Journal of Zoology

Journal of Zoology. Print ISSN 0952-8369

ORIGINAL RESEARCH

Rapid postfire color shift in a Mediterranean lizard

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Keywords
fire adaptation; coloration; global change; *Psammodromus algirus*; lizards; thermoregulation; wildfires; phenotypic flexibility.

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Editor: Anthony Herrel
Associate Editor: Donald Miles

Received 5 May 2025; revised 3 August 2025; accepted 21 October 2025

doi:10.1111/jzo.70083

Abstract

Wildfires can abruptly cause dramatic changes in the physical environment, challenging the survival and persistence of animal populations. Animals can adapt to fast-changing environments through phenotypic plasticity, yet little is known about the extent of this capacity in postfire environments. We hypothesized that Mediterranean lizards in recently burned areas would develop a lighter coloration, potentially as a response to the increased overheating risk due to vegetation loss. We quantified dorsal luminosity and color composition of *Psammodromus algirus* in burned and adjacent unburned habitats at different times since fire. Lizards inhabiting recently burned areas displayed lighter dorsal coloration, particularly during the early stages of postfire succession, with the effect being more pronounced in larger individuals. Although alternative mechanisms (e.g., stress-induced responses or reduced crypsis requirements) cannot be entirely excluded, the direction, timing, and consistency of the observed shifts are most consistent with a thermoregulatory function. These findings suggest that phenotypic flexibility in dorsal coloration may be an important mechanism for ectotherms to persist in increasingly fire-prone landscapes.

Introduction

Fire is a globally widespread ecosystem process (Keeley & Pausas, 2022; Krawchuk & Moritz, 2011) shaping the composition, structure and function of many ecosystems, including Mediterranean ones (Pausas & Keeley, 2014). Its role as an important selective pressure shaping traits and thereby, driving biodiversity, has been well documented in plants (He et al., 2019; Keeley & Pausas, 2022). Fire effects on fauna are much less known, with limited evidence of adaptive responses to cope with fires (Álvarez-Ruiz et al., 2021; Nimmo et al., 2021; Pausas & Parr, 2018). Wildfires impact fauna in many ways and their effects vary across taxa (Ensbey et al., 2023). Animals with the ability to survive or recolonize after a wildfire might need some physiological or behavioral adjustments for inhabiting the new (postfire) conditions. In addition, fire-induced changes in vegetation structure may increase exposure to predators, particularly for species that rely on vegetation for cover.

Vegetation is an important regulator of surface energy fluxes (Duveiller et al., 2018). Fire abruptly reduces plant cover creating open spaces that lead to an increase in soil and air temperatures (López-García & Caselles, 1991), while also intensifying diurnal and seasonal temperature fluctuations (Veraverbeke et al., 2012). As vegetation regenerates, the magnitude of these effects gradually diminishes (Amiro et al., 1999).

In ectotherms, thermal conditions influence most physiological functions, including metabolism, development, growth, locomotion, and reproduction (Huey, 1982; While et al., 2018). These functions occur within a thermal window bounded by the individuals' thermal tolerance (ranging between critical thermal maximum and minimum; Huey & Stevenson, 1979). Because the thermal quality of a habitat is strongly linked to vegetation (Belliure et al., 1996), the reduction of plant cover postfire may lead to operative environmental temperatures that exceed lizard's thermal tolerance (overheating), resulting in heat stress and negative effects on performance (Niehaus et al., 2012; Sinclair et al., 2016). Consequently, in recently burned areas ectotherms might show mechanisms to buffer the cost of increased risk of overheating. Although behavioral responses are typically faster, physiological plasticity can also offer rapid coping strategies. The color-mediated thermoregulation hypothesis states that, at a given solar radiation, dark-colored organisms (lower reflectance) heat up faster than the equivalent light-colored ones (Clusella-Trullas et al., 2007). This prediction is widely supported in heliothermic lizards (Geen & Johnston, 2014; González-Morales et al., 2021). The mechanisms of variation in melanism include developmental plasticity and phenotypic flexibility (Piersma & Drent, 2003). Phenotypic flexibility is the reversible transformation that individuals can show in response to rapid changes in environmental conditions over their lifespan (Pigliucci, 2001) and might incur a selective advantage (Via et al., 1995). Hormonal mechanisms may also play a role in color variation (Castrucci et al., 1997). While some empirical studies have documented substantial phenotypic changes in lizards' coloration in response to environmental changes (Lewis et al., 2017), research of such changes specifically following wildfires remains unexplored.

Under the color-mediated thermoregulation hypothesis (Clusella-Trullas, 2006), we expect phenotypic flexibility in dorsal coloration of lizards surviving a fire, given that fire modifies their thermal environment. Thus, we predict lighter coloration in lizards within recently burned areas as a plausible plastic response to mitigate heat gain from solar radiation and reduce the risk of overheating. This effect should only be apparent in early postfire years before the vegetation recovers. To test this prediction, we evaluated the dorsal coloration of the lizard *Psammodromus algirus* in recently burned areas (at different postfire ages) and in adjacent unburned areas.

Materials and methods

Species model and study sites

Psammodromus algirus is a widespread species in the eastern Iberian Peninsula where high-intensity fires are common. This medium-sized lizard actively searches for its prey and thermoregulates by basking and shuttling between sunlit and shaded sites (Belliure et al., 1996), despite having a relatively small home range (usually <100 m^2; Civantos et al., 2010). Individuals typically live from 3 to 5 years (Comas et al., 2020), and may reach sexual maturity within a year depending on resources and environmental conditions (Carretero & Llorente, 1997). This species is frequently found in recently burned areas, likely due to its high postfire survival ability (Santos et al., 2022). Given that Mediterranean wildfires typically cover areas much larger than its home range, *P. algirus* is an appropriate candidate for studying the effects of living in postfire conditions. The study area is located in the eastern Iberian Peninsula and shows a typical Mediterranean climate prone to summer wildfires (Pausas & Paula, 2012).

Sampling

We sampled five wildfires that occurred between 2018 and 2020 (Appendix S1: Table S1); time since the last fire was 3 months (one site), ~1 year (three sites), and 2 years (one site). Sampling months varied among sites according to the timing of the fires, as our aim was to capture specific postfire ages, (e.g., sampling in November for the site burned in August to assess effects 3 months postfire). As a result, two of the sampled populations (the 3-month site and one of the ~1-year sites) were surveyed in November. In these late-season surveys, only juveniles were captured (both in burned and unburned areas) likely due to reduced activity of adults during cooler months. Although the sampling periods did not always coincide with the peak activity of all age classes, each population was sampled within a short time window. In each of the five 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, see Appendix S1: Table S1).

Lizards were collected by hand or using a pole with a slip noose, maintaining distance from the wildfire's edge to ensure that the lizard's home range was completely within or outside the fire perimeter (>500 m). For each site, we captured between 21 and 50 individuals (Appendix S1: Table S1); they were then measured for snout-vent length (SVL, ±0.1 g) and weighed (±0.1 g). Lizards' sex was determined by examining femoral pores, which are more prominent in adult males (Iraeta et al., 2011); therefore, juveniles were not sexed. Lizards were kept in cotton bags right after their capture and transported to the lab (Department of Ecology at CIDE) for controlled photography. Lizards were then released at the location of capture.

Color measurements

We took a photograph of each sampled lizard in controlled conditions (Appendix S1). A total of 192 digital images were used to analyze the body color of lizards from burned (n = 89) and unburned (n = 103) habitats across five locations (Appendix S1: Table S1). For each individual, dorsal skin luminance was computed as the average luminance of the entire dorsal area. Luminance reflects perceived lightness and is a reliable proxy of dorsal melanism (Laurentino et al., 2022). Detailed information on image capture, processing, and the methodology for dorsal color and luminosity determination can be found in Appendix S1: Material and Methods.

Statistical analyses

Statistical analyses were conducted using the R software version 4.0.3 (R Core Team, 2020). Body condition was calculated as the residuals of the regression of body mass against SVL (log-transformed; Warner et al., 2016), computed separately for females, males and juveniles. To examine fire's impact on the dorsal luminosity of lizards we fitted a linear mixed-effects model (LMM) using the package "lme4" (Bates et al., 2014). We included fixed effects of fire treatment (burned and unburned), SVL, postfire time (3 months, ~1 year and ~ 2 years), the interactions between fire treatment and SVL, and fire treatment and postfire time; sampling location (5 levels) was included as a random effect to account for among-population variation. We used type III "ANOVA" with the Satterthwaite approximation of degrees of freedom to obtain the significance of fixed factors and interaction terms. Model residuals were checked for normality using the DHARMa package v. 0.2.4 (Hartig, 2019). Comparative post hoc tests for treatment and post-fire time were conducted using the "difflsmeans" function of the "lmerTest" package

(Kuznetsova et al., 2017), and the Benjamini and Hochberg correction procedure was applied to control for the false discovery rate (Ferreira, 2007). Preliminary tests examined the potential influence of other factors (sex, body condition index, parasite count and tail autotomy; see Appendix S1: Table S3); as they were not significant, these variables were excluded from the final models.

To evaluate potential differences in inefficient predation pressure between burned and unburned areas, we used tail autotomy (binary: present/absent) as a proxy (Medel et al., 1988) and fitted a generalized linear mixed model (GLMM) with fire treatment as a fixed effect and location as a random effect (binomial error distribution; Bates et al., 2014).

Lizards' dorsal-color composition was analyzed with two-dimensional nonmetric multidimensional scaling (NMDS) ordination ("metaMDS" function in "vegan" package; Oksanen et al., 2020), based on relative color abundances (proportional contribution of the 27 bins to overall color abundance). The analysis was performed separately for adults and juveniles as *P. algirus* shows ontogenetic differences in coloration, with juveniles typically displaying darker and more uniform dorsal patterns than adults (Carretero, 2002). We conducted a PERMANOVA, with 999 permutations, using the "adonis" function in "vegan" package (Anderson, 2001) to test for differences in color composition between burned and unburned. We also specified the option strata (individuals nested within location) to account for differences in colouration across locations (Oksanen et al., 2020). To identify the color bins contributing most to the dissimilarity between burned and unburned, we conducted an indicator value analysis using "multipatt" function in the R package "indicspecies" v.1.7.9 (De Cáceres & Legendre, 2009).

Finally, to compare dorsal color of lizards among our paired burned/unburned sampled locations, we calculated the distribution of color for each site and generated a color distance matrix using the earth mover's distance or Wasserstein metric (EMD) method with the "colordistance" R package (Weller, 2019; Weller & Westneat, 2019). *P. algirus* dorsal coloration can be described as a varying lighter area within a darker area (Appendix S1: Fig. S1). Thus, we used kmeans clustering in "colordistance," that is, an approach for color-based image segmentation assigning each pixel to k clusters based on RGB values, to visualize the dominant tones and their relative sizes of lizards' dorse from each population (number of clusters = 2).

Results

Dorsal luminosity

Dorsal luminosity increased with lizards' size (SVL; $F_{1,141.72} = 41.19$, $P < 0.001$, Fig. 1, Appendix S1: Table S2). Additionally, dorsal luminosity was found to be higher in burned areas compared to unburned areas ($F_{1,182.28} = 8$, $P = 0.005$), with a significant SVL × fire treatment interaction ($F_{1,182.36} = 15.58$, $P < 0.001$). That is, larger lizards (higher SVL) inhabiting burned areas exhibited higher dorsal luminosity compared to those in unburned areas. Dorsal luminosity was higher in burned areas in recent postfire conditions ($F_{2,182.53} = 12.32$, $P < 0.001$). Specifically, post hoc tests revealed higher dorsal luminosity in burned areas 3 months postfire (estimate = 7.39, SE = 1.82, $P < 0.001$) and ~ 1 year postfire (estimate = 4.83, SE = 0.94, $P < 0.001$; Appendix S1: Table S4; Fig. 1), but similar in burned and unburned areas in 2 years postfire (estimate = −3.55, SE = 1.61, $P = 0.134$; Appendix S1: Table S4; Fig. 1). None of the additional variables considered (sex, body condition index, parasite count, and tail autotomy; see Appendix S1: Table S3) had a significant effect on dorsal luminosity and were therefore excluded from the final model.

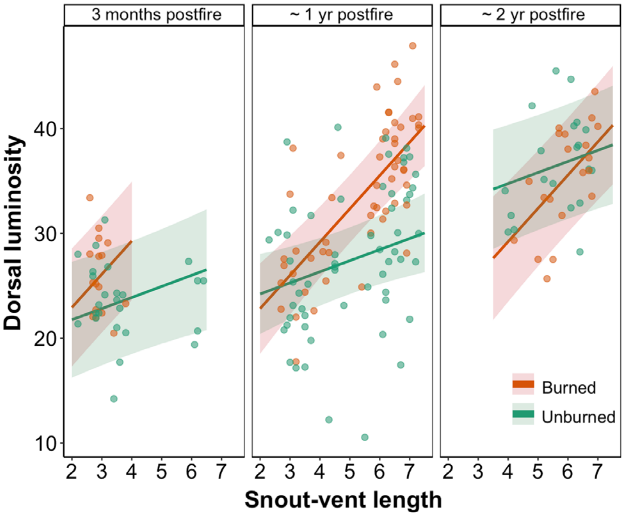

Figure 1 Lizards' dorsal luminosity in relation to lizards' size (snout-vent length, SVL) for burned areas (in red) and the corresponding paired unburned (in green). Lines are fitted values (with 95% confidence intervals) of the linear mixed model (see Appendix S1: Table S2). Symbols are the raw data ($N = 192$). The data split by populations is represented in Appendix S1: Fig. S3.

Color variations

The color composition of adult lizards differed significantly across burned and unburned areas (adonis test, $F_1 = 11.44$, $R^2 = 0.16$, $P = 0.001$; Fig. 2), with fire treatment accounting for 16% of the variation. In contrast, juveniles show no differences in color composition between burned and unburned areas (adonis test, $F_1 = 0.78$, $R^2 = 0.009$, $P = 0.4$). The color bins that best distinguish lizards in burned areas were 5 (stat = 0.285, $P = 0.023$) and 14 (stat = 0.41, $P < 0.001$), while color bin 1 was characteristic of lizards in unburned areas (stat = 0.489, $P < 0.001$). Specifically, color bins 5 and 14 corresponded to the color "grayish yellowish", while color bin 1 corresponded to "brown dark olive brown" in the ISCC–NBS System of Color Designation.

Predation proxy

To assess potential differences in inefficient predation pressure across fire treatments, we used tail autotomy as an indirect indicator. A generalized linear mixed model revealed no

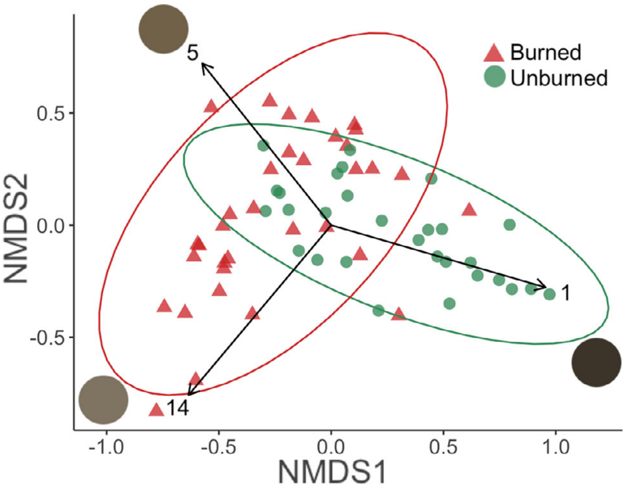

Figure 2 Nonmetric multidimensional scaling (NMDS) ordination of adult lizards in ~1-year postfire showing dissimilarities between burned and unburned in terms of coloration based on the Bray–Curtis distance coefficient. Dots (green) and triangles (red) represent lizards from unburned and burned, respectively. Ellipsoids indicate standard deviation around the centroid of each fire treatment. Arrows represent the association of the ordination with the color bins selected using multipatt(), and the large circles in the corners show the color of the corresponding bins (HEX codes: bin 1 = #3D3429, bin 5 = #716149, bin 14 = #7F7361). $N = 63$.

significant effect of fire treatment on the probability of tail loss ($\beta = 0.41 \pm 0.34$ SE, $z = 1.21$, $P = 0.224$), indicating similar rates of tail autotomy in burned and unburned areas.

Discussion

Lizards inhabiting areas recently affected by fire showed a lighter coloration compared to those in adjacent unburned areas. This color shift appears very recently after a fire (3 months), peaks in ~1-year postfire, and vanishes 2 years after the wildfire. Note that this early shift was observed only in juveniles, as no adults were sampled at the 3-month postfire site. The initial reduction and subsequent recovery of the vegetation in the Mediterranean fire-prone ecosystem, dominated by fire-adapted plant species that quickly resprout or germinate after the fire (Keeley & Pausas, 2022; Pausas & Keeley, 2014) is likely the reason behind this temporal pattern. Although we did not measure environmental temperatures directly, previous work in the region (Santos et al., 2022) found that mean temperatures in burned areas were higher than in unburned areas for at least 4-year postfire, although anomalies in maximum temperature stabilized after the second-year postfire. These anomalies may exceed the thermal physiological limits of lizards. Considering that *P. algirus* prefers microhabitats with low shrub cover (over 20 cm in height; Díaz & Carrascal, 1991), it seems that 2 years is sufficient time for the area to restore an acceptable thermal mosaic for the species. Nonetheless, behavioral adjustments, such as changes in microhabitat use (e.g. shuttling between shade and sun), may also contribute to thermoregulation in recently burned environments.

While our study design does not allow us to track individuals across time, the rapid appearance and disappearance of the lightening effect suggests that phenotypic plasticity, rather than selection, is the most likely driver. However, we cannot fully exclude the possibility that some individuals in the 1- and 2-year postfire sites were born after the fire and thus may reflect early-life environmental influences or selective survival (Laurent et al., 2016).

This fire-driven "lightening" effect is independent of sex, is consistent in adults and juveniles, and is more pronounced in larger lizards (Appendix S1: Table S5, Fig. S4). Given that having a higher surface area-to-volume ratio implies higher heat transfer coefficients (Norris, 1967), we would expect the lightening of dorsal coloration to be higher in smaller lizards as they are subjected to faster heating and cooling rates (Carrascal et al., 1992). However, ontogenetic effects may constrain their ability for color shifting, as juveniles of *P. algirus* are typically darker than adults (Carretero, 2002; Reguera et al., 2014). Behavioral differences between juveniles and adults may contribute to this pattern. Juveniles tend to bask more frequently (although for shorter periods), and are more active, than adults (Carrascal et al., 1992), which could allow them to better regulate their body temperature behaviorally and reduce their dependence on physiological adjustments such as dorsal lightening.

Altitude has been shown to influence dorsal coloration in lizards, including *P. algirus*, with darker individuals often found at higher elevations (Megía-Palma et al., 2021; Moreno-Rueda et al., 2019; Reguera et al., 2014). However, our design compared burned and unburned areas within each population, and paired sites were always selected at similar elevations and under comparable ecological conditions.

The observed color pattern aligns with the color-mediated thermoregulatory hypothesis. Prefire melanin levels could make lizards more prone to overheating postfire. Lizards employ multiple strategies to regulate their body temperature within their physiological thermal-tolerance limits (Sunday et al., 2014). The thermal properties of a lizard's habitat have a significant impact on the amount of time that it spends thermoregulating, including activities such as basking, searching for suitable basking sites, and shuttling between sun and shade (Gvoždík, 2011). Thus, fire-driven shifts in the thermal environment can impact the thermoregulatory behavior of lizards, and therefore, their life histories as a result (Herrando-Pérez et al., 2019). By adjusting their coloration, lizards may compensate for the increased temperatures in burned areas, reducing their heat gain and avoiding the energetic negative consequences of thermal retreats. This could increase their success in defending territories, mate-seeking, feeding, or fleeing from predators (Clusella-Trullas et al., 2007), and thus have important implications for lizards' fitness.

Although we did not model heat exchange directly, the timing, direction and reversibility of the observed color shifts suggest ecological relevance. These patterns are consistent with known thermoregulatory strategies in ectotherms, even if the precise thermal benefit remains to be quantified. However, dorsal lightening in a dark, postfire environment may reduce camouflage and increase exposure to predators. Such limitations in crypsis could represent a potential cost of color-mediated thermoregulation. However, while lighter dorsal coloration might imply a trade-off with crypsis in burned habitats, our data show no evidence of increased tail loss in those areas. This indicates that potential predation costs associated with color lightening are either absent or mitigated by other ecological or behavioral factors. While some lizard species exhibit short-term color changes in response to daily temperature or seasonal fluctuations (González-Morales et al., 2024; Langkilde & Boronow, 2012), there is no evidence of such mechanisms in *P. algirus*, where color variation is more closely linked to reproductive activity and body size rather than seasonal environmental changes (Carretero, 2002). Similarly, stress-induced physiological color changes, such as those observed in species like *Anolis*, typically occur within minutes and are reversible in the short term (Boyer & Swierk, 2017; Taylor & Hadley, 1970). In contrast, the color shifts observed in our study develop gradually and are sustained, which is not consistent with a typical stress response. Note that all photographs used in this study were taken under controlled temperature conditions after the lizards had spent a full day indoors, ensuring that potential short-term color changes due to ambient temperature were minimized.

Our results are in line with studies indicating that melanistic diurnal species inhabit cooler areas than lighter species, and that melanism results in greater fitness in cold environments. For instance, light morph butterflies (*Colias*) occupied warmer, less cloudy and, less windy habitats, enabling them to maintain suitable temperatures compared to darker individuals which were overheated (Watt, 1968). Similar results were observed when comparing closely related species of cordylid lizards (Clusella-Trullas, 2006). In addition, for our studied species, there is also evidence of color lightening with body size and temperature (Reguera et al., 2014). While previous studies reported spatial variation in dorsal coloration across environmental gradients (González-Morales et al., 2024; Sreelatha et al., 2025), our results provide one of the few examples of rapid, reversible shifts following a disturbance. This highlights a potentially plastic response that complements earlier findings based on long-term patterns.

Extreme temperatures can occur in burned environments, especially in the current context of climate warming (Fischer et al., 2021). To survive, lizards may rely on the phenotypic plasticity of thermal-related traits that provide a reprieve from extreme heat, keeping them within their physiological thermal-safety margin. Our study shows how a fitness-related measurement, such as coloration, can rapidly change in response to environmental alteration. The ability of *P. algirus* to quickly adjust its dorsal coloration likely favors its persistence in post-fire environments (Santos et al., 2022). Although our results are consistent with a plastic response, the possibility of alternative processes, including selection or developmental effects may also contribute, particularly at longer postfire intervals (Laurent et al., 2016). To better understand how species cope with fast-changing environments, future research should extend these findings to other ectothermic species, uncover mechanisms, and evaluate costs associated with the phenotypic flexibility of coloration. As different species have diverse levels of exposure to fire, their adaptive mechanisms, including the one examined in this study, are also anticipated to vary. This study highlights the overlooked area of animal adaptation to wildfires; as our planet warms we anticipate color lightning of ectotherms in postfire conditions to increase.

Acknowledgements

We thank the main technician, G. Benítez, and all the CIDE members who kindly helped in the fieldwork. We also thank the editor and the anonymous reviewers for their valuable comments. This work was supported by the Ministry of Economy and Competitiveness and the Ministry of Science, Innovation and Universities from the Spanish Government (grant numbers CGL2015-64086-P [FILAS], PGC2018-096569-B-I00 [FIROTIC], BES-2016-078225).

Author contributions

L.A-R., J.B. and J.P. conceived the idea. J.B. and L.A-R. collected the data. L.A-R. analysed the data and led the writing of the manuscript with the help of J.P. All authors contributed critically to the final version of the manuscript.

Data availability statement

Analyses reported in this article can be reproduced using the data provided by Álvarez-Ruiz et al. (2025).

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Supporting Information

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

Figure S1. Example of a photograph of an adult individual of *P. algirus*.

Figure S2. Example of color metrics of two adult males from a burned location (8-month postfire in Bejís) and the adjacent unburned zone. (a) Cropped dorsal areas, (b) CIELab clusters calculated by kmeans method, (c) CIElab 3D plot of pixels.

Figure S3. Dorsal luminosity comparison between burned and unburned areas. Higher values of luminosity indicate overall lighter coloration. Box plots 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 Table 2. $N = 192$.

Figure S4. Comparison of color among paired burned/unburned sampled populations using k-clustering (k = 2) and Earth Mover's distance (EMD) as the dissimilarity metric. The figure displays the color profiles of different populations and the distances between paired burned/unburned.

Table S1. Location and coordinates of study sites (Eastern Spain), fire start date, hectares burned, sampling months, time since wildfire, and number of lizards captured.

Table S2. Type III analysis of variance from the linear mixed effects model including snout-vent length (SVL), fire treatment (burned, unburned), postfire time (3 months, ~1 year, ~2 years) and their interaction as fixed effects. Location was included as random factor (5 levels). $N = 192$. Fitted values are displayed in Fig. 1. Statistically significant ($P < 0.05$) differences are highlighted in bold.

Table S3. Results of the linear mixed model (LMM) for adult lizards' dorsal luminosity as the response variable.

Table S4. Post hoc tests for effects of Fire treatment (FT: burned, unburned) and Postfire treatment (PT: 3 m, 1 year, 2 years) on lizards' dorsal luminosity. Values are least square estimates of the fixed effects "Fire treatment" and "Postfire time," 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.

Table S5. Variation in dorsal luminosity per pixel across lizards' age, sex, and fire treatments.