

Sex-specific antipredator response to auditory cues in the black spiny-tailed iguana

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Abstract

The selective pressures exerted by predation can have considerable influence on the behavior of prey species across a wide range of taxa. Within a species, this force may differ between the sexes, leading to sex-specific behavioral responses to predators. We tested whether the black spiny-tailed iguana *Ctenosaura similis* is able to use auditory cues to detect an avian predator and whether antipredator responses differ in a sex-dependent fashion. We conducted behavioral assays in which a food item was used as bait while iguanas were subjected to a recording of a Harris's hawk or white noise as a control. We found that a significantly greater percentage of individuals of either sex responded to the hawk call than to the white noise. We also found that a significantly greater percentage of females than males responded to either sound. These results suggest that not only do black spiny-tailed iguanas incorporate auditory cues into predator detection, but that antipredator behavioral responses differ between the sexes as well. Such sex-specific behaviors can be attributed to morphological and endocrine differences between male and female iguanas. These findings may also lend insight into how behavior can influence the evolution of sexual dimorphism within a species.

Introduction

Predation pressure can be an important driver of the evolution of behavioral responses to perceived danger in prey species (Lima & Dill, 1990). Predator avoidance and defense responses occur across a wide range of taxa, in the presence of both real and simulated danger for prey species (e.g., altered foraging in graybelly salamanders, Whitham & Mathis, 2000; adjustment of time taken to return to the nest in hooded warblers, Schaeff & Mumme, 2012; collective diving avoidance response in Atlantic herring, Rieucau *et al.*, 2014). Although these behaviors can increase both survival and fitness, antipredator behaviors can be costly by increasing levels of stress or causing missed opportunities for mating or foraging (e.g., pumpkinseed sunfish, Ball & Baker, 1996; copepods, Jersabek *et al.*, 2007; dogwhelks, Matassa & Trussell, 2014). Because of this high potential cost, prey must determine the risk that a predator poses, which can be highly context-specific (e.g., Balearic lizards, Cooper, Hawlena & Perez-Mellado, 2009; striped plateau lizards, Cooper, 2011; gulls, MacLean & Bonter, 2013; Rhesus macaques, Etting & Isbell, 2014) [Correction added on 22 April 2016 after first online publication: Reference Etting, Isbell & Zeh, 2014 has been corrected to Etting & Isbell, 2014]. This context can vary based on the environment, characteristics of the predator, and characteristics of the prey,

including whether the prey is a male or a female (Lima & Dill, 1990; Magnhagen, 1991).

Predator presence and risk can be evaluated using visual, chemical, olfactory, and auditory cues (Fine, 1999; Mirza, Scott & Chivers, 2001; Bernal, Rand & Ryan, 2007; McCoy *et al.*, 2012; Hermann & Thaler, 2014). In contexts that are suboptimal for detecting predators, prey may require the use of multiple cues to evaluate predatory risk (Elmasri *et al.*, 2012). The combination of cues used to detect a predator can be specific to particular taxa; for example, most birds primarily rely on their vision to scan their environment for predators (Fernandez-Juricic, Erichsen & Kacelnik, 2004), whereas some fish species may be more likely to use olfactory cues (Mirza *et al.*, 2001; Dixson, Munday & Jones, 2010). While it has not been shown that the sexes of one species differ in their use of cues, the differences in the subsequent behavioral response(s) have been documented in several species (e.g., field voles, Norrdahl & Korpimaki, 1998; mouse lemurs, Radespiel *et al.*, 1998; rats, Sommer, 2000; blackbirds and small mammals, Christe, Keller & Roulin, 2006; cichlid fish, Maan *et al.*, 2008).

The potential for sex-specific responses to predation is amplified in species that are sexually dimorphic in morphology or behavior (Norrdahl & Korpimaki, 1998; Radespiel *et al.*, 1998; Sommer, 2000; Christe *et al.*, 2006; Maan *et al.*, 2008).

In many species, the behaviors and phenotypes that confer an advantage for mate acquisition also increase the possibility of predation for the sex that employs them, which is typically males (Norrdahl & Korpimaki, 1998; Maan *et al.*, 2008). Similarly, phenotypes that differ between the sexes due to life-history traits and trade-offs can cause one sex to be better suited for avoiding predators or defending against them (Norrdahl & Korpimaki, 1998; Radespiel *et al.*, 1998; Sommer, 2000; Christe *et al.*, 2006). This is the case for species in which the sexes differ in their respective investments into growth versus reproduction, often causing females to be smaller and less aggressive than males (Cox, Butler & John-Alder, 2007). These differences between the sexes can in turn lead them to respond differently to the presence of various predatory cues (Mirza *et al.*, 2001; Bernal *et al.*, 2007).

We studied the black spiny-tailed iguana *Ctenosaura similis*, which is known to use both visual and olfactory cues to respond to potential predators (Burger, Gochfeld & Murray, 1991; Burger & Gochfeld, 1993; Farallo *et al.*, 2010). Black spiny-tailed iguanas are large, highly sexually dimorphic lizards (Fig. 1) with well-developed olfactory, visual, and auditory senses (Janzen & Brodie, 1995; Savage, 2002; Farallo *et al.*, 2010). Despite the high degree of sexual dimorphism in this species, previous research has not yet tested if predator response behaviors differ between the sexes or how they respond to other types of predator cues. Our research builds upon earlier studies of black spiny-tailed iguanas by testing whether auditory cues are used to respond to predators, and whether the response differs in a sex-dependent fashion. We predicted that foraging behaviors of these iguanas would be affected by auditory cues, and that the behavioral response to a perceived predator would differ between males and females because of sex differences in susceptibility to avian predation.

Materials and methods

The black spiny-tailed iguana is a large, diurnal, semiarid lizards that spends most of its time basking or foraging, making it easy to observe and study (Savage, 2002). We conducted this study from 24 to 27 November 2014 near Palo Verde Biological Station, Costa Rica, where these iguanas are locally abundant. We tested lizards from two neighboring sites; one at the field station of the Organization for Tropical Studies (OTS), and the other at the Palo Verde National Park Ranger

Station. Between both sites, 23 individuals were tested, consisting of two males and six females from the OTS Station, as well as five males and ten females from the ranger station.

We used audio playback experiments to test whether individual black spiny-tailed iguanas employ auditory cues to detect predators. We did this during the hottest hours of the day, generally from 0900 to 1600 h, when individuals were active and foraging, an activity during which many animals are particularly vulnerable to predation (Lima & Dill, 1990). Once we spotted an individual, one experimenter approached it with half of a sliced banana on a bright yellow plastic plate, and placed this approximately 5 m away. We used banana on a yellow plate because adult black spiny-tailed iguanas are primarily herbivorous, and rely on visual cues, especially colors like red and yellow, when foraging for fruits and flowers (Travaset, 1990; Janzen & Brodie, 1995). The sex of each individual was determined using the criteria set forth in Savage (2002). Most individuals had multicolored bead tags (Binns & Burton, 2007) from a previous study (used as identifiers), and all individuals were photographed to ensure independence of observations. Next to the plate, we placed a Bluetooth® (Kirkland, WA, USA) speaker covered with a camouflage shirt, and all experimenters retreated at least 15 m. Using a wireless connection, we played one of two auditory cues, initiated when the lizard reached a point approximately 2 m from the banana and ending when they either reached the plate or fled from the area. To simulate a predator, we used the call of a Harris's hawk *Parabuteo unicinctus*, a sympatric raptor known to pursue relatively large prey, including iguanas (Stiles & Skutch, 1989; Blazquez & Rodriguez-Estrella, 2007). We used 'white noise' as a control (obtained from <http://audacity.sourceforge.net/>). Both sounds were calibrated using a Radioshack® (Fort Worth, TX, USA) sound pressure level meter to obtain a maximum volume of 56 decibels from 10 cm away.

We measured two major response variables: latency to respond (LTR) and categorical behavioral responses. We measured LTR as the time in which the lizard moved from the 2-m mark to the banana target while the auditory cue was playing. During this time, we first categorized the individual's behavior as 'Responded' or 'No Response', based on whether or not there was any visible change in behavior as they approached the target. We then divided the 'Responded' category into two subcategories: 'Paused', in which the lizard ceased movement, waited for a brief amount of time, and then continued to the target; and 'Fled', indicating that the individ-



Figure 1 Photographs of (a) male and (b) female *Ctenosaura similis* in Palo Verde National Park, Costa Rica. Photographs by J. D. Curlis.

ual moved rapidly away, never reaching the plate. As potential covariates, we estimated the initial distance of the lizard from the banana target, and measured the time that each individual took to reach the 2-m mark from their initial position (initial approach time, IAT).

Statistical analysis

We conducted a multiple regression with all variables and all possible interactions, with LTR as the response variable. We then used a reduced model multiple regression to test the effect of sex, auditory cue, and a sex*auditory cue interaction on LTR. We used bivariate linear regression to test the following effects: initial distance on IAT, initial distance on LTR, IAT on LTR, and auditory cue on LTR. Finally, we employed chi-square analyses to test whether the presence of any response ('Paused' and 'Fled' vs. 'No Response') was affected by auditory cue or sex. We also determined whether the percentage of individuals that did not respond, paused, or fled was affected by auditory cue type or by sex. Prior to analysis, both IAT and LTR were log-transformed to fulfill the assumptions of parametric statistics. All statistical tests were conducted using JMP Pro 11 (SAS, 2014).

Results

We found a positive relationship between initial distance and IAT (Fig. 2), but not between initial distance and LTR, IAT and LTR, and auditory cue and LTR (Table 1). LTR was not affected by any variable in either the full model or the reduced model, so they were not included in subsequent analyses (see Supporting Information Table S1 and Table S2).

We found that a significantly ($X^2 = 3.884$; $df = 1$; $P = 0.049$) greater percentage of individuals responded in the presence of the hawk call (64.3%) than in the presence of

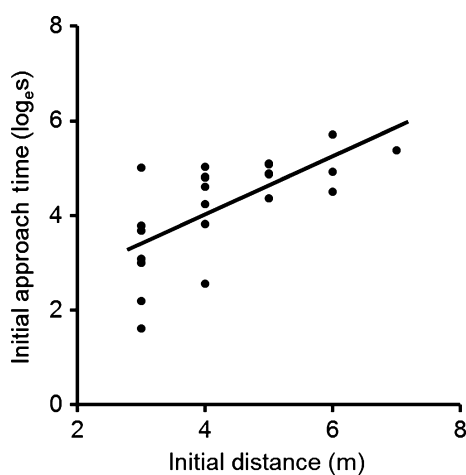


Figure 2 The relationship between initial approach time and initial distance in *Ctenosaura similis*. Initial approach time was significantly positively correlated with initial distance. Initial approach time was log-transformed. $R^2 = 0.444$.

Table 1 Bivariate analyses testing the effect of initial distance on initial approach time, the effect of initial distance on latency to respond, the effect of initial approach time on latency to respond, and the effect of auditory cue on latency to respond. Initial approach time and latency to respond were log-transformed

Variables	F Ratio	P-value
Initial distance × Initial approach time	16.783	0.0005
Initial distance × Latency to respond	0.269	0.61
Initial approach time × Latency to respond	2.369	0.1411
Auditory cue × Latency to respond	2.153	0.1596

white noise (22.2%, Fig. 3a), when combining males and females. We also found that a significantly ($X^2 = 4.537$; $df = 1$; $P = 0.033$) greater percentage of females (62.5%) than males (14.3%) responded to either noise (hawk call or white noise; Fig. 3b). When we parsed the 'Responded' category into 'Paused' and 'Fled', females were far more likely to exhibit the 'Pause' response in the presence of either the hawk call or white noise (56.3%) than males (0.0%), and a greater percentage of males did not respond in the presence of either noise (85.7%) than females (37.5%, $X^2 = 6.469$; $df = 2$; $P = 0.039$; Fig. 4). Combining the sexes, we found that a greater percentage of individuals 'Paused' or 'Fled' in the presence of the hawk call (50.0 and 14.3%, respectively) than in the presence of white noise (22.2 and 0.0%, respectively), although the response no longer significantly ($X^2 = 4.224$; $df = 2$; $P = 0.121$) differed with the type of auditory cue (Fig. 4).

Discussion

In many prey species, the selective pressures associated with predation have given rise to a suite of behavioral responses that are employed when environmental cues suggest the presence of a predator (Lima & Dill, 1990; Ball & Baker, 1996; Whitham & Mathis, 2000; Jersabek *et al.*, 2007; Schaeff & Mumme, 2012; MacLean & Bonter, 2013; Rieucan *et al.*, 2014). These responses can vary both inter- and intraspecifically, and often differ between the sexes in sexually dimorphic species (Norrdahl & Korpimäki, 1998; Radespiel *et al.*, 1998; Sommer, 2000; Fernandez-Juricic *et al.*, 2004; Christie *et al.*, 2006; Maan *et al.*, 2008; Dixon *et al.*, 2010). We found that not only do black spiny-tailed iguanas respond to auditory cues, but also that this response differs in a sex-dependent fashion. This study suggests that hearing may play a more critical role in predator detection for lizards than previously thought. It also corroborates the findings of previous studies that indicate that sex-specific behavioral responses to predators may arise as a result of sexually dimorphic morphological and physiological traits.

The fact that black spiny-tailed iguanas displayed sex-specific responses to a predatory cue may be attributed to morphological and endocrine differences between the sexes. As mentioned previously, this species exhibits pronounced sexual size dimorphism (Fig. 1), with males reaching lengths of approximately 1.5 m (including the tail) and females reaching approximately 1 m (Savage, 2002). Indeed, the larger size and

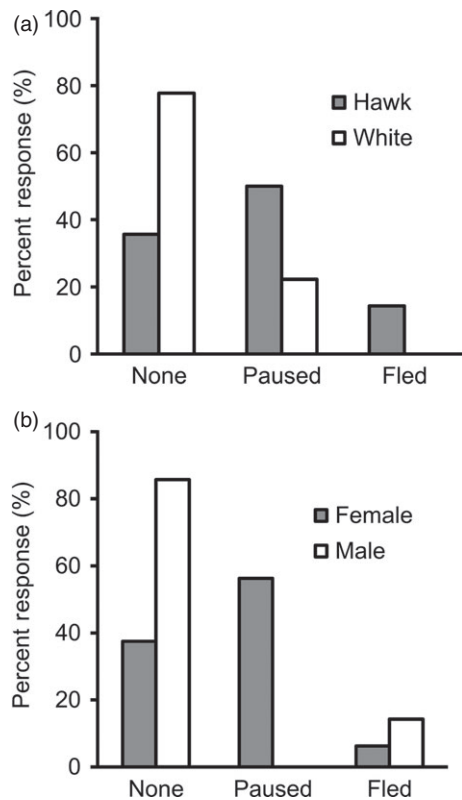


Figure 3 The percentage of individuals of *Ctenosaura similis* that responded (a) to each auditory cue type and (b) of each sex. A response was defined as either pausing, then continuing to the target or fleeing from the target when the sound was played.

exaggerated displays of male iguanas could theoretically lead to greater predation risk and therefore greater caution, opposite of what we documented in this paper. However, the smaller body size of females may make them easier targets for predators than males, simply due to the lower potential cost incurred by the predator in terms of the comparative ease to pursue, kill, carry, and/or digest females rather than males (Leutenegger & Kelly, 1977; Sih & Christensen, 2001; Hassell *et al.*, 2012). Furthermore, because maximal sprint speed is often positively correlated with lizard body size (Huey & Hertz, 1984; Bauwens *et al.*, 1995; Pagan *et al.*, 2012), females may be unable to escape from predators as easily as males. Finally, the lack of gonadal androgens may make them less aggressive than males (Barfield, Busch & Wallen, 1972; Greenberg, Chen & Crews, 1984; Golinski *et al.*, 2014). With reduced size, sprint speed, and aggression, females may be less willing to risk contact with a predator than males, and therefore more likely to respond to a predator cue when placed in a vulnerable context.

Our research also highlights the benefits of studying behavior in black spiny-tailed iguanas in semi-natural habitats near field stations in Costa Rica (Farallo *et al.*, 2010). We were able to detect differences between males and females, and between auditory cue types, with a relatively small sample size. This is

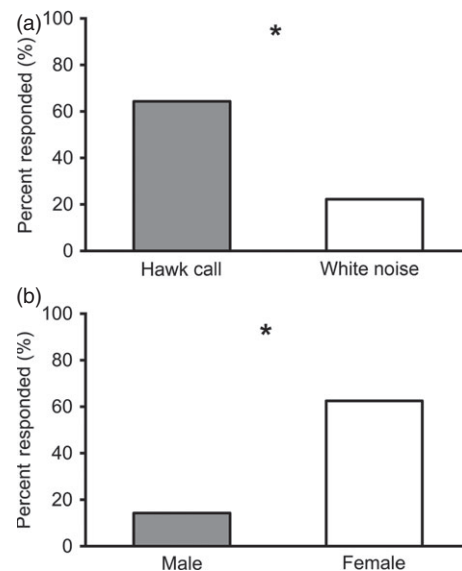


Figure 4 The percentage of individuals of *Ctenosaura similis* that did not respond; paused, then continued to the target; or fled from the target (a) in the presence of each auditory cue type (when combining both males and females) and (b) of each sex (when combining both auditory cue types).

likely because many of the lizards are habituated to humans, making behavioral observations easier (Baldwin, 1968; Burger & Gochfeld, 1990, 1999). In addition, such a habitat offers an uncommonly high degree of access to food and shelter, allowing them to live in larger, denser groups (Farallo *et al.*, 2010). However, these lizards are exposed to the same predator assemblage as conspecifics in the less human-influenced natural areas nearby (Farallo *et al.*, 2010) and still exhibit antipredator behaviors that are characteristic of the species. Future research should leverage this system to explore the determinants of sex-specific responses to different predatory cues.

While it has been well-documented that many reptiles use visual and olfactory cues to detect predators, our study suggests that they can use auditory cues as well. Although many species of fish, birds, and mammals incorporate auditory cues into predator detection (Harvey & Greenwood, 1978; Pusenius & Ostfeld, 2000; Quinn *et al.*, 2006; Simpson *et al.*, 2011), this remains relatively unstudied in lizards. However, many species of lizards can hear quite well, particularly the gekkonids (Peterson, 1966; Marcellini, 1977). Many species in this group have evolved the ability to vocalize, which they use to communicate with conspecifics (Marcellini, 1977). In addition, at least one species of non-vocal reptile, the Galapagos marine iguana *Amblyrhynchus cristatus*, recognizes heterospecific alarm calls and responds with antipredator behavior (Vitousek *et al.*, 2007). Our results confirm the importance of acoustic cues in lizards.

Finally, our results have implications for the evolution of sexual dimorphism. Sexual dimorphism in lizards often evolves due to differential sexual selection that favors combat and display traits in males and fecundity selection in females (Olsson *et al.*, 2002; Cox, Skelly & John-Alder, 2003; Cox *et al.*,

2007; Samia *et al.*, 2015). However, once established, differing phenotypes between the sexes can result in differing degrees of predation pressure, as well as different types of predators in general (Lima & Dill, 1990; Magnhagen, 1991; Hassell *et al.*, 2012; Samia *et al.*, 2015). This can, in turn, lead to differences between the sexes in response to predator cues (Norrdahl & Korpimäki, 1998; Radespiel *et al.*, 1998; Sommer, 2000; Christe *et al.*, 2006; Maan *et al.*, 2008; Samia *et al.*, 2015). As such, sex-specific predator-based selection and response to predatory cues could act as a force to further reinforce or diminish the selection that drives sexual dimorphism. Thus, differential predator-based selection pressure between the sexes could ultimately influence the evolution of sexual dimorphism.

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References

- Baldwin, J.D. (1968). The social behavior of adult male squirrel monkeys (*Saimiri sciureus*) in a seminatural environment. *Folia Primatol.* **9**, 281–314.
- Ball, S.L. & Baker, R.L. (1996). Predator-induced life history changes: antipredator behavior costs or facultative life history shifts? *Ecology* **77**, 1116–1124.
- Barfield, R.J., Busch, D.E. & Wallen, K. (1972). Gonadal influence on agonistic behavior in the male domestic rat. *Horm. Behav.* **3**, 247–259.
- Bauwens, D., Garland, T. Jr., Castilla, A.M. & Van Damme, R. (1995). Evolution of sprint speed in lacertid lizards: morphological, physiological and behavioral covariation. *Evolution* **49**, 848–863.
- Bernal, X.E., Rand, A.S. and Ryan, M.J. (2007). Sexual differences in the behavioral response of tungara frogs, *physalaemus pustulosus*, to cues associated with increased predation risk. *Ethology* **113**, 755–763.
- Binns, J. & Burton, F. (2007). Bead Tags. International Reptile Conservation Foundation and Blue Iguana Recovery Program.
- Blazquez, M.C. & Rodriguez-Estrella, R. (2007). Microhabitat selection in diet and trophic ecology of a spiny-tailed iguana *Ctenosaura hemilopha*. *Biotropica* **39**, 496–501.
- Burger, J. & Gochfeld, M. (1990). Risk discrimination of direct versus tangential approach by basking black iguanas (*Ctenosaura similis*): Variation as a function of human exposure. *J. Comp. Psychol.* **104**, 388–394.
- Burger, J. & Gochfeld, M. (1993). The Importance of the Human Face in Risk Perception by Black Iguanas, *Ctenosaura similis*. *J. Herpetol.* **27**, 426–430.
- Burger, J. & Gochfeld, M. (1999). Role of human disturbance in response behavior of Laysan albatrosses (*Diomedea immutabilis*). *Bird Behavior* **13**, 23–30.
- Burger, J., Gochfeld, M. & Murray, B.G. (1991). Role of a predator's eye size in risk perception by basking black iguana, *Ctenosaura similis*. *Anim. Behav.* **42**, 471–476.
- Christe, P., Keller, L. & Roulin, A. (2006). The predation cost of being a male: implications for sex-specific rates of ageing. *Oikos* **114**, 381–384.
- Cooper, W.E., Jr. (2011). Influence of some potential predation risk factors and interaction between predation risk and cost of fleeing on escape by the lizard *Sceloporus virgatus*. *Ethology* **117**, 620–629.
- Cooper, W.E., Jr., Hawlena, D. & Perez-Mellado, V. (2009). Effects of predation risk factors on escape behavior by Balearic lizards (*Podarcis lilfordi*) in relation to optimal escape theory. *Amphibia-Reptilia*, **30**, 99–110.
- Cox, R.M., Skelly, S.L. & John-Alder, H. (2003). A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution* **57**, 1653–1669.
- Cox, R.M., Butler, M.A. & John-Alder, H.B. (2007). The evolution of sexual size dimorphism in reptiles. In *Sex, size and gender roles: evolutionary studies of sexual size dimorphism*: 38–49. Fairbairn, D.J., Blanckenhorn, W.U. & Székely, T. (Eds). New York, NY, USA: Oxford University Press.
- Dixson, D.L., Munday, P.L. & Jones, G.P. (2010). Ocean acidification disrupts the innate ability of fish to detect predator olfactory cues. *Ecol. Lett.* **13**, 68–75.
- Elmasri, O.L., Moreno, M.S., Neumann, C.A. & Blumstein, D.T. (2012). Response of brown anoles *Anolis sagrei* to multimodal signals from a native and novel predator. *Curr. Zool.* **58**, 791–796.
- Etting, S.F. & Isbell, L.A. (2014). Rhesus macaques (*Macaca mulatta*) use posture to assess level of threat from snakes. *Ethology* **120**, 1177–1184. [Correction added on 22 April 2016 after first online publication: Reference has been corrected from Etting S.F., Isbell, L.A. & Zeh, D. to Etting S.F. & Isbell, L.A. 2014].
- Farallo, V.R., Sasa, M., Wasko, D.K. & Forstner, M.R.J. (2010). Reduced foraging in the presence of predator cues by the Black Spiny-tailed Iguana, *Ctenosaura similis* (Sauria: Iguanidae). *Phyllomedusa* **9**, 109–119.
- Fernandez-Juricic, E., Erichsen, J.T. & Kacelnik, A. (2004). Visual perception and social foraging in birds. *Trends Ecol. Evol.* **19**, 25–31.
- Fine, P.V.A. (1999). Aerial predator recognition by free-ranging *sceloporus occidentalis*. *J. Herpetol.* **33**, 128–131.
- Golinski, A., Kubicka, L., John-Alder, H. & Kratochvil, L. (2014). Elevated testosterone is required for male copulatory behavior and aggression in Madagascar ground gecko (*Paroedura picta*). *Gen. Comp. Endocrinol.* **205**, 133–141.
- Greenberg, N., Chen, T. & Crews, D. (1984). Social status, gonadal state, and the adrenal stress response in the lizard, *Anolis carolinensis*. *Horm. Behav.*, **18**, 1–11.

- Harvey, P.H. & Greenwood, P.J. (1978). Antipredator defence strategies: some evolutionary problems. In *Behavioural Ecology: an evolutionary approach*. Krebs, J.R. & Davies, N.B. (Eds). Oxford: Blackwell.
- Hassell, E.M., Meyers, P.J., Billman, E.J., Rasmussen, J.E. & Belk, M.C. (2012). Ontogeny and sex alter the effect of predation on body shape in a livebearing fish: sexual dimorphism, parallelism, and costs of reproduction. *Ecol. Evol.* **2**, 1738–1746.
- Hermann, S.L. & Thaler, J.S. (2014). Prey perception of predation risk: volatile chemical cues mediate non-consumptive effects of a predator on a herbivorous insect. *Oecologia* **176**, 669–676.
- Huey, R.B. & Hertz, P.E. (1984). Effects of body size and slope on acceleration of a lizard (*Stellio stellio*). *J. Exp. Biol.* **110**, 113–123.
- Janzen, F.J. & Brodie, E.D. III (1995). Visually-oriented foraging in a natural population of herbivorous lizards (*Ctenosaura similis*). *J. Herpetol.* **29**, 132–136.
- Jersabek, C.D., Luger, M.S., Schabetsberger, R., Grill, S. & Strickler, J.R. (2007). Hang on or run? Copepod mating versus predation risk in contrasting environments. *Oecologia* **153**, 761–773.
- Leutenegger, W. & Kelly, J.T. (1977). Relationship of sexual dimorphism in canine size and body size to social, behavioral, and ecological correlates in anthropoid primates. *Primates* **18**, 117–136.
- Lima, S.L. & Dill, L.M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68**, 619–640.
- Maan, M.E., Eshuis, B., Haesler, M.P., Schneider, M.V., Van Alphen, J.J.M. & Seehausen, O. (2008). Color polymorphism and predation in a lake victoria cichlid fish. *Copeia* **2008**, 621–629.
- MacLean, S.A. & Bonter, D.N. (2013). The sound of danger: threat sensitivity to predator vocalizations, alarm calls, and novelty in gulls. *PLoS ONE* **8**, e82384.
- Magnhagen, C. (1991). Predation risk as a cost of reproduction. *Trends Ecol. Evol.* **6**, 183–186.
- Marcellini, D. (1977). Acoustic and visual display behavior of gekkonid lizards. *Amer. Zool.* **17**, 251–260.
- Matassa, C.M. & Trussell, G.C. (2014). Prey state shapes the effects of temporal variation in predation risk. *Proc. R. Soc. B* **281**, 20141952.
- McCoy, M.W., Touchon, J.C., Landberg, T., Warkentin, K.M. & Vonesh, J.R. (2012). Prey responses to predator chemical cues: disentangling the importance of the number and biomass of prey consumed. *PLoS ONE* **7**, e47495.
- Mirza, R., Scott, J.J. & Chivers, D.P. (2001). Differential responses of male and female red swordtails to chemical alarm cues. *J. Fish Biol.* **59**, 716–728.
- Norrdaahl, K. & Korpimäki, E. (1998). Does mobility or sex of voles affect risk of predation by mammalian predators? *Ecology* **79**, 226–232.
- Olsson, M., Shine, R., Wapstra, E., Ujvari, B. & Madsen, T. (2002). Sexual dimorphism in lizard body shape: The roles of sexual selection and fecundity selection. *Evolution* **56**, 1538–1542.
- Pagan, D.N.M., Gifford, M.E., Parmerlee, J.S. & Powell, R. (2012). Ecological Performance in the Actively Foraging Lizard *Ameiva ameiva* (Teiidae). *J. Herpetol.* **46**, 253–256.
- Peterson, E.A. (1966). Hearing in the lizard: some comments on the auditory capacities of a nonmammalian ear. *Herpetologica* **22**, 161–171.
- Pusenius, J. & Ostfeld, R.S. (2000). Effects of stoat's presence and auditory cues indicating its presence on tree seedling predation by meadow voles. *Oikos* **91**, 123–130.
- Quinn, J.L., Whittingham, M.J., Butler, S.J. & Cresswell, W. (2006). Noise, predation risk compensation and vigilance in the chaffinch *Fringilla coelebs*. *J. Avian Biol.* **37**, 601–608.
- Radespiel, U., Cepok, S., Zietemann, V. & Zimmermann, E. (1998). Sex-specific usage patterns of sleeping sites in grey mouse lemurs (*Microcebus murinus*) in northwestern madagascar. *Am. J. Primatol.* **46**, 77–84.
- Rieucou, G., De Robertis, A., Boswell, K.M. & Handegard, N.O. (2014). School density affects the strength of collective avoidance responses in wild-caught Atlantic herring *Clupea harengus*: a simulated predator encounter experiment. *J. Fish Biol.* **85**, 1650–1664.
- Samia, D.S.M., Moller, A.P., Blumstein, D.T., Stankowich, T. & Cooper, W.E. (2015). Sex differences in lizard escape decisions vary with latitude, but not sexual dimorphism. *Proc. R. Soc. B* **282**, 1805.
- SAS (2014). *JMP®*, Version 11. Cary, NC: SAS Institute Inc..
- Savage, J.M. (2002). *The amphibians and reptiles of costa rica: a herpetofauna between two continents, between two seas*. Chicago, IL: The University of Chicago Press.
- Schaeff, K.M. & Mumme, R.L. (2012). Predator vocalizations alter parental return time at nests of the hooded warbler. *Condor* **114**, 840–845.
- Sih, A. & Christensen, B. (2001). Optimal diet theory: when does it work, and when and why does it fail? *Anim. Behav.* **61**, 379–390.
- Simpson, S.D., Munday, P.L., Wittenrich, M.L., Manassa, R., Dixson, D.L., Gagliano, M. & Yan, H.Y. (2011). Ocean acidification erodes crucial auditory behaviour in a marine fish. *Biol. Lett.* **7**, 917–920.
- Sommer, S. (2000). Sex-specific predation on a monogamous rat, *Hypogeomys antimena* (Muridae: Nesomyinae). *Anim. Behav.* **59**, 1087–1094.
- Stiles, G. & Skutch, A.F. (1989). *A guide to the birds of Costa Rica*. Ithaca, NY: Comstock Publishing Associates.
- Travaset, A. (1990). *Ctenosaura similis* gray (Iguanidae) as a seed disperser in a Central American deciduous forest. *Am. Midl. Nat.* **123**, 402–404.
- Vitousek, M.N., Adelman, J.S., Gregory, N.C. & St. Clair, J.J.H. (2007). Heterospecific alarm call recognition in a non-vocal reptile. *Biol. Lett.* **3**, 632–634.

Whitham, J. & Mathis, A. (2000). Effects of hunger and predation risk on foraging behavior of graybelly salamanders, *Eurycea multiplicata*. *J. Chem. Ecol.* **26**, 1659–1665.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Fully factorial linear model examining the effect of sex, auditory cue, initial distance, and initial approach time on latency to respond. Both initial approach time and latency to respond were log-transformed. $N = 23$; $F = 1.179$; $df = 11$; $P = 0.4177$.

Table S2. Reduced linear model examining the effect of sex, auditory cue, and an interaction between sex and auditory cue on latency to respond. Latency to respond was log-transformed. $N = 23$; $F = 1.4913$; $df = 3$; $P = 0.2548$.

Data S1. Resumen