

Short-term impact of a small wildfire on the lizard *Psammodromus algirus* (LINNAEUS, 1758): a Before-After-Control-Impact study (Squamata: Sauria: Lacertidae)

Kurzzeitwirkung eines kleinräumigen Buschfeuers auf *Psammodromus algirus*
(LINNAEUS, 1758): eine vorher-nachher-Vergleichsuntersuchung
(Squamata: Sauria: Lacertidae)

GREGORIO MORENO-RUEDA & ELENA MELERO & SENDA REGUERA
& FRANCISCO J. ZAMORA-CAMACHO & MAR COMAS

KURZFASSUNG

Im mediterranen Raum sind Wald- und Buschbrände wesentliche Gestaltungselemente von Landschaften, natürlichen Abfolgen von Biozönosen und der Dynamik von Arten und Lebensgemeinschaften. Doch haben in den letzten Jahren Zahl und Ausmaß solcher Brände derart zugenommen, daß der Naturschutz besorgt auf diese Entwicklung reagiert. Noch wird verbreitet angenommen, daß Reptilien von Buschbränden meist nur wenig beeinträchtigt werden oder sogar profitieren. In der vorliegenden Arbeit führten die Autoren eine vorher-nachher-Vergleichsuntersuchung durch, um die Auswirkung eines kleinräumigen Buschfeuers (16 ha) auf die Abundanz der Eidechse *Psammodromus algirus* (LINNAEUS, 1758) zu untersuchen. Die Ergebnisse legen nahe, daß die lokal betroffene Population aufgrund des Brandes zusammenbrach, obwohl Jungtiere das Brandgebiet aus der Nachbarschaft rasch wieder besiedelten. Ein knappes Jahr nach dem Brand wurde erstmalig wieder ein adulter *P. algirus* im Brandgebiet festgestellt. Die vorliegende Untersuchung zeigt, daß selbst ein sehr kleinräumiges Buschfeuer negative Auswirkungen auf mediterrane Eidechsen haben kann.

ABSTRACT

In Mediterranean environments, wildfires are key in modelling landscapes, ecological succession and the dynamics of species and communities. However, in recent years, wildfires have increased in number and extent, resulting in a conservation concern. Still, it is generally thought that reptiles are usually not harmed by wildfires, or even may be benefited. Here, the authors used a Before-After-Control-Impact design to examine the effect of a small wildfire (16 ha) on the abundance of a lizard, *Psammodromus algirus* (LINNAEUS, 1758). The findings suggest that the local population crashed as a result of the wildfire, although juvenile lizards quickly recolonized the burnt area from adjacent sites. Almost a year after the fire, an adult *P. algirus* was detected in the burnt area. Therefore, the present study highlights that even a very small wildfire may negatively impact a Mediterranean lizard.

KEY WORDS

Reptilia: Squamata: Sauria. Lacertidae; *Psammopdromus algirus*; ecology, mortality, prey availability, habitat structure; conservation, threat, wildfire; Before-After-Control-Impact study; Mediterranean environments, Sierra Nevada, Spain

INTRODUCTION

Wildfires are environmental disturbances with a key role in modelling Mediterranean landscapes (MORENO & OECHEL 1994). These blazes generate new open areas, affecting ecological succession and the dynamics of species and communities (WHELAN 1995). Hence, they are considered to have a major impact on Mediterra-

nean ecosystem functioning and community composition (BLONDEL et al. 2010). Ultimately, wildfires increase environmental heterogeneity, which in turn may favor species diversity (ALLOUCHE et al. 2012). However, in recent years, human activities have increased the number and extent of wildfires (WESTERLING et al. 2006; PAUSAS

& KEELEY 2009; PAUSAS & FERNÁNDEZ-MUÑOZ 2012), resulting in an environmental problem. In the Mediterranean basin, more than 50,000 fires occur per year, burning about 700,000 hectares (LÓPEZ-ORNAT & CORREAS 2003). Wildfires impact animals directly by causing mortality during fire (WHELAN 1995). Moreover, although fires increase spatial heterogeneity at broad spatial scales, the burnt site typically undergoes habitat simplification, which may result in reduced species richness and diversity, at least in the short-term (e.g., GREEN & SANECKI 2006; BROS et al. 2011; DAVIS & DOHERTY 2015). Hence, if the wildfires are frequent or extensive, damages caused to the ecosystem may be higher than benefits, which may drive species towards local extirpation (UNDERWOOD et al. 2009). Wildfire frequency and intensity is expected to increase with climate change (PIÑOL et al. 1998; MCKENZIE et al. 2004; BOWMAN et al. 2009) and, therefore, understanding wildfire impact on fauna is fundamental for conservation planning in Mediterranean ecosystems (DRISCOLL et al. 2010).

Given the environmental (and economic) relevance of wildfires, much research has been conducted on this topic. However, our understanding of how wildfires affect species is still limited. By generating specific habitats, wildfires may benefit certain species but harm others (SANTOS et al. 2012). In the case of reptiles, different species display opposing responses to wildfire according to habitat preferences (DOHERTY et al. 2015), foraging mode (FRIEND 1993), diurnal or nocturnal activity (LEGGE et al. 2008), biogeographic affinities (SANTOS & CHEYLAN 2013), life-history traits

(SMITH et al. 2014) and physiological adaptations (FERREIRA et al. 2016b). Still, the underlying mechanisms by which responses to wildfire differ among species are not completely clear. In fact, the temporal response along the ecological succession after the fire may be species specific (DAVIS & DOHERTY 2015). Additionally, the type of fire as well as its size and intensity may affect different species in different ways (PASTRO et al. 2011; FONTAINE & KENNEDY 2012; BROWN et al. 2014b). For example, a small wildfire may create a new area of adequate habitat for a given species. Although the fire kills the members of that species in the burnt area, individuals might recolonize the area quickly from adjacent areas and hence benefit in the short-term from the wildfire. However, if the wildfire is very extensive, recolonization might be precluded and therefore the population would be harmed by the fire over a longer term.

The ideal way to study the impact of wildfires on fauna is with a Before-After-Control-Impact (BACI) study design (CONNER et al. 2016). However, due to the unpredictable nature of wildfires, the use of this design is very constrained. Consequently, most studies compare the fauna of burnt areas with unburnt ones (Control-Impact only; e.g., RUGIERO & LUISELLI 2006; HU et al. 2013; SANTOS et al. 2014). These comparisons have the drawback that it is not certain whether the unburnt areas represent a correct control for the impacted area. The present study on the short-term impact of a small wildfire on the lizard *Psammotromus algirus* (LINNAEUS, 1758), took advantage of the exceptional situation described below.

MATERIALS AND METHODS

Preconditions. – As a part of a long-term study, in 2010 the authors gathered ecology data (relative abundance, habitat structure, and prey availability) of the lizard *Psammotromus algirus* (LINNAEUS, 1758), in six populations along an elevational gradient in the Sierra Nevada mountain ridge (SE Spain) (ZAMORA-CAMACHO et al. 2013; MORENO-RUEDA et al. 2018). In August 2013, a small fire burned 16 hec-

tares encompassing one of the study locations, sited at 700 m a.s.l. This opportunity was seized and, during April-June 2014, the study performed in 2010 was repeated in order to ascertain the immediate changes provoked by the wildfire. Moreover, repetition of the study was done also in a nearby unaffected location, at 300 m a.s.l., which served as a control given that, in 2010, it showed a similar relative abundance of liz-

ards as the area at 700 m (ZAMORA-CAMACHO et al. 2013).

Hypotheses. – *Psammodromus algirus* is a medium-sized lizard distributed in SW Europe and NW Africa, strongly linked to warm Mediterranean areas covered by shrub formations (SALVADOR 2015). It typically inhabits shrubland with vegetation 40–100 cm high and abundant plant cover (DÍAZ & CARRASCAL 1991) where it feeds on arthropods (MORENO-RUEDA et al. 2018). SALVADOR (2015) considers wildfires to constitute one of the main threats to this species, due to direct mortality, habitat fragmentation and habitat alteration. Accordingly, the authors hypothesize that the wildfire, in the very short term (less than a year), will negatively affect this lizard. Firstly, it will cause direct mortality of specimens (SMITH et al. 2012), and secondly the fire can diminish prey availability (HELLGREN et al. 2010). Thirdly, the destruction of shrubs by the fire will alter the habitat by increasing the grassland, which is suboptimal for this species (DÍAZ & CARRASCAL 1991). Therefore, the burnt area will not be optimal for this lizard until the shrubland recovers. The loss of its main refuge (shrubs) will have a negative impact on its capacity for thermoregulation (see ELZER et al. 2012), since, moreover, the location at 700 m a.s.l. presents an excessively hot habitat for the species (ZAMORA-CAMACHO et al. 2016). Furthermore, it will increase the risk of predation (MARTÍN & LÓPEZ 1995).

However, SANTOS et al. (2016), found that *P. algirus* in NE Spain declined in abundance a year after a wildfire, but recovered only two years after the fire. In another area of NE Spain, SANTOS & POQUET (2010) reported that this lizard benefited from wildfires that occurred four years earlier, since, over the medium term, fires generated new areas of shrub habitat. In addition, the physiology of this species gives it strong resistance to conditions generated by wildfires, tolerating high temperatures and low humidity (FERREIRA et al. 2016b). Thus, as an alternative one could hypothesize that this small wildfire could have little impact on this lizard.

Study design. – To test the short-term impact of the wildfire on *P. algirus* in the impacted area (16 ha, location at 700 m

a.s.l.; 36°55' N, 3°26' W), in 2014 (after impact) the relative lizard abundance, habitat structure and prey availability were estimated and compared with estimates from 2010 (before impact), and with the changes that occurred in the control area (location at 300 m a.s.l.; 36°53' N, 3°24' W) during the same period.

In 2010, to quantify lizard relative abundance (specified as the average number of lizards observed per transect inspection), four 500-m transects were laid out, approximately 2–3 weeks apart, between April 19 to June 17, in each sampling location in the Sierra Nevada mountain ridge, SE Spain (ZAMORA-CAMACHO et al. 2013). Censuses were replicated every two hours during daytime (5 replicates per day), from sunrise to sunset, and included the number of active adult and juvenile individuals seen in each transect. Juvenile lizards were distinguished from adults by body size and coloration, especially of the tail (redder in juveniles). It was assumed that the detectability of lizards is the same in all sampling locations, and the number of active individuals recorded by this procedure to be positively related to the real population density (BLOMBERG & SHINE 1996). Since reptile activity is affected by environmental temperature (MORENO-RUEDA et al. 2009), air temperature was measured 1 m above the ground, in the shade, using a thermometer Hibok 14 (accuracy 0.1 °C). In 2014, a year after the wildfire, this census was replicated at the burnt location and at the control location.

To measure the habitat structure in each sampling station, a 50-m-long string (marked every meter) was randomly staked out, five times over the land, along which the presence or absence of plants, and the height of the plants found at each one-meter mark on the string were recorded; plant height was classified as < 25 cm, 25–50 cm, and > 50 cm. The plant structure in 2010 and in 2014 was studied in both the burnt and the control locations.

To estimate the availability of potential prey for *P. algirus*, in 2010 and in 2014, the authors installed 15 pitfall traps (WOODCOCK 2005) in each location (burnt and control) for four days (however, the data from one day in the control area were lost) more than two weeks apart, coinciding with the

census period. Traps were established a minimum of 5 m apart to ensure the independence of the data (WARD et al. 2001) and remained open from early morning until dusk, coinciding with the activity period of the lizard. At sundown, the trap content was individually collected in labelled vials and preserved with ethanol (96 %). In this way, only arthropods were captured that potentially were available and could have been consumed by this diurnal lizard. Each potential prey was identified in the laboratory under a 10–40× binocular microscope and assigned to an operational taxonomic unit (OTU, SNEATH & SOKAL 1962), usually at order level, except for (1) the Formicidae family, which was separated from other Hymenoptera because of their particular morphological and ecological characteristics, and (2) larvae of undetermined order, included in a single particular OTU.

To test whether the relative abundance of lizards (adults and juveniles separately) changed between the two periods (2010 vs. 2014) and between the two zones (burnt vs. control), the difference in the number of *P.*

algirus lizards detected for each transect in 2014 was calculated, with respect to the counts gained along the transect laid out on the same day (approximately) and hour in 2010. In this way, the difference in the relative abundance was estimated with the 95 % confidence intervals (95 % CI). When this difference statistically differed from zero (according to 95 % CI), the authors concluded that the abundance increased or decreased significantly. In a similar way, it was estimated whether there were differences in the environmental temperature. To test differences in habitat structure, a Chi-square test was performed to check differences in plant cover, and another to check for differences in plant structure (frequency of plants in each category of < 25 cm, 25–50 cm and > 50 cm). To detect differences in prey availability expressed by differences in the frequency of the main prey items consumed by this lizard (Orthoptera, Coleoptera, Hemiptera, and Araneae; MORENO-RUEDA et al. 2018), the change in frequency between years and zones was compared by means of a Chi-square test.

RESULTS

In 2010, the average temperature measured during the study period was 20.48 °C (range = 15.9 to 25.9 °C), whereas in 2014 it was 21.32 °C (range = 17.5 to 24.6 °C). The average temperature was 0.84 °C higher in 2014 than in 2010, but this increase did not differ statistically from zero (95 % CI = -0.96 to 2.64 °C).

In the burnt location, the relative abundance of adult lizards per transect in 2010 was 0.5, which decreased to 0.05 in 2014 (Fig. 1). This decrease in relative abundance statistically differed from zero (mean: -0.45 lizards per transect, 95 % CI: -0.87 to -0.03). Meanwhile, in the control location, the relative abundance changed from 0.05 lizards per transect in 2010 to 0.84 in 2014, with a significant increase of 0.79 lizards per transect (95 % CI: 0.49 to 1.09). Hence, between 2010 and 2014, there was an increase in the abundance of lizards in the control area, but at the same time, lizard abundance decreased in the burnt area.

Meanwhile, the relative abundance of juvenile lizards changed from 0.5 to 0.25 individuals per transect in the burnt area between 2010 and 2014 (Fig. 1), but this change non-significantly differed from zero (mean: -0.25, 95 % CI: -0.73 to 0.23). In the control area, at the same period, the relative abundance of juvenile lizards changed from 0.26 to 0.47 individuals per transect, which also did not significantly differ from zero (mean: 0.21, 95 % CI: -0.31 to 0.73). It is noteworthy that in 2014, in the burnt area, three juvenile lizards were detected in April, two in May, and one adult in June.

Regarding habitat structure, the density of the plant cover decreased significantly in the burnt area, from 66.7 % in 2010 to 57 % in 2014 ($\chi^2 = 5.06$, $P = 0.025$; Fig. 2); the height structure of the plants did not change significantly ($\chi^2_2 = 3.10$, $P = 0.21$). Whereas, in the control area, the plant cover density increased between 2010 and 2014 (52.6 vs. 61.7 %; $\chi^2 = 4.27$, $P = 0.039$), mainly

Table 1: Number of potential prey items of *Psammodromus algirus* (LINNAEUS, 1758), collected in the pitfall traps (sample size between parentheses), for the before (2010) and after (2014) years in the impact (at 700 m a.s.l.) and control (at 300 m a.s.l.) areas. Items were assigned to seven operational taxonomic units, the category Hymenoptera does not include Formicidae, larvae refer to those of unidentified taxa. The main prey category includes the sum total for Coleoptera, Orthoptera, Araneae and Hemiptera, the main prey of *P. algirus*, according to MORENO-RUEDA et al. (2018).

Tab. 1: Die Anzahl möglicher Beuteobjekte von *Psammodromus algirus* (LINNAEUS, 1758), die in Bodenfallen (Anzahl zwischen Klammern) vor (2010) und nach (2014) dem Brandereignis im Brand- (700 m ü. M.) und Kontrollgebiet (300 m ü. M.) gefangen wurden. Die Objekte wurden sieben Kategorien zugeordnet, wobei Formicidae den restlichen Hymenopteren gegenübergestellt sind. Die Kategorie Main Prey (Hauptbeuteobjekte) beinhaltet die Gesamtmenge an Coleoptera, Orthoptera, Araneae und Hemiptera, welche nach MORENO-RUEDA et al. (2018) den Hauptbestandteil der Beute von *P. algirus* ausmachen.

	Impact area		Control area	
	2010 (60)	2014 (60)	2010 (45)	2014 (45)
Formicidae	219	286	141	226
Coleoptera	39	27	13	24
Orthoptera	7	4	39	18
Araneae	12	6	33	16
Hymenoptera	15	47	3	17
Hemiptera	13	6	10	5
Larvae	1	1	4	1
Main Prey	71	43	95	63

due to an increase in vegetation less than 25 cm high ($\chi^2_2 = 9.41$, $P = 0.009$; Fig. 2).

In 2014, the frequency of the main prey items (Coleoptera, Orthoptera, Araneae and Hemiptera according to MORENO-

RUEDA et al. 2018) of *P. algirus* captured in pitfall traps in the burnt area was 61 % of those captured in pitfall traps in 2010 ($\chi^2 = 16.90$, $P < 0.001$; Table 1). Nevertheless, in the control area, a similar decline was

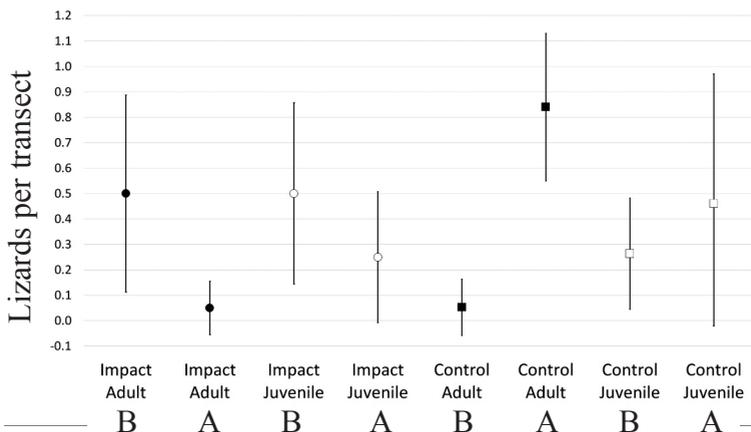


Fig. 1: Average and 95 % CI of the relative abundance (lizards per transect) of *Psammodromus algirus* (LINNAEUS, 1758), before (B) and after (A) the wildfire in the impacted (circles) and control (squares) areas, separated by juvenile (empty symbols) and adult (solid symbols) lizards.

Abb. 1: Mittelwert und 95 % Vertrauensgrenzen der relativen Häufigkeit (Individuen je Transekt) von *Psammodromus algirus* (LINNAEUS, 1758) vor (B) und nach (A) dem Buschfeuer im betroffenen (Impact, Kreise) und im Kontrollgebiet (Control, Quadrate), getrennt nach Jungtieren (leere Symbole) und Adulten (volle Symbole).

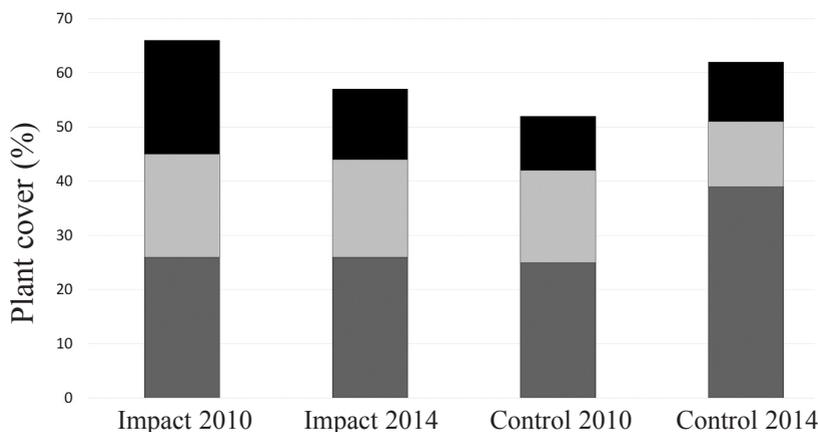


Fig. 2: Percentage of ground surface covered by vegetation in the wildfire-impacted and control areas, in both 2010 and 2014 (before and after the wildfire event) ($N = 253$ measures at each area and year). Different tones indicate the percentage of plant covers of different height (grey: < 25 cm; white: 25–50 cm; black: > 25 cm).

Abb. 2: Prozentsatz der vegetationsbedeckten Bodenoberfläche auf dem Gebiet des Buschfeuers (Impact) und der Kontrollfläche (Control) in den Jahren 2010 und 2014 (vor und nach dem Brand) ($N = 253$ Messungen in jedem Gebiet und Jahr). Verschiedene Grauwerte zeigen die jeweiligen Anteile von Pflanzen unterschiedlicher Wuchshöhe (grau: < 25 cm; weiß: 25–50 cm; schwarz: > 50 cm).

detected in the frequency of the main prey items, in that only 66 % of the number of insects captured in 2010 were trapped in 2014 ($\chi^2 = 22.85$, $P < 0.001$; Table 1). In

fact, the frequency of the main prey items did not change significantly between the two areas between the two years ($\chi^2 = 0.13$, $P = 0.72$).

DISCUSSION

Comparing the observations made in 2010 and 2014, the results show that a small wildfire had an immediate effect on the local population of *P. algirus*. The population collapsed after the fire, compared to the population prior to the fire and to the situation in the same period of time in a nearby unaffected population (in which the lizard abundance actually increased). After the wildfire, the vegetation cover was reduced as a result of the fire, although only by 15 %. The prey availability had also diminished, but apparently not only due to the fire, since a similar decrease occurred in the control area. Therefore, the population decline was probably caused by burn death of the specimens (see SANTOS et al. 2016). The relative abundance of juveniles was less reduced

than of adults. The juvenile individuals detected in the burnt area probably came from adjacent areas in the course of their dispersion, whereas only a single adult was found in the burnt area, probably a previously immigrated juvenile that had reached maturity by that time. This suggests that the population started its recovery a year after the fire, coinciding with the observation by SANTOS et al. (2016) in the case of a fire in Catalonia (NE Spain). In that study, the authors reported that the population of *P. algirus* declined the year after the fire, but that two years later it had recovered. However, in the case of SANTOS et al. (2016), the wildfire that affected the population of *P. algirus* burned an area of roughly 10,000 hectares.

However, the present study found that even a wildfire affecting a very small area (only 16 hectares) had a short-term effect on a Mediterranean reptile, which contrasts with the generalized idea that wildfires are not harmful to reptiles and may even benefit them (BURY 2004; LANGFORD et al. 2007; GREENBERG & WALDROP 2008; ASHTON & KNIPPS 2011; BROWN et al. 2014a; but see exceptions in VALENTINE et al. 2012; HU et al. 2013; MCCOY et al. 2013). For example, DUARTE et al. (2017), using a BACI design, found no short-term effect (one year later) of a fire on three species of lizards in Texas (USA). The response of reptiles to wildfires can be species-dependent (BRAITHWAITE 1987; DRISCOLL & HENDERSON 2008; DOHERTY et al. 2015). Whether or not a wildfire has immediate effects on a reptile species will probably be determined firstly by the ability of the reptile to survive the fire. For example, species that do not burrow have higher direct mortality than those that do (SMITH et al. 2012). Lizards associated with rocky environments, which use rocky fissures as shelter such as *Podarcis hispanica* (STEINDACHNER, 1870), or *Tarentola mauritanica* (LINNAEUS, 1758), appear to survive fires better than do species that live mainly associated with vegetation, such as *P. algirus* (SANTOS & POQUET 2010; SANTOS et al. 2016).

Nonetheless, even if the fire has an immediate effect, reptile populations can recover quickly (CUNNINGHAM et al. 2002; DAVID & DOHERTY 2015; SANTOS et al. 2016). As to *P. algirus*, a species associated with open areas (shrubland), its habitat seems to recover quickly after the fire (SANTOS et al. 2016). Such rapid post-fire recovery of the vegetation structure allows fast recovery of reptile populations (LINDENMAYER et al. 2008). However, whether species recover quickly or not depends on whether the wildfire generates a suitable habitat for them. The idea of a speedy recovery cannot be applied to environments with dense vegetation, in which the wildfires involve a strong change in the plant structure that will take more time to recover. In these cases, wildfires can harm species inhabiting those habitats in favor of species associated with more open habitats (PIANKA & GOODYEAR 2012; SANTOS & CHEYLAN 2013; FERREIRA et al. 2016a).

Therefore, the short-term impact of a wildfire on a reptile will depend primarily on two factors: first, whether or not the reptile is able to survive the fire, and second, whether or not the area left by the fire is habitable to the species. Species that are capable of surviving the fire and are adapted to the new habitat will not show immediate population declines in response to the fire, as is the case of *T. mauritanica* (SANTOS et al. 2016). *Psammodromus algirus* is a species that did not survive the fire, but the habitat generated immediately afterwards appeared to be adequate for it, allowing a quick recovery. This explains why this lizard disappeared just after the wildfire, but started to recover in about a year (SANTOS et al. 2016). By contrast, species adapted to late stages of plant successions, such as *Ctenophorus isolepis* (FISCHER, 1881), which is associated with dense vegetation, would show a reduction in abundance after fires, recovering slowly as the vegetation recovers (PIANKA & GOODYEAR 2012). Consequently, reptiles might be classified into three categories according to how they respond to wildfire: unaffected species, quick-recovery species, and slow-recovery species. Differences in the composition of reptile communities regarding these types of species would explain the strong variation in the results reported by different studies.

In Mediterranean environments, reptile and plant communities have coexisted with regular wildfire, and thus they should be adapted to wildfires (MORENO & OCHELL 1994). Mediterranean lizard communities frequently recover quickly after a fire or even are not affected (SANTOS & POQUET 2010; SANTOS et al. 2016; DUARTE et al. 2017). Hence, the main conservation concern is for zones that begin to suffer wildfires recently (e.g., due to climate change) where lizards are adapted to plant communities that would recover very slowly (or even not recover) after a fire (see SANTOS & CHEYLAN 2013). In such cases, wildfires will provoke local extirpations with pervasive consequences for the reptile fauna.

In general, it is thought that in a small wildfire, reptile recovery may be very fast, as a consequence of the small size of the area affected, which entails a short distance over which dispersing lizards must move

around to recolonize the burnt zone. However, comparison of the present study with that by SANTOS et al. (2016) suggests similar patterns of local extirpation and recovery, despite the enormous size difference between the two wildfires (16 vs. 10,000 hectares). Factors such as lizard density in the surrounding population (very low in the present study; see ZAMORA-CAMACHO et al. 2013), are also relevant to understand recovery dynamics, although they have rarely been considered. Most of the wildfires in Spain are relatively small

(1-500 ha; MAAMA 2016), and therefore the pattern found here is widely applicable to many cases of burning. In view of these results, the authors suggest that the generalized idea that wildfires have no impact on reptiles, and may even benefit them, should be considered with caution, since the impact of wildfires on a reptile population will depend on many factors, and in fact, as described in this study, small wildfires can have negative effects even on a typical Mediterranean species.

ACKNOWLEDGMENTS

The authors thank the staff of the Espacio Natural de Sierra Nevada (Andalusia, Spain) for their constant support. This work was partially funded by the Spanish Ministerio de Ciencia e Innovación, project CGL2009-13185. The authors F. J. Zamora-Camacho (AP2009-3505) and S. Reguera (AP2009-1325) were supported by two pre-doctoral grants from the Ministerio de Ciencia e Innovación (Ayudas para la formación de profesorado universitario – FPU programme), and M. Comas was supported by the Mini-

sterio de Economía y Competencia, through the Severo Ochoa Programme for Centres of Excellence in Research, Development and Innovation (R+D+I) [SEV-2012-0262] with the contract SVP-2014-068620. The study was carried out with permits for working with the wild fauna, issued by Junta de Andalucía and Sierra Nevada National Park (references GMN/GyB/JMIF, ENSN/JSG/JEGT/MCF, ENSN/JSG/BRL/MCF, SGMN/GyB/JMIF, and SSA/SI/MD/ps). David Nesbitt (Granada) improved the English.

REFERENCES

- ALLOUCHE, O. & KALYUZHNYY, M. & MORENO-RUEDA, G. & PIZARRO, M. & KADMON, R. (2012): Area-heterogeneity tradeoff and the diversity of ecological communities.—Proceedings of the National Academy of Sciences of the U.S.A., Washington; 109: 17495-17500.
- ASHTON, K. G. & KNIPPS, A. C. S. (2011): Effects of fire history on amphibian and reptile assemblages in rosemary scrub.— *Journal of Herpetology*, Houston, etc.; 45: 497-503.
- BLONDEL, J. & ARONSON, J. & BODIQUOY, J.-Y. & BOEUF, G. (2010): The Mediterranean region. Biological diversity in space and time. New York (Oxford University Press), pp. 382.
- BLOMBERG, S. & SHINE, R. (1996): Reptiles; pp. 218-226. In: SUTHERLAND, W. J. (Ed.): *Ecological census techniques, a Handbook*. Cambridge (Cambridge University Press).
- BOWMAN, D. M. J. S. & BALCH, J. K. & ARTAXO, P. & BOND, W. J. & CARLSON, J. M. & COCHRANE, M. A. & D'ANTONIO, C. M. & DEFRIES, R. S. & DOYLE, J. C. & HARRISON, S. P. & JOHNSTON, F. H. & KEELEY, J. E. & KRAWCHUK, M. A. & KULL, C. A. & MARSTON, J. B. & MORITZ, M. A. & PRENTICE, I. C. & ROOS, C. I. & SCOTT, A. C. & SWETNAM, T. W. & VAN DER WERF, G. R. & PYNE, S. J. (2009): Fire in the earth system.— *Science*, Washington; 324: 481-484.
- BRAITHWAITE, R. W. (1987): Effects of fire regimes on lizards in the wet-dry tropics of Australia.— *Journal of Tropical Ecology*, Cambridge, etc.; 3: 265-275.
- BROS, V. & MORENO-RUEDA, G. & SANTOS, X. (2011): Does postfire management affect the recovery of Mediterranean communities? The case study of terrestrial gastropods.— *Forest Ecology and Management*, Amsterdam; 261: 611-619.
- BROWN, D. J. & DUARTE, A. & MALI, I. & JONES, M. C. & FORSTNER, M. R. J. (2014a): Potential impacts of a high severity wildfire on abundance, movement, and diversity of herpetofauna in the lost pines ecoregion of Texas.— *Herpetological Conservation and Biology*, open access journal available at < <http://www.herpconbio.org/volumes.html> >; 9: 192-205.
- BROWN, D. J. & NOWLIN, W. H. & OZEL, E. & MALI, I. & EPISCOPO, D. & JONES, M. C. & FORSTNER, M. R. J. (2014b): Comparison of short term low, moderate, and high severity fire impacts to aquatic and terrestrial ecosystem components of a southern USA mixed pine/hardwood forest.— *Forest Ecology and Management*, Amsterdam; 312: 179-192.
- BURY, R. B. (2004): Wildfire, fuel reduction, and herpetofaunas across diverse landscape mosaics in northwestern forests.— *Conservation Biology*, Malden, Oxford; 18: 968-975.
- CONNER, M. M. & SAUNDERS, W. C. & BOUWES, N. & JORDAN, C. (2015): Evaluating impacts using a BACI design, ratios, and a Bayesian approach with a focus on restoration.— *Environmental Monitoring and Assessment*, Dordrecht; 188: 555.
- CUNNINGHAM, S. C. & BABB, R. D. & JONES, T. R. & TAUBERT, B. D. & VEGA, R. (2002): Reaction of

- lizard populations to a catastrophic wildfire in a central Arizona mountain range.– *Biological Conservation, Barking*; 107: 193-201.
- DAVIS, R. A. & DOHERTY, T. S. (2015): Rapid recovery of an urban remnant reptile community following summer wildfire.– *PLOS ONE, San Francisco*; 10: e0127925.
- DÍAZ, J. A. & CARRASCAL, L. M. (1991): Regional distribution of a Mediterranean lizard: influence of habitat cues and prey abundance.– *Journal of Biogeography, Oxford*; 18: 291-297.
- DOHERTY, T. S. & DAVIS, R. A. & VAN ETEN, E. J. B. & COLLIER, N. & KRAWIEC, J. (2015): Response of a shrubland mammal and reptile community to a history of landscape-scale wildfire.– *International Journal of Wildland Fire, Clayton South-Collingwood*; 24: 534.
- DRISCOLL, D. A. & HENDERSON, M. K. (2008): How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model.– *Biological Conservation, Barking*; 141: 460-471.
- 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, Barking*; 143: 1928-1939.
- DUARTE, A. & BROWN, D. J. & FORSTNER, M. R. J. (2017): Response of lizards to high-severity wildfires in a southern United States mixed pine/hardwood forest.– *Copeia, Washington*; 105: 609-617.
- ELZER, A. L. & PIKE, D. A. & WEBB, J. K. & HAMMILL, K. & BRADSTOCK, R. A. & SHINE, R. (2013): Forest-fire regimes affect thermoregulatory opportunities for terrestrial ectotherms.– *Austral Ecology, Carlton South*; 38: 190-198.
- FERREIRA, D. & MATEUS, C. & SANTOS, X. (2016a): Responses of reptiles to fire in transition zones are mediated by bioregion affinity of species.– *Biodiversity and Conservation, Dordrecht*; 25: 1543-1557.
- FERREIRA, C. C. & SANTOS, X. & CARRETERO, M. A. (2016b): Does ecophysiology mediate reptile responses to fire regimes? Evidence from Iberian lizards.– *PeerJ, open access journal available at <https://peerj.com/articles/>*; 4: e2107.
- FONTAINE, J. B. & KENNEDY, P. L. (2012): Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests.– *Ecological Applications, New York, Washington*; 22: 1547-1561.
- FRIEND, G. R. (1993): Impact of fire on small vertebrates in mallee woodlands and heathlands of temperate Australia. A review.– *Biological Conservation, Barking*; 65: 99-114.
- GREEN, K. E. N. & SANECKI, G. (2006): Immediate and short-term responses of bird and mammal assemblages to a subalpine wildfire in the Snowy Mountains, Australia.– *Austral Ecology, Carlton South*; 31: 673-681.
- GREENBERG, C. H. & WALDROP, T. A. (2008): Short-term response of reptiles and amphibians to prescribed fire and mechanical fuel reduction in a southern Appalachian upland hardwood forest.– *Forest Ecology and Management, Amsterdam*; 255: 2883-2893.
- HELLGREN, E. C. & BURROW, A. L. & KAZMAIER, R. T. & RUTHVEN, D. C. (2010): The effects of winter burning and grazing on resources and survival of Texas horned lizards in a thornscrub ecosystem.– *Journal of Wildlife Management, Oxford*; 74: 300-309.
- HU, Y. & URLUS, J. & GILLESPIE, G. & LETNIC, M. & JESSOP, T. S. (2013): Evaluating the role of fire disturbance in structuring small reptile communities in temperate forests.– *Biodiversity and Conservation, Dordrecht*; 22: 1949-1963.
- LANGFORD, G. J. & BORDEN, J. A. & MAJOR, C. S. & NELSON, D. H. (2007): Effects of prescribed fire on the herpetofauna of a Southern Mississippi Pine Savanna.– *Herpetological Conservation and Biology, open access journal available at <http://www.herpconbio.org/volumes.html>*; 2: 135-143.
- LEGGE, S. & MURPHY, S. & HEATHCOTE, J. & FLAXMAN, E. & AUGUSTEYN, J. & CROSSMAN, M. (2008): The short-term effects of an extensive and high-intensity fire on vertebrates in the tropical savannas of the central Kimberley, northern Australia.– *Wildlife Research, Collingwood*; 35: 33-43.
- LINDENMAYER, D. B. & WOOD, J. T. & MACGREGOR, C. & MICHAEL, D. R. & CUNNINGHAM, R. B. & CRANE, M. & MONTAGUE-DRAKE, R. & BROWN, D. & MUNTZ, R. & DRISCOLL, D. A. (2008): How predictable are reptile responses to wildfire?– *Oikos, Oxford*; 117: 1086-1097.
- LÓPEZ-ORNAT, A. & CORREAS, E. (2003) Assessment and opportunities of Mediterranean networks and action plans for the management of protected areas / Gestion des aires protégées méditerranéennes : Evaluation et opportunités des réseaux et plans d'action. Gland, Cambridge (IUCN), pp. 151.
- MAAMA (MINISTERIO DE AGRICULTURA, ALIMENTACIÓN Y MEDIO AMBIENTE) (2016): Los incendios forestales en España. Madrid (Ministerio de Agricultura, Alimentación y Medio Ambiente), pp. 30.
- MARTÍN, J. & LÓPEZ, P. (1995): Influence of habitat structure on the escape tactics of the lizard *Psammodromus algirus*.– *Canadian Journal of Zoology, Ottawa*; 73: 129-132.
- MCCOY, E. D. & BRITT, E. J. & CATENAZZI, A. & MUSHINSKY, H. R. (2013): Fire and herpetofaunal diversity in the Florida scrub ecosystem.– *Natural Areas Journal, Rockford*; 33: 316-326.
- MCKENZIE, D. & GEDALOF, Z. & PETERSON, D. L. & MOTE, P. (2004): Climatic Change, wildfire, and conservation.– *Conservation Biology, Malden, Oxford*; 18: 890-902.
- MORENO, J. M. & OECHEL, W. C. (1994): The role of fire in Mediterranean type ecosystems. Berlin (Springer-Verlag), pp. XIII, 201. [Ecological Studies No. 107].
- MORENO-RUEDA, G. & PLEGUEZUELOS, J. M. & ALAMINOS, E. (2009): Climate warming and activity period extension in the Mediterranean snake *Malpolon monspessulanus*.– *Climatic Change, Dordrecht*; 92: 235-242.
- MORENO-RUEDA, G. & MELERO, E. & REGUERA, S. & ZAMORA-CAMACHO, F. J. & ÁLVAREZ-BENITO, I. (2018): Prey availability, prey selection, and trophic niche width in the lizard *Psammodromus algirus* along an elevational gradient.– *Current Zoology, Beijing*; 64: 603-613.

- PASTRO, L. A. & DICKMAN, C. R. & LETNIC, M. (2011): Burning for biodiversity or burning biodiversity? Prescribed burn vs. wildfire impacts on plants, lizards, and mammals.– *Ecological Applications*, New York, Washington; 21: 3238-3253.
- PAUSAS, J. G. & FERNÁNDEZ-MUÑOZ, S. (2012): Fire regime changes in the Western Mediterranean Basin. From fuel-limited to drought-driven fire regime.– *Climatic Change*, Dordrecht; 110: 215-226.
- PAUSAS, J. G. & KEELEY, J. E. (2009): A burning story. The role of fire in the history of life.– *BioScience*, Berkeley; 59: 593-601.
- PIANKA, E. R. & GOODYEAR, S. E. (2012): Lizard responses to wildfire in arid interior Australia. Long-term experimental data and commonalities with other studies.– *Austral Ecology*, Carlton South; 37: 1-11.
- PIÑOL, J. & TERRADAS, J. & LLORET, F. (1998): Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain.– *Climatic Change*, Dordrecht; 38: 345-357.
- RUGIERO, L. & LUISELLI, L. (2006): Influence of small-scale fires on the populations of three lizard species in Rome.– *Herpetological Journal*, London; 16: 63-68.
- SALVADOR, A. (2015): Lagartija colilarga - *Psammotromus algirus*. In: SALVADOR, A. & MARCO, A. (Eds.): *Enciclopedia virtual de los vertebrados españoles*. Madrid (Museo Nacional de Ciencias Naturales). WWW online resource available at < <http://www.vertebradosibericos.org/reptiles/psaalg.htm> > [last accessed: November 20, 2018].
- SANTOS, X. & BADIANE, A. & MATOS, C. (2016): Contrasts in short- and long-term responses of Mediterranean reptile species to fire and habitat structure.– *Oecologia*, Berlin, Heidelberg; 180: 205-216.
- SANTOS, X. & BROS, V. & ROS, E. (2012): Contrasting responses of two xerophilous land snails to fire and natural reforestation.– *Contributions to Zoology*, Amsterdam; 81: 167-180.
- SANTOS, X. & CHEYLAN, M. (2013): Taxonomic and functional response of a Mediterranean reptile assemblage to a repeated fire regime.– *Biological Conservation*, Barking; 168: 90-98.
- SANTOS, X., & MATEOS, E. & BROS, V. & BROTONS, L. & DE MAS, E. & HERRAIZ, J. A. & HERRANDO, S. & MIÑO, A. & OLMO-VIDAL, J. M. & QUESADA, J. & RIBES, J. & SABATÉ, S. & SAURAS-YERA, T. & SERRA, A. & VALLEJO, V. R. & VIÑOLAS, A. (2014): Is response to fire influenced by dietary specialization and mobility? A comparative study with multiple animal assemblages.– *PLOS ONE*, San Francisco; 9: e88224.
- SANTOS, X. & POQUET, J. M. (2010): Ecological succession and habitat attributes affect the postfire response of a Mediterranean reptile community.– *European Journal of Wildlife Research*, Collingwood; 56: 895-905.
- SMITH, A. L. & BULL, C. M. & GARDNER, M. G. & DRISCOLL, D. A. (2014): Life history influences how fire affects genetic diversity in two lizard species.– *Molecular Ecology*, Oxford etc.; 23: 2428-2441.
- SMITH, A. L. & MEULDERS, B. & BULL, C. M. & DRISCOLL, D. A. (2012): Wildfire-induced mortality of Australian reptiles.– *Herpetology Notes*, Braunschweig; 5: 233-235.
- SNEATH, P. & SOKAL, R. (1962): Numerical taxonomy.– *Nature*, London; 193: 855-860.
- UNDERWOOD, E. C. & VIERS, J. H. & KLAUSMEYER, K. R. & COX, R. L. & SHAW, M. R. (2009): Threats and biodiversity in the Mediterranean biome.– *Diversity and Distributions*, Oxford etc.; 15: 188-197.
- VALENTINE, L. E. & REAVELEY, A. & JOHNSON, B. & FISHER, R. & WILSON, B. A. (2012): Burning in Banksia woodlands. How does the fire-free period influence reptile communities?– *PLOS ONE*, San Francisco; 7: e34448.
- WARD, D. F. & NEW, T. R. & YEN, A. L. (2001): Effects of pitfall trap spacing on the abundance, richness and composition of invertebrate catches.– *Journal of Insect Conservation*, Dordrecht; 5: 47-53.
- WESTERLING, A. L. & HIDALGO, H. G. & CAYAN, D. R. & SWETNAM, T. W. (2006): Warming and earlier spring increase western US forest wildfire activity.– *Science*, Washington; 313: 940-943.
- WHELAN, R. J. (1995): *The ecology of fire*. Cambridge (Cambridge University Press), pp. X, 346.
- WOODCOCK, B. (2005): Pitfall trapping in ecological studies; pp. 37-57. In: LEATHER, S. R. (Ed.): *Insect sampling in forest ecosystems*. Oxford (Blackwell Publishing).
- ZAMORA-CAMACHO, F. J. & REGUERA, S. & MORENO-RUEDA, G. & PLEGUEZUELOS, J. M. (2013): Patterns of seasonal activity in a Mediterranean lizard along a 2200 m altitudinal gradient.– *Journal of Thermal Biology*, Oxford, Braunschweig; 38: 64-69.
- ZAMORA-CAMACHO, F. J. & REGUERA, S. & MORENO-RUEDA, G. (2016): Thermoregulation in the lizard *Psammotromus algirus* along a 2200-m elevational gradient in Sierra Nevada (Spain).– *International Journal of Biometeorology*, Berlin, Heidelberg; 60: 687-697.

DATE OF SUBMISSION: March 8, 2018

Corresponding editor: Heinz Grillitsch

AUTHORS: Gregorio MORENO-RUEDA (Corresponding author < gmr@ugr.es >)¹, Elena MELERO¹, Senda REGUERA¹, Francisco J. ZAMORA-CAMACHO² & Mar COMAS³)¹ Departamento de Zoología, Facultad de Ciencias, Universidad de Granada, E-18071, Granada, Spain.² Departamento de Biogeografía y Cambio Global, Museo Nacional de Ciencias Naturales-CSIC, C/ José Gutiérrez Abascal 2, E-28006 Madrid, Spain.³ Estación Biológica de Doñana (EBD-CSIC), Avda. Américo Vespucio 26, Sevilla E-41092, Spain.