredator behavior.

Our results are also consistent with previous studies’ findings showing that human exposure altered responses over time (Greenberg and Holekamp 2017; McGowan et al. 2014; Samia et al. 2015; Smith et al. 2015; Williams et al. 2019). The skinks we studied did not change their short-term behavior nor their later risk assessment when human vocalizations were broadcast in areas

where humans were only intermittent visitors, but did change their behavior in areas where humans had a consistent presence. Both species modified their behavior in ways that reflect increased perceptions of risk, but only in residential areas. This suggests that exposure to humans alters risk assessment, or our ability to study it. This finding differs from that reported in other studies where species closer to humans tend to be more tolerant and less fearful (Evans et al. 2010; Lowry et al. 2011; Møller 2008; 2012; Uchida et al. 2019) suggesting that each study system have their own ways of responding to humans based off different stimuli/experiences. For instance, dik-diks foraged more when within 0.5 km of human residence after hearing alarm call playbacks compared to dik-diks further than 0.5 km (Coleman et al. 2008). Similarly, dark-eyed juncos (*Junco hyemalis*) became less fearful of humans in urban areas compared to non-urban areas (Diamant et al. 2023).

There is a growing literature on the effects of urbanization on boldness and other aggressive and antipredator behaviors (Baxter-Gilbert et al. 2019; Lapeidra et al. 2016; Patankar et al. 2021; Sadoul et al. 2021; Samia et al. 2015). Future cognitive studies should explicitly recognize that where animals are studied, with respect to their exposure to humans, can influence their response and hence our ability to quantify cognitive traits and abilities. Thus, while studying animals in their natural environment may be essential to understand the adaptive value of cognition (Goumas et al. 2020; Pritchard et al. 2016), animals' prior experiences and surroundings may influence our ability to quantify their cognitive abilities. An important conclusion from this study is that context matters when asking cognitive questions about animals' perception, learning, memory, and decision making (Dukas 2004; Goumas et al. 2020; Shettleworth 2001). After all, there is a notable difference between trials that ask foraging questions versus those that ask fear related questions. It is important to study cognition in the wild because cognitive abilities

evolved to solve problems animals face in nature (Cole et al. 2012; Keagy et al. 2009; Raine and Chittka 2008). Furthermore, research like this is important because it can inform those involved in wildlife management and conservation about how animals process information (Greggor et al. 2020; Stanton et al. 2023). Nevertheless, as this study has shown, it is essential to consider anthropogenic influences and context when conducting research on seemingly “wild” animals.

Acknowledgements

We thank the staff at University of California Berkeley's Gump Research Station for their hospitality and facilities. We thank Andy Lin for his assistance with our statistical analysis, Luc Arnal for providing the human audio recordings used here (16_scrmsent1.wav, 16_sentmatch1.wav, 18_scrmsent3.wav, 18_sentmatch3.wav, 20_scrmsent4.wav, 20_sentmatch4.wav, 21_scrmsent2.wav, 21_sentmatch2.wav), and two anonymous reviewers for making a series of astute suggestions that improved our paper.

Ethics Statement

Permission to work in Mo'orea was granted by Convention d'accueil number 130005820 approved on 24 November 2023. Experiments were approved by UCLA IACUC protocol number 2000-147 approved on 28 November 2023. Animals were not captured or otherwise touched, experiments were brief, and animals appeared to resume normal behavior soon after the experiments.

Data Availability

Data and code are archived at OSF:

https://osf.io/6cmxn/?view_only=40d4a59c6e6449df9cdb5100c746799f

Authors' Contributions

C.B., L.H., D.J., A.L., and D.T.B. conceived the project, designed the experiments and wrote the first draft of the manuscript. Experiments were executed by the first four people. S.O. and D.T.B. supervised the analysis and interpretation. All authors edited and revised the initial draft and approved of its publication.

Conflict of Interest

The authors declare that they have no competing interests.

Funding

We thank the University of California Los Angeles Department of Ecology and Evolutionary Biology for partial support.

References

- Anikin A, Pisanski K, Reby D, 2020. Do nonlinear vocal phenomena signal negative valence or high emotion intensity? *R Soc Open Sci* 7:201306.
- Arnal LH, Flinker A, Kleinschmidt A, Giraud AL, Poeppel D, 2015. Human screams occupy a privileged niche in the communication soundscape. *Curr Biol* 25:2051–2056.
- Audacity®: Free audio editor and recorder 2014. Audacity Team.
- Baxter-Gilbert J, Riley JL, Whiting MJ, 2019. Bold New World: Urbanization promotes an innate behavioral trait in a lizard. *Behav Ecol Sociobiol* 73:105.
- Blumstein DT, 2025. Non-linear phenomena in marmot alarm calls: a mechanism encoding fear? *Phil Trans R Soc B* (in press)
- Blumstein DT, Sanchez M, Philson CS, Bliard L, 2023. Is flight initiation distance associated with longer-term survival in yellow-bellied marmots, *Marmota flaviventris*? *Anim Behav* 202:21–28.
- Blumstein DT, Récapet C, 2009. The sound of arousal: The addition of novel non-linearities increases responsiveness in marmot alarm calls. *Ethology* 115:1074–1081.
- Carrasco MF, & Blumstein DT, 2012. Mule deer *Odocoileus hemionus* respond to yellow-bellied marmot *Marmota flaviventris* alarm calls. *Ethology* 118:243–250.
- Cole EF, Morand-Ferron J, Hinks AE, Quinn JL, 2012. Cognitive ability influences reproductive life history variation in the wild. *Curr Biol* 22:1808–1812.

- Coleman A, Richardson D, Schechter R, Blumstein DT, 2008. Does habituation to humans influence predator discrimination in Gunther's dik-diks *Madoqua guentheri*? *Biol Lett* 4:250–252.
- Di Giovanni J, Fawcett TW, Templeton CN, Raghav S, Boogert NJ, 2022. Urban gulls show similar thermographic and behavioral responses to human shouting and conspecific alarm calls. *Front Ecol Evol* 10:891985.
- Diamant ES, MacGregor-Fors I, Blumstein DT, Yeh PJ, 2023. Urban birds become less fearful following COVID-19 reopenings. *Proc R Soc B* 290:20231338.
- Dukas R, 2004. Evolutionary biology of animal cognition. *Ann Rev Ecol Evol Syst* 35:347–374.
- Evans J, Boudreau K, Hyman J, 2010. Behavioural syndromes in urban and rural populations of song sparrows. *Ethology* 116:588–595.
- Fallow PM, Pitcher BJ, Magrath RD, 2013. Alarming features: Birds use specific acoustic properties to identify heterospecific alarm calls. *Proc R Soc B* 280:20122539.
- Frid A, Dill LM, 2002. Human-caused disturbance stimuli as a form of predation risk. *Cons Ecol* 6:art11
- Fuong H, Keeley KN, Bulut Y, Blumstein DT, 2014. Heterospecific alarm call eavesdropping in nonvocal, white-bellied copper-striped skinks, *Emoia cyanura*. *Anim Behav* 95:129–135.
- Goumas M, Lee VE, Boogert NJ, Kelley LA, Thornton A, 2020. The role of animal cognition in human-wildlife interactions. *Front Psychol* 11:589978.
- Greenberg JR, Holekamp KE, 2017. Human disturbance affects personality development in a wild carnivore. *Anim Behav* 132:303–312.

- Greggor AL, Berger-Tal O, Blumstein DT, 2020. The rules of attraction: The necessary role of animal cognition in explaining conservation failures and successes. *Ann Rev Ecol Evol Syst* 51:483–503.
- Hettena AM, Munoz N, Blumstein DT, 2014. Prey responses to predator's sounds: A review and empirical study. *Ethology* 120:427–452.
- Huber A, Barber ALA, Faragó T, Müller CA, Huber L, 2017. Investigating emotional contagion in dogs (*Canis familiaris*) to emotional sounds of humans and conspecifics. *Anim Cognit* 20:703–715.
- Ito R, Mori A, 2010. Vigilance against predators induced by eavesdropping on heterospecific alarm calls in a non-vocal lizard *Oplurus cuvieri cuvieri* (Reptilia: Iguania). *Proc R Soc B* 277:1275–1280.
- Journey L, Drury JP, Haymer M, Rose K, Blumstein DT, 2013. Vivid birds respond more to acoustic signals of predators. *Behav Ecol Sociobiol* 67:1285–1293.
- Karp D, Manser MB, Wiley EM, Townsend SW, 2014. Nonlinearities in meerkat alarm calls prevent receivers from habituating. *Ethology* 120:189–196.
- Keagy J, Savard JF, Borgia G, 2009. Male satin bowerbird problem-solving ability predicts mating success. *Anim Behav* 78:809–817.
- Lapiedra O, Chejanovski Z, Kolbe JJ, 2017. Urbanization and biological invasion shape animal personalities. *Global Change Biol* 23:592–603.
- Łopucki R, Klich D, Kiersztyn A, 2021. Changes in the social behavior of urban animals: More aggression or tolerance? *Mammal Biol* 101:1–10.

- Lowry H, Lill A, Wong BBM, 2013. Behavioural responses of wildlife to urban environments. *Biol Rev* 88:537–549.
- Lüdecke D, Ben-Shachar M, Patil I, Waggoner P, Makowski D, 2021. Performance: An R package for assessment, comparison, and testing of statistical models. *J Open Sci Soft* 6:3139.
- Maigrot AL, Hillmann E, Briefer, EF, 2022. Cross-species discrimination of vocal expression of emotional valence by Equidae and Suidae. *BMC Biol* 20:106.
- Martín, J, Luque-Larena, JJ, López, P, 2009. When to run from an ambush predator: Balancing crypsis benefits with costs of fleeing in lizards. *Anim Behav* 78:1011–1018.
- McGowan MM, Patel PD, Stroh JD, Blumstein DT, 2014. The effect of human presence and human activity on risk assessment and flight initiation distance in skinks. *Ethology* 120:1081–1089.
- von Merten S, Oliveira FG, Tapisso JT, Pustelnik A, Mathias MDL et al., 2022. Urban populations of shrews show larger behavioral differences among individuals than rural populations. *Anim Behav* 187:35–46.
- Møller AP, 2008. Flight distance of urban birds, predation, and selection for urban life. *Behav Ecol Sociobiol* 63:63–75.
- Møller AP, 2012. Urban areas as refuges from predators and flight distance of prey. *Behav Ecol* 23:1030–1035.
- Morton ES, 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *Amer Natur* 111:855–869.

- Patankar S, Jambhekar R, Suryawanshi KR, Nagendra H, 2021. Which traits influence bird survival in the city? A review. *Land* 10:92.
- Pritchard DJ, Hurly TA, Tello-Ramos MC, Healy SD, 2016. Why study cognition in the wild (And how to test it): Cognition in the wild. *J Exp Anal Behav* 105:41–55.
- R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing.
- Raine NE, Chittka L, 2008. The correlation of learning speed and natural foraging success in bumble-bees. *Proc R Soc B* 275:803–808.
- Reby D, Charlton BD, 2012. Attention grabbing in red deer sexual calls. *Anim Cognit* 15:265–270.
- Sadoul B, Blumstein DT, Alfonso S, Geffroy B, 2021. Human protection drives the emergence of a new coping style in animals. *PLOS Biol* 19:e3001186.
- Samia DSM, Nakagawa S, Nomura F, Rangel TF, Blumstein DT, 2015. Increased tolerance to humans among disturbed wildlife. *Nat Comm* 6:8877.
- Shettleworth SJ, 2001. Animal cognition and animal behaviour. *Anim Behav* 61:277–286.
- Smith JA, Suraci JP, Clinchy M, Crawford A, Roberts D et al., 2017. Fear of the human ‘super predator’ reduces feeding time in large carnivores. *Proc R Soc B* 284:20170433.
- Smith JA, Wang Y, Wilmers CC, 2015. Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proc R Soc B* 282:20142711.

- Stanton LA, Wilkinson CE, Angeloni L, Benson-Amram S, Schell CJ et al., 2023. Animal behavior, cognition, and human–wildlife interactions in urban areas. In: Lambert M, & Schell C eds. *Urban Biodiversity and Equity*. *New York: Oxford University Press* 177–202.
- Suraci JP, Clinchy M, Zarette LY, Wilmers CC, 2019. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecol Lett* 22:1578–1586.
- Townsend SW, Manser MB, 2011. The function of nonlinear phenomena in meerkat alarm calls. *Biol Lett* 7:47–49.
- Uchida K, Suzuki KK, Shimamoto T, Yanagawa H, Koizumi I, 2019. Decreased vigilance or habituation to humans? Mechanisms on increased boldness in urban animals. *Behav Ecol* 30:1583–1590.
- Vitousek MN, Adelman JS, Gregory NC, Clair JJHS, 2007. Heterospecific alarm call recognition in a non-vocal reptile. *Biol Lett* 3:632–634.
- Wickham H, 2016. ggplot2: Elegant graphics for data analysis. Available at: ggplot2.tidyverse.org
- Wickham H, François R, Henry L, Müller K, Vaughan D, 2023. dplyr: A grammar of data manipulation. R package version 1.1.4.
- Williams DM, Nguyen PT, Chan K, Krohn M, Blumstein DT, 2020. High human disturbance decreases individual variability in skink escape behavior. *Curr Zool* 66:63–70.
- Yan KM, Pinto SP, Vartany C, Blumstein DT, 2019. Shift down, look up: A test of the non-linearity and fear hypothesis in a non-vocal skink. *Ethology* 125:153–158.

Ydenberg RC, Dill LM, 1986. The economics of fleeing from predators. *Adv Study Behav* 16: 229–249.

Zanette LY, Frizzelle NR, Clinchy M, Peel MJS, Keller CB et al., 2023. Fear of the human “super predator” pervades the South African savanna. *Curr Biol* 33:4689-4696.e4.

Accepted Manuscript

Table 1. Ethogram of antipredator or vigilant behaviors in blue-tailed and white-bellied copper-striped skinks (modified from Yan et al. 2019)

Behavior	Definition
Look	Fixed body and head position, scored following each visible head movement
Walk ^a	Locomotion using all four legs
Run ^a	Quick locomotion using all four legs
Jump ^a	Hop off initial position
Tail wag	Tail movement
Bloat	Expanding body with no locomotion or head movement. Scored with each expansion
Out of sight	Not in observer's view, either from vegetation obstruction or after disappearing into the foliage

^a Combined to create total locomotion

Table 2. The response of blue-tailed and white-bellied copper-striped skinks to playbacks. Estimates are from the linear models. P-values are from permutation tests to quantify the effect of treatment on locomotion rate and looking rate and a general linear model to quantify the effect of treatment on flight initiation distance (FID). Significant factors from linear models or permutation tests (bold) and marginally non-significant factors (italicized) are identified. The treatment effects' reference is the kingbird playback, the human use effect reference is nonresident areas, the interactions' reference is Kingbird*Nonresident, and the observers are each compared to Observer 1.

	Blue-tailed		White-bellied copper-striped	
	Estimate	<i>P</i>-value	Estimate	<i>P</i>-value
a) <u>Locomotion rate</u>				
Intercept	3.105	<0.001	0.141	0.437
Treatment:Talk	0.058	0.226	0.216	0.880
Treatment:Scream	-0.114	0.025	0.108	0.944
Human use:Resident	-0.020	0.705	1.252	0.366
Talk*Resident	0.946	0.947	-0.792	0.706
Scream*Resident	0.176	0.018	-0.322	0.872

Observer 2	-0.088	0.021	-1.444	0.137
Observer 3	-0.047	0.312	-2.665	0.012
Observer 4	-0.107	0.005	-0.701	0.545

b) Looking rate

Intercept	4.307	0.002	-0.107	0.936
Treatment:Talk	0.466	0.794	-0.081	0.961
Treatment:Scream	-4.339	0.013	2.113	0.148
Human use:Resident	-3.423	0.066	0.568	0.699
Talk*Resident	3.752	0.164	0.940	0.981
Scream*Resident	6.998	0.005	-1.935	0.295
Observer 2	-2.098	0.138	0.025	0.981
Observer 3	-1.512	0.346	-0.531	0.593
Observer 4	-3.296	0.015	1.566	0.127

c) FID

Intercept	0.315	0.410	1.206	0.009
Treatment:Talk	-0.145	0.060	-1.001	0.004
Treatment:Scream	-0.432	0.029	-0.664	0.039
Human use:Resident	-0.274	0.199	-1.036	0.002
Talk*Resident	0.590	0.060	1.251	0.003
Scream*Resident	0.678	0.029	1.131	0.005
Observer 2	-0.062	0.731	-0.002	0.989
Observer 3	-0.066	0.751	-0.071	0.721
Observer 4	-0.019	0.902	-0.496	0.009
Starting Distance	0.422	0.0002	0.387	0.004

Figure Legends

Figure 1. Photos of a) blue-tailed skink (*Emoia impar*) and white-bellied copper-striped skink (*Emoia cyanura*).

Alt Text: Photos of blue-tailed skink and white-bellied copper-striped skink.

Figure 2. Photo of study sites in Mo'orea.

Alt Text: Photo of study sites in Mo'orea.

Figure 3. Sample spectrograms of the three different stimuli broadcast to skinks.

Alt Text: Spectrograms of stimuli broadcast to skinks.

Figure 4. Box plots illustrating the changes from baseline in locomotion rates (a, d), looking rates (b, e) as a function of playback stimulus of blue-tailed skinks and white-bellied copper-striped skinks in nonresidential and residential locations respectively. The effect of playback type on the relationship ($\pm 95\%$ CI) between starting distance and flight initiation distance in blue-tailed skinks (c) and white-bellied copper-striped (f). Each dot is the response to a single experiment. Figures include adjusted R^2 values and model p-values.

Alt Text : Four box plots illustrating how skinks responded to playback and flight initiation experiments.

Figure 1



Accepted Manuscript

Figure 2

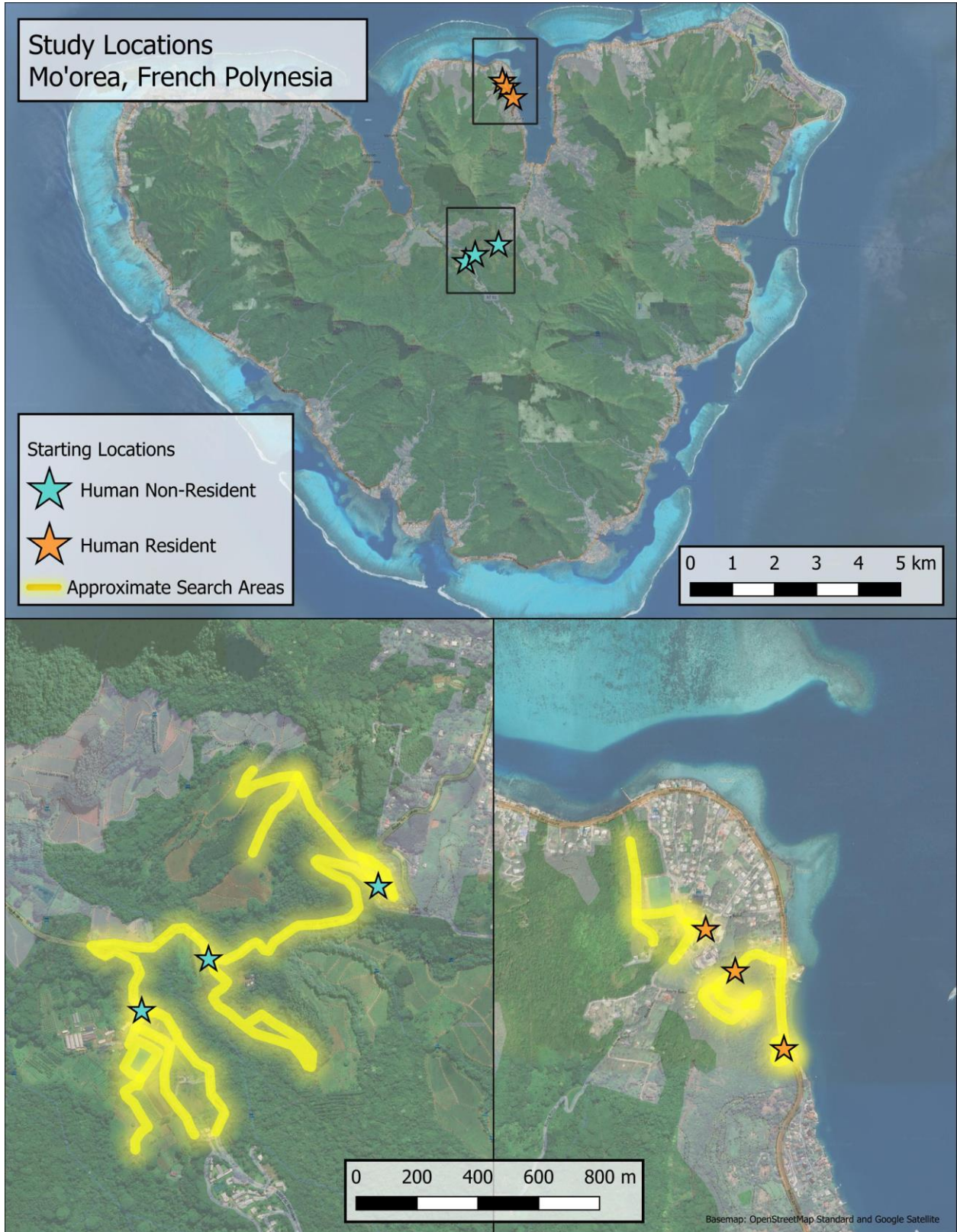
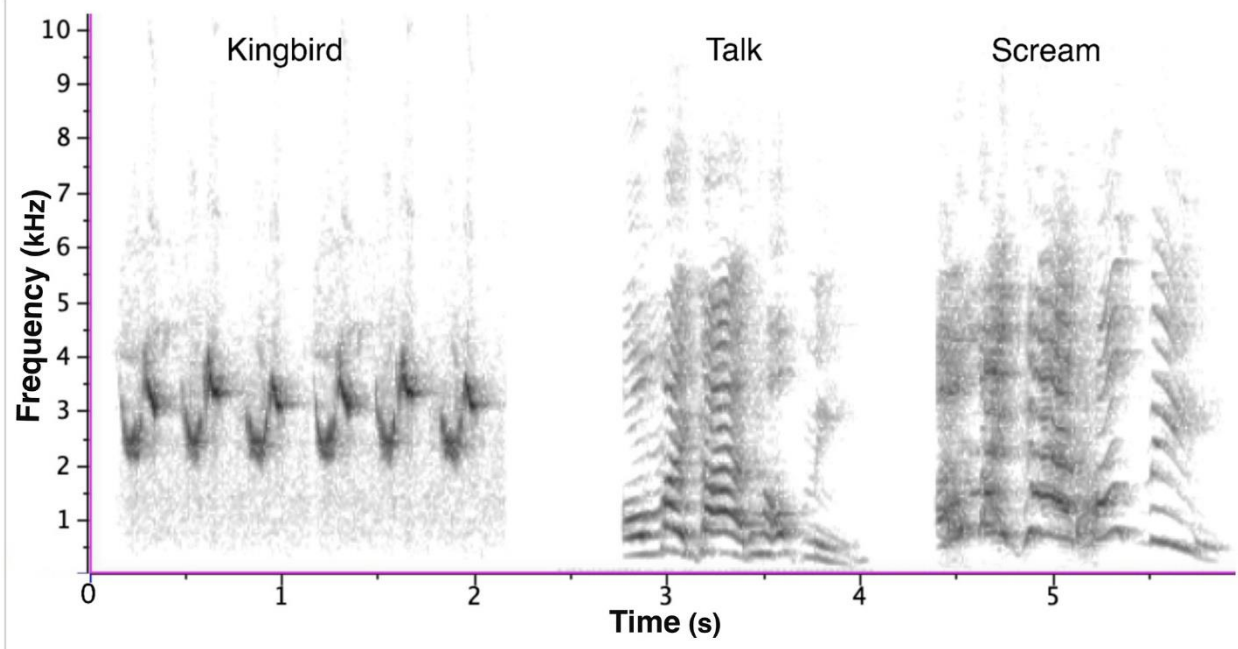


Figure 3



Accepted Manuscript

Figure 4

