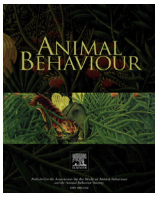
Animal Behaviour 196 (2023) 91–102

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Lizards' response to the sound of fire is modified by fire history

Lola Álvarez-Ruiz [a, *], Juli G. Pausas [a, *], Daniel T. Blumstein [b], Breanna J. Putman [b, c, d]

[a] Centro de Investigaciones sobre Desertificación (CIDE-CSIC), Valencia, Spain
[b] Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA, U.S.A.
[c] Department of Herpetology, Natural History Museum of Los Angeles County, Los Angeles, CA, U.S.A.
[d] Department of Biology, California State University, San Bernardino, CA, U.S.A.

ARTICLE INFO

Article history:
Received 28 June 2022
Initial acceptance 26 August 2022
Final acceptance 1 November 2022

MS. number: 22-00319

Keywords:
fire adaptation
fire avoidance
fire detection
flight initiation distance
global change
reptile
vigilance

Many animals survive wildfires; however, the mechanisms used to detect and respond to fire have been poorly studied. Sensory cues like sight and sound are used to recognize threats (e.g. predators) and elicit escape responses in prey. Similarly, these cues might be used to detect an approaching wildfire. We tested whether the western fence lizard, *Sceloporus occidentalis*, responds to the sound of fire as a threat. We predicted that lizards living in burned areas would be more sensitive to the sound of fire than lizards in adjacent and urban areas, where fire suppression could have induced relaxed selection on fire responsiveness. We compared the behaviours of lizards following an experimental playback where we broadcast the sound of fire along with other control sounds (a predator, a common nonpredatory bird and a novel nonpredatory bird). We conducted our playbacks in 2019 in recently burned areas (using the survivors from the 2018 Woolsey Fire, southern California, U.S.A.), unburned adjacent areas and urban areas. We found that in burned areas, lizards responded more to the sound of fire than all three controls, but in urban areas, they responded more to both the sound of a predator and the sound of fire. Our results suggest that lizard responses to fire sounds are greater in an area that has recently experienced a wildfire than in an unburned area, and that urban areas create a complex evolutionary landscape that also increased antipredator behaviour for other biologically relevant stimuli.

Fire is a natural process in many ecosystems around the world, and the need to incorporate its role into the understanding of fire-prone ecosystems' ecology has been increasingly recognized (Keeley et al., 2012; Pausas & Keeley, 2009). Much is known about the role of fire in plant ecology and evolution (Keeley & Pausas, 2022), yet fire is also a threat faced by animals. Although knowledge about the effects of fire on animals is quickly growing (Nimmo et al., 2019, 2021; Pausas & Parr, 2018), only a few studies have provided evidence of adaptive behavioural responses that animals have acquired to detect and survive fires. In fact, such effects vary across taxa (Legge et al., 2022). For instance, in relation to fire avoidance, mammals seek refuge in underground burrows and flee into adjacent unburned areas (Garvey et al., 2010; Geluso et al., 1986), some lizards shelter in crevices or under rocks (Smith et al., 2012) and nonflying invertebrates have been observed digging into the soil or climbing to the tops of trees when a fire is approaching (Dell et al., 2017; Sensenig et al., 2017). However, the sensory cues that trigger such behavioural responses are generally unknown. There is evidence that some lizards, bats and possums can detect smoke, eliciting movement to a safe site (Álvarez-Ruiz et al., 2021; Doty et al., 2018; Nowack et al., 2016; Stawski et al., 2015), and at least one species of frog flees to less flammable sites in response to the sound of fire (Grafe et al., 2002).

Fires are likely to be an important selective pressure on animal behaviour since only individuals with detection and escape traits would potentially survive (Nimmo et al., 2022; Pausas & Parr, 2018). Thus, those individuals or populations with ‘fire-savvy’ traits are likely to respond to cues associated with fire (Nimmo et al., 2021); in fact, there is evidence that animals from areas with eco-evolutionary histories with wildfire are more fire-savvy than those from habitats that lack a history with fire (Álvarez-Ruiz et al., 2021).

Urbanization is also quickly spreading worldwide. Species vary in their degree of urban tolerance (Sol et al., 2013), and this human-driven disturbance may tame animals, making them less responsive to threats (Geffroy et al., 2020; Thompson et al., 2022). Given that urban areas usually do not burn or are actively protected from

---

* Corresponding authors.
E-mail addresses: lolaalvarez.r@gmail.com (L. Álvarez-Ruiz), juli.g.pausas@ext.uv.es (J. G. Pausas).

https://doi.org/10.1016/j.anbehav.2022.12.002
0003-3472/

wildfires, urbanization could be expected to induce relaxed selection on fire responsiveness in animals. Yet, fire risk is increasing as the urban–wildland interface grows in many areas globally (Modugno et al., 2016; Radeloff et al., 2018), creating a complex interplay between urbanization, fire suppression and anthropogenic fire ignitions. Few studies have explored how fire interacts with habitat loss and fragmentation (Driscoll et al., 2021; Jennings et al., 2016; Ramalho et al., 2018) and none have examined how urbanization-driven behavioural changes might affect animal responses to fires and fire-related cues.

Lizards as a study group are ideal for testing animal responses to fire sensory cues because they occur across various habitats, are generally abundant in the habitats in which they occur, are easy to observe and catch in the wild, and use visual, auditory and olfactory cues to detect and respond to threats. In fact, lizards have a highly directional well-developed auditory system (Brittan-Powell et al., 2010; Christensen-Dalsgaard & Manley, 2005). For instance, adult male brown anoles, *Anolis sagrei*, use the sounds of specific bird calls as indicators of predation risk from birds (Cantwell & Forrest, 2013; Huang et al., 2011).

Yet, mechanisms behind observed patterns of reptile responses to fire remain unclear, making generalizations difficult (Driscoll et al., 2010). After a wildfire, little mortality is observed in burrowing lizards (Rochester et al., 2010; Smith et al., 2012) and their persistence indicates that their populations are resilient to wildfires (Santos et al., 2022). One of the proposed mechanisms is that reptiles may detect the smoke of fire in advance and then move to a safe site. Populations of the Algerian sand racer, *Psammodromus algirus*, living in fire-prone areas reacted more to smoke than conspecifics from areas that rarely burned, suggesting that fire is likely to be an evolutionary driver for animals that shapes adaptions to fire cues in fire-prone ecosystems (Álvarez-Ruiz et al., 2021).

Here we asked to what extent lizards can also use sound for detecting the threat of an oncoming wildfire. We hypothesized that lizards that survived a major wildfire would have enhanced fire detection abilities. To test this hypothesis, we studied western fence lizards, *Sceloporus occidentalis* (suborder Iguania, family Phrynosomatidae). *Sceloporus* auditory nerve fibres are connected to hair-cells that respond to frequencies from 2.5 to 43 kHz. They lack hair-cells for 1 kHz, which defines a low- and high-frequency hair-cells area (Köppl & Manley, 1992; Manley, 2000; Turner, 1987). Thus, fence lizards are capable of responding to acoustic stimuli, which makes them a suitable species to study the use of acoustic cues as a mechanism to detect threats.

We studied lizards' responses to acoustic stimuli in three different habitat types: recently burned areas (which putatively contained individuals that survived the fire), those living in the adjacent unburned areas and urban areas. Our experimental playback treatments included fire and different controls (a sympatric predator, a nonsympatric predator and a nonsympatric bird). If lizards have the ability to respond to fire (e.g. because of a strong evolutionary history with this threat), we would expect to find significant high-level responses to the sound of fire in all three habitats. However, if a large and high-intensity fire selected survivors that had heightened responses to fires, or fire survivors learnt from the experience, we would then expect the highest level of response within recently burned sites compared to unburned and urban sites.

METHODS

Species and Study Sites

Western fence lizards are native to and widely distributed in southern California where they are found in a variety of habitats including recently burned areas (indicating some ability to survive wildfires; Rochester et al., 2010) and urban areas (commonly found in home yards and gardens, showing urban tolerance; Putman et al., 2019).

Between April and July 2019, we studied the response of fence lizards to auditory playbacks in three habitat types with contrasting levels of disturbance: recently burned wildlands, unburned wildlands and unburned urban environments. For each habitat we sampled three plots (replicates; Appendix Table A1). Wildland sites were located in the Santa Monica Mountain Range, in southern California. This ecosystem, in a warm and dry Mediterranean climate, is subject to frequent high-intensity fire (Keeley & Fotheringham, 2001). In November 2018, the Woolsey Fire burned ca. 39 200 ha in Los Angeles and Ventura Counties. Our burned study plots were selected in three different valleys within the Woolsey Fire boundaries (see coordinates in Appendix Table A1). Unburned plots were located in the surrounding areas of the fire and lizards were studied at least 500 m from the fire edge to ensure that the lizard's home range (rarely exceeding 100 m; Davis & Ford, 1983; Massot et al., 2003) was fully inside or outside the fire perimeter. Urban plots were selected within urbanized areas in Los Angeles where lizards must cope with other threats and stimuli (e.g. different suites of predators and human disturbances). All plots (except for urban plots) were selected in areas with similar vegetation before the fire. The lizard's abundance, measured as the number of individuals per sampling day, was similar in the three habitats ($F_2 = 2.148$, $P = 0.132$; Table A2).

Behavioural Observations

One observer (always the same person) conducted the behavioural assays in the field from 1 April to 1 July 2019. Experiments were conducted between 1030 and 1830 hours, in temperatures of 19–35 °C, and only during periods of limited wind (0–8 km/h, < 3 on the Beaufort scale).

We examined the response of wild lizards to four playback treatments: a fire stimulus and three controls that allowed us to interpret possible reactions to stimuli. All presented sound stimuli were within the hearing range of the lizards (Fig. 1). The fire stimulus treatment consisted of a recorded sound of a wildfire. To be able to infer whether fires were perceived as a threat, we broadcast the calls of a predatory threat, the sympatric American kestrel, *Falco sparverius*. To test whether lizards responded to any sounds, we broadcast a familiar sound for the lizards, the song of a nonpredatory bird that coexists with them, the house finch, *Haemorhous mexicanus*. To determine whether lizards responded to novel sounds, we broadcast the sounds of a nonthreatening, nonsympatric bird, the bananaquit, *Coereba flaveola*, a bird that the lizards had no ecological or evolutionary experience with and whose call does not resemble those of local birds. Each lizard received only one of the four treatments and, to avoid any possible carryover effects, each time we applied a different stimulus in a predetermined order.

Fire sound was obtained from the General 6000 sound effects library (Sound Ideas, Ontario, Canada, http://www.sound-ideas.com). The original sound was a stereo recording stored as a digital audio track. We randomly selected five fragments, each 30 s in duration, with a linear ramp of 10 ms at the beginning and the end of the sound. We obtained five bird vocalizations of each control from the Macaulay Library at the Cornell Lab of Ornithology and the Xeno-Canto repository (five exemplars per treatment; Fig. 1, Appendix Table A3). We used Audacity 2.3.1 (Audacity Team, 2013) to adjust the amplitude of each sound, which was calibrated for the Bluetooth loudspeaker Ultimate Ears Boom 2 (Ultimate Ears, Irvine/Newark, CA, U.S.A.) and Apple iPhone 7 (Apple Inc., Cupertino, CA,

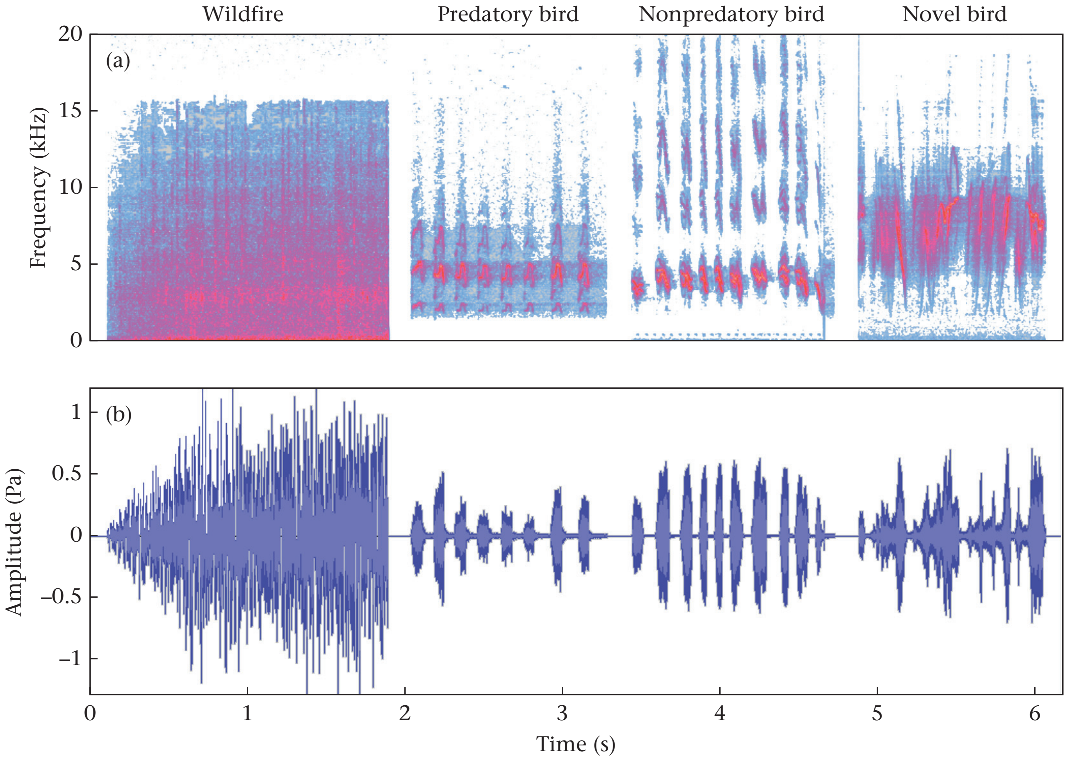


Figure 1. Representative spectrograms and waveforms of acoustic stimuli used to study lizards' reaction to the sound of fire and controls. Sampling rate 44.1 kHz, 1024-point FFT. (a) The spectrogram shows the energy levels of the sound at a particular frequency at a particular time. Warmer colours represent higher energy levels. (b) The waveform displays amplitude on a linear scale. The dark blue part of the waveform displays the tallest peak in the area represented. The light blue part of the waveform displays the average root mean square value for the same group of samples. Note that it does not represent how loudness is actually perceived, which is best represented on a logarithmic scale, measured in decibels. All sounds were calibrated to be broadcast at 85 dB.

U.S.A.) using a sound level meter (Sper Scientific digital sound meter model number 840029, Sper Scientific, Scottsdale, AZ, U.S.A.). All sounds were calibrated to be broadcast at 85 dB (±1 dB SPL measured 1 m from speaker, peak response, weighting A), which is the approximate sound level of natural calls.

To find focal lizards, we slowly walked around each site looking for adult lizards, scanning at all heights. We moved through a given spot only once to prevent resampling the same individuals. Once a lizard was located, we carefully approached it to avoid disturbance, set up the portable loudspeaker 3–5 m from the lizard, and then moved about 10 m away to quietly observe the subject using binoculars. If the lizard retreated into its burrow, we waited for it to emerge. Before starting the trials, we noted the initial angle between the loudspeaker and the lizard's snout.

After an initial 2 min acclimation period, we proceeded to quantify each subject's behaviour quietly dictating behavioural transitions into a voice recorder (Apple iPhone 7). Focal observations lasted 2 min: we started each playback with a baseline period of silence (30 s pretreatment) followed by a treatment or control sound broadcast (30 s) and another period of silence (60 s posttreatment). After each trial, we measured the soil temperature using a noncontact infrared thermometer (model eT650D, ennoLogic, Eugene, OR, U.S.A.), and the air temperature, humidity and wind speed using a pocket weather meter (model 5000, Kestrel, Boothwyn, PA, U.S.A.).

Flight Initiation Distance Measurement

Fence lizards also use visual cues to identify potential predators (Fine, 1999; Fitch, 1940) and then respond to danger by moving to a refuge (Greene, 1988). Once each behavioural assay was concluded, we measured the flight initiation distance (FID), the distance at which an animal flees from an approaching threat. FID is a risk assessment measurement such that longer FIDs correspond to an increased perception of risk in animals (Cooper, 2015; Cooper & Blumstein, 2015; Stankowich & Blumstein, 2005). We quantified FID because it provides another way to study the response to a stimulus because exposure to threatening stimuli can affect later risk assessments. Therefore, if lizards fled during the sound experiment, we waited until they emerged to measure FID. Once the lizard was relaxed and not moving (i.e. foraging, basking, or perched and looking around), the observer (dressed all in black, hair up) walked at a fixed velocity (0.5 m/s) directly towards it. The observer noted the starting distance (the total distance between the lizard and the observer when the trial was started) and the FID (the distance from the observer at which it began to move away from its initial location). Distances were measured using a transect tape after the trial.

Lizards run to refuge or cover to escape their predators; thus, risk increases with the distance to refuge. After each FID trial, we measured the height at which the lizard was found and the distance each lizard was from the closest refuge (±5 cm; independently of whether the lizard fled or not) as it can influence lizards' risk perception and FID (Samia et al., 2015).

Morphological Measurements

Once the FID trials were concluded, we captured (when possible) the lizards using a lasso tied to the end of a fishing pole and measured the lizard's body temperature using a noncontact infrared thermometer (model eT650D, ennoLogic). We also measured the body length (snout–vent length, SVL ±0.01 cm) and weight (±0.1 g; see Appendix Table A1); adults were sexed by the presence (male) or absence (female) of femoral pores and enlarged postanal scales. We calculated body condition as the residuals of the regression of body mass on SVL (Green, 2001; Warner et al., 2016). All lizards were released at the location of capture after the measurements were taken.

Data Processing

We developed an ethogram to analyse the behaviour of each lizard during the playback trials. Our ethogram followed Yan et al. (2019) and included stand and look, walk, run, forage, push-ups, other and out of sight (see Appendix Table A4 for a detailed description of the behaviours). Focal samples were scored and analysed using JWatcher (version 1.0; Blumstein & Daniel, 2007). We summarized responses of lizards to the playbacks into two behavioural indicators: (1) sign of threat detection and (2) activity. In lizards, eavesdropping on heterospecific alarm calls is a common phenomenon to identify nearby threats and reduce the cost and risk of predation (Fuong et al., 2014; Vitousek et al., 2007). Looking behaviour is associated with antipredator and vigilance behaviour (McElroy, 2019). Therefore, we calculated the change in rates of looking as a sign of threat detection to test our hypotheses about risk perception. To analyse lizards' activity, we calculated the rates of the other behaviours scored (foraging, push-ups and locomotion, i.e. walk and run).

Not all trials were of equal length (because lizards sometimes ran out of sight), so rates were calculated as the number of times that the behaviour occurred divided by the total time the lizard was in sight. We subtracted the calculated rate from the rate of each baseline behaviour (preplayback) to obtain a sensitive measure of responses to the playback. From this, a positive change value reflected an increase in the rate, while a negative change value reflected a decrease in the rate compared to baseline.

Statistical Analyses

All statistical analyses were performed using the R software version 4.0.3 (R Core Team, 2020). To examine whether changes in lizards' rates of looking varied between habitat and playback treatments, we fitted a linear mixed-effects model (LMM) using the package lme4 (Bates et al., 2014). We included fixed effects of playback treatment (fire, predatory bird, nonpredatory bird and novel bird), habitat (burned, unburned and urban), an interaction between treatment and habitat, and a random effect of sampling location. We used ‘anova’ type III with the Satterthwaite approximation of degrees of freedom to obtain *F* values and *P* values of fixed factors and the interaction term. Normality of model residuals was checked using the DHARMa package v. 0.2.4 (Hartig, 2019). We also used the ‘difflsmeans’ function of the lmerTest package (Kuznetsova et al., 2017) to conduct comparative post hoc tests for treatment and habitats. The Benjamini and Hochberg correction procedure was applied to control the false discovery rate (Benjamini & Hochberg, 1995; Ferreira, 2007).

Lizards' responses to stimuli may be influenced by other factors; thus, we first demonstrated that lizards' rates of looking were independent of their sex, body size, body temperature, wind speed, speaker distance, initial head orientation, distance to the closest refuge and tail autotomy (Appendix Table A5); thus, these variables were not included in the final models.

Other behaviours such as foraging, push-ups, walking and running occurred at low frequencies (see Appendix Fig. A1); because of their rarity (i.e. the analyses were zero-inflated), we represented these behaviours as binary variables (yes/no). To analyse the effect of habitat and treatment on whether lizards exhibited these behaviours (foraging, push-ups, walking and running) or not, we fitted generalized linear mixed-effect models (GLMER) with a binomial error structure using the lme4 package. We included fixed effects of playback treatment, habitat, its interaction and sampling location as random effects. Normality of model residuals was checked using the DHARMa package v. 0.2.4 (Hartig, 2019).

To study variation in FID, we fitted a LMM as a function of starting distance, habitat, treatment, lizard attributes (sex, body size, body condition index, tail autotomy), climatic variables (soil and air temperature, humidity, wind speed) and distance to the closest refuge. A similar model was fitted to study variation in the distance to the closest refuge. For both analyses, sampling location was included as a random factor; we added variables sequentially in order of their contribution to the remaining explained variance and kept the most parsimonious final model (see Appendix Table A5). Again, residual distributional assumptions of these models were checked using the DHARMa package v. 0.2.4 (Hartig, 2019).

Ethical Note

The project adhered to the ASAB/ABS guidelines for the treatment of animals in research. All methods were approved by the UCLA Animal Research Committee (ARC-2016—051-03C).

RESULTS

We successfully performed 199 playback trials and captured 152 of the subjects (86 females, 71 males; Appendix Table A1).

When faced with the treatments, the most typical lizard's response was ‘looking’. Overall, lizards modified their rates of looking across habitats and treatments, with a significant treatment*habitat interaction (Fig. 2, Appendix Table A6).

In unburned areas, lizards did not vary their rate of looking as a function of playback type (Fig. 2, Table 1). In burned areas, lizards looked more in response to the sound of fire compared to the three control treatments (Fig. 2, Table 1). In urban areas, lizards' reaction to the predator playback was higher than the reaction to the nonpredatory bird playback (Fig. 2, Table 1).

Post hoc tests revealed looking rate in response to the fire playback was higher in burned areas than in unburned areas (Fig. 2,

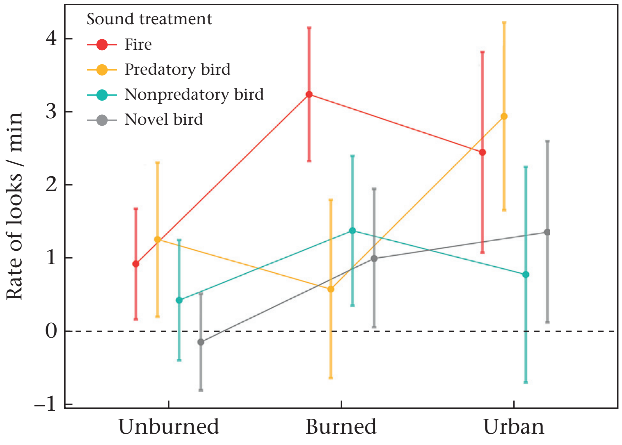


Figure 2. Difference from baseline in mean (± 95% confidence interval) rate of looks/min in the 90 s including and immediately after playback of treatments (fire, predator, nonpredatory bird and novel bird) in the three habitats (unburned, burned and urban). The dashed line (zero) represents no difference in rates from the baseline rates. For statistical significance see Tables 1, A6 and A7. *N* = 199 subjects.

Table 1
Post hoc tests for effects of habitat and sound treatment on lizards' rate of looks/min

Habitat*Treatment	Estimate	SE	*df*	*t*	Lower CI	Upper CI	*P*
Burned*Fire −Burned*Predator	2.655	0.733	187	3.622	1.209	4.101	0.006
Burned*Fire − Burned*Nonpredatory bird	1.860	0.745	187	2.495	0.390	3.331	0.046
Burned*Fire − Burned*Novel bird	2.233	0.733	187	3.047	0.787	3.679	0.015
Burned*Fire − Unburned*Fire	2.312	0.712	187	3.249	0.908	3.716	0.01
Burned*Fire −Unburned*Predator	1.979	0.712	187	2.780	0.575	3.383	0.028
Burned*Fire − Unburned*Nonpredatory bird	2.807	0.722	187	3.888	1.382	4.231	0.004
Burned*Fire − Unburned*Novel bird	3.378	0.745	187	4.531	1.907	4.848	0.001
Burned*Fire − Urban*Nonpredatory bird	2.457	0.712	187	3.453	1.053	3.861	0.006
Burned*Fire − Urban*Novel bird	1.874	0.733	187	2.557	0.428	3.320	0.045
Burned*Predator − Urban*Predator	−2.358	0.733	187	−3.217	−3.804	−0.912	0.01
Unburned*Fire − Urban*Predator	−2.015	0.712	187	−2.832	−3.419	−0.611	0.026
Urban*Fire − Burned*Predator	1.869	0.744	187	2.513	0.402	3.337	0.046
Urban*Fire − Unburned*Nonpredatory bird	2.021	0.733	187	2.758	0.575	3.467	0.028
Urban*Fire − Unburned*Novel bird	2.592	0.756	187	3.428	1.100	4.084	0.006
Urban*Predator − Unburned*Nonpredatory bird	2.510	0.722	187	3.477	1.086	3.934	0.006
Urban*Predator − Urban*Nonpredatory bird	2.161	0.712	187	3.036	0.757	3.565	0.015
Urban*Predator − Burned*Novel bird	1.936	0.733	187	2.642	0.490	3.382	0.037
Urban*Predator − Unburned*Novel bird	3.081	0.745	187	4.133	1.610	4.551	0.002

Values are least-square estimates of the fixed effects 'habitat' and 'treatment', and their interaction term in the LMM, containing location as random factor. *P* values were adjusted using the Benjamini & Hochberg correction to control the false discovery rate. Only significant interactions are shown. CI: confidence interval.

Tables 1, A7). Looking rate in response to the predatory bird playback was lower in burned areas than in urban areas (Fig. 2, Table 1). Yet, looking rate to the nonpredatory bird and novel bird playbacks across habitats did not differ significantly from each other.

We found no effect of habitat or sound treatment on the proportion of lizards that exhibited foraging or locomotion behaviours (Appendix Fig. A1, Table A8). However, lizards were more likely to perform push-ups in the fire sound treatment than in the novel bird sound treatment across all habitat types and in urban than in unburned environments (Appendix Fig. A1, Table A9). The interaction between habitat and sound treatment was not significant and was removed from the final model.

Smaller lizards and lizards that had suffered tail autotomy were found closer to refuge (Appendix Table A10). Also, we found lizards closer to refuge in urban habitats than in unburned wildland habitats (Appendix Tables A10, A11). Of the 199 sound trials performed, 16 lizards fled during the playbacks and five of those resurfaced for the FID tests. Of the 188 FID trials performed, 36 lizards fled and could not be captured. For the FID analysis, we only used data of the individuals that we also captured ($N = 152$). FID was independent of lizards' habitat (burned, unburned or urban) and the playback to which they were exposed (fire, predatory bird, nonpredatory bird or novel bird) prior to the FID trial. The best predictors of lizards' FID to human approach were distance to the closest refuge and body condition index, although the effect of these variables was only marginally significant (Appendix Table A12).

DISCUSSION

Western fence lizards survived the Woolsey Fire, and we sought to determine whether putative survivors had different fire-responsive behaviours than lizards that had not experienced this natural perturbance. Our results suggest that fence lizards that survived the fire (in burned plots) were more responsive to the sound of fire than those in adjacent unburned plots. Furthermore, only lizards in urban areas exhibited significant increases in vigilance (looks) during playbacks of American kestrel (a predatory bird) calls compared with songs of nonpredatory species, suggesting that lizards in wildland habitats, in both burned and unburned areas, cannot distinguish between the calls of birds that they might perceive as threatening and those that they perceive as nonthreatening or are novel to them (control sounds).

Lizards' occurrence and relative abundance in all burned sampled plots implies a high survival rate, suggesting a high resilience capacity of the species after experiencing large wildfires. Given the small home range and the limited dispersal ability of the species relative to the scale of the wildfire, this resilience is likely caused by postfire survival and local population persistence from refugia and not by colonization from unburnt areas, as suggested for other lizards (Santos et al., 2022).

The enhanced response to the fire stimulus of lizards in burned areas could be the result of a selection event, whereby only lizards with developed fire detection traits survived, or it may be the result of learning from fire experience or both. The fact that the population density was not substantially different in the different habitats implies a high survival rate, which is consistent with the response to fire sounds being learned. However, results from our current study cannot distinguish between mechanisms underlying behavioural differences between sites. Further research employing common garden experiments that test laboratory-reared offspring under controlled environmental conditions and/or transcriptomic work that associates differentially expressed genes with population level differences in behaviour would improve our understanding of this.

A high survival rate suggests that this species is likely to be adapted to recognize fires as a threat and respond with evasive behaviours. Our results suggest that the sound of fire triggers an alert response in those lizards that have experienced a wildfire, as we observed increased rates of looking or vigilance when lizards in burned plots heard the sound of wildfire. This suggests that the fire cue provoking a locomotive escape response could be another stimulus, such as the sight or smell of smoke. An oncoming fire can be detected by scent, sound and visible cues. Lizards could use one or several of these cues, depending on the main sense they rely on to detect threats, and the decision to escape could be a trade-off between the risk of mortality for not evacuating early and missed opportunity costs if the fire fails to arrive (Nimmo et al., 2021). For instance, other species of lizards that occur in fire-prone habitats attempt to physically escape the area after smelling smoke (Álvarez-Ruiz et al., 2021; Mendyk et al., 2020), as expected from their chemoreception abilities (Baeckens et al., 2017). Additionally, at least one frog species is able to recognize and flee from the sound of fire, as expected from anurans that use hearing to communicate (Grafe et al., 2002). Furthermore, multisensory integration between odour and sound modulates the way in which some animals perceive their environment (Halene et al., 2009). Although the sound of fire triggers alertness in lizards, this sensory information alone might not be enough to elicit an escape response in an incongruous sensory context (Cohen et al., 2011; Seo & Hummel, 2011). Alternatively, the intensity of the sound stimulus presented during our playback experiment might not have been representative of a life-threatening wildfire and, therefore, lizards had subdued responses.

Urban lizards reacted to the sound of fire in a similar way as lizards inhabiting both unburned and burned areas (the mean response lies between these two habitats; Fig. 1). They were also more alert to predatory sounds than lizards from burned environments. Moreover, urban lizards were more likely to be seen doing push-ups than lizards in unburned environments. Push-ups are used for species recognition, mate choice and defence of territories (Martins, 1991; Sheldahl & Martins, 2000), and might serve as a pursuit deterrent signal (antipredator function; Leal & Rodríguez-Robles, 1997). All this suggests that urban lizards are more sensitive to threatening sounds, which does not support the hypothesis that relaxed selection in urban habitats would decrease responsiveness to fire stimuli (Geffroy et al., 2020). This may be because urban lizards are exposed to more risks (e.g. from domestic pets and/or human activities) than lizards in nonurban habitats, and only the most alert ones could survive. Cats, *Felis catus*, and other domesticated animals have higher population densities in urban areas and they exert a higher predation pressure on lizards, mammals and birds (Koenig et al., 2002; Loyd et al., 2013). Indeed, indicators of predation increase with urbanization in southern alligator lizards, *Elgaria multicarinata*, in southern California, suggesting that predation pressure is higher in these urban areas (Putman et al., 2021). The presence of additional stimuli in urban environments, such as human foot traffic, bicycles and motor vehicles might also make lizards more vigilant and sensitive to potential threats, such as fire. In this sense, the enhanced response to fire cues in urban environments might be a general response to a potentially threatening stimulus, rather than a specific response to fire per se.

Our FID results suggest that the lizards did not modify their evasion response following exposure to the sounds of predators or fire (there was no difference across habitats). However, urban lizards stayed closer to the refuge than nonurban lizards suggesting this might be an adaptive response in urban habitats (Batabyal et al., 2017; Putman et al., 2020), again, perhaps as a response to increased risks found in such habitats.

Overall, our study shows that both natural and human-driven disturbances such as fire and urbanization can shape the behaviour of animals. Lizards were more alert in these habitats compared to unburned wildland habitats. The ability to recognize and detect potential new threats is a life-saving trait in disturbed environments. Our results suggest that wildfires shape lizards' behaviour in a way that results in survivors being more aware of the sound of fire. The mechanism behind these behavioural differences is unknown; fire-responsive behaviours could be acquired during the life of the animal (through learning) or through differential survival of individuals during the fire (those with fire-savvy traits survive). However, antipredator and surveillance responses come at a cost and can affect individual fitness. In other words, lizards in recently burned habitats might forego foraging and/or reproductive opportunities if they are over-responding to potential risks. Further research is needed to understand the mechanism behind the observed behavioural responses.

Species vary in the degree to which they have been exposed to fires and we observed within-species variation in the response to fire cues. Similarly, species vary in their degree of urban tolerance which also conditions their fire response. Behavioural studies like this one provide a better understanding of the joint effects of fire and urbanization in an increasingly urban ‘Pyrocene’. Such studies are needed for a wide range of species to identify vulnerable species, predict potential effects, and guide management and conservation of affected environments and species.

Author Contributions

All authors conceptualized and designed the study, L.A-R. collected field data, L.A-R. performed data analysis, L.A-R. drafted the manuscript, J.G.P, D.TB. and B.J.P. supervised and contributed critically to the final version of the manuscript.

Data Availability

Analyses reported in this article can be reproduced using the Mendeley Data repository provided in Álvarez-Ruiz et al. (2022): https://doi.org/10.17632/cmddbrxc87.1.

Declaration of Interest

The authors declare no conflict of interest.

Acknowledgments

We thank Hellen Lin for her assistance in the field and Jon McCann for logistical support. We are grateful to Daniel and Susan Gottlieb (The Gottlieb Native Garden) for allowing the study at their garden; to Scott Logan for his guidance in the garden; and to the Griffith Park neighbours, Gerry Hans, Lisa Grezo, Rémi Kessler, Caroline Schweich, Linda Othenin-Girard and Annette Sikand who made their yards available for this study. We also thank the Santa Monica Mountains National Recreation Area for the permit to conduct this research. This work was supported by Ministry of Economy and Competitiveness and Ministry of Science, Innovation and Universities from the Spanish Government (grant numbers CGL2015-64086-P, PGC2018-096569-B-I00 and BES-2016-078225).

References

Álvarez-Ruiz, L., Belliure, J., & Pausas, J. G. (2021). Fire-driven behavioral response to smoke in a Mediterranean lizard. *Behavioral Ecology, 32*(4), 662–667. https://doi.org/10.1093/beheco/arab010

Álvarez-Ruiz, L., Pausas, J. G., Blumstein, D. T., & Putman, B. J. (2022). Lizards' response to the sound of fire is modified by fire history. Mendeley Data, v1 https://doi.org/10.17632/cmddbrxc87.1.

Baeckens, S., Herrel, A., Broeckhoven, C., Vasilopoulou-Kampitsi, M., Huyghe, K., Goyens, J., & Van Damme, R. (2017). Evolutionary morphology of the lizard chemosensory system. *Scientific Reports, 7*(1), 1–13. https://doi.org/10.1038/s41598-017-09415-7

Batabyal, A., Balakrishna, S., & Thaker, M. (2017). A multivariate approach to understanding shifts in escape strategies of urban lizards. *Behavioral Ecology and Sociobiology, 71*(5), 1–8. https://doi.org/10.1007/S00265-017-2307-3

Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2014). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1). https://doi.org/10.18637/jss.v067.i01

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Methodological), 57*(1), 289–300. https://doi.org/10.1111/J.2517-6161.1995.TB02031.X

Blumstein, D., & Daniel, J. (2007). *Quantifying behavior the JWatcher way.* Sinauer.

Brittan-Powell, E. F., Christensen-Dalsgaard, J., Tang, Y., Carr, C., & Dooling, R. J. (2010). The auditory brainstem response in two lizard species. *Journal of the Acoustical Society of America, 128*(2), 787–794. https://doi.org/10.1121/1.3458813

Cantwell, L. R., & Forrest, T. G. (2013). Response of *Anolis sagrei* to acoustic calls from predatory and nonpredatory birds. *Journal of Herpetology, 47*(2), 293–298. https://doi.org/10.1670/11-184

Christensen-Dalsgaard, J., & Manley, G. A. (2005). Directionality of the lizard ear. *Journal of Experimental Biology, 208*(6), 1209–1217. https://doi.org/10.1242/JEB.01511

Cohen, L., Rothschild, G., & Mizrahi, A. (2011). Multisensory integration of natural odors and sounds in the auditory cortex. *Neuron, 72*(2), 357–369. https://doi.org/10.1016/J.NEURON.2011.08.019

Cooper, W. E. (2015). Theory: Models of escape behavior and refuge use. In W. E. Cooper, & D. T. Blumstein (Eds.), *Escaping from predators: An integrative view of escape decisions* (pp. 17–60). Cambridge University Press.

Cooper, W. E., & Blumstein, D. T. (2015). Escape behavior: Importance, scope, and variables. Escaping from predators: An integrative view of escape decisions. In

W. E. Cooper, & D. T. Blumstein (Eds.), *Escaping from predators: An integrative view of escape decisions* (pp. 3–14). Cambridge University Press.

Davis, J., & Ford, R. G. (1983). Home range in the western fence lizard (*Sceloporus occidentalis occidentalis*). *Copeia, 1983*(4), 933. https://doi.org/10.2307/1445094

Dell, J., O'Brien, J., Doan, L., Richards, L., & Dyer, L. (2017). An arthropod survival strategy in a frequently burned forest. *Ecology, 98*(11), 2972–2974. https://doi.org/10.1002/ecy.1939

Doty, A. C., Currie, S. E., Stawski, C., & Geiser, F. (2018). Can bats can sense smoke during deep torpor? *Physiology & Behavior, 185*, 31–38.

Driscoll, D. A., Armenteras, D., Bennett, A. F., Brotons, L., Clarke, M. F., Doherty, T. S., Haslem, A., Kelly, L. T., Sato, C. F., Sitters, H., Aquilué, N., Bell, K., Chadid, M., Duane, A., Meza-Elizalde, M. C., Giljohann, K. M., González, T. M., Jambhekar, R., Lazzari, J., … Wevill, T. (2021). How fire interacts with habitat loss and fragmentation. *Biological Reviews, 96*(3), 976–998. https://doi.org/10.1111/BRV.12687

Driscoll, D. A., Lindenmayer, D. B., Bennett, A. F., Bode, M., Bradstock, R. A., Cary, G. J., Clarke, M. F., Dexter, N., Fensham, R., Friend, G., Gill, M., James, S., Kay, G., Keith, D. A., MacGregor, C., Russell-Smith, J., Salt, D., Watson, J. E. M., Williams, R. J., & York, A. (2010). Fire management for biodiversity conservation: Key research questions and our capacity to answer them. *Biological Conservation, 143*(9), 1928–1939. https://doi.org/10.1016/J.BIOCON.2010.05.026

Ferreira, J. A. (2007). The Benjamini-Hochberg method in the case of discrete test statistics. *International Journal of Biostatistics, 3*(1). https://doi.org/10.2202/1557-4679.1065

Fine, P. V. A. (1999). Aerial predator recognition by free-ranging *Sceloporus occidentalis*. *Journal of Herpetology, 33*(1), 128–131. https://doi.org/10.2307/1565553

Fitch, H. W. (1940). *A field study of the growth and behavior of the fence lizard* (Vol. 44, pp. 151–172). University of California Publications in Zoology.

Fuong, H., Keeley, K. N., Bulut, Y., & Blumstein, D. T. (2014). Heterospecific alarm call eavesdropping in nonvocal, white-bellied copper-striped skinks, *Emoia cyanura*. *Animal Behaviour, 95*, 129–135. https://doi.org/10.1016/J.ANBEHAV.2014.07.005

Garvey, N., Ben-Ami, D., Ramp, D., & Croft, D. B. (2010). Survival behaviour of swamp wallabies during prescribed burning and wildfire. *Wildlife Research, 37*(1), 1. https://doi.org/10.1071/WR08029

Geffroy, B., Sadoul, B., Putman, B. J., Berger-Tal, O., Garamszegi, L. Z., Møller, A. P., & Blumstein, D. T. (2020). Evolutionary dynamics in the Anthropocene: Life history and intensity of human contact shape antipredator responses. *PLoS Biology, 18*(9), Article e3000818. https://doi.org/10.1371/journal.pbio.3000818

Geluso, K. N., Schroder, G. D., & Bragg, T. B. (1986). Fire-avoidance behavior of meadow voles (*Microtus pennsylvanicus*). *American Midland Naturalist, 116*(1), 202–205. https://doi.org/10.2307/2425953

Grafe, T. U., Döbler, S., Linsenmair, K. E., Dö, S., & Linsenmair, K. E. (2002). Frogs flee from the sound of fire. *Proceedings of the Royal Society B: Biological Sciences, 269*(1495), 999–1003. https://doi.org/10.1098/rspb.2002.1974

Green, A. J. (2001). Mass/length residuals: Measures of body condition or generators of spurious results? *Ecology, 82*(5), 1473–1483. https://doi.org/10.1890/0012-9658(2001)082[1473:MLRMOB]2.0.CO;2

Greene, H. W. (1988). Antipredator mechanisms in reptiles. In C. Gans, & R. B. Huey (Eds.), *Biology of the reptilia* (pp. 1–152). Alan R. Liss.

Halene, T. B., Talmud, J., Jonak, G. J., Schneider, F., & Siegel, S. J. (2009). Predator odor modulates auditory event-related potentials in mice. *NeuroReport, 20*(14), 1260–1264. https://doi.org/10.1097/WNR.0B013E32833300CDE

Hartig, F. (2019). DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. https://cran.r-project.org/web/packages/DHARMa/index.html.

Huang, B., Lubarsky, K., Teng, T., & Blumstein, D. T. (2011). Take only pictures, leave only fear? The effects of photography on the West Indian anole *Anolis cristatellus*. *Current Zoology, 57*(1), 77–82. https://doi.org/10.1093/czoolo/57.1.77

Jennings, M. K., Lewison, R. L., Vickers, T. W., & Boyce, W. M. (2016). Puma response to the effects of fire and urbanization. *Journal of Wildlife Management, 80*(2), 221–234. https://doi.org/10.1002/JWMG.1018

Keeley, J. E., Bond, W. J., Bradstock, R. A., Pausas, J. G., & Rundel, P. W. (2012). *Fire in Mediterranean ecosystems: Ecology, evolution and management*. Cambridge University Press. https://doi.org/10.1017/CBO9781139033091

Keeley, J. E., & Fotheringham, C. J. (2001). Historic fire regime in southern California shrublands. *Conservation Biology, 15*(6), 1536–1548. https://doi.org/10.1046/j.1523-1739.2001.00097.x

Keeley, J. E., & Pausas, J. G. (2022). Evolutionary ecology of fire. *Annual Review of Ecology, Evolution and Systematics, 53*. https://doi.org/10.1146/annurev-ecolsys-102320-095612

Koenig, J., Shine, R., & Shea, G. (2002). The dangers of life in the city: Patterns of activity, injury and mortality in suburban lizards (*Tiliqua scincoides*). *Journal of Herpetology, 36*(1), 62–68. https://doi.org/10.1670/0022-1511(2002)036[0062:TDOLITC]2.0.CO;2

Köppl, C., & Manley, G. A. (1992). Functional consequences of morphological trends in the evolution of lizard hearing organs. In D. B. Webster, R. R. Fay, & A. N. Popper (Eds.), *The evolutionary biology of hearing* (pp. 489–509). Springer-Verlag. https://doi.org/10.1007/978-1-4612-2784-7_31.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software, 82*(13), 1–26. https://doi.org/10.18637/JSS.V082.I13

Leal, M., & Rodríguez-Robles, J. A. (1997). Signalling displays during predator-prey interactions in a Puerto Rican anole, *Anolis cristatellus*. *Animal Behaviour, 54*(5), 1147–1154. https://doi.org/10.1006/anbe.1997.0572

Legge, S., Rumpff, L., Woinarski, J. C. Z., Whiterod, N. S., Ward, M., Southwell, D. G., Scheele, B. C., Nimmo, D. G., Lintermans, M., Geyle, H., Garnett, S. T., Hayward-Brown, B., Ensbey, M., Ehmke, G., Ahyong, S. T., Blackmore, C. J., Bower, D. S., Brizuela-Torres, D., Burbidge, A. H., … Zukowski, S. (2022). The conservation impacts of ecological disturbance: Time-bound estimates of population loss and recovery for fauna affected by the 2019-2020 Australian megafires. *Global Ecology and Biogeography, 31*, 2085–2104. https://doi.org/10.1111/geb.13473

Loyd, K. A. T., Hernandez, S. M., Carroll, J. P., Abernathy, K. J., & Marshall, G. J. (2013). Quantifying free-roaming domestic cat predation using animal-borne video cameras. *Biological Conservation, 160*, 183–189. https://doi.org/10.1016/J.BIOCON.2013.01.008

Manley, G. A. (2000). The hearing organs of lizards. In R. J. Dooling, R. R. Fay, & A. N. Popper (Eds.), *Comparative hearing: Birds and reptiles* (pp. 139–196). Springer. https://doi.org/10.1007/978-1-4612-1182-2_4.

Martins, E. P. (1991). Individual and sex differences in the use of the push-up display by the sagebrush lizard, *Sceloporus graciosus*. *Animal Behaviour, 41*(3), 403–416. https://doi.org/10.1016/S0003-3472(05)80841-3

Massot, M., Huey, R. B., Tsuji, J., & Van Berkum, F. H. (2003). Genetic, prenatal, and postnatal correlates of dispersal in hatchling fence lizards (*Sceloporus occidentalis*). *Behavioral Ecology, 14*(5), 650–655. https://doi.org/10.1093/beheco/arg056

McElroy, E. J. (2019). Antipredator behavioral mechanisms: Avoidance, deterrence, escape, and encounter. In V. L. Bels, & A. P. Russel (Eds.), *Behavior of lizards* (pp. 143–188). CRC Press/Taylor & Francis. https://doi.org/10.1201/9781498782739-6.

Mendyk, R. W., Weisse, A., & Fullerton, W. (2020). A wake-up call for sleepy lizards: The olfactory-driven response of *Tiliqua rugosa* (Reptilia: Squamata: Sauria) to smoke and its implications for fire avoidance behavior. *Journal of Ethology, 38*, 161–166. https://doi.org/10.1007/s10164-019-00628-z

Modugno, S., Balzter, H., Cole, B., & Borrelli, P. (2016). Mapping regional patterns of large forest fires in Wildland–Urban Interface areas in Europe. *Journal of Environmental Management, 172*, 112–126. https://doi.org/10.1016/J.JENVMAN.2016.02.013

Nimmo, D. G., Avitabile, S., Banks, S. C., Bliege Bird, R., Callister, K., Clarke, M. F., Dickman, C. R., Doherty, T. S., Driscoll, D. A., Greenville, A. C., Haslem, A., Kelly, L. T., Kenny, S. A., Lahoz-Monfort, J. J., Lee, C., Leonard, S., Moore, H., Newsome, T. M., Parr, C. L., … Bennett, A. F. (2019). Animal movements in fire-prone landscapes. *Biological Reviews, 94*(3), 981–998. https://doi.org/10.1111/brv.12486

Nimmo, D. G., Carthey, A. J. R., Jolly, C. J., & Blumstein, D. T. (2021). Welcome to the Pyrocene: Animal survival in the age of megafire. *Global Change Biology, 27*(22), 5684–5693. https://doi.org/10.1111/GCB.15834

Nimmo, D. G., Jolly, C. J., & Carthey, A. J. R. (2022). Megafire: The Darwinian guillotine? *Australian Zoologist, 42*(2), 217–222. https://doi.org/10.7882/AZ.2022.022

Nowack, J., Delesalle, M., Stawski, C., & Geiser, F. (2016). Can hibernators sense and evade fires? Olfactory acuity and locomotor performance during deep torpor. *Science of Nature, 103*(9–10), 73. https://doi.org/10.1007/s00114-016-1396-6

Pausas, J. G., & Keeley, J. E. (2009). A burning story: The role of fire in the history of life. *BioScience, 59*(7), 593–601. https://doi.org/10.1525/bio.2009.59.7.10

Pausas, J. G., & Parr, C. L. (2018). Towards an understanding of the evolutionary role of fire in animals. *Evolutionary Ecology, 32*(2–3), 113–125. https://doi.org/10.1007/s10682-018-9927-6

Putman, B. J., Gasca, M., Blumstein, D. T., & Pauly, G. B. (2019). Downsizing for downtown: Limb lengths, toe lengths, and scale counts decrease with urbanization in western fence lizards (*Sceloporus occidentalis*). *Urban Ecosystems, 22*(6), 1071–1081. https://doi.org/10.1007/s11252-019-00889-z

Putman, B. J., Pauly, G. B., & Blumstein, D. T. (2020). Urban invaders are not bold risk-takers: A study of 3 invasive lizards in Southern California. *Current Zoology, 66*(6), 657–665. https://doi.org/10.1093/CZ/ZOAA015

Putman, B. J., Williams, R., Li, E., & Pauly, G. B. (2021). The power of community science to quantify ecological interactions in cities. *Scientific Reports, 11*(1). https://doi.org/10.1038/S41598-021-82491-Y

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Radeloff, V. C., Helmers, D. P., Anu Kramer, H., Mockrin, M. H., Alexandre, P. M., Bar-Massada, A., Butsic, V., Hawbaker, T. J., Martinuzzi, S., Syphard, A. D., & Stewart, S. I. (2018). Rapid growth of the US wildland-urban interface raises wildfire risk. *Proceedings of the National Academy of Sciences of the United States of America, 115*(13), 3314–3319. https://doi.org/10.1073/PNAS.1718850115/SUPPL_FILE/PNAS.201718850SI.PDF

Ramalho, C. E., Ottewell, K. M., Chambers, B. K., Yates, C. J., Wilson, B. A., Bencini, R., & Barrett, G. (2018). Demographic and genetic viability of a medium-sized ground-dwelling mammal in a fire prone, rapidly urbanizing landscape. *PLoS One, 13*(2), Article e0191190. https://doi.org/10.1371/JOURNAL.PONE.0191190

Rochester, C. J., Brehme, C. S., Clark, D. R., Stokes, D. C., Hathaway, S. A., & Fisher, R. N. (2010). Reptile and amphibian responses to large-scale wildfires in southern California. *Journal of Herpetology, 44*(3), 333–351. https://doi.org/10.1670/08-143.1

Samia, D. S. M., Nakagawa, S., Nomura, F., Rangel, T. F., & Blumstein, D. T. (2015). Increased tolerance to humans among disturbed wildlife. *Nature Communications, 6*(1), 1–8. https://doi.org/10.1038/ncomms9877

Santos, X., Belliure, J., Gonçalves, J. F., & Pausas, J. G. (2022). Resilience of reptiles to megafires. *Ecological Applications, 32*(2), e2518. https://doi.org/10.1002/EAP.2518

Sensenig, R. L., Kimuyu, D. M., Carlos Ruiz-Guajardo, J., & Veblen, K. E. (2017). Fire disturbance disrupts an acacia ant–plant mutualism in favor of a subordinate ant species. *Ecology, 98*(5), 1455–1464. https://doi.org/10.1002/ecy.1797

Seo, H. S., & Hummel, T. (2011). Auditory–olfactory integration: Congruent or pleasant sounds amplify odor pleasantness. *Chemical Senses, 36*(3), 301–309. https://doi.org/10.1093/CHEMSE/BJQ129

Sheldahl, L. A., & Martins, E. P. (2000). The territorial behavior of the western fence lizard, *Sceloporus occidentalis*. *Herpetologica, 56*, 469–479.

Smith, A., Meulders, B., Bull, C. M., & Driscoll, D. (2012). Wildfire-induced mortality of Australian reptiles. *Herpetology Notes, 5*, 233–235.

Sol, D., Lapiedra, O., & González-Lagos, C. (2013). Behavioural adjustments for a life in the city. *Animal Behaviour, 85*(5), 1101–1112. https://doi.org/10.1016/J.ANBEHAV.2013.01.023

Stankowich, T., & Blumstein, D. T. (2005). Fear in animals: A meta-analysis and review of risk assessment. *Proceedings of the Royal Society B: Biological Sciences, 272*(1581), 2627–2634. https://doi.org/10.1098/RSPB.2005.3251

Stawski, C., Matthews, J. K., Körtner, G., & Geiser, F. (2015). Physiological and behavioural responses of a small heterothermic mammal to fire stimuli. *Physiology and Behavior, 151*, 617–622. https://doi.org/10.1016/j.physbeh.2015.09.002

Thompson, M. J., Capilla-Lasheras, P., Dominoni, D. M., Réale, D., & Charmantier, A. (2022). Phenotypic variation in urban environments: Mechanisms and implications. *Trends in Ecology & Evolution, 37*(2), 171–182. https://doi.org/10.1016/J.TREE.2021.09.009

Turner, R. G. (1987). Neural tuning in the granite spiny lizard. *Hearing Research, 26*(3), 287–299. https://doi.org/10.1016/0378-5955(87)90064-5

Vitousek, M. N., Adelman, J. S., Gregory, N. C., & St Clair, J. J. H. (2007). Heterospecific alarm call recognition in a non-vocal reptile. *Biology Letters, 3*(6), 632–634. https://doi.org/10.1098/RSBL.2007.0443

Warner, D. A., Johnson, M. S., & Nagy, T. R. (2016). Validation of body condition indices and quantitative magnetic resonance in estimating body composition in a small lizard. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology, 325*, 588–597. https://doi.org/10.1002/jez.2053

Yan, K. M., Pinto, S. P., Vartany, C., & Blumstein, D. T. (2019). Shift down, look up: A test of the non-linearity and fear hypothesis in a non-vocal skink. *Ethology, 125*(3), 153–158. https://doi.org/10.1111/eth.12839

Appendix

Table A1

Location of the nine study sites (in southern California, U.S.A.) in the three environments studied (burned, unburned and urban), coordinates, distance to fire edge, number of experimental playbacks, number of sampling days, sampled lizards per day and number of lizards captured

Ecosystem type	Location name	Coordinates	Minimum distance to fire edge (km)[1]	No. of experimental playbacks	No. of sampling days/sampled lizards per day	No. of lizards captured	
						♀	♂
Burned wildland	Backbone	34°04′28.4′N; 118°48′47.1′W	5.8	30	4/7.5	7	19
	Backbone West	34°05′23.0′N; 118°52′10.1′W	1.5	18	4/4.5	4	11
	Chesebro	34°10′38.0′N; 118°43′41.9′W	1.7	16	4/4	12	3
Unburned wildland	Marvin	34°07′32.9′N; 118°33′07.0′W	11.9	21	2/10.5	8	6
	Satwiwa	34°08′47.0′N; 118°57′51.5′W	2.5	22	4/5.5	12	6
	Stunt	34°05′39.4′N; 118°38′52.6′W	5.4	25	4/6.25	9	9
Urban	Sage Hill	34°04′27.3′N; 118°27′16.9′W	23.4	24	7/3.43	2	11
	Griffith Park	34°07′08.8′N; 118°18′38.8′W	34.1	23	7/3.29	9	10
	Gottlieb Garden	Beverly Hills, LA	26.8	20	2/10	7	7
Total				199		70	82

[1] This is the distance from the centre of the studied population to the edge and it was calculated by making a polygon with the location of each lizard.

Table A2

Result of the linear mixed model (LMM) for the number of lizards found per sampling day

Site	Estimate	SE	t	P
Intercept	5.333	1.454	3.668	**0.019**
Unburned	1.928	2.104	0.916	0.405
Urban	−0.503	2.041	−0.247	0.818

Location was included as a random factor. $N = 38$ subjects. Statistically significant ($P < 0.05$) difference is highlighted in bold.

Table A3

Source of acoustic stimuli and samples

Treatment	Sample no.	Type	Link	Catalogue no.	Location of recording
House finch (nonpredatory bird)	1	Song	https://macaulaylibrary.org/asset/56843	56843	Why, Arizona, U.S.A.
	2	Song	https://macaulaylibrary.org/asset/22938	22938	Kern, California, U.S.A.
	3	Song	https://macaulaylibrary.org/asset/12932	12932	Kern, California, U.S.A.
	4	Song	https://www.xeno-canto.org/72282	XC72282	Milwaukee, Wisconsin, U.S.A.
	5	Song	https://www.xeno-canto.org/268458	XC268458	Douglas, Arizona, U.S.A.
American kestrel (predatory bird)	1	Call	https://www.xeno-canto.org/348428	XC348428	Sierra San Pedro Martir, Baja California, Mexico
	2	Call	https://macaulaylibrary.org/asset/107973	107973	Tompkins, New York, U.S.A.
	3	Call	https://www.xeno-canto.org/297550	XC297550	Terlingua, Texas, U.S.A.
	4	Call	https://www.xeno-canto.org/127418	XC127418	Chicauma, Chile
	5	Call	https://www.xeno-canto.org/147272	XC147272	Otay Lakes, California
Bananaquit (novel bird)	1	Song	https://macaulaylibrary.org/asset/110066	110066	Mato Grosso, Brazil
	2	Song	https://macaulaylibrary.org/asset/67156	67156	Aragua, Venezuela
	3	Song	https://macaulaylibrary.org/asset/67153	67153	Aragua, Venezuela
	4	Song	https://macaulaylibrary.org/asset/67147	67147	Cojedes, Venezuela
	5	Song	https://macaulaylibrary.org/asset/67154	67154	Carabobo, Venezuela

Table A4
Ethogram of western fence lizards' behaviour (modified from Yan et al., 2019)

Behaviour	Definition
Stand and look	Fixed body and head position. Scored with time head moved (interpreted as a shift in gaze)
Walk	Locomotion using all four legs
Run	Fast locomotion using all four legs
Forage	Slow locomotion in search widely for food
Push-ups	No change in position. Lizard's head and trunk are raised and lowered by extension and flexion of the front legs.
Other	Other behaviours not listed
Out of sight	Lizard was not in view of observer

Table A5
Results of the linear mixed model (LMM) for lizards' rate of looks/min

Model	*df*	AIC	χ^2	*P*	Estimates
Null	2	685.42			1.308 [Intercept]
Treatment	3	677.67	13.754	**0.003**	2.237 [Intercept]; −0.708 [P]; −1.519 [NP]; −1.584 [N]
+ Habitat	2	672.27	9.395	**0.009**	2.6 [Intercept]; −0.726 [P]; −1.54 [NP]; −1.577 [N]; −1.183 [UB]; 0.126 [U]
+ Sex	1	674.18	0.092	0.761	
+ SVL	1	672.34	1.933	0.164	
+ Lizard body temp	1	673.3	0.975	0.323	
+ Wind speed	1	674.26	0.009	0.921	
+ Speaker distance	1	674.21	0.065	0.799	
+ Initial head orientation	5	673.61	0.667	0.414	
+ Distance to closest refuge	6	673.04	1.231	0.267	
+ Tail autotomy	1	673.97	0.3	0.584	

The only variables included in the final model (treatment and habitat) were selected by the stepwise procedure (variables added sequentially in order of their contribution to the remaining explained deviance). Note that each row is an independent model. Results of the models adding the rest of the variables (sex, SVL, lizard body temperature, wind velocity, speaker distance, initial head orientation and tail autotomy) once treatment and habitat were in the model are also shown; all are nonsignificant (note that each row is an independent model). The estimates of the fixed effects of the corresponding model are shown in the rightmost column. $N = 152$ subjects. SVL: snout − vent length; P: predatory bird; NP: nonpredatory bird; N: novel bird; UB: unburned; U: urban. Statistically significant ($P < 0.05$) differences are highlighted in bold.

Table A6
Effect of habitat (burned, unburned, and urban), treatment (fire, predatory bird, nonpredatory bird and novel bird) and their interaction on lizards' rate of looks/min

Predictors	Sum of squares	Mean square	Numerator *df*	Denominator *df*	*F*	*P*
Habitat	57.791	28.895	2	187	6.525	**0.002**
Treatment	69.310	23.103	3	187	5.217	**0.002**
Habitat*Treatment	66.320	11.053	6	187	2.496	**0.024**

The table shows type III ANOVA (analysis of variance) results from the linear mixed-effects model with Gaussian distribution including fixed effects of playback treatment, habitat and their interaction. $N = 199$ subjects. Statistically significant ($P < 0.05$) differences are highlighted in bold.

Table A7
Variation in rate of looks/min across habitats and treatments

Habitat	Treatment	Mean	SE	*df*	Lower CI	Upper CI
Burned	Fire	3.238	0.510	187	2.231	4.245
Unburned	Fire	0.926	0.496	187	−0.053	1.904
Urban	Fire	2.453	0.526	187	1.415	3.491
Burned	Predatory bird	0.583	0.526	187	−0.455	1.621
Unburned	Predatory bird	1.259	0.496	187	0.281	2.238
Urban	Predatory bird	2.941	0.510	187	1.934	3.948
Burned	Nonpredatory bird	1.378	0.543	187	0.306	2.450
Unburned	Nonpredatory bird	0.431	0.510	187	−0.576	1.438
Urban	Nonpredatory bird	0.781	0.496	187	−0.198	1.759
Burned	Novel bird	1.005	0.526	187	−0.033	2.043
Unburned	Novel bird	−0.140	0.543	187	−1.212	0.932
Urban	Novel bird	1.364	0.526	187	0.326	2.402

CI: confidence interval.

Table A8
Effect of habitat (burned, unburned and urban) and treatment (fire, predatory bird, nonpredatory bird and novel bird) on proportion of lizards' exhibiting push-ups, locomotion (i.e. walk and run) or foraging behaviour

	df	Push-ups		Locomotion		Foraging	
		χ^2	*P*	χ^2	*P*	χ^2	*P*
Habitat	2	6.852	**0.032**	3.995	0.136	3.948	0.14
Treatment	3	9.19	**0.027**	5.048	0.168	0.859	0.835

The table shows type III ANOVA (analysis of variance) results from the generalized linear mixed-effects model with binomial distribution including fixed effects of playback treatment and habitat. The interaction between factors was tested and removed from the final model because it was not significant. $N = 199$ subjects. Statistically significant ($P < 0.05$) differences are highlighted in bold.

Table A9
Differences in the probability of lizards doing push-ups between playback treatments and habitats.

Predictors	Contrast	Estimate	SE	*df*	*z*	*P*
Treatment	Fire − Predatory bird	0.93	0.528	Infinite	1.763	0.291
	Fire − Nonpredatory bird	1.121	0.551	Infinite	2.033	0.176
	Fire − Novel bird	1.817	0.687	Infinite	2.647	**0.04**
	Predatory bird − Nonpredatory bird	0.191	0.607	Infinite	0.315	0.989
	Predatory bird − Novel bird	0.887	0.731	Infinite	1.213	0.618
	Nonpredatory bird − Novel bird	0.697	0.747	Infinite	0.932	0.788
Habitat	Unburned − Burned	−0.419	0.583	Infinite	−0.719	0.752
	Unburned − Urban	−1.288	0.53	Infinite	−2.428	**0.04**
	Burned − Urban	−0.869	0.491	Infinite	−1.769	0.18

The table shows the results of linear contrasts that were calculated from the binomial model presented in Table A8. $N = 199$ subjects. Statistically significant ($P < 0.05$) differences are highlighted in bold.

Table A10
Results of the linear mixed model (LMM) for lizards' distance to closest refuge (log transformed) before starting the FID trials

Model	*df*	AIC	χ^2	*P*	Estimate
Null		300.23			3.948 [Intercept]
SVL	1	289.12	13.111	**< 0.001**	1.979 [Intercept]; 0.03 [SVL]
+ Habitat	2	285.48	7.641	**0.022**	2.167 [Intercept]; 0.027 [SVL]; 0.189 [UB]; −0.2 [U]
+ Tail autotomy	1	282.03	5.448	**0.02**	2.356 [Intercept]; 0.025 [SVL]; 0.149 [UB]; −0.268 [U]; −0.252 [Tail autotomy Yes]
+ Soil temperature	1	280.71	3.324	0.068	1.916 [Intercept]; 0.025 [SVL]; 0.16 [UB]; −0.254 [U]; −0.253 [Tail autotomy Yes]; 0.013 [Soil temperature]
+ Lizard body temp	1	282.54	0.168	0.682	
+ Sex	1	283.63	0.077	0.782	
+ BCI	1	281.65	1.057	0.304	
+ Air temperature	1	282.2	0.507	0.476	
+ Humidity	1	281.92	0.785	0.376	
+ Wind speed	1	280.93	1.782	0.182	

The variables included in the final model (SVL, habitat, tail autotomy and soil temperature) were selected by the stepwise procedure (variables are added sequentially in order of their contribution to the remaining explained deviance). Results of the models adding the rest of the variables once SVL, habitat, tail autotomy and soil temperature were in the model are also shown; all are nonsignificant (note that each row is an independent model). Interactions between factors were checked and were not significant. The estimates of the fixed effects of the corresponding model are shown in the rightmost column. $N = 152$ subjects. SVL: snout − vent length; BCI: body condition index; UB: unburned; U: urban. Statistically significant ($P < 0.05$) differences are highlighted in bold.

Table A11
Differences in lizards' distance to closest refuge between habitats

Contrast	Estimate	SE	*df*	*t*	*P*
Burned − Unburned	−0.16	0.131	5.56	−1.222	0.487
Burned − Urban	0.254	0.144	8.14	1.764	0.241
Unburned − Urban	0.414	0.136	6.62	3.038	**0.047**

The table shows the results of linear contrasts that were calculated from the lineal mixed model presented in Table A9. $N = 152$ subjects. Statistically significant ($P < 0.05$) difference is highlighted in bold.

Table A12
Results of the linear mixed model (LMM) for lizards' flight initiation distance

Model	*df*	AIC	χ^2	*P*	Estimate
Null		1675.7			77.072 [Intercept]
Distance to shelter	1	1674	3.677	0.055	62.975 [Intercept]; 0.218 [Distance to shelter]
+ BCI	1	1673.1	2.852	0.091	63.505 [Intercept]; 0.021 [Distance to shelter]; 62.088 [BCI]
+ Starting distance	1	1673.8	1.387	0.239	
+ Height	1	1673.5	2.456	0.117	
+ Treatment	1	1677.8	1.35	0.717	
+ Habitat	1	1676.1	1.081	0.582	
+ SVL	1	1674.1	1.083	0.298	
+ Sex	1	1674.4	0.699	0.403	
+ Lizard body temp	1	1675	0.096	0.757	
+ Tail autotomy	1	1673.3	1.817	0.178	
+ Air temperature	1	1673.8	1.33	0.249	
+ Soil temperature	1	1675.1	0.005	0.982	
+ Humidity	1	1673.4	1.784	0.182	
+ Wind speed	1	1675.3	0.67	0.413	

The only variables included in the final model (distance to shelter and BCI) were selected by the stepwise procedure (variables are added sequentially in order of their contribution to the remaining explained deviance). Results of the models adding the rest of the variables once distance to shelter and BCI were in the model are also shown; all are nonsignificant (note that each row is an independent model). Interactions between factors were checked and were not significant. The estimates of the fixed effects of the corresponding model are shown in the rightmost column. $N = 152$ subjects. SVL: snout − vent length; BCI: body condition index.

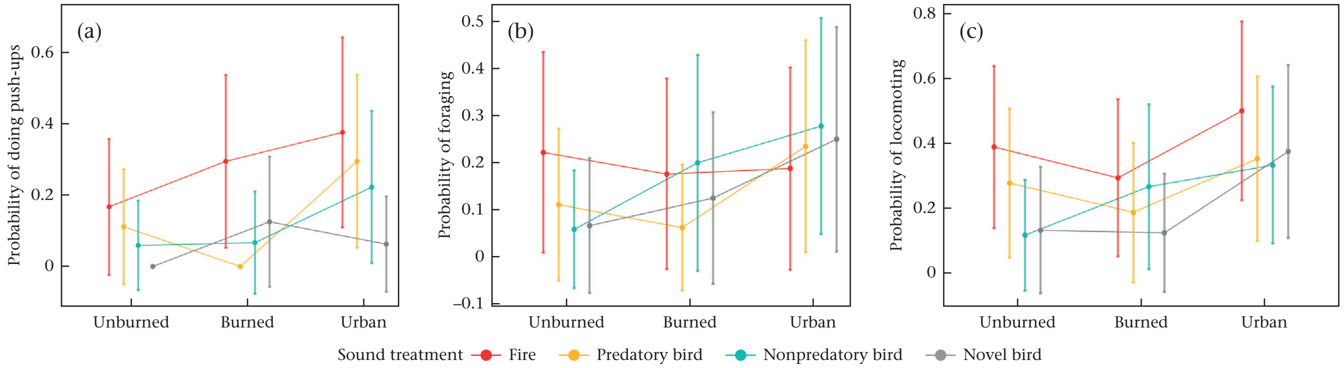


Figure A1. Proportion of lizards (a) exhibiting push-ups, (b) foraging or (c) locomoting in the 90 s including and immediately after playback of treatments (fire, predator, nonpredatory bird and novel bird) in the three habitats (unburned, burned and urban). Points represent means and lines represent 95% confidence intervals. For statistical significance see Table A8. $N = 199$ subjects.

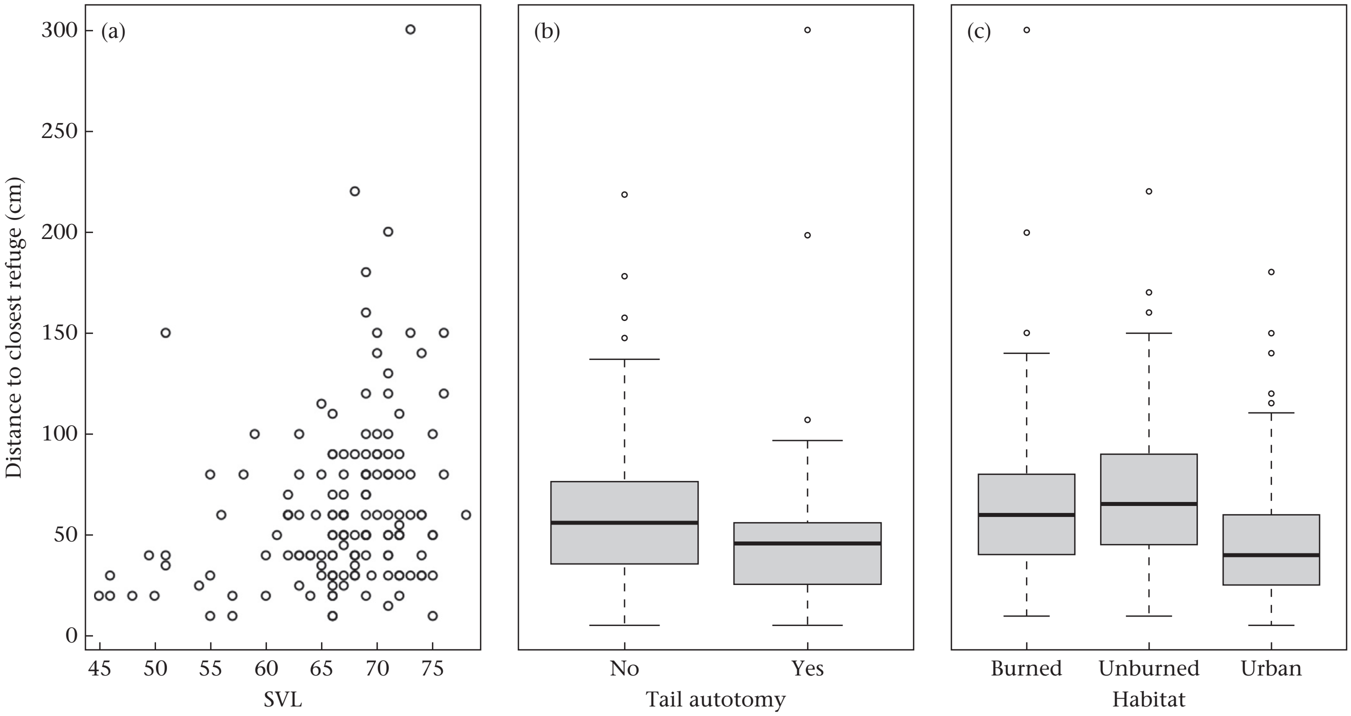


Figure A2. Lizards' distance to closest refuge in relation to (a) snout–vent length (SVL), (b) tail autotomy and (c) habitat. Box plots (b) and (c) illustrate the median (thick horizontal lines), the first and third quartiles (box edges), values within the range of 1.5 times the interquartile range (whiskers) and values beyond the end of whiskers (circles). For statistical significance see Tables A10 and A11. $N = 152$ subjects.

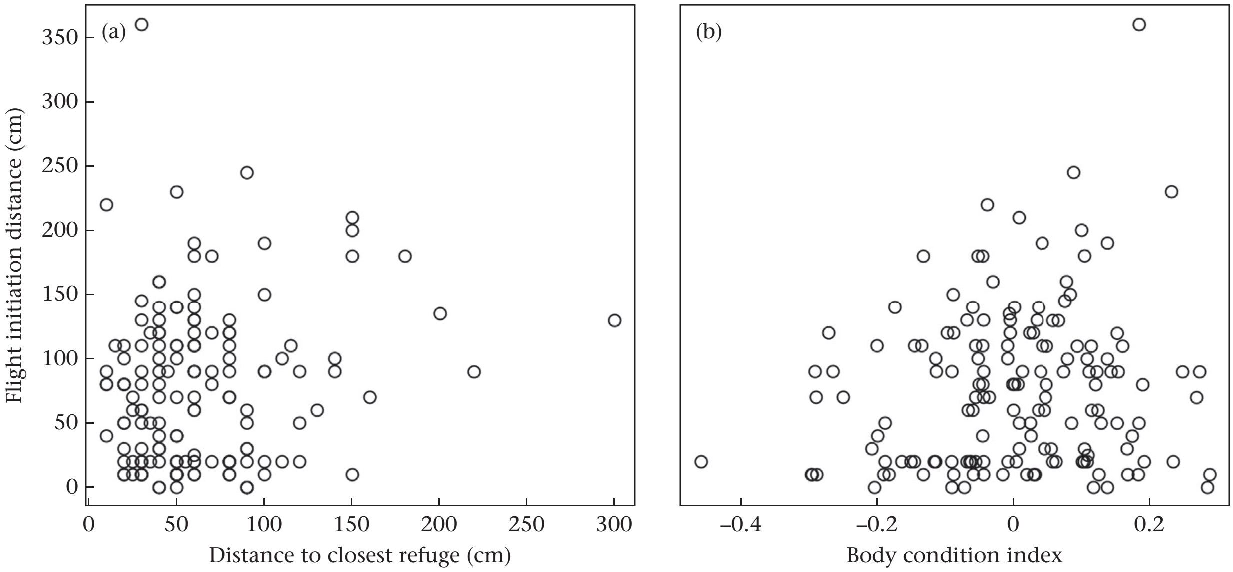


Figure A3. Flight initiation distance in relation to (a) distance to closest refuge and (b) body condition index. For statistical significance see Table A12. $N = 152$ subjects.