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Cite this article: Álvarez-Ruiz L, Belliure J, Santos X, Pausas JG. 2021 Fire reduces parasite load in a Mediterranean lizard. *Proc. R. Soc. B* 20211230.
https://doi.org/10.1098/rspb.2021.1230

Received: 31 May 2021
Accepted: 22 June 2021

Subject Category:
Ecology

Subject Areas:
ecology, health and disease and epidemiology

Keywords:
ectoparasites, global change, mite, *Ophionyssus*, *Psammodromus algirus*, wildfire

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Electronic supplementary material is available online at rs.figshare.com.

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Fire reduces parasite load in a Mediterranean lizard

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Wildfires are a natural disturbance in many ecosystems. However, their effect on biotic interactions has been poorly studied. Fire consumes the vegetation and the litter layer where many parasites spend part of their life cycles. We hypothesize that wildfires reduce habitat availability for parasites with consequent potential benefits for hosts. We tested this for the lizard *Psammodromus algirus* and its ectoparasites in a Mediterranean ecosystem. We predicted that lizards in recently burned areas would have lower parasite load (cleaning effect) than those in unburned areas and that this phenomenon implies that lizards spending their entire lives in postfire conditions experience a lower level of parasitism than those living in unburned areas. We compared the ectoparasite load of lizards between eight paired burned/unburned sites, including recent (less than 1 year postfire) and older fires (2–4 years). We found that lizards' ectoparasites prevalence was drastically reduced in recently burned areas. Likewise, lizards in older burned areas showed less evidence of past parasitic infections. Fire disrupted the host–parasite interaction providing the opportunity for lizards to avoid the negative effects of ectoparasites. Our results suggest that wildfires likely fulfil a role in controlling vector-borne diseases and pathogens and highlight ecological effects of wildfires that have been overlooked.

1. Background

Fire is an intrinsic and natural process in many ecosystems, and the need to incorporate its role into the understanding of fire-prone ecosystems' ecology has been increasingly recognized [1,2]. The knowledge of the role of fire in the ecology and evolution of plants is robust, with extensive breadth and depth [1]. Whereas this understanding for animals is quickly growing [3–5], little is known for other biodiversity components such as biotic interactions.

One of the most relevant interactions in nature is parasitism [6]. Parasites cause adverse effects on a range of behavioural, physiological, genomic and demographic factors of hosts [7,8]. Hosts have selected different antiparasitic strategies (e.g. behavioural [9]; physiological [10]) among which the immunological response is probably the most complex [11,12]. Nevertheless, developing an immune response is energetically costly and it implies trade-offs with other vital attributes [13]. Therefore, parasite prevalence is considered one of the main factors modulating the dynamics of host populations ([14]; reviewed in [15]).

In fire-prone ecosystems, fire abruptly consumes most vegetation and litter, where many ectoparasites spend the independent terrestrial stages of their life cycles [16,17]. Therefore, ectoparasite populations are likely to be reduced immediately after a fire (cleaning effect). In fact, early humans and native cultures have used fire for clearing the ground from parasites and diseases [2,18], and agricultural societies use fire to reduce livestock diseases [19–21]. There are examples of livestock–parasite reduction such as ticks and mites after prescribed burns [22,23]. These vertebrate parasites can in turn be vectors for other parasites and pathogens such as Lyme disease [24] and

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hemogregarines [25,26]; thus, fire reduces the transmission of vector-borne diseases by direct and indirect effects on vectors. However, the role of fire in reducing parasites in wild populations remains unexplored.

Fire may provide a significant parasite cleaning effect from which hosts could benefit. This effect should be especially relevant for host species with the ability to survive fires and remain postfire living in burned areas. That is the case of species with traits and strategies that confer them some fire survival [5,27,28] and that show limited mobility and small home ranges; hosts with large home ranges may alternate between burned and unburned patches and thus the potential cleaning effect by fire may be blurred. In this study, we explore the effect of fire on the biotic interaction of parasitism in wild conditions. We selected a lizard as model system because many lizard species survive wildfires by seeking refuge in burrows, crevices, under rocks or among roots within the burn (e.g. burrowing lizards [29–31]), and they often spend their entire lives within a burned area due to their small home ranges [32], low vagility and dispersal rates [33]. Specifically, we selected the ground-dwelling Mediterranean lizard *Psammodromus algirus* and its ectoparasites (mites) as a case study.

We hypothesized that wildfires reduce the habitat for ectoparasites, and thus lizards in postfire conditions benefit from this clean environment by showing a lower parasite load than those in unburned areas. To test this, we compared lizard's parasite load (number of ectoparasites) in recent burned (less than 1-year postfire) and in paired unburned sites. We also tested if this cleaning effect of fire implies that lizards spending their entire lives in postfire conditions show lower evidence of past parasitic infections than those living in unburned areas. For this, we compared an indicator of the cumulative parasitic infection (number of raised ventral scales), in lizards in older burned (more than two years from fire) and in paired unburned sites.

2. Methods

(a) Study system

Psammodromus algirus is a medium-sized ground-dwelling lizard with a lifespan of 3–5 years [34]; it is widespread in Mediterranean landscapes of the Iberian Peninsula where high-intensity fires are common. Although it is a habitat-generalist species [35], it prefers habitats with low shrub cover [36]. Moreover, *P. algirus* is often found in recently burnt areas, suggesting a high ability to survive fire [37–39]. Dispersal ability of *P. algirus* is low (less than 20 m; [40]), and its home range (usually less than 100 m^2; [41]) is smaller than the typical wildfires occurring in the Mediterranean area [42,43]. Due to its relatively low mobility, individuals of this species are appropriate candidates to benefit from a postfire reduction of parasites as it is expected to fully inhabit within the burned area.

In our study areas, endoparasite prevalence in *P. algirus* is low, probably due to the xeric conditions of their habitat [44], whereas ectoparasites are common. Specifically, we focused on mites of the genus *Ophionyssus* (Gamasid mites; Acari: Macronyssidae) that are ectoparasites of *P. algirus* [45] and act as vectors of hemoparasites [26]. *Ophionyssus* species have a complex life cycle that includes five developmental stages on both the host and the soil [17]. The time for completion of the development of an individual from egg to adult varies with environmental conditions, being faster in wet and warm environments [17]. According to morphological characteristics [46], we identified both larvae and nymphs in our sampled lizards (electronic supplementary material, figures S1–S3).

Ticks (Acari: Ixodidae) were also present in *P. algirus*, but a preliminary analysis suggested a very low prevelance (only approx. 2% of sampled adult lizards infected and no presence on juveniles), and thus they were not considered in this study.

(b) Lizard sampling and parasite quantification

The study was undertaken on the east of the Iberian Peninsula, an area that shows a typical Mediterranean climate where wildfires are common in summer [47,48]. Sampling locations were dominated by shrublands (mainly *Quercus coccifera*, *Cistus* sp. pl. *Ulex parviflorus*, *Rhamnus alaternus*, *Pistacia lentiscus*, *Arbutus unedo*, *Rosmarinus oficinalis*, *Juniperus oxycedurs*, *Chamerops humilis*, *Brachypodium retusum*), alternated with pine woodlands (*Pinus halepensis*) and some evergreen oak patches (*Quercus ilex*).

We identified eight locations for the study, where wildfires had occurred between 2012 and 2018 (electronic supplementary material, table S1). The sampling was carried out between 2016 and 2018. In each of the eight locations, we sampled lizards in the burned area and in an adjacent unburned area; both the burned and unburned areas had similar pre-fire characteristics (vegetation, topography). Lizards were collected by hand or using a pole with a slip noose, always far from the edge of the wildfire to ensure that the lizard's home range was fully inside or outside of the fire perimeter. All lizards were measured (snout–vent length, SVL; ±0.01 cm) and weighed (±0.1 g). Sex determination was carried out by observing lizards' femoral pores that are more conspicuous in adult males [49]; therefore, the sex of juvenile individuals could not be determined. All individuals were released back to the location of capture.

Mites are usually found under the ventral scales and on the dorsal scales of the tail of *P. algirus* (electronic supplementary material, figure S4). Ventral scales of this species are smooth and imbricate, but they raise up when an ectoparasite is present [50,51] and some remain raised up even after ectoparasites detach from the host ([52]; see also electronic supplementary material, figure S5). Successive parasitic infections increases the number of raised ventral scales in lizards over time, so that, this measurement provides an indicator of the level of parasitic infections that individuals have experienced through their lives. Parasite load may vary due to the phenology of the parasites at the moment of sampling [53]; therefore, while the number of mites observed measures parasite load at the moment of sampling, raised ventral scales are an indicator of past infection [52].

To test the cleaning effect of fire, we used three locations with a time since fire lower than 1 year (hereafter 'recent' wildfires) where we performed a direct count of mites (adults and nymphs) on the lizards using a magnifying glass (10×). We carefully explored the cotton bags where lizards where kept until processed and we added any mite found there to the parasite's load of the corresponding lizard. To test if as a result of the cleaning effect of fire, lizards in postfire conditions suffer less cumulative parasitic infections than those living in unburned areas, and considering the life expectancy of *P. algirus* (*ca* 3 years; [34]), we sampled lizards at five locations in which the time since fire was 2–4 years (hereafter, 'older' wildfires). In such cases, we counted the number of raised ventral scales of the lizards in order to estimate the level of parasitism in lizards that have spent most of their lives under postfire conditions.

(c) Statistical analyses

We calculated the body condition index (BCI) as the residuals of the regression of body mass on SVL (log-transformed); this was computed separately for each sex and age group [54].

Due to the large amount of zeros in parasite counts (51 and 53% for the count in recent and older wildfires, respectively), we fitted hurdle generalized linear mixed models (GLMMs) using the R package 'glmmTMB' v. 0.2.3 [55]. Hurdle models

Table 1. Results of the hurdle mixed models for (*a*) the number of mites for recent wildfires and (*b*) the number of raised ventral scales for older wildfires, of lizards inhabiting burned and adjacent unburned areas. Note that in zero-inflation models, positive coefficients indicate lower parasitism and negative coefficients higher parasitism. For qualitative variables (treatment, location), the squared brackets show the factor level related to the coefficient shown. Models are displayed in figures 1 and 2.

parameter	estimate	s.e.	*Z*	*p*-value
(*a*) number of mites (<1 year postfire, $n = 117$)				
zero-inflation model				
intercept	1.579	0.731	2.160	0.031*
fire treatment [burned]	3.157	0.590	5.350	<0.001***
SVL	−0.732	0.198	−3.696	<0.001***
BCI	0.256	1.164	0.220	0.826
conditional model				
intercept	0.243	0.646	0.376	0.707
fire treatment [burned]	−0.212	0.474	−0.448	0.654
SVL	0.171	0.122	1.394	0.163
BCI	−1.064	1.209	−0.88	0.379
(*b*) number of raised ventral scales (2–4 year postfire, $n = 241$)				
zero-inflation model				
intercept	−1.884	0.651	−2.895	0.004**
fire treatment [burned]	2.290	0.611	3.751	<0.001***
BCI	0.167	1.754	0.095	0.924
conditional model				
intercept	−1.379	0.487	−2.829	0.005**
fire treatment [burned]	−0.374	0.183	−2.045	0.041*
SVL	0.418	0.079	5.324	<0.001***
BCI	1.031	0.598	1.725	0.084

are partitioned in a binary process that allows us to analyse the prevalence of parasites (containing zero values), and a counting process by which we can assess the intensity of the infection when it occurred (containing the positive counts).

To analyse the number of mites on lizards (recent fires), we fitted a Hurdle GLMM with a truncated negative binomial (truncated_nbinom2) error distribution, where burned versus unburned condition, sex, BCI and SVL were considered as fixed factors and location (3 levels) was included as a random factor. The use of a zero-truncated negative binomial regression allowed accounting for data overdispersion.

For the analysis of the number of raised ventral scales (older fires), we fitted a Hurdle GLMM with a negative binomial (nbinom2) error distribution, where burned versus unburned condition, sex, BCI and SVL were considered as fixed factors and location (5 levels) was included as a random factor. In both regressions, interactions among fixed factors were also tested.

Models were constructed using maximum-likelihood estimation via Template Model Builder (TMB); as implemented in the R package 'glmmTMB' version 0.2.3 [55]. Model selection was based on the lowest Akaike's information criterion (AIC); uniformity of residuals was checked using the DHARMa package v. 0.2.4 [56]. All statistics were implemented in R v. 3.6.1 [57].

3. Results

(a) Recent wildfires (less than 1-year postfire)

We sampled 117 lizards (32 adults, 85 juveniles) from three recently burned areas (3, 8 and 9 months postfire; electronic supplementary material, table S1) and their corresponding paired unburned areas.

The number of mites in adult lizards was independent of their sex ($p = 0.086$; electronic supplementary material, table S2), and, therefore, for subsequent analyses, we merged the data from juveniles (undetermined sex) and adults.

The probability of an individual being parasitized declined in burned compared to unburned areas (18% and 74% respectively; zero-inflated model: $p < 0.001$, table 1*a*), such that living in unburned environments was associated with a 4 times higher chance of carrying parasites. The probability of infection increased with lizards' size (SVL; but the interaction with fire condition was not significant; table 1*a*), and it was independent of their body condition (BCI; zero-inflated model: n.s., table 1*a*). For the parasitized lizards, the average number of mites was similar between burned (3.6 ± 3.6) and unburned (4.3 ± 4.5) areas (conditional model: n.s., table 1*a*), although the maximum number of mites found in burned areas was 2.3 times lower than in unburned areas (10 in burned versus 23 in unburned areas; figure 1). The number of parasites was not related to lizard SVL and BCI (conditional model: n.s., table 1*a*).

(b) Older wildfires (2–4 years postfire)

We sampled a total of 241 lizards (142 adults, 99 juveniles) from 5 different locations (5 paired burned/unburned areas;

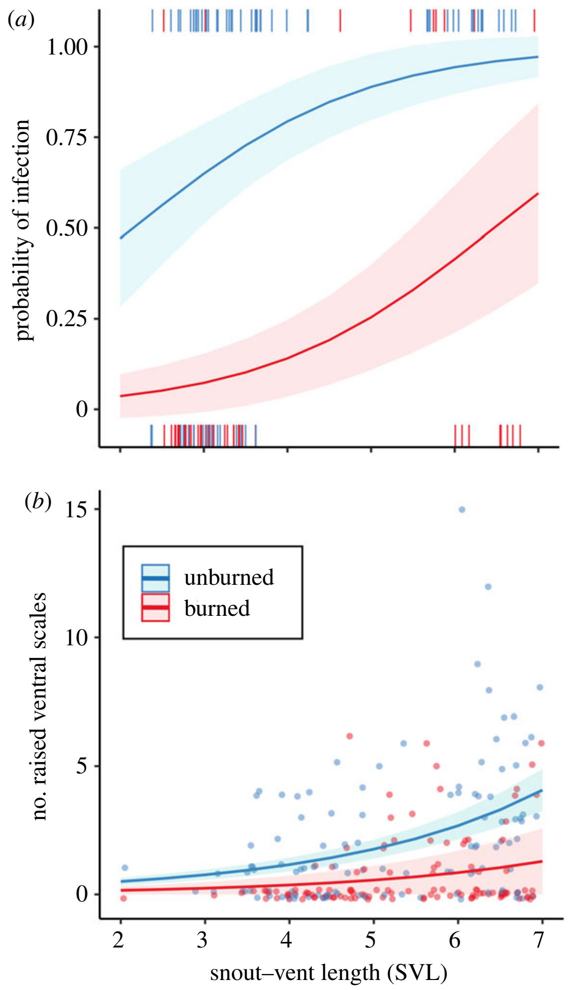

Figure 1. (*a*) Lizards' mite load in relation to lizards' size (SVL) for recently burned areas (less than 1 year from fire; red) and the corresponding paired unburned (blue). Lines are predicted values (and confidence intervals) of conditioned on the zero-inflation component (probability of mite infection) of the hurdle mixed model. For the statistical significance, table 1*a*. Raw binomial data ($n = 117$) are represented as short vertical lines on the horizontal axes at $y = 0$ and 1. The data split by populations is represented in electronic supplementary material, figure S6. (*b*) Number of raised scales in relation to lizards' size (SVL) for burned areas (older wildfires, 2–4 years; in red) and the corresponding paired unburned (in blue). Lines are predicted values (with confidence intervals) of the zero-inflation component of the hurdle mixed model. Symbols are the raw data ($n = 241$). For the statistical significance, table 1*b*. The data split by populations is represented in electronic supplementary material, figure S7. (Online version in colour.)

electronic supplementary material, table S1) that experienced fire 2 and 4 years ago.

The number of raised scales on adult lizards was independent of their sex (zero-inflated model: $p = 0.428$, conditional model: $p = 0.985$; electronic supplementary material, table S2), thus for the subsequent analyses, we merged the data of juveniles (undetermined sex) and adults.

Lizards living in burned environments were less likely to show raised ventral scales (approx. 29% prevalence, zero-inflated model: $p < 0.001$, table 1*b*), in comparison with those lizards inhabiting unburned areas (approx. 68% prevalence). For the parasitized lizards, those from burned areas showed lower number of raised ventral scales (2.7 ± 1.7) than lizards from the adjacent unburned areas (3.4 ± 2.8; figure 2, conditional model: $p < 0.046$, table 1*b*). Moreover, the maximum number of raised ventral scales found in burned areas was 2.5 times lower than in unburned areas (6 in burned versus 15 in unburned areas). The number of raised scales increased with lizard's size (SVL), but the interaction with fire treatment was not significant (table 1*b*).

4. Discussion

We studied the disruption of a negative biotic interaction, parasitism, by the natural perturbation of wildfires. Our results showed that fire reduces the ectoparasite load of *P. algirus* (the cleaning effect), suggesting that postfire environments provide a temporal window of opportunity for lizards to avoid the negative effects of ectoparasites. This finding is consistent with the decreased parasite load in livestock after prescribed fires [58]. The reduced ectoparasitism is not only observed just after the fire, but expands through the entire life of the lizards inhabiting the postfire environment (i.e. less evidence of past parasitism). Given that ectoparasites may induce costs to reptiles [8,59,60], including to *P. algirus* [61,62], confronting a postfire scenario with reduced parasite load is likely to be advantageous for lizards.

Parasitism increased with lizards' size (probability of carrying mites, table 1*a*; and raised ventral scales, table 1*b*). This is because size correlates with age so older individuals had more chances of getting infected [63]. We did not detect an improvement of lizard's body condition as a result of the fire-driven parasite reduction (table 1). This is because body condition is a poor indicator of fitness in relation to parasitism [64,65], and is strongly influenced by environmental resources (which are likely to change postfire). Parasitism likely affects other life attributes different from body conditions (i.e. colour ornaments; [62,66]). That is, independently of their body condition, lizards in postfire environments should benefit from lower parasitism-related stress.

Evidence suggest that the disruption by fire of antagonistic interactions can be beneficial to plants (lowering seed predation and diseases [67,68]). Similarly, here, we provide evidence of the disruption of a parasite–host interaction that is likely to result in a benefit for lizards. To our knowledge, this is the first evidence of a disruption of an ectoparasite–host interaction by fire in wild populations.

The parasite reduction in the environment could be mediated by direct mortality through the burning of vegetation and soil litter. This is the most plausible mechanism considering that *Ophionyssus* spends part of its cycle on the ground [17], and, therefore, fire-driven mortality is likely to occur (e.g., for fire-driven mortality of a soil acari, see [69]). By contrast, postfire changes in environmental conditions are unlikely to explain the observed pattern; while the drier postfire conditions may limit parasite development [70], the increased postfire temperatures can also favour it [71].

The observed reduction of lizard ectoparasitism in burned areas could also be mediated by changes in the spatial habitat structure. For instance, the lower prevalence of chytrid infection in boreal toads in recently burned areas is likely due to limitations in pathogen exposure and persistence in the new postfire habitat [72]. The reduced postfire litter and plant cover may limit lizards' exposure to mites as *P. algirus* actively searches for food in the litter beneath shrubs or trees [73,74]. On the other hand, lizards likely spread their parasites when sharing favourable microsites, such as shelters or suitable places for sun basking [75]. Fire, by opening the vegetation, increases the number of these favourable places [76,77], and thus reduces the lizard density in those microsites and the transmission risk among individuals [78]. Caution must be taken when extrapolating these structural effects on animals with very different ecology. For example, in animals typical of understory (closed) environments, fire diminished the availability of microsites for the host and this led to an increase in the encounter rate, and thus in the prevalence of infection (e.g. hantavirus in rodents from boreal forests; [79]).

The reported fire-driven changes in vector populations presumably occur in many other fire-prone ecosystems but remain largely unexplored. Disturbances reducing the abundance of vectors would eventually limit the parasite abundance and its persistence in the ecosystem [80]. Our findings support the possible role of wildfires in providing ecosystem services (*sensu* [18]) by controlling vector-borne diseases (i.e. Lyme disease) and pathogens (i.e. hemogregarines) in natural systems and thus, reducing risk and exposure for humans and livestock.

This study highlights an ecological role of wildfires that has been overlooked. Understanding the role of fire in the complex networks of interactions that characterize biodiversity is essential to comprehend ecological and evolutionary processes as well as for conservation purposes in a changing world.

Data accessibility. Analyses reported in this article can be reproduced using the data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.g79cnp5pc [81].

The data are provided in electronic supplementary material [82].

Authors' contributions. L.A.-R.: data curation, formal analysis, investigation, methodology, validation, visualization, writing—original draft, writing—review and editing; J.B.: conceptualization, data curation, methodology, supervision, writing—review and editing; X.S.: data curation, investigation, writing—review and editing; J.G.P.: conceptualization, funding acquisition, investigation, project administration, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. We declare we have no competing interests.

Funding. This work was supported by Ministry of Economy and Competitiveness and Ministry of Science, Innovation and Universities from the Spanish Government (grant nos CGL2015-64086-P, PGC2018-096569-B-I00, BES-2016-078225). CIDE is a joint institute of the Spanish National Research Council (CSIC), the University of Valencia and the regional government of Valencia (Generalitat Valenciana).

Acknowledgements. We thank the main field technician G. Benítez. We also thank R. Megía-Palma, S. Reguera, R. Drechsler and all CIDE members who helped with the fieldwork.

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