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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. This is partly because the large home-range and scarcity of predators makes 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 (*Aquila fasciata*) that were being simultaneously tracked by GPS/GSM dataloggers in four neighbouring territories.

Methods - One of the territories was burnt in a wildfire and the other three were used for comparison. We computed the home-range area by comparing individual 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 – as the individual flew directly away from the burning area. However, after a few days the individual recovered its 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 neither the short nor long-term. This could be the result of an adaptation by this species to the frequent and recurrent wildfires in the Mediterranean area.

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

Introduction

The current increase in wildfires across the world is likely to have an impact on animal populations. 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 unaffected or even benefiting by wildfire or a postfire environment (Jaffe and Isbell 2009; Hovick *et al.* 2017). In fact, many animals may have behavioural traits for dealing with wildfire (Pausas and Parr 2018).

The interaction between vertebrate herbivores and wildfires is relatively well-known, especially in savannas (Archibald and Hempson 2016). However, interaction between wildfires and predators is poorly understood. This lack of information may be partly because response to wildfires is highly species-specific (Geary *et al.* 2020), but also because large predators are not abundant and have large home-ranges – and this makes their study difficult. Nevertheless, the role of wildfire in influencing predator behaviouris 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 iconic predators with great conservation value. 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.* 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 migrate 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 behaviour of the Bonelli's eagle (*Aquila fasciata*) in a Mediterranean landscape. GPS 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 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 other 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 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

The Bonelli's eagle is a raptor classified as 'near threatened' in Europe (BirdLife International 2015) and 'endangered' in Spain (Madroño *et al.* 2004). Its habitat includes forest areas, scrub, and open areas where there are rabbits, hares, pigeons, corvids, and partridges. 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 surroundings. The area covers approximately 400 km^2 and varies from 100 to 1106 meters above sea level. The climate is Mediterranean with an 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. pl.*). 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 a metropolitan area of more than 2.5 million inhabitants (Valencia; National Institute of Statistics, www.ine.es).

In summer 2016, a wildfire (the 'Artana wildfire') affected 1556 ha of the study area. This wildfire affected the municipalities of Alcudia de Veo, Artana, Onda, and Tales and was active between 25 July and 1 August 2016. The wildfire developed during the first three days (25-27 July) (see Fig. S1 in Supplementary Material for details). This wildfire affected 100% of the core territory (including the nest site) of one pair of eagles which were 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 had been fitted with 48 g solar-powered GPS/GSM dataloggers (e-obs GmbH, Munich, Germany). The territories are located in the municipalities of Alfondeguilla, Tales, Soneja, and Ayódar (Fig. 1; see Table S1 in Supp. Mat. for details). In each of these territories, male and female pairs were captured at the same time (between 2015 and 2016; Table S1 in Supp. Mat.). The weight of the dataloggers was 1.66 – 2.86% (average = 2.25%, sd = 0.38%) of the body mass of the eagle, i.e., below the 3% threshold established to avoid negative effects on the animal behaviour (Kenward 2001). The duty cycle of the dataloggers was programmed to record a GPS location at five-minute 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 was retrieved, stored, and managed through the Movebank online repository (http://www.movebank.org/).

The female in Tales (named Carla or F_TAL; Table S1), which was one of the pair in whose home range the wildfire occurred, lost her datalogger on 04/20/2016 and thus was not tagged during the wildfire (July/August 2016). She was recaptured and tagged again on 12/12/2016.

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 coordinates: 735229, 4421213). To do so, we considered GPS locations in accordance with the available information on the evolution 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 Jun and 31 Aug (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 animate 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 eagle – including seven individuals (Table S1 in Supp. Mat.) – to compute home-range indicators using kernel density estimation methods (KDE) (Worton 1989) for three short-term periods: before (1 Jun – 24 Jul), during (25 Jul – 1 Aug), and after (2 Aug – 31 Aug) 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 10947, 1735, and 6199 GPS locations on average, before, during, and after the fire (Table S2 in Supp. Mat. for details). Pairwise comparisons between periods for each variable and for each individual were performed with a non-parametric Kruskal-Wallis analysis and a *posthoc* Wilcoxon test by pair samples (Table S3 in

Supp. Mat. for statistical details). Territorial maps of 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, 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 Table S1, in Supp. Mat.) for periods that expand larger temporal windows as follows: i) from the tagging day until the day before the wildfire (24 Jul); ii) from the day after the wildfire (2 Aug) 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 ten individuals were considered in total (Table S2, in Supp. Mat.)There is evidence that the replacement individuals assumed the same territorial behaviourr as the previous one (Perona et al., 2019; López-López et al., 2020). Thereby, the final number of GPS locations considered were on average 35193, 18652, 50556, and 37253 for each temporal window, respectively (see Table S2 in Supp. Mat. for details). Pairwise comparisons between periods for each variable and for each individual were performed with a non-parametric Kruskal-Wallis analysis and a *posthoc* Wilcoxon test by pair samples (see Table S4 in Supp. Mat. for statistical details). For all statistical analysis 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). 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 Jul; 8.35 ± 3.44 km) than afterwards (29 Jul – 1 Aug; 3.47 ± 3.25 km; $p < 0.001$, Kruskal-Wallis test). The proportion of GPS location (i.e., the proportion of time) within the wildfire perimeter was much lower during the first period (6.02%, n = 748) than afterwards (60.37%, n = 752). The residence time of the male within the fire perimeter was similar before the fire (15.24 ± 9.99 h/entry) and afterwards (14.80 ± 9.42 h/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 two hours of the fire, following the wind direction (NW), but remained within its home-range. The wildfire reached 85% of its final extension that night and affected the nest where two chicks had been hatched a couple of months previously. During the next day, there were still some active fire fronts, and considerable firefighter activity ini the study area (including continuous movement of fire-fighting 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 the animation of these movements, in Figshare Repository 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 just afterwards (Fig. 3; Fig. S2 and Table S3 in Supp. Mat. for statistical details). A similar but not significant pattern was observed for the 50% kernel (i.e., the core area) and the distances travelled (TDD, SLM, Fig. 3). The pair in Alfondeguilla (named M_ALF and F_ALF) that were about 4.5 km from the fire also showed some increase in their 95% and 50% kernels during the wildfire – and a quick recovery (Fig. S2 and Table S3 in Supp. Mat. for statistical details; Fig. S3 and S4 in Supp. Mat. 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 (Fig. S2 and Table S3 in Supp. Mat. for statistical details; Fig. S5-S8 in Supp. Mat. for map territories).

Long-term differences in home-range

The pair which 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 ± 5.29 km^2), during (4.90 ± 3.15 km^2), and after (10.18 ± 6.89 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, for each of the eight individuals (four pairs), the four long-term periods (i: from tagged to the wildfire; ii: from the wildfire to end of 2016; iii: for 2017; and iv: for 2018) there were no differences in any of the variables considered in this study (95% kernel, 50% kernel, TDD, and SLM) for any individual (see Table S4 in Supp. Mat.; Fig. S9-S12 in Supp. Mat.).

Discussion

We showWe, for the first time, the effect of fire on the 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 due to the forest habitat destruction in the first case, and by the postfire 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 the Bonelli's eagle in Valencia (Spain). In contrast, wildfires were a significant positive factor for the golden eagle, probably due to the increased availability of open habitats that favour prey and accessibility for hunting. On the contrary, Kochert *et al.,* (1999) showed that wildfires decreased the breeding performance of golden eagles in the first 4-6 years after large wildfires (increasing afterwards).

We found that despite a wildfire affecting most of eagle's core area (according to the 50% kernel density contour), the activity of the individual whose territory was almost completely burnt was hardly affected. This individual moved away from the core territory during the first days of the wildfire (when the fire was most intense), but never went out of 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). When the wildfire was less intense (during the last days of the wildfire), the eagle spent most of the time within the burnt area, including around the flames. Once the fire was extinguished, all home-range parameters return quickly to pre-wildfire levels (Fig. S2 in Supp. Mat.). The analysis of this individual behaviour at the same dates in following years showed that there were no similar changes in the eagle's activity, suggesting that the observed behavioural change during 2016 was probablydue to the wildfire.

Fortunately, there were three additional neighbouring Bonelli's eagle pairs which 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 (Fig. S2 in Supp. Mat.). 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 (including off-road vehicles and fire-fighting 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 the fire is burning hot. However, their 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 two years after fire. In fact, the pair whose territory was directly affected by the fire, reproduced successfully in the second year after the wildfire in 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. Postfire 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).

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 would be able to deal with some fire activity. Our study case is based on a relatively small fire (ca. 1500 ha).

Finally, it is worth noticing the importance of this serendipitous event, as we were able to analyse 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.

Authors' contribution

S.M., V.U. and P.L.L conceived the ideas, designed methodology and collected the data. S.M. analysed the data and wrote the manuscript. J.P., V.U. and P.L.L. contributed critically to the drafts and gave final approval for publication.

Conflict of interest

Authors declare that no conflict of interest exists.

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Data Availability Statement

All data used in this study are publicly available upon request to data managers in the online data repository Movebank (www.movebank.org), project 'Bonelli's eagle University of Alicante Spain' (project ID = 58923588).

References

Archibald S, Hempson GP (2016). Competing consumers: contrasting the patterns and impacts of fire and mammalian herbivory in Africa. *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**(1703), 20150309.

Beschta RL, Painter LE, Ripple W J (2018). Trophic cascades at multiple spatial scales shape recovery of young aspen in Yellowstone. *Forest Ecology and Management* **413**, 62-69.

BirdLife International (2015). *Aquila fasciata*. The IUCN Red List of Threatened Species 2015: e.T22696076A60132541. Downloaded on 20 October 2020.

Blakey RV, Siegel RB, Webb EB, Dillingham CP, Johnson M, Kesler DC (2020). Multi-scale habitat selection by Northern Goshawks (*Accipiter gentilis*) in a fire-prone forest. *Biological Conservation*, **241**, 108348.

Bonta M, Gosford R, Eussen D, Ferguson N, Loveless E, Witwer M (2017). Intentional fire-spreading by 'Firehawk' raptors in Northern *Australia. Journal of Ethnobiology*, **37**(4), 700-718.

Bracis C, Bildstein KL, Mueller T (2018). Revisitation analysis uncovers spatio-temporal patterns in animal movement data. *Ecography*, **41**(11), 1801-1811.

Del Moral JC, Molina B (Eds.) (2018). 'El águila perdicera en España, población reproductora en 2018 y método de censo' (SEO/BirdLife. Madrid, Spain)

Engstrom RT (2010). First-order fire effects on animals: review and recommendations. *Fire Ecology*, **6**(1), 115-130.

Geary WL, Doherty TS, Nimmo DG, Tulloch AI, Ritchie EG (2020). Predator responses to wildfire: A global systematic review and meta-analysis. *Journal of Animal Ecology,* **89**, 955-71.

Geluso KN, Bragg TB (1986). Fire-avoidance behavior of meadow voles (*Microtus pennsylvanicus*). *American Midland Naturalist*, 202-205.

Hovick TJ, McGranahan DA, Elmore RD, Weir JR, Fuhlendorf SD (2017). Pyric-carnivory: Raptor use of prescribed fires. *Ecology and Evolution*, **7**(21), 9144-9150.

Jaffe KE, Isbell LA (2009). After the fire: benefits of reduced ground cover for vervet monkeys (*Cercopithecus aethiops*). *American Journal of Primatology: Official Journal of the American Society of Primatologists*, **71**(3), 252-260.

Kenward RE (2001). 'A Manual for Wildlife Radio Tagging'. (Academic Press)

Kochert MN, Steenhof K, Carpenter LB, Marzluff JM (1999). Effects of fire on golden eagle territory occupancy and reproductive success. *The Journal of wildlife management*, 773-780.

Long K (2009). Burrowing bandicoots – an adaptation to life in a fire-prone environment? *Australian Mammalogy,* **31**, 57–59.

López-López, P., Perona, A. M., Egea-Casas, O., Morant, J., & Urios, V. (2021). Tri-axial accelerometry shows differences in energy expenditure and parental effort throughout the breeding season in long-lived raptors. *Current Zoology*, zoab010

Leahy L, Legge SM, Tuft K, McGregor HW, Barmuta LA, Jones ME, Johnson CN (2016). Amplified predation after fire suppresses rodent populations in Australia's tropical savannas. *Wildlife Research, 42*, 705–716.

Madroño A, González GG, Atienza JC (Eds.). (2004). 'Libro rojo de las aves de España.' (Organismo Autónomo Parques Nacionales)

McGregor HW, Legge S, Jones ME, Johnson CN (2016). Extraterritorial hunting expeditions to intense fire scars by feral cats. *Scientific reports*, **6**, 22559.

Moreno S, Villafuerte R (1995). Traditional management of scrubland for the conservation of rabbits *Oryctolagus cuniculus* and their predators in Doñana National Park, Spain. *Biological Conservation,* **73**, 81-85.

Nimmo DG, Avitabile S, Banks SC, Bliege Bird R, Callister K, Clarke MF, Dickman CR, Doherty TS, Driscoll DA, Greenville AC, Haslem A, Kelly LT, Kenny SA, Lahoz-Monfort JJ, Lee C, Leonard S, Moore H, Newsome TM, Parr CL, Ritchie EG, Schneider K, Turner JM, Watson S, Westbrooke M, Wouters M, White M, Bennett AF. (2019). Animal movements in fire-prone landscapes. *Biological Reviews,* **94**, 981-998.

Pausas JG, Parr CL (2018). Towards an understanding of the evolutionary role of fire in animals. *Evolutionary Ecology*, **32**(2-3), 113-125.

Perona, A.M., Urios., V., López-López, P. (2019). Holidays? Not for all. Eagles have larger home ranges on holidays as a consequence of human disturbance. *Biological Conservation* 231:59-66

R Core Team (2019). R: A language and environment for statistical computing. *R Foundation for Statistical Computing*, Vienna, Austria. URL https://www.R-project.org/.

Ripple WJ, Beschta RL (2004). Wolves and the ecology of fear: can predation risk structure ecosystems?. *BioScience*, **54**(8), 755-766.

Schwalb-Willmann, J.; Remelgado, R.; Safi, K.; Wegmann, M. (2020). moveVis: Animating movement trajectories in synchronicity with static or temporally dynamic environmental data in R. *Methods in Ecology and Evolution*.

Signer J, Balkenhol N (2015). Reproducible home-ranges (rhr): A new, user-friendly R package for analyses of wildlife telemetry data. *Wildlife Society Bulletin*, **39**(2), 358-363.

Signer J, Fieberg J, Avgar T (2019). Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecology and evolution*, **9**(2), 880-890.

Smith JK, Lyon LJ (2000). ‘Wildland fire in ecosystems: effects of fire on fauna’ (Vol. 2). (US Department of Agriculture, Forest Service, Rocky Mountain Research Station)

Steenhof K, Newton I (2007). Assessing nesting success and productivity. *Raptor research and management techniques*, 181-192.

Urios V (1986). Biología, Requerimientos Ecológicos y Relaciones Interespecífica del Águila Real *Aquila chrysaetos homeyeri* Severtrov, 1888 y del Águila Perdicera *Hieraetus fasciatus fasciatus* Viellot, 1822 (Accipitriformes, Accipitridae) en la Provincia de Valencia. Tesis de licenciatura. Universidad de Valencia.

Woinarski JCZ, Recher HF (1997). Impact and response: a review of the effects of fire on the Australian avifauna. *Pacific Conservation Biology*, **3**(3), 183-205.

Worton BJ (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164-168.

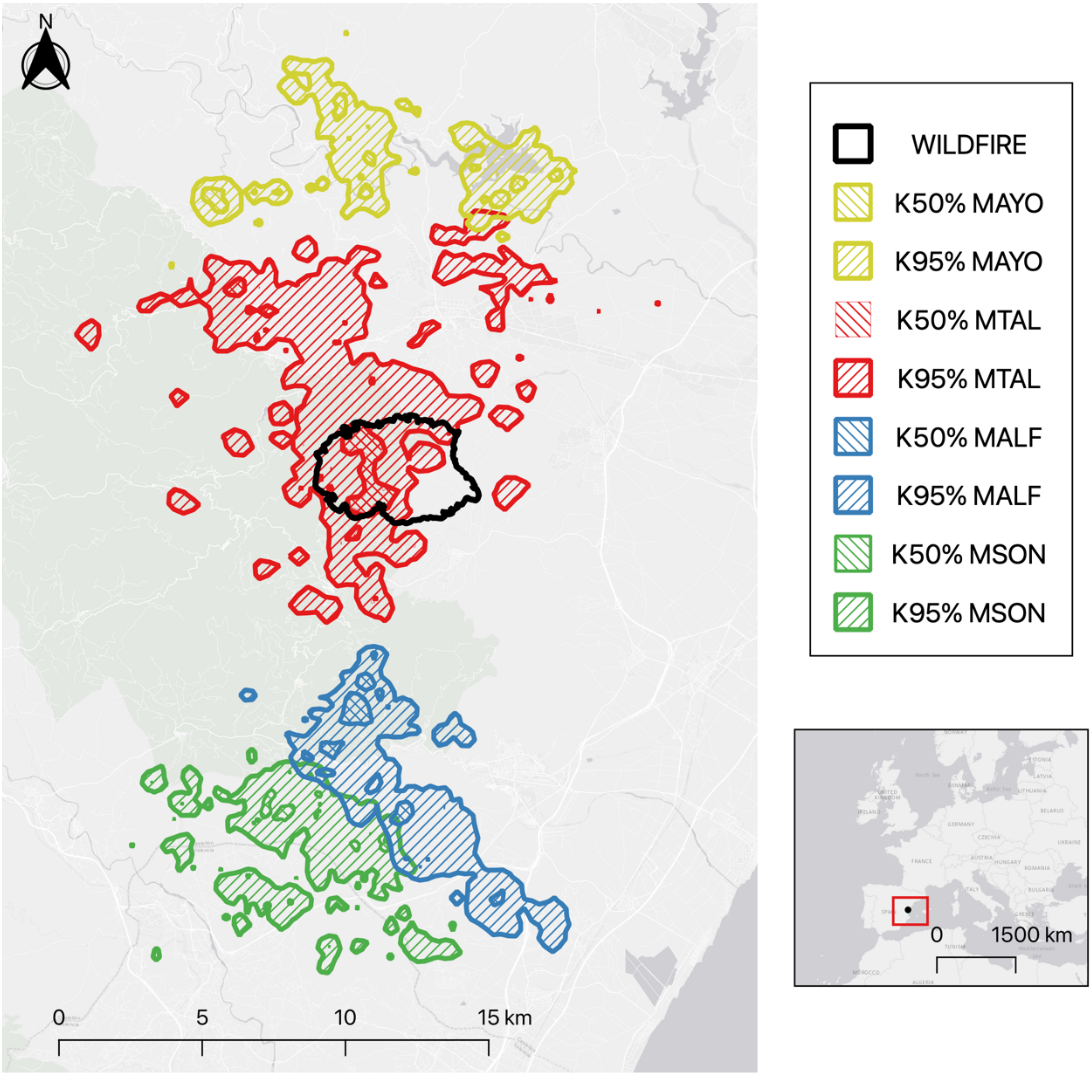

Figure 1: Locations of the four male territories of each pair of the Bonelli's eagle in the study area (MAYO, MTAL, MALF, and MSON; see Table S1). Territories are indicated as the 50% and 95% kernel distribution obtained from GPS locations. The wildfire (black line) affected the core of one of the pair of Bonelli's eagles (MTAL named Carbo; in red).

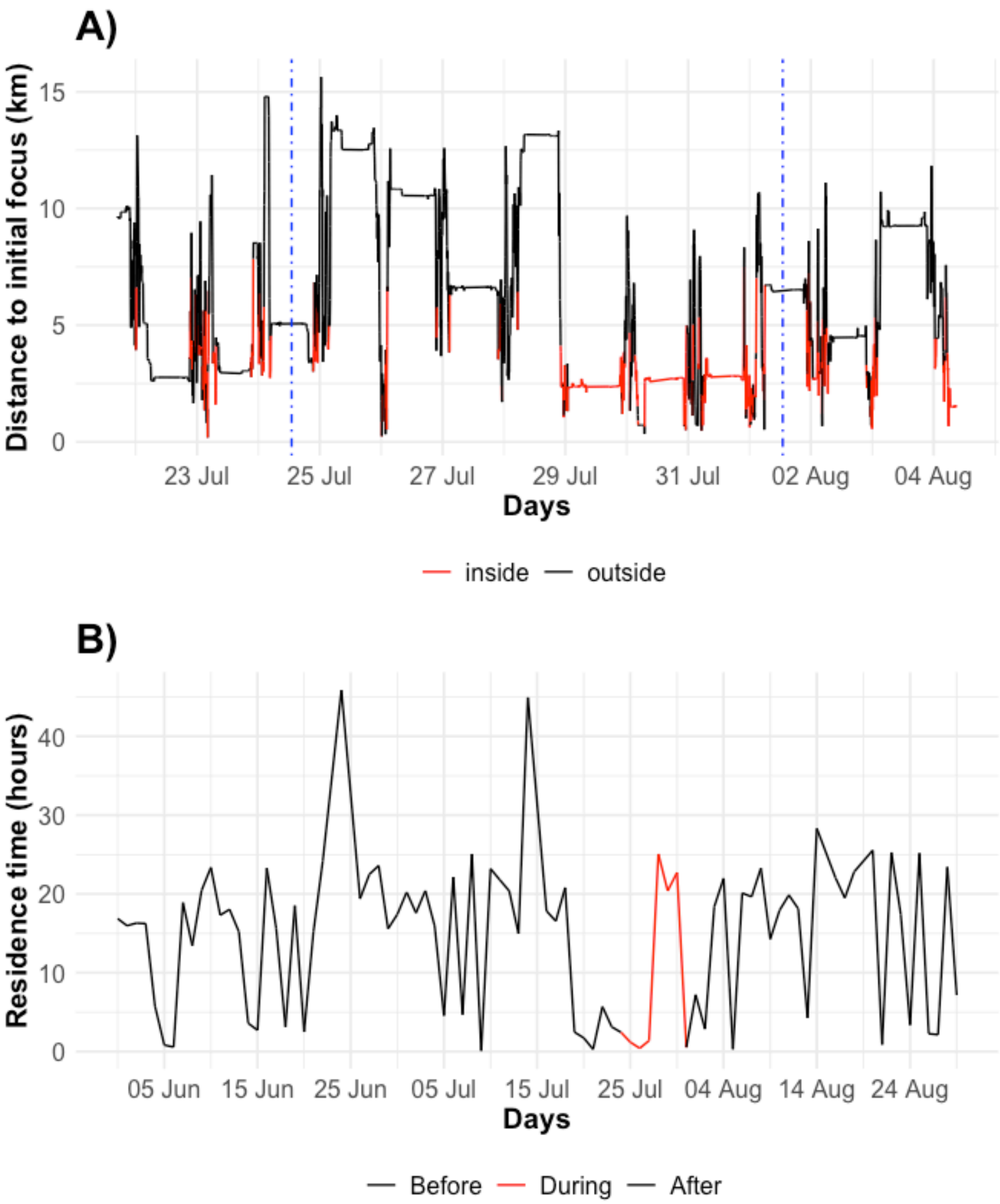

Figure 2: Behaviour of the Bonelli's eagle male directly affected by the wildfire (M_TAL) before, during, and after the catastrophic event. A) Distance (km) of the individual to the fire ignition point between 22 July and 5 August (in red when he was within the fire perimeter, the vertical blue lines indicate the beginning and the end of the wildfire. B) Residence time (hours) within the fire perimeter between 1 June – 31 August (red line shows the time when the wildfire took place).

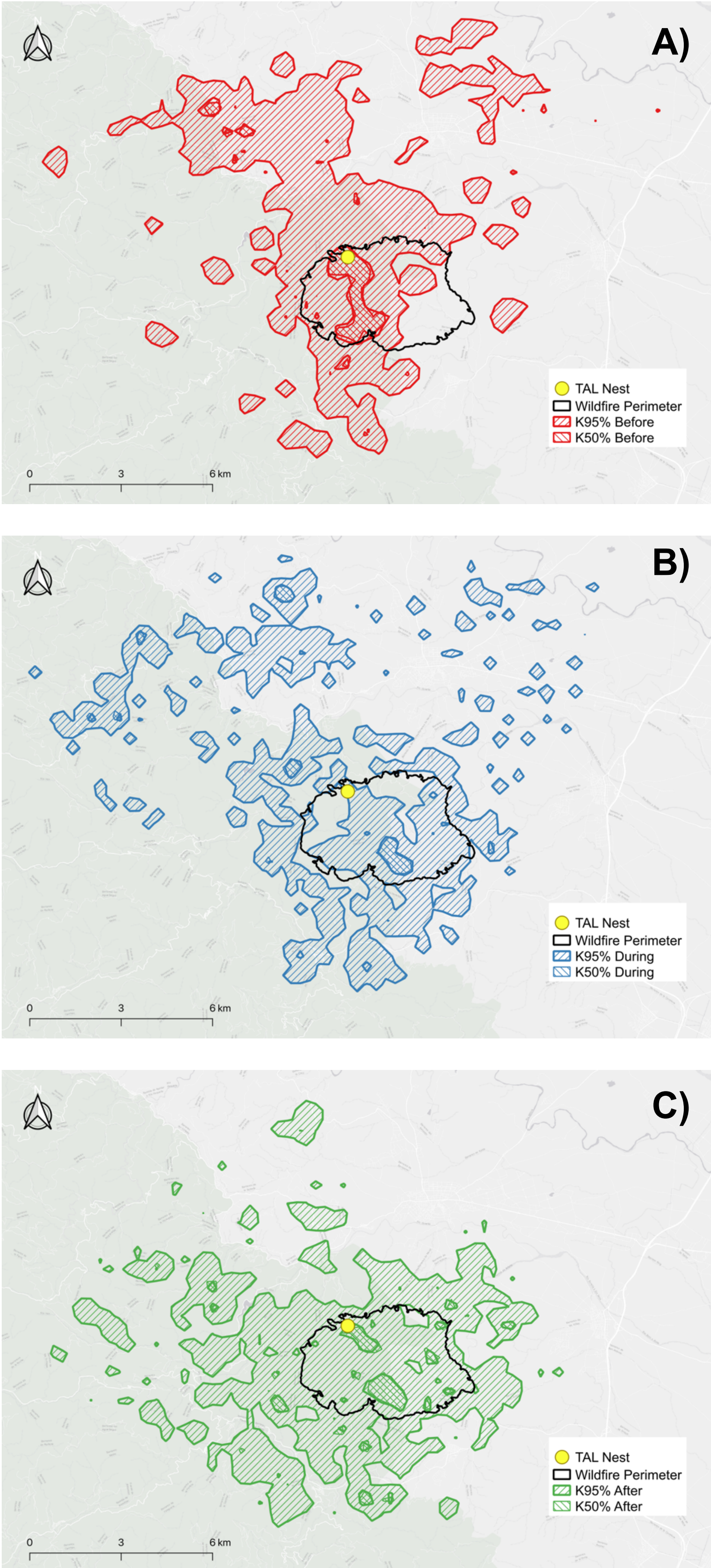
A)
TAL Nest
Wildfire Perimeter
K95% Before
K50% Before
0
3
6 km
B)
TAL Nest
Wildfire Perimeter
K95% During
K50% During
0
3
6 km
C)
TAL Nest
Wildfire Perimeter
K95% After
K50% After
0
3
6 km

Figure 3: Home-range according to the spatial estimators 95% and 50% kernels of the Bonelli's eagle male directly affected by the wildfire (M_TAL). The fire perimeter (black polygon) and the nest (yellow dot) are shown: A) before the wildfire (red; 1 Jun – 24 Jul); B) during the wildfire (blue; 25 Jul – 1 Aug); and C) after the wildfire (green; 2 Aug – 31 Aug).