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ORIGINAL RESEARCH

A new view of territoriality in large eagles: the territory pre-exists regardless of their occupants

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Abstract

Knowledge of vertebrate territoriality and spatial use is a topic of great interest in the study of animal behaviour and conservation biology. Investigating the plasticity of territory boundaries, the shape of territories and how territories can be modified depending on their owners is important to deepen our knowledge of the behaviour of territorial species. We analysed the variation and tested the similarity of the distribution area of individuals from the same territory between 2015 and 2021, using data from 51 Bonelli's eagles (*Aquila fasciata*) from 22 different territories, tagged with GPS/GSM transmitters in eastern Spain. We calculated the percentage of overlap between the territories of the same individual in different years using the 95% kernel density estimator. We also analysed the changes in territory size and shape following the replacement of territory owners either by a single individual or by the whole pair. Our results show that territories retain the same shape and extent regardless of the occupying members, and that their boundaries change little over time. Identifying and maintaining large eagle territories, regardless of their owners, is therefore key to ensuring the long-term recovery of these threatened species.

Introduction

The study of dispersal patterns and territoriality is essential for understanding animal populations. There are several criteria for defining territoriality in animals. One of them could be from a behavioural point of view, and there are different definitions of territoriality, such as *Area-defended territoriality*, with aggression and warnings at territorial boundaries (Maher & Lott, 1995). This idea of area-defended territoriality was originally defined as the defence of a territory by a male against other males of the same species (Kaufmann, 1983). Some authors have defined territoriality as involving a fixed spatial area (Brown, 1975; Kaufmann, 1983), while others have suggested that defended areas may change over time and across space and may be mobile (Wilson, 1975). Another term is *Site-specific dominance*, which defines territory as the home range of an aggressive and dominant animal against intruders (Emlen, 1957). This definition supports the idea of territorial exclusion and the existence of overlapping areas between neighbouring territories with hostile owners (Wittenberger, 1981). Territoriality can also be defined in ecological terms, such as *Exclusive use* of a defined area (Maher & Lott, 1995), without taking into account animal behaviour. In addition, the shape or size of territories may vary according to population density, food availability and quality, habitat characteristics and the individuals that inhabit them (Maher & Lott, 2000).

Most vertebrates limit their activities to a specific area during certain periods in the annual cycle, known as the home range. When individuals defend all or part of this home range against others of the same species, it is referred to as a territory (Odum & Kuenzler, 1955). A territory is a specific area within an animal's home range where the animal has exclusive or priority use. It may be the entire home range or a partial section of it (Powell, 2000).

Understanding the spatial use of species is crucial for conservation. When determining the limits and zoning of protection areas for avian species, such as in the case of Special

Protection Areas (SPAs), the location of nests is taken into account. Proposed limits (e.g. a defined radius around a nest site) typically coincide with geographical features or areas that are easy for the administrations to delimit, as outlined in Council Directive 79/409/EEC of 2 April 1979 on the conservation of wild birds, particularly in the case of raptors. Therefore, understanding the territorial limits and their consistency over time is crucial for establishing clear criteria for delimiting and extending protected areas. As such, SPAs encompass both occupied and unoccupied territories.

Some studies have analysed the behaviour and use of space of Bonelli's eagle by examining its reproductive cycles (e.g. López-López, de La Puente, et al., 2016), feeding (e.g. Barton & Houston, 1994; Costantini et al., 2005) and territorial occupation (e.g. Martinez et al., 2008). The study of territories has been approached from different perspectives, such as habitat selection (e.g. Barrientos & Arroyo, 2014; Tanferna et al., 2013), individual fidelity (e.g. Martínez-Miranzo et al., 2016; Pérez-García et al., 2013), or seasonal differences (e.g. López-López et al., 2021; Morollón, et al., 2022a). However, to date, no research has been conducted on the shape of the territories and how their boundaries change or are maintained over time, regardless of the individuals that occupy them.

The Bonelli's eagle (*Aquila fasciata*) is a territorial raptor that defends its territory in pairs. It exhibits typical cooperative hunting behaviour, with males and females flying together (Morollón, et al., 2022a). This species has a wide distribution across Europe, North Africa, and southern Asia, and is mostly found in Mediterranean habitats with evergreen forests and abrupt topography. The species is classified as "Near Threatened" (NT) in Europe (BirdLife International, 2015) and "Vulnerable" (VU) in Spain (SEO/BirdLife, 2021).

The aim of this study is to investigate whether the spatial stability of territories remains consistent over time and is not influenced by their owners. The study examines the capacity of territory boundaries to change, the shape of territories, and how territories can be modified depending on their owners between 2015 and 2021. Here, we evaluate the spatial use of various Bonelli's eagle individuals in the same territory and analyses the eagles' movement behaviour over the years. We hypothesised that if the territory remains stable over time regardless of its occupants, there would be no differences in annual territory size among individuals occupying each territory during consecutive years (i.e., the null hypothesis). On the contrary, we hypothesised that if individuals occupying the same territory exhibit different spatial use patterns, resulting in varying annual territory sizes over time, there would be no stability or delimitation of the territories themselves independent of their occupants (i.e., the alternative hypothesis).

Materials and methods

Study area

The study area was situated in eastern Spain, encompassing the provinces of Albacete, Alicante, Castellón, Cuenca, and Valencia, covering an area of approximately 10 000 km^2 with altitudes ranging from sea level to 1814 m a.s.l. The climate was Mediterranean, with an average annual temperature that varied between 8°C in the interior mountains and 17°C in the coastal areas. The dominant landscape was dominated by Mediterranean scrublands, oak forests (*Quercus faginea* and *Quercus suber*), and Mediterranean evergreen forests (*Quercus ilex, Pinus halepensis* and *Pinus nigra*). Additionally, the area contained rainfed and irrigated cropland, with the former located inland and the latter in coastal areas. The study area was densely populated situated approximately 50–100 km from three metropolitan areas with a combined population of over 1.75 million inhabitants (Albacete, Castellón, and Valencia; Instituto Nacional de Estadística, www.ine.es).

Tracking

Between 2015 and 2021, we trapped 26 males and 25 females of adult and subadult Bonelli's eagles in 22 different breeding territories (Fig. 1; Table S1) using a remotely activated folding ground net. The trap was always monitored by the researchers who were hidden nearby, and was only activated once the target individuals were inside. In most cases (16 territories), both male and female members of the pair were trapped together. When we detected a replacement of one member of the pair (usually after the death of the previous member), we trapped and tagged the new member (Table S1).

All individuals were fitted with GPS/GSM solar energy transmitters manufactured by e-obs GmbH (Munich, Germany) and Ornitela (Vilnius, Lithuania) using a backpack configuration that employed a Teflon tubular harness sewn with cotton thread. The harness was designed to allow a unit to fall off at some point in the future. The transmitters weighed between 48 and 50 g respectively, which represented 1.66 to 2.86% (mean = 2.25%, SD = 0.38%) of the eagles' body mass (males = 1.88 kg, SD = 0.12 kg, range = 1.70–2.06 kg; females = 2.50 kg, SD = 0.18 kg, range = 2.16–2.90 kg). These weights were below the 3% threshold established to avoid negative effects on behaviour (García et al., 2021; Kenward, 2001). The transmitters were programmed to record a GPS location at five-minute intervals (López-López et al., 2021), from 1 h before sunrise to 1 h after sunset year-round during the study period (2015–2021). The data from the transmiters were managed and stored using the Movebank online repository (http://www.movebank.org/).

Ethics statement

Trapping and marking activities were conducted under permissions issued by regional authorities (Conselleria de Agricultura, Medio Ambiente, Cambio Climático y Desarrollo Rural, Generalitat Valenciana and Consejería Agricultura, Medio Ambiente y Desarrollo Rural, Castilla-La Mancha, Spain). All efforts were made to minimize handling time to reduce stress on the eagles. Most of the individuals were captured and tagged during the non-breeding season to prevent any changes in their behaviour during this sensitive period. In all cases where individuals were tagged during the breeding season, we made sure that the birds had either failed to reproduce or did not reproduce that year (Table S1; López-Peinado & López-López, 2023).

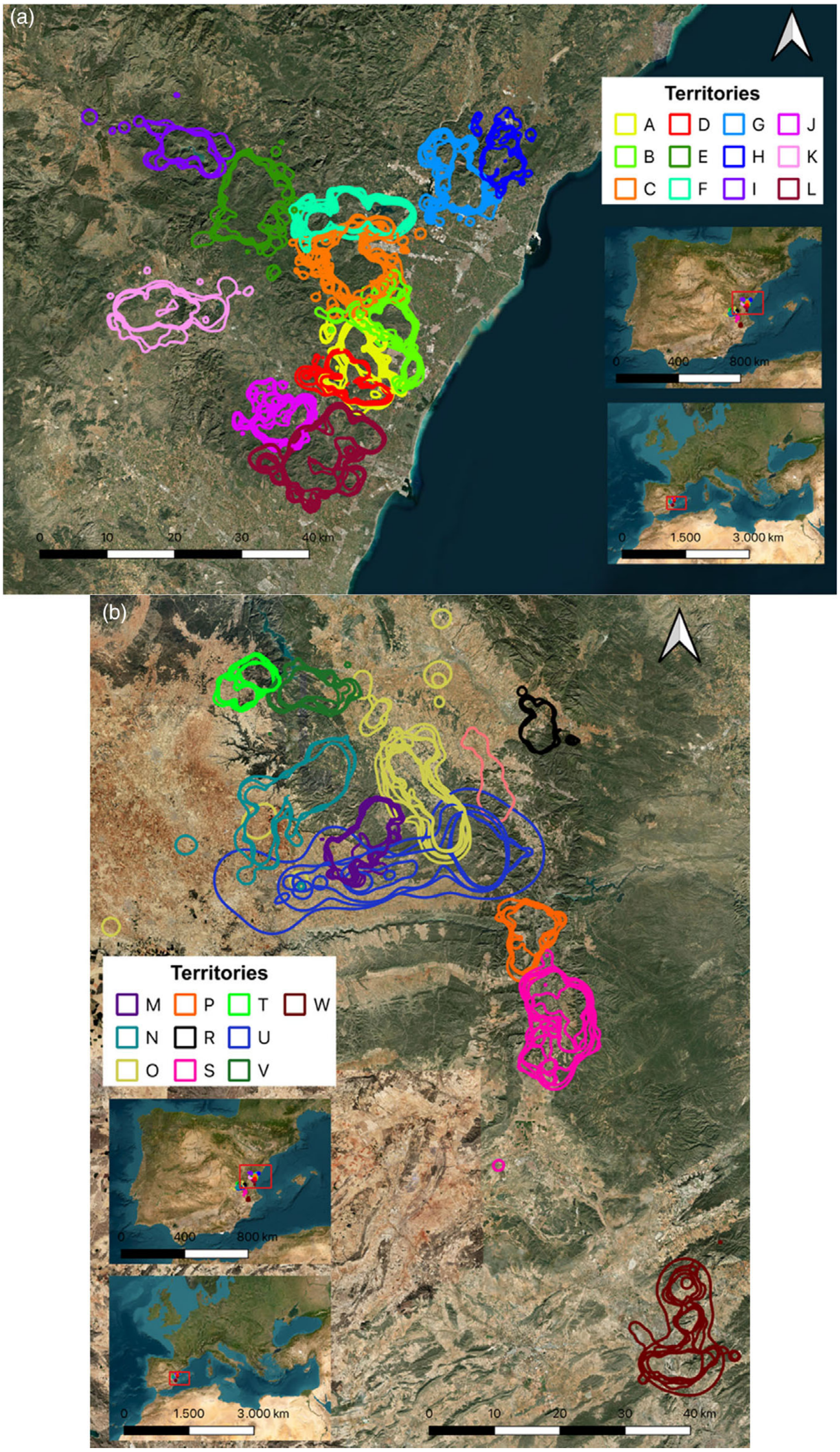

Figure 1 Territorial overlap of 51 Bonelli's eagles tracked by high-resolution GPS/GSM telemetry from 2015 to 2021 in eastern Spain. The individuals occupying the same territory are shown in a different colour. (a) Individuals occupying territories close to the coast (provinces of Castellón, and Valencia). (b) Individuals marked in inner lands (provinces of Albacete, Cuenca, and inner Valencia).

Territory analysis

We used kernel density methods (KDE; Worton, 1989) to calculate annual territory size and evaluate space use. We assumed that the annual home ranges we calculated represented the territory of an individual since each annual home range corresponds to the defended area and the exclusive use area of each pair or individual, i.e. the territory. We computed the 95% annual kernel isopleth (K95%) considered as the total area of the territory (Kie et al., 2010; Samuel et al., 1985). The isopleths are the curves that connect the points where the function has the same constant value. We analysed data for each individual from the next day after tagging until the end day of data transmission (e.g. animal's death, end of transmission). We used the "reproducible home range" (*rhr*) R package for statistical computing (R Core Team, 2020; Signer & Balkenhol, 2015). The annual kernels were calculated based on the available data for each individual from January 1st to the December 31st, provided that there were more than 15 days of monitoring (Morollón, et al., 2022b).

We analysed the annual territorial overlap between all the individuals occupying the same territory over the years (including the replaced individuals). To this end, we calculated the percentage of annual overlap between the total territory sizes (K95%) of individuals from the same territory using the *raster* R package (Hijmans, 2020). We computed the proportion of one individual's annual territory of covered by another individual's annual territory (which could be the same individual in a different year) was calculated as follows: Overlap[A,B] = Area[A,B]/Area[A]. The overlap percentages were computed by comparing the area of the intersection between the two annual territories (Area[A,B]) and the area of the annual territory of the individual A (Area[A]). We computed for the same individual these overlap percentages over the years, as well as with the other occupants of the same territory, including the other individual of the pair and any the turnover individuals, if applicable. We calculated the average overlap for each territory and the total overlap percentage average to avoid pseudo-replication. We also made maps of all the 95% annual kernel isopleths, so that we could compare the shapes of different individuals occupying the same territory. We identified the 22 specific territories using the letters A–S. These maps were created using QGIS software version 3.22.6 (QGIS Development Team, 2022).

Additionally, we described the turnover events where a territory owner was replaced by another individual who was subsequently tagged. We compared the percentage of overlap between the territories of the previous and new individuals in these cases. Turnovers were classified as *Single turnover* when only one member of the pair was replaced or *Double turnover* when both members were replaced. We calculated the average overlap percentage using only the annual territories of the individuals who had a turnover event.

Results

In this study, we tracked 51 eagles and used 4 791 080 GPS locations (mean per individual = 101 098.42 locations; SD = 81 578.23 locations; range = 1016–257 640 locations).

The annual territory was measured using the 95% kernel density estimator, which yielded an average of 79.79 ± 54.42 km^2 (n = 161 annual 95% kernels) with a range between 23.47 and 555.23 km^2.

On average, individuals occupying the same territory had an 80.95 ± 5.58% overlap in their annual territory area (n = 22 overlapping percentages, one for each territory; see Table S2). The range was from 91.03 ± 4.71% (Territory R, n = 30) to 71.99 ± 24.08% (Territory U, n = 12; Fig. 1; see Tables S3–S24).

There were seven territories (A, B, D, F, H, P, and S) with changes in ownership, resulting in a total of eight replacements: six single turnovers (A, B, F, H, P, and S territories) and two double turnovers (B and D territories). The average overlapping percentage of territory size during these turnover events was 85.54 ± 9.71% (n = 14 overlapping percentages between turnover individuals), with a range between 66.50 and 99.30% (Table 1, Figs 2 and 3).

Discussion

This study presents the fixed shape of Bonelli's eagle territories and how their boundaries are maintained over time, regardless of the individuals that occupy them.

Our results indicate that the area and the shape of the territories remain consistent over the years, with a high percentage of overlap (80.95 ± 5.58%) between individuals inhabiting the same territory. The territory remains constant regardless of whether it is used by one pair, a new pair, or a pair formed by a previous and a new individual. Our study is the first to examine the overlap between different occupants of territory in Bonelli's eagles, as well in other vertebrate species. Previous studies have only measured individual inter-annual fidelity or overlap between sexes. The fidelity percentage between owners recorded in our study was higher than the individual fidelity found in previous studies carried out on the same species using GPS (27.3%, n = 7, Pérez-García et al., 2013; 76.8%, n = 8, Martínez-Miranzo et al., 2016), probably due to the different types of analyses and variables used in the different studies. However, the percentage of overlap between sexes recorded using a radio-tracking methodology (98.6%, n = 10, Bosch et al., 2010) was higher than that recorded here, probably due to the small sample size of this analysis and the use of outdated techniques. The overlapping percentage of inter-annual fidelity is higher in this raptor species than in others such as the Golden eagle (*Aquila chrysaetos*; 60%, n = 8, radio-tracking, Marzluff et al., 1997; 70% (99% kernel), n = 17, GPS, Watson et al., 2014), and Spanish imperial eagle (*Aquila adalberti*; 75%, n = 8, radio-tracking, Fernández et al., 2009). Therefore, our results demonstrate the fidelity of owners to the same territory, whose boundaries tend to remain stable over time. When comparing our annual territory size results with the daily territory size of Bonelli's eagle in previous studies, we found that the annual territory size is 30% larger than the daily territory (mean = 54.86, SD = 20.57 km^2, range = 22.44–116.11 km^2; Morollón, et al., 2022a). This comparison can be used as a reference for future studies to determine which measure to use.

Table 1 Overlap percentages and information of the turnover events

Type of turnover	Territory	Sex	Remplaced individual	New individual	Period	Anual overlap %	Causes of turnover	Tables and Figures
Single	A	Male	Abel	Adan	2016–2017	89.2	Abel died in September 2016 by unknown causes and was replaced by Adan, which was tagged in January 2017	Figure 2a; Table S3
Single	B	Female	Berta	Boira	2015	66.5	Berta died in July 2015 by a collision with a power line and was replaced by Boira, tagged in November 2015	Table S4
Single	F	Female	Flora	Fauna	2016–2017	93.0	Flora died in December 2016 by electrocution at a power line and was replaced by Fauna, tagged in May 2017	Figure 2b; Table S8
Single	H	Male	Helios	Heackel	2016–2017	95.1	Helios died in January 2017 by electrocution at a power line and was replaced by Haeckel, tagged in April 2017	Figure 2c; Table S10
Single	P	Male	Popper	Pino	2019–2020	97.2	Popper died in October 2019 by collision with a power line and was replaced by Pino, tagged in June 2020)	Figure 2d; Table S18
Single	S	Female	Sabina	Salvia	2019–2020	99.3	Sabina died in February 2020 by collision with a fence and was replaced by Salvia, tagged in June 2020	Figure 2e; Table S20
Double	B	Male	Boira	Bruma	2016–2017	89.7 (Bruma) and 84.0 (Boj)	Boira and Blas drowned in an irrigation pond in June 2016 López-López, Urios, and Cervera (2016) and were replaced by individuals from the floating population, Boj, and Bruma in 2017, which were tagged at the same time in April 2017	Figure 3a; Table S4
		Female	Blas	Boj	2016–2017	92.2 (Bruma) and 84.3 (Boj)		
Double	D	Male Female	Dino Dora	Adan Aura	Tables S5 and S24 for all percentages		Dino and Dora were poisoned at the same time in March 2018 López-López and Urios (2018) and Adan and Aura (neighbours of the A territory) occupied both territories (territories A and D) only 2 ays after the death of the pair Dino-Dora.	Figure 3b; Tables S6 and S24

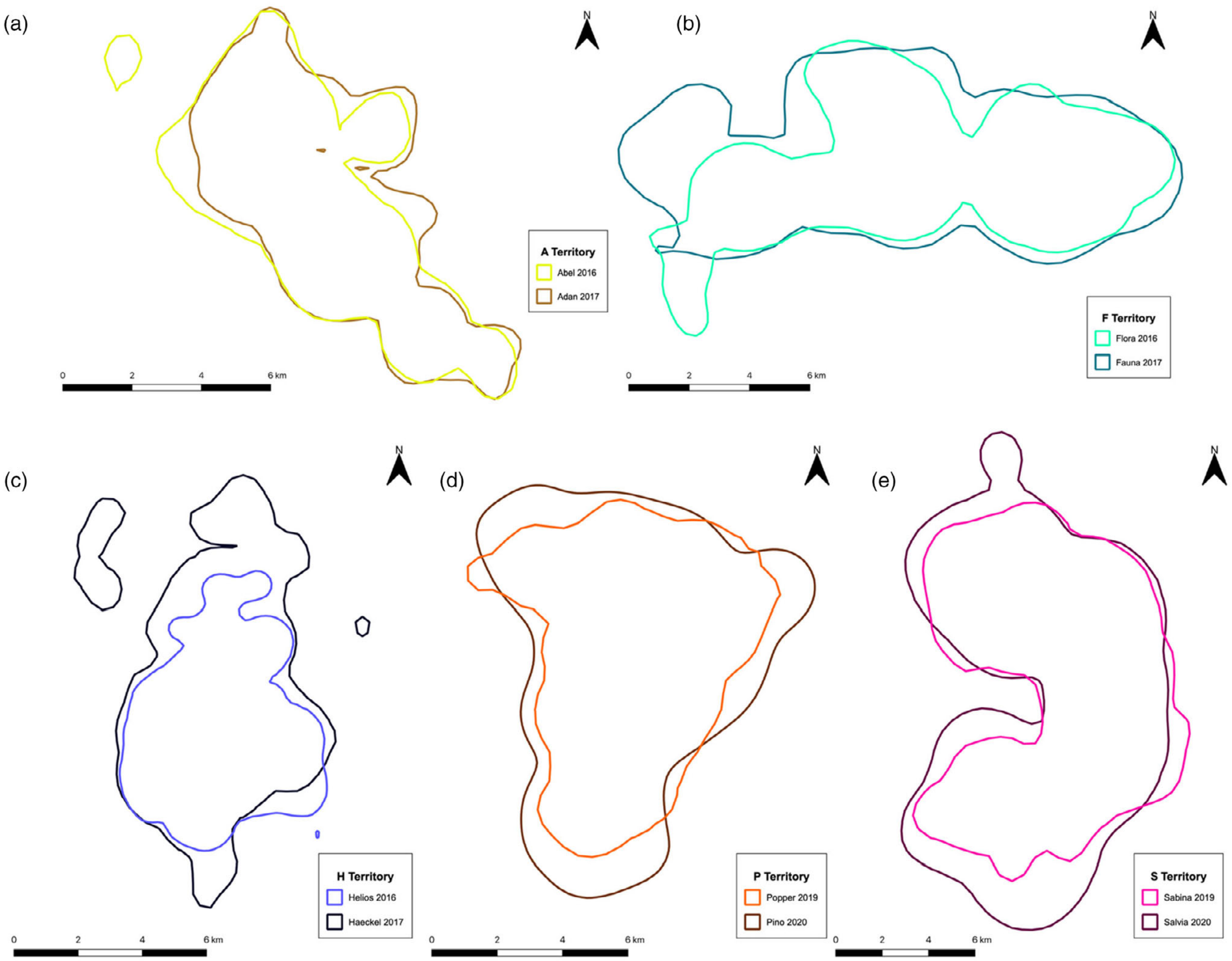

Figure 2 Comparison of annual territories (K95%) following a simple turnover event. (a) Turnover between A territorial males. (b) Turnover between F territorial females. (c) Turnover between H territorial males. (d) Turnover between P territorial males. (e) Turnover between S territorial females.

Our overlap analysis indicates that, in addition to their extension, the shape of the territories is also preserved. However, the maps (Fig. 1) reveal that the shape of the territories varies between neighbouring pair. Some territories were elongated, others were rounded, and some were more irregular. This variation likely due to the physiognomy of the terrain, and mantained distinct boundaries and shapes across individuals and over time.

In one instance of a double turnover in this study, a new pair took over the territory with a high degree of overlap (Fig. 3a; Table S4). In the second instance, a neighbouring pair occupied almost the entire new territory, except for the most distant parts, while maintaining the territorial boundaries (Fig. 3b; Tables S6, S8 and S25.). In essence, individuals that occupy vacant territories, whether they were a new or neighbouring pair, inhabit a pre-existing limited space its own boundaries and shape, rather than creating their own. Furthermore, in the rare instances where there are gaps between territories, no nests or pairs were found during the study. Conversely, individuals from the floating population were detected.

For single replacements, our findings indicate that the new member of the pair adjust the boundaries of its territory to match those of the previous occupant, as well as the other member of the pair (the non-substituted individual). It is important to note that the percentage of overlap between replaced individuals (85.54 ± 9.71%) is higher in most cases (9 out of 14 cases, almost 65%; Table 1) than the overall percentage of overlap (80.95 ± 5.58%; Table S2).

Until now, it was believed that territorial boundaries were maintained due to pressure from neighbouring pairs (Adams, 2001; Fryxell & Lundberg, 1997; López-Sepulcre & Kokko, 2005) and will disappear when the defending pair died. Among other factors, the constancy of the landscape and food resources also play a role. For instance, a forest fire forced golden eagles to move to neighbouring areas (Kochert et al., 1999), but it was demonstrated that Bonelli's eagles

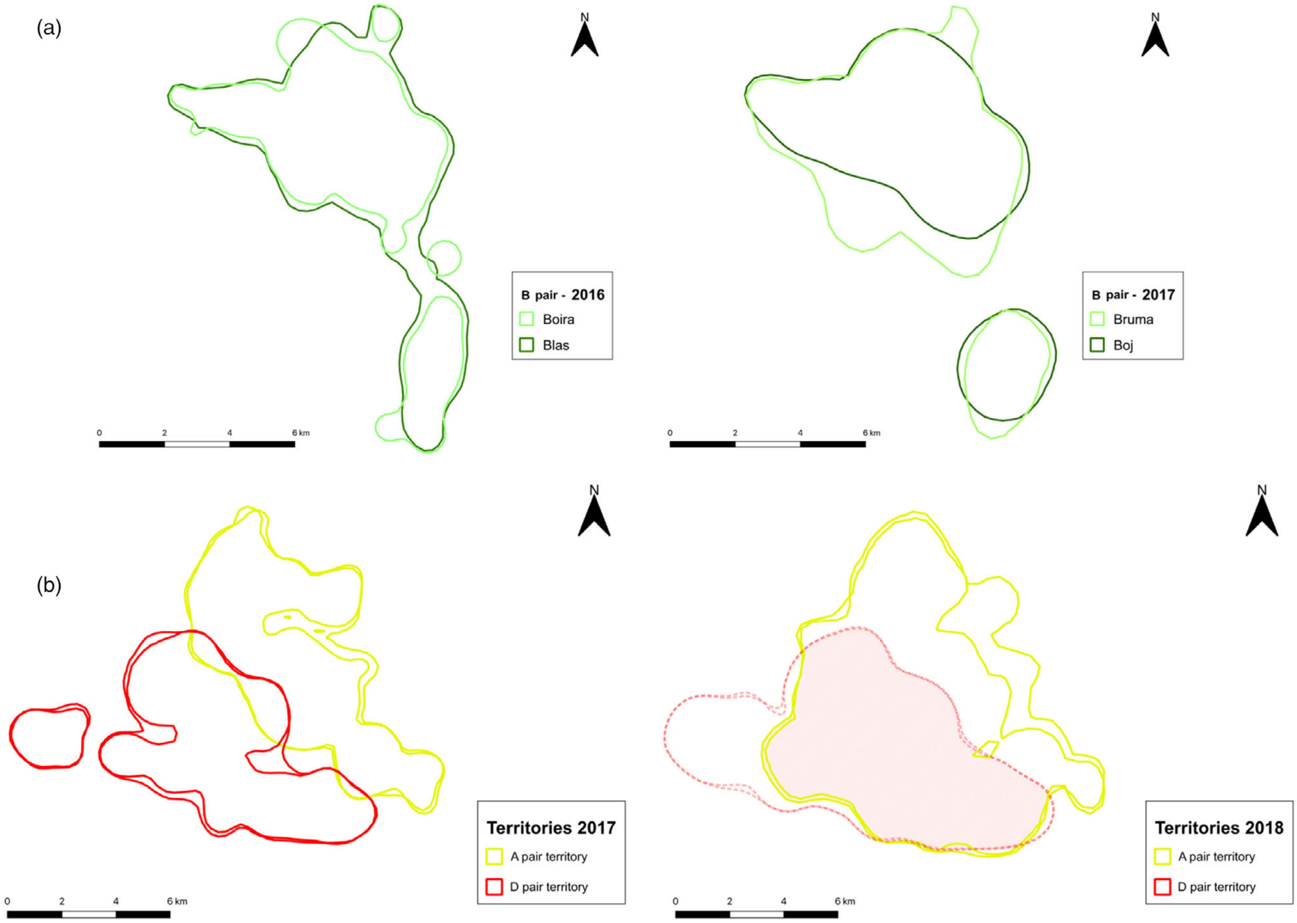

Figure 3 Comparison of annual territories (K95%) following a double turnover event. (a) Turnover between B territorial pairs. (b) Turnover between D territory (in red) and A territory (in yellow) in 2017 (top) and 2018 (bottom). In 2018, the D territory is represented by a dashed red line to remember where it was before.

were not affected by forest fires in the medium and long term (Morollón, Pausas, et al., 2022).

These pressures would alter the boundaries and shape of the territory, eventually leading to occupation by neighbouring pairs. Furthermore, the boundaries of the territories of the pair inhabiting the empty territory would also lose their shape. Several examples demonstrate that the territories are maintained even when they are empty, and new pairs that occupy the territories preserve the previous limits and shapes.

The evolution of territoriality in many strategies reflects the balance between benefit and cost (Ord, 2021). Species whose males use territories to monopolize access to females may incur higher costs than those that defend only food resources (Adams, 2001; Ord, 2021). However, Wilson (1975) argued that territories could change in time and space and may not be fixed spaces. Conversely, Brown (1975) and Kaufmann (1983) argued that territories are fixed spaces. We consider that the existence of stable territories, regardless of the individuals occupying them, may confer an evolutionary advantage. This advantage can be divided into two points: (1) territoriality increases population stability, and floating individuals form a buffer against fluctuations (López-Sepulcre & Kokko, 2005); (2) the age of the individuals and the quality of a territory (measured as reproductive success) are correlated (Ferrer & Bisson, 2003). Therefore, we observe a constant struggle within the floating population to occupy the best territories. This is usually achieved through agonistic replacement of a pair member or, in the case of a natural loss, by occupying the vacant territory as soon as possible (see also Penteriani et al., 2011, 2015). Our field observations indicate that replacement after a vacancy typically occurs within a few weeks. Throughout the study period, the formation of new territories by tracked animals was not recorded. The best specimens settle in the best territories, which are the ones that favour the continuity of the population.

To effectively protect sedentary raptors, such as Bonelli's eagles and other similar species, it is crucial to know the extent of their entire territory, not just their nest location. Our research shows that these territories have fixed boundaries that persist even when unoccupied and reused. This valuable insight into their spatial ecology can be extended to other raptors and can aid in designing protective measures. Protecting top predators like Bonelli's eagle also safeguards many other species, enhancing the value of this approach in protected area design. This perspective can optimize land protection by aligning protected areas with their functional, occupied regions, regardless of population fluctuations. Identifying and preserving these territories, regardless of their occupancy and condition, may streamline conservation efforts and facilitate species recovery.

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Author contributions

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

Conflict of interest

The authors declare that no conflict of interest exists.

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). The projects are: "Bonelli's eagle University of Alicante Spain" (project ID = 58923588), "Bonelli's eagle Alicante Spain" (ID = 430140799), "Bonelli's eagle University of Valencia Spain" (ID = 193515984) and "Movement ecology of large raptors in Spain" (ID = 640908212).

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Supporting Information

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

Table S1. Summary information of 51 Bonelli's eagles monitored by GPS/GSM telemetry in eastern Spain (period: 2015–2021).

Table S2. Territorial averages of the overlap percentages, standard deviation (SD) and number of annual territories (*n*).

Table S3. Inter-annual overlap percentages of territory A's individuals.

Table S4. Inter-annual overlap percentages of territory B's individuals.

Table S5. Inter-annual overlap percentages of territory C's individuals.

Table S6. Inter-annual overlap percentages of territory D's individuals.

Table S7. Inter-annual overlap percentages of territory E's individuals.

Table S8. Inter-annual overlap percentages of territory F's individuals.

Table S9. Inter-annual overlap percentages of territory G's individuals.

Table S10. Inter-annual overlap percentages of territory H's individuals.

Table S11. Inter-annual overlap percentages of territory I's individuals.

Table S12. Inter-annual overlap percentages of territory J's individuals.

Table S13. Inter-annual overlap percentages of territory K's individuals.

Table S14. Inter-annual overlap percentages of territory L's individuals.

Table S15. Inter-annual overlap percentages of territory M's individuals.

Table S16. Inter-annual overlap percentages of territory N's individuals.

Table S17. Inter-annual overlap percentages of territory O's individuals.

Table S18. Inter-annual overlap percentages of territory P's individuals.

Table S19. Inter-annual overlap percentages of territory R's individuals.

Table S20. Inter-annual overlap percentages of territory S's individuals.

Table S21. Inter-annual overlap percentages of territory T's individuals.

Table S22. Inter-annual overlap percentages of territory U's individuals.

Table S23. Inter-annual overlap percentages of territory V's individuals.

Table S24. Inter-annual overlap percentages of territory W's individuals.

Table S25. Overlap percentages of A territory (original territory) compared with the previous year (2017) before the death of D territorial pair (Dino and Dora) and overlap percentages of the new territory occupied (D) by the A territorial pair.