Experimental food subsidies keep eagles inside protected areas: implications for conservation and resource management

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1. Introduction

Conservation and management of mobile species poses significant challenges, as they range over vast areas making it difficult to prioritize area-based protection. These species face a variety of threats throughout their life cycle, such as barriers, conflicts, persecution, poisoning, and loss of habitats (Singh and Milner-Gulland, 2011; Augé et al., 2014; Allen and Singh, 2016). Thus, obtaining data on their demographic parameters, habitat utilization, and behaviour is vital for evaluating their population viability (Caughley, 1994; Pakazhenthi et al., 2005).

In recent decades, birds of prey have experienced one of the most severe population declines among all animal groups for various reasons (McClure et al., 2018; Buechley et al., 2019). Habitat degradation, direct persecution, poisoning, wind turbine collisions, electrocution on power lines, and collisions with man-made infrastructures are among the most common causes of mortality among birds of prey worldwide (e.g., Morkill and Anderson, 1991; Anderson et al., 1999; Carrete et al., 2009; Garvin et al., 2011; Hille and Collar, 2011; Quinn, 2011; Dixon et al., 2013; Brochet et al., 2019). Moreover, their status as top and mesopredators in ecosystems makes them particularly vulnerable to changes in other trophic levels (McClure et al., 2018).

A number of conservation measures have been adopted around the world to protect raptors, and these include better protection of nesting areas, reducing persecution, collisions with infrastructure, banning of certain environmental contaminants such as DDT and lead, and establishment of protected areas (PAs). PAs are a key conservation tool aimed at preserving native species and their habitats (Rojas, 1992; Bertzky et al., 2012; Le Saout et al., 2013; Geldmann et al., 2013). However, highly mobile raptors may range over much larger areas outside PAs for foraging, resting, wintering and fulfilling other basic needs (Phipps et al., 2013; Di Franco et al., 2018; De Alban et al., 2021). Therefore, the effectiveness of PAs in conserving raptors may be questionable (Loucks...
et al., 2008; Joppa and Pfaff, 2009; Baldi et al., 2017; Chacón-Prieto et al., 2021), as the likelihood of mortality outside PAs may be multiple folds higher (Devictor et al., 2007). An alternative to increasing the attractiveness of PAs for raptors could be through improved foraging opportunities. Supplementary feeding, hereafter feeding, has been used as a management measure to divert certain target animal species from risk zones or attract to contain them in certain areas by increasing the attractiveness through creating better foraging opportunities (Anderssen et al., 2005; Ewen et al., 2015; Thierry et al., 2020).

Artificially providing more food in certain areas has been shown to have positive effects on survival and reproduction in mammals and birds (Boutin, 1990; Elliott et al., 2001; Rea, 2003; González et al., 2006; Armstrong et al., 2007; Siriwardena et al., 2007; Ferrer et al., 2013; Pearson and Husby, 2021; Marinković et al., 2021). It has also been shown to increase the efficiency of territory use and reducing the home range size (Gilbert et al., 2007; López-López et al., 2014; Genoro et al., 2020; Arkumarev et al., 2021; Penteriani et al., 2021), which may favour the management of some of these species. Nonetheless, not all species or individuals may react to food in the same way (Siriwardena et al., 2008; Kovalczyk et al., 2011; Steyaert et al., 2014; Todorov et al., 2020). On the other hand, there are demonstrated risks of the use of feeding in the long term. Excessive spatio-temporal predictability of feeding may result in an ecological trap for the populations dependent on such feeding (Ewen et al., 2011). The attraction of many individuals in supplementary feeding stations (SFS) may facilitate the spread of diseases and parasites (Putman and Staines, 2004; Sorensen et al., 2014; Becker et al., 2015; Murray et al., 2016; Blanco and Díaz de Tuesta, 2021), increase direct and indirect intraspecific competition due to density-dependency effects (Carrete et al., 2006) and increase the risk of predation (Cortés-Avizanda et al., 2009; Pearson and Husby, 2021). Similarly, artificial feeding leads to imbalances in the food web that may have a negative impact on the target species or other species in ecosystems (Cortés-Avizanda et al., 2010). Notwithstanding, most studies highlight the positive effect of this technique when used for scientific and conservation purposes (Oro et al., 2008), but others recommend its utilization at specific times and places, intermittently (Murray et al., 2016). Aiming for the best management solutions, several studies support that improving the natural availability of food in ecosystems is the measure that has shown better results and could be more feasible to maintain in the long term (Villanueva, 1996; Siriwardena et al., 2008; Cortés-Avizanda et al., 2010; Angerbjörn et al., 2013; Zikmund et al., 2021).

Spain is a stronghold of large birds of prey in Europe, and raptors have benefited from protection in National and Natural Parks (Del Moral and Molina, 2018). Originally established to preserve scenic landscapes, the creation of these PAs sometimes had more aesthetic than wildlife-oriented motives (Watson et al., 2014; Dietz et al., 2020). While the nesting areas are included within PAs, birds must leave them often to find food outside, exposing them to highly human modified landscapes where the probability of mortality is much higher from collisions with powerlines, electrocution and persecution (Sergio et al., 2005), among other causes. Likewise, conservation efforts have already been implemented to maintain raptors within PAs by employing measures like supplementary feeding or habitat management (e.g., Moreno and Villafuerte, 1995). Nevertheless, continuous monitoring of the feeding behaviour and demographics of birds are necessary to assess the positive effects and long-term viability of such measures.

We conducted an experiment in a PA in eastern Spain, which is known to be a stronghold for Bonelli’s eagles. The study aimed to evaluate the effects of feeding on the eagles’ space use and demographic

Fig. 1. Location of the study area in eastern Spain (right), comprising the Sierra de Espadan Natural Park (dark red) and the Special Conservation Area for Birds (yellow), presented alongside a map of Spain (left) and the Castellón province (grey). Supplementary feeding stations (SFS) utilized during the study are indicated as black dots on the map. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
parameters. The study was conducted for two years (2018 and 2019) and involved GPS-tagged individuals, which were monitored during experimental feeding sessions and non-feeding days. The primary objective was to assess if increased food availability within PAs would lead to reduced space use outside the protected area. Additionally, the study aimed to: (i) determine if space use decreased on days when supplementary feed was available; (ii) evaluate the habitats used inside and outside the PAs; (iii) determine if riskier habitats (i.e., those including powerlines) and suburban areas were used when food was not provided; and (iv) make management recommendations for conservation purposes.

2. Materials and methods

2.1. Study area

This study was carried out in the province of Castellón in eastern Spain and was focused around the Sierra de Espadán Natural Park (NP) and its Special Conservation Area for Birds. This conservation area is part of the Natura 2000 network (N2000) and can be identified by the code ES0000468 (Fig. 1). The N2000 area encompasses an area of about 653 km$^2$, stretching from the sea level up to 1106 m. The NP itself is located within the N2000 network and comprises an area of 312 km$^2$. Climatologically, the area belongs to a Mediterranean climate with an annual average temperature varying from 17 $^\circ$C in coastal areas to 8 $^\circ$C in inner highlands. The vegetation comprises of coniferous forests (Pinus spp.), broad-leaved forests (Quercus spp.) and Mediterranean low shrublands with Salvia rosmarinus, Thymus spp. and transitional shrublands dominated by Quercus coccifera. The area also includes irrigated and non-irrigated agricultural lands, as long as old abandoned agricultural lands. Red-legged partridges (Alectoris rufa), common wood pigeons (Columbia palumbus), wild and urban rock doves (Columbia spp.), rabbits (Oryctolagus cuniculus), hares (Lepus granatensis) and ocellated lizards (Timon spp.) inhabit the area as potential prey for the Bonelli’s eagle. A more detailed description of the study area can be found in López-López et al. (2006, 2007a) and Perona et al. (2019).

2.2. Study species

The Bonelli’s eagle is a long-lived bird of prey and a top predator of the Mediterranean ecosystems (Cramp, 1980; Ontiveros, 2016). It is considered “Least concern” in Europe (“BirdLife International”, 2023), “Vulnerable” in Spain (Real Decreto, 139/2011) and “Endangered” in the Valencian Region (DOGV ORDEN 2/2022). Its overall population has decreased in the Iberian Peninsula in recent years (Del Moral and Molina, 2018). The causes of this decrease include the decline of prey availability and a high unnatural mortality, especially in adults mainly due to electrocution, collision with power lines, drowning in irrigation ponds and direct persecution (BirdLife International, 2023; Morollon et al., 2022a, 2022b; López-López et al. unpublished data).

The species hunts preferably in open areas for pigeons, rabbits and red-legged partridges (Martínez et al., 2014). Nonetheless, dietary studies shown that Bonelli’s eagles’ diet is broad as they feed on mammals, birds and reptiles (Moleon et al., 2009; Ontiveros, 2016).

The Bonelli’s eagle is considered a priority species for conservation according to the Spanish and the Valencian regional Government. As a consequence, a number of PAs included in the N2000 network were designated to protect this species (López-López et al., 2007b). In the particular case of the Valencian Community, 82 % of the breeding pairs place their nests inside N2000 PAs (authors unpublished information).

2.3. Trapping and tagging

A total of 10 territorial Bonelli’s eagles from 6 different territories, 5
males and 5 females, were trapped by means of a folding net between 2015 and 2017 and equipped with 48 g solar-powered GPS/GSM data-loggers (e-obs GmbH, Munich, Germany). Both members of the pair were captured and tracked in territories 2, 3, 5 and 6 (Fig.X). We only captured and tracked a male of territory 1 and a female of the territory 4. The pair from territory 6 was killed after start of the experiment. The male was found illegally poisoned as consequence of the conflict with the local pigeons’ fanciers. Transmitters’ duty cycle was programmed to record one GPS location at five minutes intervals, from 1 h before sunrise to 1 h after sunset, year-round (see details in Perona et al., 2019; Morollón et al., 2022a, 2022b, 2022c). The weight of transmitters was 1.6–2.4 % of eagles’ body mass which is within the recommended limits to avoid negative effects on behaviour (Bodey et al., 2018; Kenward, 2000). 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 (Kays et al., 2022).

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

2.4. Before-After Control-Impact (BACI) experiment

Following a Before-After Control-Impact (BACI) study design (Smith et al., 1993; Jooedsson et al., 2020) our study period spanned from 2016 to 2021. We included data of the two years before (2016 and 2017), during (2018 and 2019), and after the experiment (2020 and 2021). SFS were established within the core area of greatest use (kernel 50 %) in the six territories of Bonelli’s eagle within the Sierra de Espadán N2000 (Fig. 1) in places close to the usual nests (mean ± sd from the used nest to the SFS = 776 ± 781 m; range = 229–2238 m), visibly accessible to the eagles, easily accessible to the workers of the Sierra de Espadan Natural Park and not frequented by hikers. Kernels were computed using kernel density estimation in the “adehabitatHR” R package (version 0.4.19) (Calenge, 2006). Feeding was conducted in elevated places where artificial wood platforms were installed as perches, avoiding carnivores and carrion-eating mammals (González et al., 2006). In each platform we installed camera traps to record the visit of eagles and other sporadic wildlife. Cameras (model Moultrie M-999i) were set 1 m away from the platform. To bait eagles, we firstly used domestic sanitized pigeons provided by the “El Saler” Wildlife Recovery Centre (Valencia). When eagles got used to the SFS, we fed them with eviscerated rabbits acquired from a local butcher shop. All the territories were fed twice per week from March until June in 2018, and from November 2018 until May 2019, including two breeding seasons.

We compared the metrics recorded during the experiment divided as the days that we had supplied food (“Impact”) and on the days that we did not (“Control”) and we assigned the same calendar days as “fed” or “not fed” during the previous (“Before”) and the next (“After”) two years, with the aim of controlling that the differences between the presence and absence of extra-food did not appear during the years we did not supply food.

2.5. Statistical analysis

Similar to Singh et al. (2021), we fitted binomial generalized mixed-effects models with the eagles’ location relative to PAs (inside/outside) as response variable and the feeding supplementation of the day (fed/not fed) as predictor. Eagles’ identification was used as a random factor accounting for the individual variation of the response to the treatment.

We fitted the models for the NP and the N2000, separately.

Secondly, we analysed habitat use by means of the landscape classes...
Fig. 4. Predicted probability of Bonelli’s eagle GPS locations inside of the Natural Park (NP, below) and Special Area of Conservation (N2000) “Before”, “During” and “After” the experiment on days without supplementary feeding (red dots) and on days with supplementary feeding (yellow dots). Bars show 95 % confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
3. Results

We conducted the feeding experiment in 2018–2019, where feeding was carried out on 77 days. Overall, we obtained a total of 1,808,450 GPS locations of eagles. Out of these, 732,581 locations were recorded before the feeding experiment (in 2016–2017), 759,394 during (in 2018–2019; Fig. 2), and 316,475 after feeding (2020–2021).

We found that eagles locations were more probable of being inside of both the PAs in the days when they were fed (Fig. 3, Natural Park: ΔAIC = 478.95, estimate = 0.038, R² = 0.289, p < 0.001; N2000: ΔAIC = 2491.58, estimate = 0.087, R² = 0.259, p < 0.001). This result was consistent for both sexes and between years (Supplementary Material Fig. S1).

The best model (Natural Park: ΔAIC = 1033.10; N2000: ΔAIC = 915,564.70) that predicted probability of locations inside of the PAs was the one including “period” (Before/During/After) and feeding (or Not) and their interaction as the best predictors (Fig. 4).

We fitted binomial generalized mixed-effects models using the “lme4” package for R (version 1.1.30) (Bates et al., 2014). An information-theoretical approach based on Akaike’s Information Criterion (AIC) was then used for model selection (Anderson and Burnham, 2002), selecting models with a ΔAIC ≤ 2 units as the best models. ΔAIC between the best model and the second best model was expressed in absolute value in results. All analyses were conducted in R statistical software (version 4.2.1) (R Core Team, 2023).

4. Discussion

This study represents a robust evaluation of a conservation and management intervention implemented at the ground level for a free-ranging and highly mobile species. Frequently, management interventions are implemented within PAs, yet evaluations of their effectiveness are infrequent. Therefore, this study provides a strong foundation to assess such interventions aimed at reducing anthropogenic conflicts and promoting population recovery, as well as to evaluate the efficacy of PAs. This is often debated in scientific and conservation literature (Rojas, 1992; Naughton-Treves et al., 2005; López-López et al., 2007b; Goldmann et al., 2013; Le Saout et al., 2013;
The Bonelli’s eagle has been breeding for decades in our study area. Nonetheless, breeding performance was not the highest in the region (López-López et al., 2007a) and adult mortality is unnaturally higher than in other regions (Real et al., 2001; Hernandez-Matias et al., 2015). In fact, mortality outside PAs is larger than inside them as recorded by GPS telemetry (authors’ unpublished data). In our study area, despite the presence of breeding platforms and core home range areas being mostly inside PAs (Morollón et al., 2022b), Bonelli’s eagle, as other predators (e.g., Margalida et al., 2016), must go outside of these limits to obtain food. Increasing the availability of prey may be a key aspect to allow the conservation of top predators such as the Bonelli’s and the Golden eagle (Aquila chrysaetos), present in the area, as well as facilitating the presence and attraction of other protected species such as the Spanish imperial eagle (Aquila adalberti), the Iberian wolf (Canis lupus signatus) and the Iberian lynx (Lynx pardinus), a group of species that are increasing their breeding range in the Iberian Peninsula (López-Bao et al., 2018; Morandini et al., 2020; Ministerio para la Transición Ecológica y el Reto Demográfico e Instituto de Conservación da Natureza e das Florestas (ICNF), 2022).

The use of feeding as a management tool demonstrates how increasing food availability within PAs makes it easier for target species to stay inside protection zones. Our results show that we were successful for both sexes and the years with feeding. Our results are consistent with previous studies in which mammals and birds reduce and change their movements when they had received feeding. Nonetheless, feeding has negative effects too. The reduction in movement as consequence of feeding has the potential to cause habituation in animals. This phenomenon can have either positive (more control in management) or negative impacts (wildlife human-dependent) on populations depending on the circumstances (Elliott et al., 2001; González et al., 2006; Marínkovíc et al., 2021). In addition, negative effects such as reduced productivity have been documented (Carrete et al., 2006). Furthermore, not all species and individuals respond positively to feeding (Kowalczyk et al., 2011; Steyaert et al., 2014; Todorov et al., 2020), and these points need to be considered when planning feeding as a long-term management tool.

Outside of PAs, Bonelli’s eagles showed a higher preference for habitat types that are favorable for hunting, such as sclerophyllous vegetation. This highlights the importance of using food supplementation as a management tool to retain eagles within PAs. Eagles spending more time outside of PAs are exposed to higher risks. In general, eagles predominantly used sclerophyllous vegetation, which provides an open and suitable habitat for hunting (Ontiveros et al., 2005; Real et al., 2016), and coniferous forests, where they rest for long periods. Burnt areas were also used within PAs, as after wildfires, vegetation communities change and grasslands become more prevalent, providing more food sources for partridges and pigeons (Morollón et al., 2022c). Additionally, eagles used transitional woodland-shrub habitat, an open habitat that is preferred by rabbits (Ontiveros et al., 2005). Outside of PAs, eagles spent more time in scattered woody vegetation areas, particularly males during days without feeding. Furthermore, eagles that do not share SFS can reduce the risk of spreading diseases and parasites (Putman and Staines, 2004; Sorensen et al., 2014; Becker et al., 2015; Murray et al., 2016; Blanco and Díaz de Tuesta, 2021), as well as the risk of intraspecific aggression (Carrete et al., 2006; Cortés-Avizanda et al., 2009; Pearson and Husby, 2021).

4.1. Synthesis and conservation applications

We started the experiment with the hypothesis that an increase in local food availability would retain the eagles within the PAs, and our results successfully confirm this assumption. However, the long-term use of artificial feeding may have negative consequences (Villanueva, 1996; Cortés-Avizanda et al., 2010; Belotti et al., 2014). Therefore, the future goal should be to enhance the occurrence, abundance, and...
availability of local prey. Improving shrublands, pastures, and creating water refuges and traditional agricultural practices can help increase rabbit, partridge, and pigeon populations, the main prey for eagles (Moreno and Villafuerte, 1995; Lombardi et al., 2003; Palma et al., 2006; Delibes-Mateos et al., 2009). Such an increase in food availability would also benefit other sympatric species such as the golden and the Spanish Imperial eagles and would ultimately increase the effectiveness in terms of species’ conservation within PAs in the long-term (Azmanis et al., 2009; Ferrer et al., 2013, 2018).

Credit authorship contribution statement

Study conception and design: P.L.L., V.U.; data collection: P.L.L.; data analysis: A.L.P., N.S; interpretation of results: A.L.P., N.S., P.L.L.; graph design and elaboration: A.L.P., N.S.; draft manuscript preparation: A.L.P. All authors reviewed the results and approved the final version of the manuscript.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data used in this study are publicly available in the online data repository Movebank (www.movebank.org), project ‘Bonelli’s Eagle University of Alicante Spain’ (project ID = 58923588), and project ‘Bonelli’s Eagle University of Valencia Spain’ (project ID = 193515984).

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