



Holidays? Not for all. Eagles have larger home ranges on holidays as a consequence of human disturbance



Arturo M. Perona^{a,*}, Vicente Urios^b, Pascual López-López^a

^a Cavanilles Institute of Biodiversity and Evolutionary Biology, Terrestrial Vertebrates Group, University of Valencia, C/Catedrático José Beltrán 2, E-46980 Paterna, Valencia, Spain

^b Vertebrates Zoology Research Group, CIBIO Research Institute, University of Alicante, Apdo. 99, E-03080 Alicante, Spain

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ABSTRACT

Human-wildlife conflicts are the object of raising concern in conservation biology. People living in urban areas are rapidly increasing worldwide and consequently the temporal pattern of occupation of natural areas for recreation is changing as well, resulting in an ever-increasing concentration of people during weekends and holidays. This is particularly evident in affluent societies, where more recreationists visit natural areas on holidays and weekends, causing disturbance to wildlife in the so-called “weekend effect”. Here, we tested the response to disturbance of 30 Bonelli's eagles tracked by high-frequency GPS/GSM telemetry. We analysed daily home-range size, a measure of changing behaviour that integrates their vital requirements, throughout the annual cycle, considering three different levels (95%, 75% and 50% kernel density estimators). Our results showed that eagles made a higher ranging effort on weekends and holidays throughout the annual cycle. This was particularly evident during the non-breeding period, when larger home-ranges were observed. Higher ranging effort can lead to conservation problems such as extra energy expenditure, hunting interference, and eventually nest and/or territory abandonment, decreasing eagles' fitness. Measures aimed at reducing human-wildlife conflicts including spatio-temporal limitation of leisure activities particularly during the most critical periods (i.e., incubation, chick rearing) are urgently needed. Finally, where possible, high quality information of animal movement should be incorporated into conservation plans in order to delineate efficient spatially-explicit management measures.

1. Introduction

Today, more than a half of the world's population lives in urban areas, and is expected to increase to nearly 70% in 2050 (United Nations, Department of Economic and Social Affairs, Population Division, 2018; <https://esa.un.org/unpd/wup/>). This implies a reduction in the amount of people living in rural areas (Seto et al., 2012), resulting in a change of landscape use from a source of primary productivity to a source of potential recreation (Paracchini et al., 2014). Currently, almost a third of world's protected areas are under intense human pressure, which is especially evident in Europe (Jones et al., 2018). The amount of outdoor recreational activities in protected areas is rapidly rising in recent years, reaching many billions of visitors per year in Europe and North America, an issue of conservation concern (Balmford et al., 2015; Tablado and Jenni, 2017).

Given the intensification of recreational activities, the amount of human-wildlife interactions is expected to increase and, hence, the

effects on vulnerable species as well (Balmford et al., 2015; Bennett et al., 2011; Knight and Gutzwiller, 1995; Monti et al., 2018; Spaul and Heath, 2016, 2017). Outdoor recreational activities can result in human disturbance in many ways, affecting habitat use, dispersal, distribution, population dynamics, changes in reproductive rates, or even survival (Holmes et al., 1993; Knight and Cole, 1991; Ruhlen et al., 2003; Tablado and Jenni, 2017). The impact of human disturbance to wildlife is of growing global conservation concern with examples across all vertebrate taxa (e.g., George and Crooks, 2006; González et al., 2006; Lusseau and Bejder, 2007; Monti et al., 2018; Richardson and Miller, 1997; Spaul and Heath, 2017).

Non-consumptive activities such as walking, hiking, climbing, bird-watching, cycling are among the most practiced by recreationists (Cordell et al., 2009; González et al., 2006; Knight and Gutzwiller, 1995; Steven et al., 2011). Moreover, disturbance caused by off-road motorized recreation is of important concern in natural areas (López-López et al., 2006; Spaul and Heath, 2016). For example, according to

* Corresponding author.

E-mail address: armarpe2@alumni.uv.es (A.M. Perona).

data published in the latest Europarc-Spain yearbook (EUROPARC-Spain, 2017), all protected natural areas in Spain received 23 million visitors in 2014, with increasing numbers since the previous report. In the particular case of the Valencian Community (where the study area is located), > 50 trail running races with an average of 450 participants/race were reported in 2015 (EUROPARC-Spain, 2017).

On the other hand, although decreasing in the latest decades, consumptive uses of wildlife such as hunting are still a cause of human disturbance on endangered birds (González et al., 2006) and mammals (Hertel et al., 2016; Paton et al., 2017). Both consumptive and non-consumptive activities have a direct response on wildlife, either causing flight or changes in habitat use, modulating physiological anti-predator response, inducing panic responses including self-injury or damage to mates, altering breeding site selection, causing interference in parental care, foraging behaviour and even temporal dynamics (i.e., nocturnality), among others (Gaynor et al., 2018; González et al., 2006; Knight and Cole, 1991; Ruhlen et al., 2003; Tablado and Jenni, 2017; Zuberogoitia et al., 2008). Although animals may be habituated to recreation in territories with regular human presence, the level of response varies with the intensity of recreationists' behaviour in association with animals' perception of potential danger. These include situations in which hunters and pedestrians disembark from motorized vehicles or birdwatchers who constantly stop and stare around (González et al., 2006; Spaul and Heath, 2017). Short-term responses to human disturbance may include avoidance, reduced breeding success and changes in feeding and breeding areas, which may also have long-term consequences such as habitat abandonment and eventually population decline (Blumstein, 2006; Lusseau and Bejder, 2007; Morant et al., 2018). Therefore, a better understanding of animal response to disturbance is of major interest in order to manage outdoor recreation and thus to achieve better conservation of threatened species, particularly in human populated areas.

The Bonelli's eagle (*Aquila fasciata*) is a long-lived resident raptor distributed across the Palearctic, Indo-Malayan and, marginally, the Afro-tropical regions (Ferguson-Lees and Christie, 2001). In the second half of the 20th century, the species declined drastically throughout its European range owing to habitat degradation, declining prey availability and unnatural elevated mortality, mainly due to direct persecution, including poaching and poisoning, but also electrocution on electric pylons (Real and Mañosa, 1997; Real et al., 2001; BirdLife International, 2018). The Iberian Peninsula is particularly important since it holds 80% of European population, with 733–768 pairs according to the latest survey conducted in 2005 (Del Moral, 2006). The species is legally listed as Vulnerable in Spain (Royal Decree 139/2011) and as Endangered according to IUCN national red list due to rapid decline in important areas of its breeding range (Real, 2004). Bonelli's eagles inhabit coastal regions and mid-altitude mountainous areas all over the Iberian Peninsula and, unlike other large eagles such as the Golden eagle (*Aquila chrysaetos*) or the Spanish Imperial eagle (*Aquila adalberti*), its range overlaps many urban areas across the Mediterranean region (Muñoz et al., 2005; López-López et al., 2006; Carrascal and Seoane, 2009a). As a consequence, the species is under high human pressure, which, in turn, can cause disturbance, breeding failure and ultimately death, with important consequences on population dynamics (Carrascal and Seoane, 2009b; López-López et al., 2007; Real et al., 2001). For this reason, the Bonelli's eagle can be considered as an adequate target species to study how potential human disturbance due to outdoor recreation activities could affect its ranging behaviour.

Many people living in cities take weekends and holidays as an opportunity to spend time in natural areas, resulting in an increase of outdoor recreation during these periods (i.e., weekend-effect) (Barrueto et al., 2014; Bautista et al., 2004; Lafferty, 2001; Longshore and Thompson, 2013; Rogala et al., 2011; Spaul and Heath, 2016, Stalmaster and Kaiser, 1998). Most of the studies about human disturbance and recreation have been focused on direct observable measures like flushing behaviour and how different types of recreation can

affect animals' response to human presence (e.g., González et al., 2006; Monti et al., 2018; Spaul and Heath, 2017). However, there is a lack of knowledge about how disturbance can affect animals' space use across the annual cycle. Here, our main goal is to evaluate the effects of weekends and holidays (i.e., considered as a proxy of increased human disturbance) on eagles' ranging behaviour throughout the annual cycle. If eagles' space use is not affected by outdoor activities, no differences in home-range size would be expected between holidays and weekdays (i.e., null hypothesis). In contrast, eagles may be forced to range more extensively due to higher human presence and thus home-range size should be higher during weekends and holidays (i.e., alternative hypothesis). To test these predictions, we used high-frequency telemetry data to quantify animals' home-range as an integrated measure of eagles' behaviour, reflecting spatial requirements for vital needs, including prey capture, roosting and breeding.

2. Material and methods

2.1. Study area

This study was conducted in eastern Spain, including Castellón and Valencia provinces. Breeding territories were located in Natura 2000 protected areas and their surroundings, encompassing Sierra de Espadán and Sierra Calderona Natural Parks (from 40°09'N to 39°36'N and from 0°44'W to 0°05'E). The area covers approximately 1600 km² from sea level to 1106 m above sea level. Climatologically, the area belongs to a Mediterranean climate with an annual average temperature varying from 17 °C in coastal areas to 8 °C in inner highlands. The dominant landscape includes different types of vegetation, mainly forest patches dominated by evergreen forests (*Pinus halepensis*, *Pinus nigra*), oak forests (*Quercus rotundifolia*, *Quercus suber*) and Mediterranean shrublands dominated by *Rosmarinus officinalis* and *Quercus coccifera*. The area also includes irrigated and non-irrigated agricultural lands, the former located in coastal areas and the latter in inner lands. With > 2.5 million people in the surrounding areas in 2017, the study area is a high-density populated area (Spanish National Institute of Statistics, www.ine.es). A more detailed description of the study area can be found in López-López et al. (2006, 2007).

2.2. Monitoring

A total of 30 territorial Bonelli's eagles, 16 males and 14 females, were trapped in 12 different territories by means of a folding net between 2015 and 2017, and equipped with 48 g solar-powered GPS/GSM dataloggers (e-obs GmbH, Munich, Germany). Both pair members, male and female, were trapped together except in territory #5 where only a single individual was tracked. When a mortality event happened during the study period, the new individual recruited in the territory was tagged. Transmitters' duty cycle was programmed to record one GPS location at five minute intervals, from 1 h before sunrise to 1 h after sunset, year-round. The weight of transmitters was 1.66–2.86% (average = 2.25%, sd = 0.38%) of eagle body mass, below the 3% threshold established to avoid negative effects on behaviour (Kenward, 2001). Tags were fixed in a backpack configuration using a teflon tubular harness designed to ensure that the harness would fall off at the end of the tag's life. Data were retrieved, stored and managed by means of the Movebank online repository (www.movebank.org).

2.3. Ethics statement

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

2.4. Home-range analysis

We computed home-ranges by means of kernel density estimation (KDE) methods (Worton, 1989) using the “reproducible home ranges” package (*rhr*) in R software for statistical computing (Signer and Balkenhol, 2015; R Core Team, 2018). We used the reference bandwidth “ h_{ref} ” as smoothing parameter for all individual home-range estimation (see e.g., Kie et al., 2010; Kie, 2013; Schuler et al., 2014). Although “ h_{ref} ” may be positively biased (i.e., it can include areas that are not part of an animal's home range), it performs better (i.e., closer match between estimated and true home ranges) with increasing sample size, so it is particularly recommended when sample size is large, as in our case (Kie, 2013). In addition, large eagles may explore extensive areas in short time intervals and hence using other smoothing parameters may lead to over-smoothing situations. We used different isopleths levels in order to assess multiple levels of space use and to allow comparison with similar studies. Kernel 50% isopleth (KDE50) was considered as the core area, including the nest and the most used area; kernel 95% isopleth (KDE95) was considered as the total home-range area (Samuel et al., 1985; Seaman and Powell, 1996); and we also computed 75% isopleth as a balanced area of active use, where individuals spend most of the time, including roosting and feeding areas (KDE75). A complete review can be found in Laver and Kelly (2008) and Kie et al. (2010).

We computed daily kernels for each bird and annotated them as weekdays (Monday–Friday) or weekend days (Saturday–Sunday) during the study period, which was established from the first capture on May 19th 2015 to 31st December 2017. We excluded the tagging day and the day after from analyses to be conservative with potential anomalous behaviour. We also defined holidays according to the Spanish calendar (Table S1). Then, we rearranged the annotated dataset of daily kernels to include weekends as part of “holidays”. In order to account for temporal variations in space use throughout the annual cycle, we considered two different status: “breeding” and “non-breeding”. Breeding status was defined using individuals' data combining fieldwork observations and detailed tracking information. If eagles initiated courtship and started reproduction but failed for whatever reason, we considered data before failure as “breeding” and as “non-breeding” afterwards. We considered an average span of incubation of 39 days from egg-laying and an average fledging date of 63 days after the hatching date (Cadahía et al., 2008). Taking into account that males hardly contribute to incubation (Real, 1991), and to avoid underestimation of home-range size, repeated locations of incubating females on the nest were excluded from the analysis.

2.5. Statistical analysis

We used Generalized Linear Mixed Models (GLMMs) (Zuur et al., 2009), to analyse variation in home-range size in relation to four fixed binary factors: “holidays”, “sex”, “age” and “status”. “Age” was determined by detailed plumage examination at capture, allowing differentiation between subadults (i.e., birds in their third and fourth calendar year) and adults (i.e., birds from fifth calendar year onwards). We considered “territory”, “individual” and “year” as random factors. “Individual” was nested into “territory” to account for the hierarchical structure (i.e., non-independence) of data (Harrison et al., 2018). Daily home-range sizes according to the three different spatial estimators (KDE50, KDE75, KDE95) were logarithmically transformed and were used as response variables. Overall, we built a unique model for each spatial estimator, pooling both breeding and non-breeding status together. The model included the four additive variables and their combined interactions. We used the package “lme4” (Bates et al., 2015) for the analysis.

We calculated the conditional and marginal R^2 following Nakagawa and Schielzeth (2013) in order to assess the relative contribution of each random and fixed factor by means of the R package

“piecewiseSEM” (Lefcheck, 2016). Statistical significance was set at $p < 0.05$. All computations were done in R version 3.5.1 (R Core Team, 2018).

Once we obtained the results of GLMMs, we checked whether variations in home range size between weekdays and weekends were statistically supported or just the outcome of a statistical artefact. Provided that days within weekends and weekdays could be intrinsically auto-correlated (i.e., the two days within a weekend are more similar than among different weekends), we randomized the variable “holidays” using a Monte Carlo simulation approach (Gotelli and Ellison, 2004). To this end, we randomized the binary values of the variable “holidays” keeping the original structure of data (i.e., conserving the same number of “weekdays” and “holidays” as in the real dataset) and then we reran the GLMMs with the variable “holidays” randomized. We repeated this analysis with 10 different set of randomizations of the variable “holidays” and analysed the effects with the three different spatial estimators (KDE50, KDE75, KDE95).

3. Results

Overall, 1.4 million GPS locations were used in this study. Individuals were tracked on average 347 ± 267 days (range = 3–957 days). The average number of tracking days (\pm SD) was 219 ± 160 and 107 ± 78 days for weekdays and holidays, respectively (Table 1). On average, 138 ± 24 GPS locations per day were used for computing daily kernels. During the study period, 10 eagles were found dead (three by electrocution at power lines, two drowned in irrigation ponds, and the other five by different causes, including shooting, natural disease, collision with power lines and one unknown) (Table 1).

Our results showed that home range size can be explained by the additive effects of “holidays”, “sex” and “status” as well as the interactions between “sex” and “status” and “sex” and “age” (Table 2). This was consistent for both larger spatial estimators (i.e., KDE95 and KDE75). However, “holidays” was not included as a significant predictor of home-range size at the smaller spatial estimator (i.e., KDE50; Table 2). Interestingly, “holidays” was not modulated by any other factor provided that interactions between “holidays” and other variables were not significant. The interaction between sex and age was not significant across the three different spatial estimators (Table 2). Results of $R^2_{conditional}$ corresponding to the effect of combined fixed and random factors were 0.26, 0.27 and 0.25 according to KDE95, KDE75 and KDE50, respectively. The variance explained by random factors (obtained as $R^2_{conditional} - R^2_{marginal}$) was 0.19 for both KDE95 and KDE75 levels, and 0.17 for KDE50.

Overall, home-range size was higher on holidays than weekdays, almost throughout the annual cycle, with lower differences observed in January, June and September. Larger differences in home-range size were found in autumn and winter months (Fig. 1). Although “holidays” was not included as a significant predictor of home range size for core areas (i.e., KDE50) ($p = 0.081$), eagles showed larger home-range size during holidays throughout the annual cycle for this spatial estimator (Fig. 1). Importantly, none of the 10 models with the variable “holidays” randomized showed a significant effect of the type of day on home-range size variation (Table S2).

During breeding, eagles showed an average daily home-range size on holidays of 34.22 ± 26.93 km², 13.53 ± 11.39 km² and 5.71 ± 5.11 km² according to KDE95, KDE75 and KDE50, respectively. By contrast, average values of home-range size on weekdays were 29.87 ± 23.65 km², 12.01 ± 10.29 km² and 5.14 ± 4.65 km² according to KDE95, KDE75 and KDE50.

During non-breeding, the average daily home-range size on holidays was 48.90 ± 34.92 km², 22.05 ± 16.85 km², and 10.10 ± 8.18 km² according to KDE95, KDE75 and KDE50, respectively. Average home-range size on weekdays was 45.80 ± 34.28 km², 20.54 ± 16.21 km², and 9.38 ± 7.77 km² according to KDE95, KDE75 and KDE50,

Table 1

Summary information of 30 territorial Bonelli's eagles tracked by GPS/GSM telemetry in eastern Spain during the period 2015–2017. Individuals that died during the study are indicated with an asterisk.

Individual	Pair	Sex	Age	Tagging date	No. locations	Weekdays	Holidays	Average locations/day ± sd
1*	1	Male	Adult	19/05/2015	70,860	322	150	149 ± 47
2	1	Female	Adult	19/05/2015	98,759	572	265	110 ± 72
3*	2	Male	Adult	10/06/2015	4173	259	125	158 ± 30
4*	2	Female	Adult	10/06/2015	60,836	18	7	164 ± 30
5	3	Male	Adult	28/10/2015	98,749	529	264	61 ± 30
6	3	Female	Adult	28/10/2015	69,371	336	167	141 ± 42
7	4	Male	Adult	29/10/2015	113,566	489	236	156 ± 26
8	4	Female	Adult	29/10/2015	122,536	504	246	158 ± 23
9*	2	Female	Subadult	06/11/2015	27,833	149	80	121 ± 50
10	5	Male	Adult	06/06/2016	84,064	385	187	147 ± 34
11	6	Male	Adult	08/06/2016	87,590	385	187	152 ± 28
12*	6	Female	Subadult	08/06/2016	26,785	131	59	141 ± 51
13	7	Male	Adult	07/10/2016	62,454	277	138	150 ± 28
14	7	Female	Subadult	07/10/2016	60,104	278	139	142 ± 36
15*	8	Male	Adult	06/10/2016	14,621	75	37	129 ± 20
16	8	Female	Adult	06/10/2016	63,516	274	139	151 ± 25
17*	9	Male	Adult	09/12/2016	4571	29	13	105 ± 34
18*	9	Female	Adult	09/12/2016	11,788	75	31	111 ± 42
19	1	Male	Subadult	31/01/2017	52,126	222	112	155 ± 24
20*	2	Male	subadult	11/04/2017	11,757	41	29	83 ± 15
21	2	Female	Subadult	11/04/2017	42,449	173	92	159 ± 30
22	8	Male	Subadult	20/04/2017	37,032	151	71	166 ± 23
23	6	Female	Subadult	18/05/2017	32,354	155	73	142 ± 52
24	10	Male	Adult	05/06/2017	30,712	143	67	141 ± 33
25*	11	Male	Subadult	06/06/2017	497	4	0	124 ± 54
26	11	Female	Adult	06/06/2017	32,834	142	67	141 ± 21
27	10	Female	Adult	14/06/2017	31,366	136	65	157 ± 29
28	12	Male	Adult	11/07/2017	26,859	117	57	146 ± 31
29	12	Female	Adult	11/07/2017	26,805	117	57	146 ± 28
30	11	Male	Subadult	13/09/2017	15,823	72	38	141 ± 21

Table 2

Generalized Linear Mixed Model (GLMMs) results of variation in home-range size using three different spatial estimators. Significant variables are highlighted in bold.

Dep. variable	Variable	Estimate	Std. error	t	χ ²	p-Value	
k95	Holidays	0.070	0.029	2.423	5.868	0.015	
	Sex	0.462	0.041	11.281	46.952	0.000	
	Status	0.474	0.025	18.639	341.472	0.000	
	Age	-0.208	0.055	-3.808	14.539	0.000	
	Holidays * sex	-0.018	0.019	-0.964	0.925	0.336	
	Holidays * status	-0.006	0.028	-0.208	0.043	0.835	
	Holidays * age	-0.018	0.024	-0.738	0.543	0.461	
	Sex * status	-0.416	0.029	-14.255	200.930	0.000	
	Status * age	0.112	0.040	2.778	7.935	0.005	
	Sex * age	0.088	0.064	1.383	1.881	0.170	
	k75	Holidays	0.064	0.031	2.086	4.352	0.037
		Sex	0.585	0.045	13.009	51.092	0.000
		Status	0.615	0.027	22.759	504.577	0.000
Age		-0.178	0.059	-3.021	9.127	0.003	
Holidays * sex		-0.022	0.020	-1.112	1.233	0.267	
Holidays * status		0.005	0.030	0.176	0.031	0.861	
Holidays * age		-0.024	0.026	-0.915	0.836	0.361	
Sex * status		-0.528	0.031	-17.032	285.457	0.000	
Status * age		0.089	0.043	2.075	4.481	0.034	
Sex * age		0.082	0.070	1.170	1.354	0.245	
k50		Holidays	0.060	0.035	1.746	3.051	0.081
		Sex	0.667	0.050	13.415	52.044	0.000
		Status	0.690	0.030	22.766	504.876	0.000
	Age	-0.201	0.066	-3.060	9.342	0.002	
	Holidays * sex	-0.028	0.022	-1.243	1.543	0.214	
	Holidays * status	0.018	0.034	0.538	0.288	0.591	
	Holidays * age	-0.040	0.029	-1.401	1.969	0.161	
	Sex * status	-0.598	0.035	-17.213	291.241	0.000	
	Status * age	0.135	0.048	2.815	8.143	0.004	
	Sex * age	0.039	0.078	0.501	0.211	0.646	

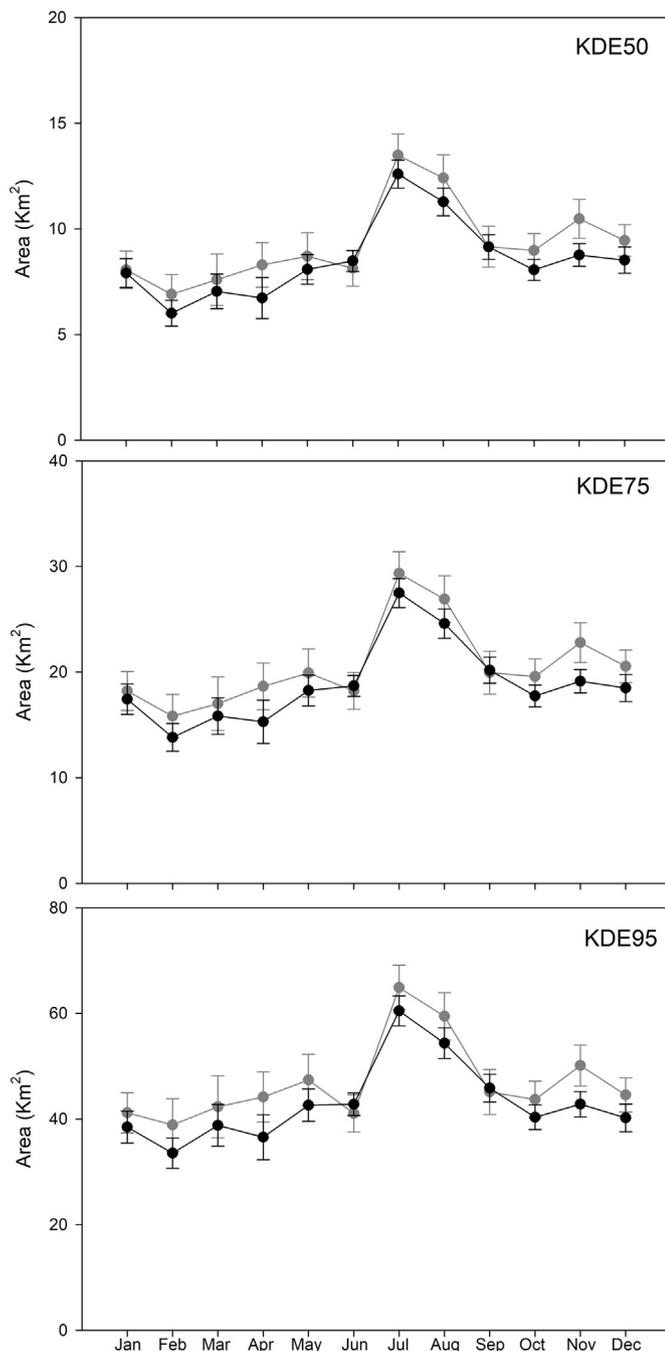


Fig. 1. Monthly average home-range size (km^2) for the whole annual cycle according to three isopleths levels (50%, 75% and 95%). Weekdays are represented with black lines and dots, and holidays are represented in grey. Error bars show 95% confidence intervals.

respectively. Some pairs, one in 2016 and four in 2017, failed to breed during the study period. Hence, for these individuals we considered home-range size from failure date in advance as non-breeding status.

4. Discussion

Improving our knowledge about the effects of human disturbance on animals' spatial ecology throughout the annual cycle is vital to understand underlying ecological processes which are very important to improve decision making for wildlife conservation. Although some papers were published about changes in habitat use and home-range due to human disturbance (e.g., Andersen et al., 1990; Coppes et al.,

2017; Longshore and Thompson, 2013; Martin et al., 2010), to the best of our knowledge, this is the first study that integrates high-frequency telemetry to test the effect of human disturbance on raptors' spatial ecology.

Overall, our results showed that eagles had larger home-ranges during holidays and weekends throughout the annual cycle, considering the two larger spatial estimators (KDE95 and KDE75). Eagles travelled longer distances on these days and thus, spent more time away from their nest and core areas. On the contrary, differences in home-range size were not statistically significant for the smaller spatial estimator (KDE50). This is expected since KDE50 represents the core area surrounding the nest, where eagles show strong site fidelity, particularly during the breeding season (Bosch et al., 2010). Behavioural changes in space-use during holidays are of conservation concern especially taking into account the environmental context. Bonelli's eagles' territories in our study area are under high human pressure. Core areas in the study area are under protection regulations including Natural Parks, Natura 2000 network and Important Bird Areas. Notwithstanding, eagles usually left protected areas to perform most of their main activities such as roosting or hunting. Out of protected areas, animals are more threatened by the concurrence of a substantial human infrastructure in highly populated areas (Tucker et al., 2018). During weekends and holidays, with eagles covering larger home-ranges, the probability of contact with human threats is thus higher. The protected areas in our study area (i.e., Sierra de Espadán and Sierra Calderona Natural Parks) are surrounded by an extended network of human infrastructure, including an extensive network of power lines and roads. Interaction with power lines, as collision with wires and especially electrocution, is considered the main cause of mortality in this species, accounting for > 50% mortality cases (Chevallier et al., 2015; Guil et al., 2015; Rollan et al., 2010). In fact, four eagles in this study were found dead resulting from interactions with power lines, three electrocutions and one collision, all of them out of protected areas. These results are similar to those obtained by Pérez-García et al. (2011) in the same region, who found that the majority of electrocution events take place out of protected areas (82% versus 18% of raptor casualties recorded outside and inside Special Protected Areas, respectively; $N = 323$).

Leisure activities can cause disturbance on wildlife in many ways, including anti-predatory responses such as fleeing or flushing (Blumstein, 2006; Bötsch et al., 2018; Spaul and Heath, 2017), which have consequences in behavioural patterns, altered energy expenditure, and even avoidance of nesting, roosting and hunting areas (Tablado and Jenni, 2017). Wildlife responses can cause more conflicts with human infrastructure, particularly increasing risk of vehicle collisions (Coppes et al., 2017; Lima et al., 2015), power outages and even fires as a consequence of bird electrocution (Dwyer et al., 2014). Human activities can also cause physical alteration to landscapes, decreasing habitat quality (Bautista et al., 2004; Fernández-Juricic et al., 2005; Lambertucci et al., 2009). Although these effects can lead to long-term changes in behavioural patterns, the fact that eagles change their behaviour only in days with high human activity, evidences that the mere presence of humans within eagles' territories is enough to cause disturbance. Furthermore, single disturbance events, occurring during particularly important periods, such as territory formation or nest settling, may lead to short-term changes in habitat use and can eventually cause breeding failure (Tablado and Jenni, 2017).

It is important to take into account that human disturbance may differ depending on timing, frequency and environmental characteristics. The degree of disturbance could be enhanced if animals fail to find alternative foraging areas, thereby reducing their fitness. Furthermore, animals with no alternative suitable habitats may be less willing to abandon their territories (Gill et al., 2001), which is especially important to territorial raptors with limited nest availability and foraging niches (Spaul and Heath, 2016). This is particularly important in our study area, which is highly covered by dense pine forests, especially in inner areas far from the coastland, where eagles have

limited access to hunting habitats.

Frequent disturbances across the annual cycle could negatively affect birds from reaching the optimal physical egg-laying condition in the months previous to the breeding period (Madsen, 1995), and disturbances over the first stages of breeding season can decrease laying and hatching success (González et al., 2006; Spaul and Heath, 2016). Additionally, although difficult to take into account and measure, animal personality is an aspect to keep in mind, as not all individuals react in the same way to the same stimuli and thus animals exhibit different levels of tolerance and habituation to human presence (Blumstein, 2006; Bötsch et al., 2018; Fernández-Juricic et al., 2001, 2005). In our case, we included the variable “individual” as a random factor to account for the potential effects of individuals' personality on spatial behaviour. According to our results, random factors (i.e., territory, individual and year) explained 19% (KDE95 and KDE75) and 17% (KDE50) of the variance of the models. Most of this variation could be attributed to small differences in individuals' behaviour in the same territory after a turnover due to death of the previous owner (seven cases recorded throughout the study period).

On the other hand, hunting activities may lead to relocation of birds, increasing flushing distances and interference in roosting and foraging (Väänänen, 2001). In our study area, eagles' non-breeding season concurs with the game hunting season. In addition, hunting activities usually happen on weekends. According to González et al. (2006), hunters have the highest probability to cause flight reaction since they usually remain in an eagles' territory for some time, accompanied by dogs, stopping frequently, changing their walking direction, leaving paths and importantly, looking at the sky. Moreover, hunters are associated with motorized vehicles and this mixed behaviour of motorized vehicles and pedestrian activity has the highest probability to cause fleeing (Spaul and Heath, 2016, 2017). Furthermore, persecution is still a serious threat to eagles. Although the mortality rate by shooting seems to be decreasing in our study area (Martínez-Abraín et al., 2009), the single shot eagle found dead in our study was shot on a weekend.

Finally, Bonelli's eagles' annual cycle is complex, and home-ranges change constantly throughout the year and among individuals, depending on environmental conditions, prey availability and competition (Martínez-Miranzo et al., 2016; Real et al., 2016). Differences in space use on weekends can be explained as a consequence of eagles' avoidance of places intensively used by humans only when the pressure is intensive. In fact, there is no other factor changing between weekdays and holidays. In weekdays, corresponding with less human pressure in the territories, eagles behave differently, which is in agreement with other studies that suggest human avoidance and changes in behavioural patterns on weekends (Gaynor et al., 2018; Longshore and Thompson, 2013; Nix et al., 2018).

4.1. Management implications and concluding remarks

Studies focusing on human-wildlife interactions are important to inform management strategies, since outdoor recreation in natural areas is rapidly increasing (Balmford et al., 2015), causing disturbance to wildlife, that can lead to important conservation problems. Wildlife are bound to overlap their home-ranges with human activities, so management plans to promote coexistence and wildlife conservation are needed (Kazmierow et al., 2000; Kelly et al., 2004; Martin et al., 2010). To deal with disturbance by recreation appropriately, it is necessary to take into account time-space variables, in addition to habitat characteristics and, to a lesser extent, individuals' personalities. Therefore, measures aimed at reducing the number of human-wildlife conflicts should include spatio-temporal limitation of leisure activities, particularly during the most critical periods. Nest abandonment during critical stages of the breeding season (i.e., egg laying or when nestlings have limited thermoregulation capacity) has very negative consequences owing to temperature loss, which can lead to hatching

failure, or higher probability of nestling predation, decreasing productivity (González et al., 2006; Tablado and Jenni, 2017). Measures aimed at establishing buffer zones (Fernández-Juricic et al., 2001), trail regulations (D'Acunto et al., 2018), and non-stopping zones around critical points (Spaul and Heath, 2017) are thus encouraged. Given the latest advances in individual tracking technologies, where possible, we highly recommend incorporating high quality telemetry information of animal movement into conservation decision making. This will allow delineating efficient spatially-explicit management measures, taking into account the actual space use of individuals, instead of using buffer areas of arbitrary radii around nest sites or critical areas to limit human activities.

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