Fire-driven behavioral response to smoke in a Mediterranean lizard

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Abstract

The evolutionary role of fire in animals has been poorly explored. Reptiles use sensory cues such as smell (chemoreception) to detect threats and flee. In Mediterranean ecosystems, fire is a threat faced by reptiles. We hypothesized that the Mediterranean lizard *Psammodromus algirus* recognizes the threat of fire by detecting the smoke, which triggers a behavioral response that enhances survival in fire-prone ecosystems. We predicted that lizards from fire-prone ecosystems will be more sensitive to fire stimulus than those from ecosystems that rarely burn. We conducted a terrarium experiment in which lizards from habitats with contrasted fire regimes (fire-prone vs. non-fire-prone) were exposed to smoke vs. control (false smoke) treatment. We found that in populations from fire-prone habitats, more lizards reacted to smoke, and their behavioral response was more intense than in lizard populations from non-fire-prone habitats. Our results suggest that an enhanced response to smoke may be adaptive in lizards from fire-prone ecosystems as it increases the chance for survival. We provide evidence that fire is likely an evolutionary driver shaping behavioral traits in lizard populations exposed to frequent wildfires. Understanding ecological and evolutionary processes shaping animal populations is relevant for species conservation in a changing fire regime world.

Keywords: fire adaptation, fire avoidance, global change, *Psammodromus algirus,* reptile, smoke detection.

Introduction

Fire is an inherent disturbance in the Mediterranean biome (Keeley et al. 2012) and its role as a selective pressure is now well accepted, especially in plants (Bond et al. 2004; He et al. 2011; Keeley et al. 2011; Pausas 2015). Plants are immobile, and thus, they have evolved structural traits for in situ persistence that are easily recognized in the field (survival and population persistence traits; (Pausas et al. 2004; Keeley et al. 2011). In contrast, animals are mobile, and thus, behavioral traits to avoid fires are expected to be particularly important (Pausas and Parr 2018). Although in fire-prone ecosystems there is an abundant and diverse fauna, the knowledge about adaptive traits to fire in animals remains poorly explored (Pausas and Parr 2018).

Individuals within a population differ in their behavior (Bell et al. 2009) and this has fitness implications (Dingemanse et al. 2004; Wolf et al. 2007). This variation could lead to different evolutionary trajectories for populations under different selective pressures (Wolf and Weissing 2012; Dall and Griffith 2014). Very few studies have provided evidence on adaptive behavioral traits to deal with fire in animals. Some bats and possums can detect smoke even when in torpor, and thus they arouse and move to a safe site (Scesny and Robbins 2006; Stawski et al. 2015; Nowack et al. 2016; Doty et al. 2018). And some frogs can recognize the sound of fire and flee to less flammable sites (Grafe et al. 2002). Many animals show fire avoidance behavior, (i.e: mammals seek refuge in underground burrows and flee into adjacent unburned areas (Geluso et al. 1986; Garvey et al. 2010) and non-flying 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 fire cues for such behaviors are unknown. Climate change along with shifts in ignition patterns and fuel

structure are driving changes in fire regimes across the globe (Pausas and Keeley 2019). The resulting unprecedented wildfire activity make fire a key potential selective agent; thus, there is a need to ascertain to what extent animals may have the capacity to detect and avoid fires (Koltz et al. 2018; Pausas and Parr 2018).

Despite wildfires having strong effects on reptile communities (Friend 1993; Santos and Cheylan 2013), burrowing lizards often show high postfire survival (Palis 1995; Floyd et al. 2002; Santos and Poquet 2010). Due to their body size, they are likely to survive sheltering in crevices, under rocks, or among roots. Lizards' survival to wildfires could depend on landscape attributes (e.g., ecosystem structure, shelter availability, and natural barriers), individual characteristics of the animal (e.g., flee speed, body size, and body shape), and fire characteristics (e.g., heterogeneity, intensity, velocity, and severity). In all these cases, the ability to quickly detect fires and react appropriately enhances survival and thus, it provides fitness benefits.

Reptiles perceive sensory cues through the smell (chemoreception, Schwenk 1995; Baeckens et al. 2017), allowing them to recognize threats, evaluate risks, and flee to a safe hiding place. Fire-derived chemicals in the smoke can act as a cue (Nowack et al. 2018). We hypothesize that, in fire-prone ecosystems, there is a selection for individuals with increased sensitivity for detecting smoke and reacting accordingly. Specifically, we predict that lizard populations living in fire-prone ecosystems (i.e., those subject to recurrent fires) are better recognizing smoke as a threat (detection and escape behavior), than lizard populations (of the same species) living in ecosystems that rarely burn. Supporting this prediction would suggest a selection for a behavior that enhances survival under recurrent fires. We tested this prediction for a common lizard in eastern Iberia.

Material and methods

Species model and study sites

Psammodromus algirus is a medium-sized lacertid lizard from the western Mediterranean region (Carranza et al. 2006), with a lifespan of 3-5 years (Comas et al. 2019). In eastern Iberian Peninsula, *P. algirus* inhabits a great variety of habitats from forests to open vegetation, and tends to select microhabitats with low shrub cover (Diaz and Carrascal 1991; Martín and Lopez 2002). It also occurs in recently burned areas, suggesting some postfire survival ability (Santos and Poquet 2010; Ferreira et al. 2018). Given that this species is common in both fire-prone and non-fire-prone habitats, it constitutes a good species model to study variations in their behavior in response to fire stimuli.

We selected two habitat types in eastern Spain with contrasted fire regimes: fire-prone and non-fire-prone type. The fire-prone habitat corresponded to a mosaic of Mediterranean shrublands (mainly *Cistus sp. pl. Ulex parviflorus*, *Quercus coccifera, Rhamnus alaternus, Pistacia lentiscus, and Arbutus unedo*) and *Pinus halepensis* (Aleppo pine) woodlands, with isolated oak trees (*Quercus suber* and *Quercus ilex*). These ecosystems are very flammable and are located in a warm and dry Mediterranean climate; therefore, they are subject to frequent high-intensity fire (Pausas and Fernández-Muñoz 2012; Pausas and Paula 2012). The non-fire-prone habitat corresponded to coastal sand dunes with sparse vegetation composed by *Ammophila arenaria*, *Elymus farctus*, *Eryngium maritimum*, *Salicornia sp.*, and some *Phragmites sp.* and *Juncus sp.* patches. In these ecosystems wildfires are rare or very small due to their low amount and continuity of biomass.

Three sites were sampled for each habitat type (Table 1); sites were all separated each other by at least 20 km (mean distance = 82.6 km). As an indicator of the recent fire history of the area, we computed the area burned around each site (in a circle of 10 km radius) during the last 42 years from fire maps provided by the local government (Generalitat Valenciana). Historical burnt area was lower around non-fire-prone sites than around fire-prone sites (Table 1). Sampling sites had not burnt in at least the last 20 years except for two fire-prone sites (Artana and Gátova), that partially burned during the two years before the study.

Sampling and experimental procedure

We collected adult and juvenile lizards from both sexes in each of the six sites (Table 1) by hand or using a pole with a slip noose. In the two fire-prone sites that partially burnt in the last two years, we sampled both unburned and adjacent burned areas. We avoided sampling close to the fire edge, so individuals sampled unlikely moved in/out the burned area. Considering the lifespan of *P. algirus,* we expected adult lizards inhabiting these burned areas to be survivors of the wildfire.

Lizards were transported to the lab inside cotton bags, and were held captive for the experimental assays. All individuals were measured (snout-vent length, SVL; ± 0.01 cm) and weighed (± 0.1 g), see Supplementary material, Table S1; adults were also sexed (males show more conspicuous femoral pores, Iraeta et al. 2011). 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 completion of the study.

Trials were conducted in an experimental terrarium (100 x 50 x 40 cm) with opaque walls, a thin layer of substrate, and one refuge in the center. The terrarium was located in a room at constant temperature and isolated from external noises. Focal lizards were sequentially exposed to two different treatments: true smoke coming from burning pine needles (Smoke treatment), and false smoke coming from an odorless electric vaporizer (Control). This experimental design implies the same smoke visual cues in both treatments, but only the Smoke treatment provided real fire odor (fire chemical cues).

Each individual remained in the terrarium for 45 minutes (acclimatization) before the assays. Assays lasted 10 minutes: 5 minutes in absence of stimulus and 5 minutes under treatment (Control or Smoke), during which a video camera recorded the interior of the terrarium from an aerial view to follow the focal individual behavior. The treatment application consisted on insufflating the true or false smoke inside the terrarium using a 1L syringe. We considered the first 3 seconds after the treatment application as adjusting time to the new conditions, and thus were discarded for the analyses. Each lizard was subjected to both experimental treatments, in random order. The first experimental trial was performed the day after capture and the alternative treatment was performed the next day.

Once all assays were concluded, we watched the video recordings to analyze lizard behavior, and registered the time that the lizard spent performing any activity using a chronometer. The behavioral expressions showed by the individuals were: standing immobile, head movement, tongue flicking, walking, running, and scratching the terrarium, and we approached activity as seconds spent in expressions different to standing immobile. To evaluate differences in the quick recognition of smoke as a threat, we focused on the first minute after the application of the treatment. Specifically we aimed to identify the

individual ability in 1) detecting fire, and 2) offering a behavioral response. We considered that individuals detected fire (yes/no; binary variable) if they showed any activity different from standing immobile for 3 or more seconds during the first minute after the application of the treatments. We evaluated the intensity of their behavioral response as total seconds of activity (i.e., time different from standing immobile; continuous variable) during the same period.

Statistical analyses

We successfully performed a total of 216 trials, 107 for Control and 109 for Smoke treatments; 8 Control and 6 Smoke assays were discarded due to technical failures at the treatment application. To analyze lizard's reaction (i.e., at least 3 seconds of activity during the first minute after treatment application) and behavioral response (i.e., total seconds of activity during the first minute after treatment application) as a function of treatment (Smoke vs Control) and habitat (fire-prone vs non-fire-prone), we used a hurdle mixed model. We also checked the effect of sex, snout-vent length (SVL), and the order of treatment application.

The high incidence of zero counts contained in our data (46.8% of no reactions, Table 2) made hurdle model especially appropriate (Potts and Elith 2006). Hurdle models are partitioned into two processes: the first process estimates the presence or absence of reaction (containing zero values), and the second one estimates the duration of the reaction, once they reacted to the treatment (containing the positive counts).

We fitted a hurdle generalized linear mixed model (GLMMs) with a negative binomial error distribution ('nbinom2') where location (6 levels) and individual (112 levels) were included as random factors. We used the function 'ggpredict()' from the package 'ggeffects' (Lüdecke 2018) to compute the predicted values of lizard activity conditioned on the fixed effects and the zero inflation component without conditioning on random effects.

Of the three fire-prone sites, two were partially affected by fire during the last two years. Therefore, we also examined whether previous experience with wildfires influences lizards' ability to detect and react to smoke. Given the limited sample size, the hurdle models provided a poor (overdispersed) fit, thus we fitted generalized linear mixed models (GLMMs) with negative binomial error distribution for the lizards' behavioral response (total seconds of activity in one minute, including zeros), where individual was included as random factor. We first compared the behavior of lizards from the recently unburned fire-prone site (P. Coeli) with the lizards from the two partially burnt fire-prone sites (Artana and Gatova) with a GLMM including the treatments (Control or Smoke), and location (P. Coeli, Artana and Gatova) as fixed factors, and individual (57 levels) as random factor. Then, for the two fire-prone sites with recently burned areas (Gatova and Artana), we compared the behavior of lizards sampled in the burned areas (which survived a wildfire) with those from the unburned areas. In that case, we fitted the GLM including the treatments (Control or Smoke), wildfire experience (yes or no), and location (Artana and Gatova) as fixed factors, and individual (30 levels) as random factor.

Models were constructed using maximum likelihood estimation via Template Model Builder (TMB) as implemented in the R package 'glmmTMB' version 0.2.3 (Brooks et al.

2017). Model selection was based on the lowest Akaike's information criterion (AIC); uniformity of residuals was checked using the DHARMa package version 0.2.4 (Hartig 2019).

We also checked that activity of the lizards one minute before application of the treatment was not related to habitat type (Supplementary material, Fig. S1, Table S2). All analyses were performed in R software version 3.4.2 (R Core Team 2019).

Results

Lizards' reaction and behavioral response to the treatments were independent of their sex (hurdle model: zero-part p= 0.447, conditional part p= 0.289), SVL (zero-part p= 0.374, conditional part p= 0.379), and the order in which they received the treatments (first Smoke vs. first Control; zero-part p= 0.855, conditional part p= 0.921), thus, these variables were not included in the final models. When confronting the Smoke treatment, lizards were more likely to show a reaction (~83% reactions, Table 2; zero-inflated model: P<0.001, Table 3a, Fig. 1) compared to the Control treatment (~23% reactions). The interaction between treatment and habitat was significant (P=0.015; Table 3a); that is, lizards from fire-prone and non-fire-prone ecosystems reacted similarly to the Control (22% and 25% of reactions, respectively), but differed in their reaction to Smoke, with lizards from fire-prone areas more likely to react (93% of reactions) than lizards from non-fire-prone areas (71% of reactions; Table 3a).

When lizards showed a reaction, their behavioral response (total seconds of activity; conditional part of the model, Table 3b) was determined by their habitat (P= 0.015) and the

treatment (P= 0.024). That is, lizards from fire-prone habitats showed a higher level of activity when confronted with the Smoke treatment than those from non fire-prone habitats (Fig. 1).

There were no differences in the behavioral response to the treatments across the three fire-prone sites, regardless of a recent (during the last two years) or a lack of wildfire experience (no significant interaction; Supplementary material, Table S3). Moreover, adult lizards from recently burned patches (which likely survived a wildfire) showed the same behavioral response to both Smoke and Control treatments than individuals from the corresponding unburned areas (Fig. 2; no significant interaction; Supplementary material, Table S4).

Discussion

A high proportion of the lizards detected smoke through olfaction, and showed a behavioral response that is consistent with threat avoidance and escape behavior (running and scratching the terrarium). The reaction to this fire stimulus was more common, and the behavioral response more intense, in lizard populations living in fire-prone areas compared to those inhabiting areas that rarely burn. This enhanced response to smoke in lizards from fire-prone habitats was independent of age and sex. Additionally, despite the limited number of individuals sampled in very recently burned areas, the results suggest that experience (i.e., to have survived a previous fire) is unlikely to explain the response to smoke. Altogether these results suggest that the ability to detect and respond to smoke may

be an adaptive behavior of this species for living in fire-prone ecosystems. To our knowledge, this is the first evidence of smoke detection by reptiles in wild populations.

There is evidence for lizards using olfaction to escape other threats such as predators (Downes 2002). Anti-predator behavior is costly and should disappear when predation pressure relaxes (Blumstein 2002; Blumstein and Daniel 2005). For instance, lizards from populations where a predator was absent for the past 100 years reacted less vigorously to its scent than the predator-sympatric lizard populations (Van Damme and Castilla 1996). In contrast, some lizards can recognize the scent of the invasive predators and deploy anti-predator behaviors in response, despite having a very short period of co-occurrence (within 15 years, Ortega et al. 2017; and 150 years, Webster et al. 2018).

In Mediterranean ecosystems, wildfires are a common disturbance factor that can potentially kill many plants and animals in a short time, acting as a strong selective pressure (Keeley et al., 2012). In these ecosystems, fire can be quick and intense; early detection and reaction to fire cues is essential for animal survival, and therefore, the avoiding fire through escape behavior is likely subject to natural selection. *P. algirus* uses smell to detect a wildfire and flee, as expected from their chemoreception abilities (Baeckens et al. 2017). Wildfire smoke contains toxic and irritating compounds, thus, a certain reaction was expected from all lizards regardless of their provenance. However, we observed higher sensitivity to smoke in lizard populations from fire-prone ecosystems than in those from non-fire-prone ecosystems. We also observed some, although much lighter, reaction to the Control treatment. The reaction to the odorless visual simulation of smoke is in agreement with the fact that lizards also use visual cues to detect threats (Amo et al. 2004). The

response to this stimulus, however, is unrelated to fire, since this response was similar in lizards from the two habitats (fire-prone/non-fire-prone).

Some previous observations during prescribed burns have documented apparent escape behavior (burrowing and climbing trees) in lizards (Bishop and Murrie 2004; Beane 2006). However, they do not delve into the mechanism that these species use to detect wildfires. Recently, there was reported an anecdotic case of reptile smoke detection through olfaction from a fortuitous smoke exposition event in captive lizards of the species *Tiliqua rugosa* (Mendyk et al. 2020). In the same event, there were 13 different reptile species that did not react to smoke, suggesting that smoke reaction cannot be generalized in reptiles. First, because the cues to trigger a fire escape could be species-specific. Second, and more importantly, the fire history of the lizards' population plays a key role in determining their fire response. Our results suggest that populations that have been subjected to the selective pressure by fire would have enhanced their sensitivity to smoke and their behavioral response as adaptive traits.

Escape is a flexible instinctive behavior under cognitive control that has evolved to avoid harm from threats in the environment (Evans et al. 2019). This behavior may vary spatially with changes in animal's perception of risk across the landscape (Gaynor et al. 2019). Predation is a well-recognized selective force shaping escape behavior in natural populations (Curio 1976). In fact, field studies have documented rapid evolution of behavioral traits when animal populations face environmental changes (Lapiedra et al. 2018). Our results suggest that natural disturbances such as wildfires likely drive the evolution of animal traits for fire survival (Pausas and Parr 2018).

In conclusion, we provide the first experimental evidence of an olfactory-driven detection and the consequent behavioral response of a lizard to a fire cue (smoke); and that this response was enhanced in populations living in ecosystems where fire is common compared to populations inhabiting ecosystems that rarely burn. We suggest that fire acts an evolutionary driver, shaping sensorial and behavioral traits in lizards.

Data availability statement

Analyses reported in this article can be reproduced using the data provided by Álvarez-Ruiz et al. 2021.

Permit

Permission to handle our study animals was given by the Conselleria d'Agricultura, Canvi Climatic i Desenvolupament Rural of the Generalitat Valenciana. Expte:333/18 (FAU18_32).

Table 1. Location of the six study sites (eastern Spain), habitat type, sampling date, cumulative area burned in the last 42 years, number of fires, and their average size, and number of sampled lizards. Cumulative area burned was estimated in the area of a circle of 10 km radius around the center of each population and using 42 years of data; the number of fires was estimated by counting all the fires that took place entirely or partially within the circle; and the average fire size was calculated with the total areas of the wildfires, even if they exceeded the circle.

Location	Habitat type	Province and coordinates	Sampling date	Hectares burned	N of fires/mean size (ha)	N of sampled lizards
Albufera	Non-fire-prone coastal dunes	Valencia 39°18'; 0°17'	Sep-Oct 2017	95.41	6/12.2	16
Santa Pola	Non-fire-prone coastal dunes	Alicante 38°11': 0°36'	Sep-Oct 2018	54.01	7/5.8	20
Canet	Non-fire-prone coastal dunes	Valencia 39°42'; 0°11'	Sep-Oct 2018	411.88	5/70.5	20
Porta Coeli	Fire-prone wildland	Valencia 39°38'; 0°28'	Sep-Oct 2017	7995.32	21/380.7	21
Gátova	Fire-prone wildland	Valencia 39°49';0°31'	Mar-May 2018	12969.69	18/720.5	19
Artana	Fire-prone wildland	Castellón 39°56';0°17'	Mar-May 2018	2023.07	21/96.9	19

Table 2. Number of reacting and non-reacting individuals for each treatment (Control or Smoke) and habitat (fire-prone and non-fire-prone). The statistical analysis is shown in Table 3a.

Habitat	Treatment	Reaction	No reaction
Fire-prone	*Control*	12	43
	Smoke	53	4
Non fire-prone	*Control*	13	39
	Smoke	37	15

Table 3. Results of the hurdle mixed model for the existence of reaction (yes or no; zero-inflation model; a) and the behavioral response (seconds of activity in one minute; conditional model; b) to the treatments (Control and Smoke) of lizards inhabiting fire-prone (Fire) and non-fire-prone (No Fire) habitats. The model includes location as random variable. N=216.

Parameter	Estimate	Std. Err.	Z	P
a) Zero-inflation model[1]				
Intercept	1.273	0.485	3.072	<0.002***
Treatment [Smoke]	-4.392	0.981	-4.479	<0.001***
Habitat [No Fire]	-0.197	0.517	-0.381	0.703
Treatment [Smoke]:Habitat [No Fire]	2.036	0.839	2.427	0.015*
b) Conditional model				
Intercept	3.038	0.145	20.905	<0.001***
Treatment [Smoke]	0.335	0.148	2.266	0.024*
Habitat [No Fire]	-0.296	0.122	-2.436	0.015*

[1] Estimates in the zero-inflation model represents the probability of 0 (no reaction), so negative coefficients indicate higher reaction.

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