



Wildfire response of GPS-tracked Bonelli's eagles in eastern Spain

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ABSTRACT

Background. Little is known about the interaction between predators and wildfires, in part because the large home range and scarcity of predators make their study difficult, and their response is strongly species-specific. **Aims.** In this paper, we study, for the first time, the effect of wildfire on the behaviour of Bonelli's eagles (*Aquila fasciata*) simultaneously tracked by GPS/GSM dataloggers in four neighbouring territories. **Methods.** One territory was burnt in a wildfire and the other three were used for comparison. We computed the home-range area by comparing individual spatial and temporal behaviour before, during and after the fire event using kernel density estimators and movement parameters. **Key results.** Our results show an immediate negative effect during the first days of the wildfire for an individual inhabiting the burnt territory – the individual flew directly away from the burning area. However, after a few days, the individual recovered their usual behaviour. The three neighbouring pairs did not show significant differences in behavioural parameters before, during and after the wildfire. **Conclusions and implications.** Our results suggest that occasional wildfires do not affect the distribution and density of Bonelli's eagles in the short or medium-term (two years after fire). This could be the result of adaptation by this species to the frequent and recurrent wildfires in the Mediterranean area.

Keywords: conservation, datalogger, kernel density, management, Mediterranean, raptors, telemetry, territory.

Introduction

The current increase in wildfires across the world is likely to have an impact on animal populations (Pausas and Keeley 2019). For instance, there is evidence of decreasing vertebrate populations due to direct mortality by wildfire (Engstrom 2010), or indirectly by changes to habitat quality (Hovick *et al.* 2017). However, there are also examples of vertebrates that were unaffected by or even benefited from wildfire or in a post-fire environment (Jaffe and Isbell 2009; Nappi and Drapeau 2009; Nappi *et al.* 2010; Hovick *et al.* 2017). Many animals may have behavioural traits for dealing with wildfire (Pausas and Parr 2018).

The interaction between vertebrate herbivores and wildfires is quite well known, such as in savannas (Archibald and Hempson 2016) or tropical forests (Cherry *et al.* 2018). However, the interaction between wildfires and predators is poorly documented and understood. This lack of information may be partly because the response to wildfires is highly species-specific in predators (Geary *et al.* 2020), but also because large predators are not abundant and have large home ranges (Lotka 1925), and this makes their study difficult. Nevertheless, the role of wildfire in influencing predator behaviour is of special interest as changes in their population may have cascading effects on trophic networks (Ripple and Beschta 2004; Beschta *et al.* 2018) and, thus, they are crucial in the functioning of ecosystems. Raptors are an example of iconic predators with high conservation value (Donazar *et al.* 2016).

Several studies have focused on the influence of wildfires on the behaviour and conservation of raptors. For example, there is observational evidence of raptors hovering above wildfires and catching animals fleeing the wildfire front or feeding on animals killed by fire (Woinarski and Recher 1997; Smith and Lyon 2000; Bonta *et al.* 2017; Hovick *et al.*

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2017). However, flames and smoke can also threaten them by killing individuals, damaging their health, or even destroying their nests. Wildfires also radically change the landscape and vegetation structure and so raptors, even if not directly affected by a wildfire, may be forced to move to neighbouring landscape areas (Kochert *et al.* 1999). The few published studies on how wildfire affects raptors show both negative (Kochert *et al.* 1999; Blakey *et al.* 2020) and positive effects (Woinarski and Recher 1997; Smith and Lyon 2000; Bonta *et al.* 2017; Hovick *et al.* 2017). The consequences are likely to vary depending on the habitat preferences of the species (e.g. forest and non-forest raptors) although a detailed analysis remains to be done.

We aim to understand the effect of a wildfire on the spatial and temporal behaviour of Bonelli's eagle (*Aquila fasciata*) in a Mediterranean landscape. GPS (global positioning system) telemetry enables us to overcome the difficulties of working with fauna with large home ranges (McGregor *et al.* 2016; Nimmo *et al.* 2019). Here, we leverage information on a wildfire that occurred in the summer of 2016 and affected most of the core of the home range of an eagle (including the cliffs where its nest was located) that was being tracked by GPS telemetry. This provided a unique opportunity to compare the eagle's movements before, during and after the wildfire, and make a comparison with neighbouring eagles simultaneously tracked by GPS telemetry that were unaffected by the wildfire. Finding no differences between pre- and post-fire home range and movement behaviour would suggest that the spatial ecology of the eagle was unaffected by the fire. In contrast, eagles may be forced to move away to an unburnt area, or expand their home range if the quality of the habitat is reduced by wildfire.

Materials and methods

Species

Bonelli's eagle is a raptor classified as 'near threatened' (NT) in Europe (BirdLife International 2015) and 'vulnerable' (VU) in Spain (SEO/BirdLife 2021). Its habitat includes forest areas, scrub and open areas where there are rabbits, hares, pigeons, corvids and partridges (López-López *et al.* 2006; Martínez-Miranzo *et al.* 2016). According to the latest national survey, conducted in 2018, it is estimated that there are between 711 and 745 pairs in Spain, nesting mainly in cliffs and trees (Del Moral and Molina 2018).

Study area

This study was carried out in the south of the province of Castellón (eastern Spain; Fig. 1). The breeding territories of the eagles were in the Sierra de Espadán Nature Park (from 40°09'N to 39°36'N) and its surroundings. The area covers approximately 400 km² and varies from 100 to 1106 m above sea level. The climate is Mediterranean with an

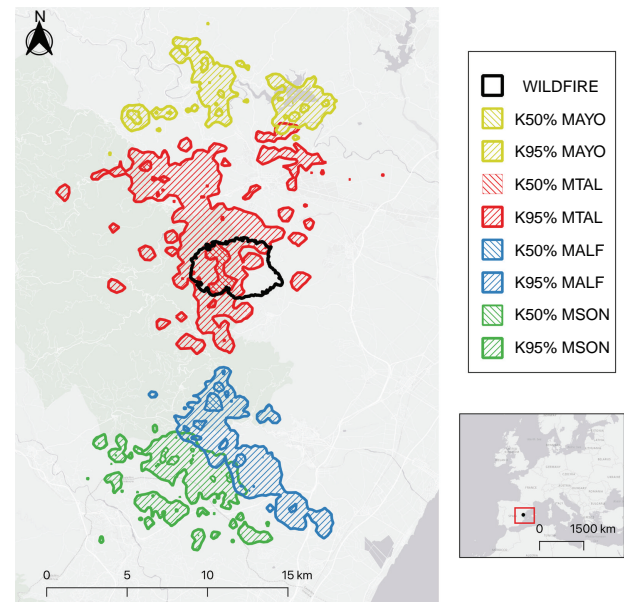


Fig. 1. Locations of the four territories of the males from each pair of the Bonelli's eagle in the study area (Male AYODAR, MaleTALES, Male ALFONDEGUILLA and Male SONEJA; see Supplementary Table S1). Territories are indicated as the 50 and 95% kernel distribution obtained from GPS locations. The wildfire (black line) affected the core of the territory of one pair of Bonelli's eagles (MTAL, named Carbo; in red).

average annual temperature that varies between 17°C in the coastal areas and 8°C in the inland mountains. The landscape includes various types of vegetation, mainly patches of pine forest (*Pinus halepensis*, *P. pinaster*), evergreen oak forests (*Quercus rotundifolia*, *Q. suber*) and Mediterranean scrub (*Rosmarinus officinalis*, *Quercus coccifera*, *Cistus* sp.). The area also includes unirrigated and irrigated farmlands, the former located in the interior and the latter in coastal areas. The study region is highly populated as it is located approximately 50 km from two metropolitan areas of more than 1.5 million inhabitants in total (Castellón and Valencia; National Institute of Statistics, www.ine.es).

In summer 2016, a wildfire (the Artana wildfire) affected 1556 ha of the study area and was active between 25 July and 1 August 2016. The municipalities of Alcudia de Veo, Artana, Onda and Tales were affected. The fire advanced during the first 3 days (25–27 July) (see Supplementary Fig. S1). This wildfire affected 100% of the core territory (including the nesting site) of one pair of eagles that was being GPS-tracked (named Carbo and Carla, in the municipality of Tales) (Fig. 1).

Tracking

A total of four territorial pairs of Bonelli's eagle were fitted with 48-g solar-powered GPS/GSM (Global System for Mobile communication) dataloggers (e-obs GmbH, Munich, Germany). The territories are located in the municipalities

of Alfondeguilla, Tales, Soneja and Ayódar (Fig. 1; see Supplementary Table S1). In each of these territories, male and female pairs were captured at the same time (between 2015 and 2016; Supplementary Table S1). The weight of the dataloggers was 1.66–2.86% (average 2.25%, s.d. 0.38%) of the body mass of the eagle, i.e. below the 3% threshold established to avoid negative effects on animal behaviour (Kenward 2001). The duty cycle of the dataloggers was programmed to record a GPS location at 5-min intervals. Tags were affixed in a backpack configuration using a Teflon tubular harness designed to ensure that it fell off at the end of the tag's life. GPS data were retrieved, stored and managed through the Movebank online repository (<http://www.movebank.org/>).

The female in Tales (named Carla or F_TAL; Supplementary Table S1), which was one of the pair in whose home range the wildfire occurred, lost her datalogger on 20 April 2016 and thus was not tagged during the wildfire (July–August 2016). She was recaptured and tagged again on 12 December 2016.

Ethics statement

Handling activities were authorised and conducted with permission issued by regional authorities (Conselleria de Agricultura, Medio Ambiente, Cambio climático y Desarrollo Rural, Generalitat Valenciana) and all efforts were made to minimise handling time to avoid any suffering for the eagles.

Data analysis

The Artana wildfire directly affected the territory in Tales where a male individual (Carbo, M_TAL) was tagged. We first studied the movements of this eagle during the wildfire by analysing distances in relation to the fire ignition point (UTM (Universal Transverse Mercator) coordinates 30S 735229, 30S 4421213). To do so, we considered GPS locations in accordance with the available information on the progression of the wildfire provided by the Valencia Fire Service (Dirección General de Prevención de Incendios Forestales, Generalitat Valenciana). We also analysed the eagle's residence time as the number of hours within the wildfire perimeter in each entry for the periods between 1 June and 31 August (i.e. including the days of the fire). This was done using the R package 'recurse' (Bracis *et al.* 2018; R Core Team 2018). A non-parametric Kruskal–Wallis analysis was made to identify if there were differences in the travelled distance during the wildfire or the residence time before and after the wildfire. We animated the movements of M_TAL during the wildfire with the R package 'moveVis' (Schwalb-Willmann *et al.* 2020).

We then used the overall territories of the four Bonelli's eagles – which included seven individuals (Supplementary Table S1) – to compute home-range indicators using kernel density estimation methods (KDE) (Worton 1989) for three short-term periods: before (1 June–24 July), during (25 July–1 August), and after (2 August–31 August) the wildfire.

Specifically, we computed daily 50 and 95% kernels (K50 and K95% respectively) using the R package 'Reproducible Home-Range' (*rhr*) (Signer and Balkenhol 2015). We also computed the total daily distance travelled (TDD) and the average daily distance travelled between consecutive points (or step length mean, SLM), using the R package 'Animal Movement Tools' (*amt*) (Signer *et al.* 2019). These indicators were computed using 10 947, 1735 and 6199 GPS locations, on average, before, during, and after the fire respectively (Supplementary Table S2). Pairwise comparisons between periods for each variable and for each individual were performed with a non-parametric Kruskal–Wallis analysis and a post-hoc Wilcoxon test by pair samples (Supplementary Table S3 for statistical details). Territorial maps for the seven individuals were made to visualise the kernel density estimators' results before–during–after the wildfire.

For M_TAL, we also computed the four home-range indicators (K50, K95%, TDD and SLM) for the same dates as the fire year (before, during and after) but in the next and the second year after the wildfire (i.e. in 2017 and 2018). A non-parametric Kruskal–Wallis analysis was carried out to identify any differences in home-range indicators for the same dates as the wildfire in the following years.

Finally, we computed the same home-range indicators (K50, K95%, TDD and SLM) for the territories of the same four Bonelli's eagles (10 individuals; long-term analysis in Supplementary Table S1) for periods that expand larger temporal windows as follows: (i) from the tagging day until the day before the wildfire (24 July); (ii) from the day after the wildfire (2 August) until the end of 2016; (iii) throughout 2017 (first year after the wildfire); and (iv) throughout 2018 (second year after the wildfire). During these longer periods, some tagged individuals died, some GPS tags stopped working, and some individuals were replaced – and so the 10 individuals were considered in total (Supplementary Table S2). There is evidence that the replacement individuals assumed the same territorial behaviour as the previous ones (Perona *et al.* 2019; López-López *et al.* 2021). Thereby, the final number of GPS locations used in the analyses were on average 35 193, 18 652, 50 556 and 37 253 for each temporal window, respectively (see Supplementary Table S2 for details). Pairwise comparisons between periods for each variable and for each individual were performed with a non-parametric Kruskal–Wallis analysis and a post-hoc Wilcoxon test by pair samples (see Supplementary Table S4 for statistical details). For all statistical analyses, a significance level of $P < 0.05$ was set.

Results

Movement of the individual directly affected by wildfire

During the first days of the wildfire, the male in the Tales territory (M_TAL) moved away from the flames (Fig. 2a).

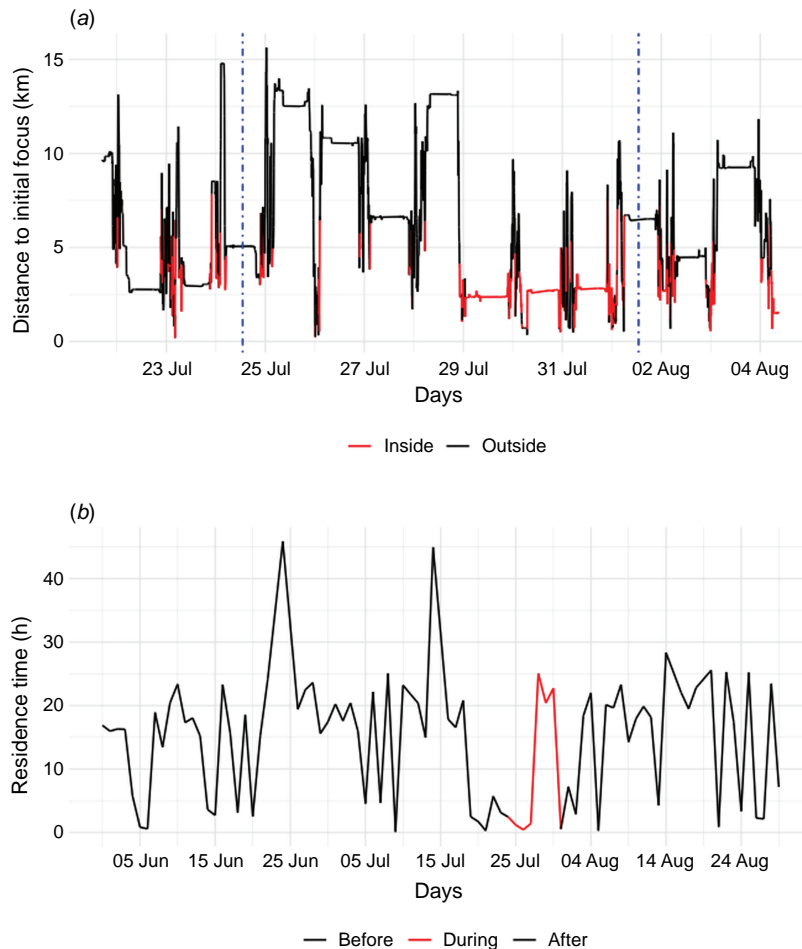


Fig. 2. Behaviour of the male Bonelli's eagle directly affected by the wildfire (M_TAL) before, during and after the fire event. (a) Distance (km) of the individual from the fire ignition point between 22 July and 5 August (in red when it was within the fire perimeter; the vertical blue lines indicate the beginning and end of the wildfire). (b) Residence time (h) within the fire perimeter between 1 June and 31 August (red line shows the time when the wildfire took place).

From the fifth day, however, this individual returned to the fire and spent most of the time within the fire perimeter, even when the fire was still burning (Fig. 2a). That is, the distance of the individual to the ignition point was significantly higher during the first fire days (25–28 July; 8.35 ± 3.44 km, range: 0239.24–15.63 km) than after (29 July–1 August; 3.47 ± 3.25 km, range: 0346.35–13.33 km; $P < 0.001$, Kruskal–Wallis test). The proportion of GPS locations (i.e. the proportion of time) within the wildfire perimeter was much lower during the first period (6.02%, $n = 748$) than after (60.37%, $n = 752$). The residence time of the male within the fire perimeter was similar before (15.24 ± 9.99 h per entry) and after fire (14.80 ± 9.42 h per entry; $P = 0.059$, Kruskal–Wallis test; Fig. 2b).

Looking at the detailed movements of this male, we observed that this individual moved 6 km away from the ignition point in the first 2 h of the fire, following the wind direction (NW), but remained within its home range. The wildfire reached 85% of its final extent that night and affected the nest where two chicks had fledged a couple of months previously. The next day, there were still some active fire fronts and considerable firefighter activity in the study area (including the continuous movement of firefighting

planes). The individual remained outside the burnt area and at the limits of its territory. It then made a change in its direction from west to east at 11 am, and visited the initial point of the wildfire, where the flames were already extinguished. At 1 pm, this individual crossed most of the burnt area, heading northwards, and remained outside the rest of the day. A similar pattern was observed during the following days, when it never left its territory and flew over the edges of the wildfire even when there was still some fire activity. It flew over areas that were burning slowly (without the wind of the first days). On the last day of the wildfire, the individual remained most of the day within the burnt area in the southern part of its territory where the wildfire originated, and for the first time since the wildfire, it spent the night within the burnt area (see an animation of these movements in Figshare Repository [10.6084/m9.figshare.19209918](https://figshare.com/10.6084/m9.figshare.19209918)).

Short-term differences in home-range

The 95% kernel of M_TAL increased during the wildfire, but it quickly decreased to pre-fire levels straight after (Fig. 3, Supplementary Fig. S2, Supplementary Table S3 for statistical details). A similar but not significant pattern was observed for

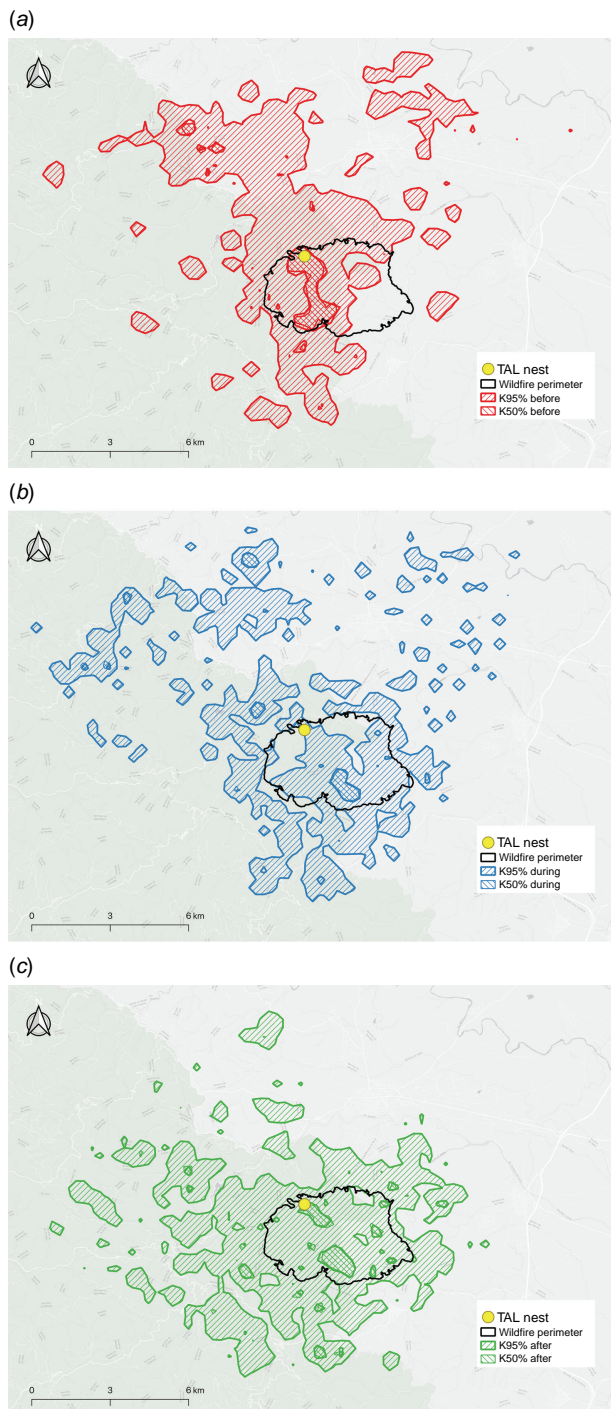


Fig. 3. Home range according to the spatial estimator 95 and 50% kernels of the male Bonelli's eagle directly affected by the wildfire (M_TAL). The fire perimeter (black polygon) and nest (yellow dot) are shown: (a) before the wildfire (red; 1 June–24 July); (b) during the wildfire (blue; 25 July–1 August); and (c) after the wildfire (green; 2 August–31 August).

the 50% kernel (i.e. the core area) and the distances travelled (TDD, SLM, Fig. 3). The pair in Alfondoguilla (named M_ALF and F_ALF) that were ~4.5 km from the fire also showed some

increase in their 95 and 50% kernels during the wildfire – and quick recovery (Supplementary Fig. S2, Supplementary Table S3 for statistical details; Supplementary Figs S3, S4 for map territories). The other two pairs (located in Soneja and in Ayódar municipalities – 6.8 and 8.6 km away from the wildfire) were also weakly affected by the wildfire according to their home range as estimated with 95 and 50% kernels (Supplementary Fig. S2, Supplementary Table S3 for statistical details; Supplementary Figs S5–S8 for map territories).

Long-term differences in home-range

The pair that was affected by the wildfire (i.e. M_TAL and F_TAL) hatched two chicks in 2016. In the year after the fire (2017), they did not hatch any chicks, and they hatched one in 2018. In 2017, for the same dates, there were significant differences in the 50% kernels ($P = 0.031$; Kruskal–Wallis test) of the male before ($7.13 \pm 5.29 \text{ km}^2$), during ($4.90 \pm 3.15 \text{ km}^2$) and after ($10.18 \pm 6.89 \text{ km}^2$) the fire. This is the opposite pattern to 2016 (the year when the fire occurred). There were no differences in the remaining variables. In the following year, 2018, and for the same dates, there were no significant differences in any of the four variables considered (all $P > 0.05$; Kruskal–Wallis test).

If we compare the four long-term periods (i: from tagging date to the wildfire; ii: from the wildfire to the end of 2016; iii: for 2017; and iv: for 2018) for each of the eight individuals (four pairs), there were no differences in any of the variables considered in this study (95% kernel, 50% kernel, TDD, and SLM) for any individual (see Supplementary Table S4, Supplementary Figs S9–S12).

Discussion

We show, for the first time, the effect of fire on the spatial and temporal behaviour of a Bonelli's eagle, an endangered European raptor. Because these eagles had been previously tagged with GPS telemetry, we were able to analyse in detail the response of a Bonelli's eagle to wildfires. Previous studies on the goshawk (*Accipiter gentilis*; Blakey *et al.* 2020) and on the golden eagle (*Aquila chrysaetos*; Kochert *et al.* 1999) concluded that both species were negatively affected by fire owing to forest habitat destruction in the first case and post-fire reduction of its main prey (rabbits) in the second case. Urios (1986) analysed the distribution of Bonelli's and golden eagle territories, including those that had been burnt in recent years, and concluded that wildfires did not affect the distribution of Bonelli's eagle in Valencia (Spain). In contrast, wildfires were a significant positive factor for the golden eagle, probably owing to the increased availability of open habitats that favour prey and accessibility for hunting. In contrast, Kochert *et al.* (1999) showed that wildfires decreased the breeding performance of golden eagles in the first 4–6 years after large wildfires (increasing afterward).

Also, [Tapia et al. \(2017\)](#) showed how land cover change (e.g. through high-intensity, low-frequency fires) can negatively affect forest species owing to possible loss of forest canopy. However, species that are not strictly forest specialists, such as the common buzzard (*Buteo buteo*) may benefit from open habitats (e.g. scrublands) for hunting.

Despite a wildfire affecting most of the eagle's core area (according to the 50% kernel density contour), its activity was hardly affected and the individual moved away from the fire but did not leave its home range (95% kernel). The reason why it did not leave its territory may be related to interactions with neighbours, as this species is highly territorial ([Urios 1986](#)). The consistency in the spatial behaviour of this individual the two years following the fire suggest that changes observed during 2016 were probably due to the wildfire event.

Fortunately, there were three additional neighbouring Bonelli's eagle pairs that were also simultaneously GPS-tracked. The home-range areas of these three pairs were not directly burnt by the wildfire. Some showed changes in their activity during the fire dates but quickly recovered after the wildfire (Supplementary Fig. S2). We consider that these slight changes in their activity could be a direct response to the smoke, or more likely, to the high level of firefighting activity in the area (which included off-road vehicles and firefighting planes).

Our results suggest that Bonelli's eagles were unaffected by wildfires in the short and medium term. Bonelli's eagles, like other birds, can move away when a fire is burning hot. However, their spatial and temporal behavioural response after the catastrophic event did not differ from that observed before. Our results did not show any change in their behaviour during the 2 years after the wildfire. In fact, the pair whose territory was directly affected by the fire reproduced successfully in the second year after the wildfire on the same cliffs (some of which were completely burnt). Note that long-lived raptors do not breed every year ([Steenhof and Newton 2007](#)). The resilience of this species to wildfires was already suggested after overlaying regional distribution maps of this species in eastern Spain on fire frequency maps ([Urios 1986](#)). Our results suggest that the main prey (rabbits and pigeons) were unaffected by the wildfire. This could be explained by the ability of many small mammals to survive fire by sheltering in burrows ([Geluso and Bragg 1986](#)). Burrowing behaviour could be an adaptive response in animals in fire-prone ecosystems ([Long 2009](#); [Pausas and Parr 2018](#)). In addition, fires increase open spaces and while this favours rabbits ([Moreno and Villafuerte 1995](#)), Bonelli's eagles may also benefit from the increased visibility of their prey after a fire. In general, post-fire conditions increase the attractiveness of burnt areas to predators ([Leahy et al. 2016](#); [McGregor et al. 2016](#)), including other raptors ([Barnard 1987](#); [Hovick et al. 2017](#)) and colonisation may occur from nearby areas, as they take advantage of these newly available open areas.

Negative consequences of wildfires on raptors have been documented, for instance, in forest species ([Blakey et al. 2020](#)). However, in fire-prone ecosystems such as those of the study area, located in the European Mediterranean region, it is likely that many species, both flora and fauna, could be able to deal with some fire activity ([Pausas and Keeley 2019](#)). Animal adaptation to fire is not easy to detect, but there is increasing recognition of the importance of understanding behavioural traits to assess animals' response to wildfires ([Pausas and Parr 2018](#); [Nimmo et al. 2019](#); [Álvarez-Ruiz et al. 2021](#)). Further, this knowledge is urgently needed for a wide range of species as the Earth is warming and fire regimes are quickly changing ([Pausas and Keeley 2021](#)). Our study case is based on a fairly small fire (~1500 ha), yet it has allowed us to improve our knowledge on the response of a European endangered species to a global change driver.

Finally, it is worth noting the importance of this serendipitous event, as we were able to analyse the behavioural response of several individuals of the same species distributed across neighbouring territories thanks to a fire occurring where eagles were already being tracked simultaneously by GPS-telemetry.

Supplementary material

Supplementary material is available [online](#).

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Conflicts of interest. The authors declare that no conflict of interest exists.

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