Protected areas enter a new era of uncertain challenges: extinction of a non-exigent falcon in Doñana National Park

F. Sergio, J. Blas, A. Tanferna & F. Hiraldo

Department of Conservation Biology, Estación Biológica de Doñana – CSIC, Seville, Spain

Abstract

Protected areas are supposed to maintain viable populations of plant and animal taxa and shield them from anthropogenic threats, but this role is increasingly under scrutiny. Here, we document the alarming extinction of a small falcon, the Eurasian hobby Falco subbuteo, in Doñana National Park, an iconic protected area renowned for its rich predator community. Hobbies were originally abundant at 50–60 pairs and acted as unique specialist hunters of swifts and dragonflies. This diet implies a unique niche within the raptor assemblage and frequent ranging over agricultural areas surrounding the park. The high density of other raptors likely constrained habitat availability. Predation was the main cause of breeding failure, and hatching and breeding success were always low, especially in drought years, and declined progressively through time. The extinction occurred rapidly after 2000 with several clues suggesting the synergistic contribution of prey depletion, farmland intensification, chemical contamination, predation and climate warming. Lack of detailed monitoring prevented a clear assessment of the relative role of these factors, but most of them seemed traceable to farming practices and climate change, i.e. large-scale drivers generated outside the Park. The documented extinction is alarming because this species is not particularly exigent, it may imply widespread declines of other species, and because this loss adds to the imminent local extinction of another raptor with profoundly different requirements, suggesting mounting, broad-level pressures affecting the whole ecosystem. This unforeseen, rapid extinction in a Park that dedicates much effort to raptor management offers unforseen, rapid extinction in a Park that dedicates much effort to raptor management offers broad-scale reflections. Climate change and growing anthropogenic pressures will make unexpected species losses increasingly common in protected areas, which will face growing difficulties in identifying decline-drivers and in performing their protective task. Increased knowledge, quality monitoring and rapid management action will be needed for protected areas to deliver their role, but this will require increased funding.

Introduction

One of the main functions of protected areas is to support viable animal and plant populations, especially of endangered species, and shield them from major anthropogenic pressures on the environment (IUCN, 1994; Naughton-Treves et al., 2005). The delivery of such protective tasks has been demonstrated in several studies (e.g. Beale et al., 2013; Magdaong et al., 2014; Virkkala et al., 2014; Gray et al., 2016), and challenged in others (e.g. Liu et al., 2001; Craigie et al., 2010; Laurance et al., 2012; Palacin & Alonso, 2018; Geldmann et al., 2019), but is still rarely monitored and increasingly under scrutiny (Gaston et al., 2008; Ferraro & Pressey, 2015; Joppa et al., 2016). This growing interest in the evaluation of parks’ performance is prompted by the fact that protected areas are expensive, that their funding is limited, that their biodiversity-conservation function ever more urgent and that they are increasingly subjected to downgrading, downsizing and degazettement pressures, reinforcing the need to ensure their cost-effectiveness and efficiency (Mascia & Pailler, 2010; Qin et al., 2019). For example, some authors have called for the need to identify low-efficiency protected areas and divert their funding to better performing ones or even substitute them with new, more efficient ones (Fuller et al., 2010). All this has shifted conservation attention from reserve quantity to quality and promoted increased attention on species losses and declines in protected areas, as obvious early warning signals of performance deterioration.

Here, we document the extinction of the local population of a once abundant falcon, the Eurasian hobby Falco subbuteo, from Doñana National Park, an iconic protected area for its rich predator community. Hobbies were originally abundant at 50–60 pairs and acted as unique specialist hunters of swifts and dragonflies. This diet implies a unique niche within the raptor assemblage and frequent ranging over agricultural areas surrounding the park. The high density of other raptors likely constrained habitat availability. Predation was the main cause of breeding failure, and hatching and breeding success were always low, especially in drought years, and declined progressively through time. The extinction occurred rapidly after 2000 with several clues suggesting the synergistic contribution of prey depletion, farmland intensification, chemical contamination, predation and climate warming. Lack of detailed monitoring prevented a clear assessment of the relative role of these factors, but most of them seemed traceable to farming practices and climate change, i.e. large-scale drivers generated outside the Park. The documented extinction is alarming because this species is not particularly exigent, it may imply widespread declines of other species, and because this loss adds to the imminent local extinction of another raptor with profoundly different requirements, suggesting mounting, broad-level pressures affecting the whole ecosystem. This unforeseen, rapid extinction in a Park that dedicates much effort to raptor management offers broad-scale reflections. Climate change and growing anthropogenic pressures will make unexpected species losses increasingly common in protected areas, which will face growing difficulties in identifying decline-drivers and in performing their protective task. Increased knowledge, quality monitoring and rapid management action will be needed for protected areas to deliver their role, but this will require increased funding.
internationally renowned for its dense and diverse predator assemblage. In particular, we summarize past knowledge on this falcon population to hypothesize potential mechanisms of local extinction and we use the outcome results to offer a reflection on the role and challenges faced by protected areas in modern conservation. Hereafter, for simplicity, we use the term “extinction” to refer to the local extinction of this specific population.

Materials and methods

Study species

The Eurasian hobby (hereafter ‘hobby’) is a small-sized falcon typical of lowland farmland and other open landscapes interspersed with mature woodland, or with clumps, groves or lines of tall trees (Sergio et al., 2001). Eggs are typically laid in June in stick nests originally built by other species, almost invariably corvids or raptors (Chapman, 1999). Hobbies typically subsist on a diet of flying insects, such as dragonflies or flying beetles, ants and termites, but raise their offspring on an avian diet, typically dominated by open-sky or open-landscapes species such as swifts, swallows, larks or sparrows (Sergio et al., 2001). The species is widespread throughout Europe with a favourable conservation status, but declines have been recently reported for Spain, where this study was conducted (BirdLife International, 2015; Palacín, 2021). However, trends need to be interpreted with caution because this species is notoriously poorly monitored and challenging to survey, due to its late breeding secretive habits, difficulty of nest-finding and generally low density (rarely > 5 pairs/100 km², Sergio et al., 2001), which makes it the least known of European raptors.

Study area

The protected area of Doñana (hereafter Doñana) is located in south-western Spain (36°56′51″N 6°21′31″O36°56′51″ N 6°21′31″O) and includes 542 km² of National Park, instituted in 1969, and 538 km² of buffering Natural Park, instituted in 1989 (Supporting Information Figure S1a). The National Park is dominated by five main habitat types: (1) seasonal marshland, usually flooded during winter and progressively drying during the spring-summer; (2) Mediterranean scrubland; (3) sparse grassland, mainly located along the interface between Mediterranean scrubland and the marshes; (4) mobile sand dunes along the Atlantic Ocean shore and (5) stone pine Pinus pinea plantations. The Park is mainly embedded in a farmland matrix, which has become progressively more intensive, especially since the 1990s with the spreading of strawberry cultivation.

Doñana is one of the most biodiversity-rich parks of Europe, currently listed as a Ramsar Site, a World Heritage Site and a UNESCO’s Man and the Biosphere Reserve. It is also an iconic area for conservation action at the national and international level. For example, its institution sparked the creation of the World Wide Fund (García Novo & Marín Cabrera, 2006). Although protected areas are usually relegated to lands of low economical value (e.g. Scott et al., 2001), Doñana is a relatively large park (>1000 km²) centred around a seasonal wetland in prime fertile land along a river estuary. Such location has caused an exponentially growing anthropogenic pressure at the park borders, especially by rapid habitat conversion to intensive farmland, with consequent impacts on the water table that sustains the reserve wetlands. The park is also world-renowned for its high density and diversity of charismatic vertebrate predators, which contributes to the attraction of several hundred thousand visitors annually and is a key focus for conservation management (e.g. Ferrer & Hiraldo, 1991; López et al., 2009). Thus, the loss or decline of predatory species is considered by the Park Authority as a highly alarming conservation priority. In past decades, the Park has dedicated a large effort to intensive management specifically targeted to diurnal raptors. Such activities have mainly focused on (1) restricting access to large buffer-areas of up to 1.5-km radius centered on Spanish imperial eagle Aquila adalberti nests, (2) providing supplementary feeding in the form of dead rabbits and carrion and (3) retrofitting electricity pylons with designs potentially conducive to raptor electrocution (e.g. Ferrer & Hiraldo, 1991). These activities were neither designed nor expected to enhance the hobby population due to its dietary specialization and low vulnerability to electrocution, except for curtailing human disturbance close to many nests included in imperial eagle buffer zones.

Field procedures

The areas where hobbies were monitored are shown in Supporting Information Figure S1b. Because of the suspicious paucity of observations of the species since 2000, despite the frequent presence of raptor biologists in the area (see below), in 2018 and 2019, we conducted an intensive search for nests and territorial pairs. To this aim, we visited and observed all the traditional nest areas historically occupied by the species (see Section on Historical information) and all other sites judged as potentially suitable for breeding (basically any site with mature enough trees to hold a raptor nest). Each site was visited several times between mid-June and mid-August. A subset of 28 territories was thoroughly searched again in 2020.

In both these recent surveys and in previous historical ones (see Section on Historical information), territorial pairs were located by observing displaying individuals and listening to their territorial and courtship calls in May-June. Nests were found by examining all raptor and corvid nests in areas occupied by territorial pairs during the main incubation period of the species, between mid-June and mid-July. Once a nest was located, it was usually visited at least three times: the first during incubation, the second just after hatching and the third when the young were ready to fledge (>25 days old). This enabled the collection of data on clutch size, hatching success (percentage of eggs that hatch), the number of nestlings raised to fledging age per nest (for all breeding pairs and for pairs that successfully raised at least one fledgling) and overall breeding success (proportion of pairs that successfully reared fledglings). Hereafter, we collectively...
refer to these as measures of breeding performance. Nest contents were checked by directly climbing the nest tree or by means of a mirror or a camera attached to the end of a telescopic pole. Laying date was calculated by subtracting 30 days from the date of hatching. Hatching date was calculated by backdating nestlings from feather development, using information contained in Morata (1971), Cramp & Simmons (1980) and Heredia et al. (1983). Estimates of breeding success were only calculated for nests found in incubation, in order to avoid biasing the figures towards successful nests discovered when they already contained nestlings. Causes of nest failure were annotated whenever they could be ascertained, as well as their temporal occurrence during the breeding cycle (e.g. in incubation or after hatching). Whenever possible, prey remains found inside or below the nest and its immediate surroundings were identified to genus or species level. The diet was strongly dominated by common swifts Apus apus and pallid swifts Apus pallidus (see Results). Because in many cases it was impossible to discriminate between the remains of these two similar species, we re-applied to these unidentified swifts the relative percentages of the two species, as assessed in the 39 cases in which they could be discerned (e.g. because the whole body of the bird was found in the nest: \( N = 22 \) pallid and 17 common swifts).

### Historical information

To reconstruct the historical distribution of the species and summarize past knowledge on this population, we integrated information from several sources: (1) the research team of F. Hiraldo, which worked intensively on the species in the 1970s and 1980s (Heredia et al., 1983); (2) the “Equipo de Seguimiento de Procesos Naturales de the EBD-CSIC”; (3) the “Grupo de Conservación” of Doñana National Park and (4) the field diaries of dozens of researchers, field workers, visitors, volunteers, gamekeepers, park managers and wardens, active in Donana since the 1970s. Field diaries were studied meticulously in order to map nests and occupied territories as precisely as possible. However, in some cases, the nest or territory location could only be approximated and probably entailed spatial errors of 100–200 m. Because of such approximation, these were discarded from spatial analyses (see below). Also, inspection of available data and conversations with historical field workers suggested that, up to 2000, most nest areas were occupied whenever checked, suggesting a stable population. However, the search effort was very uneven and difficult to quantify, and different portions of the Park were surveyed in different periods, which prevented a thorough analysis of temporal changes in abundance for the whole population or even portion of it. Thus, the available data only allow the reconstruction of the cumulative population distribution for the 1980s and 1990s and its comparison with the 2018–2020 surveys. In particular, search effort specifically targeting hobbies was lower between 2000 and 2017. However, nests of other raptor species were inspected annually during mid-June to mid-July (fully overlapping the local incubation period) over an area cumulatively holding 20–30 traditional hobby territories. The indirect monitoring effort in these years was sufficient to be confident that, had hobbies been as abundant as in earlier decades, many nests would have been accidentally encountered.

### Statistical analyses

We employed a logistic regression generalized linear model (GLM, with binomial errors and a logit link function) to analyse the environmental and biotic factors (Supporting Information Table S1) discriminating between hobby territories (i.e. one randomly chosen nest used within each territory) and an equal number of random locations. The model was implemented in R 3.6.2 (R Core Team, 2020). For this analysis, we only used 30 hobby territories located within the National Park, because these were mapped with sufficient precision and had available information on proximity to ravens Corvus corax and other raptors (see below). Random locations were generated in Qgis 3.6 and then moved to the nearest mature tree (>10 m tall) which is known to have supported a raptor or raven nest in the 1980s and 1990s (see Chefaoui & Lobo, 2008 for a discussion about the limitations of habitat selection designs based on random locations or pseudo-absences). In addition, because hobbies are territorial and solitary nesters, the minimum nearest neighbour distance (NND) among random locations was set to be the same as the minimum NND among hobby territories. We chose predictor variables (listed in Supporting Information Table S1) that measured: (1) the distance to potential hunting grounds (e.g. villages with swift breeding colonies) or to sources of human disturbance (e.g. paths or roads), (2) the proximity and exposure to potential nest-providing and predator species (ravens, goshawks Accipiter gentilis or black kites Milvus migrans) and (3) the structure and composition of the landscape within 1.1 km of the nest, which is half the NND in the Doñana population.

To reduce collinearity and the number of variables presented to the GLM, we employed the method of variable reduction proposed by Green (1979). In this method, pairs of strongly intercorrelated variables \((r > 0.6)\) are considered as estimates of a single underlying factor. Only one of the two is retained for analysis, usually the one likely to be perceived as more important by the study organism. Of the remaining variables, only those for which marginally significant univariate differences \((P < 0.1)\) were detected between nest-sites and random locations were included in multivariate analyses. The variables eventually fitted to the model are outlined in Table 2. All continuous explanatory variables were standardized before being fitted to the logistic GLM, following Zuur et al. (2013). We used an AICc model selection procedure through the MuMIn package of R to identify the most parsimonious and plausible model among all possible alternative model subsets discriminating between hobby territories and random locations. A model was considered more plausible when it was at least 2 AICc-units less than the other(s).

Because Doñana is a composite wetland subject to years of severe drought that is known to affect the breeding performance of other raptors (Sergio et al., 2011) and because
local wetland inundation rates have declined in recent years (Díaz-Paniagua & Aragónés, 2015; Schmidt et al., 2017), we also tested whether hobby breeding performance varied between years of drought and years of normal inundation. Furthermore, to evaluate the status of the Doñana hobby population within a broader perspective, we compared the local density and breeding success to the mean values published for other European populations (reviewed in Sergio et al., 2001).

Differences in means, medians or frequencies were tested by means of *t* tests, Mann–Whitney U tests and *χ²* tests (Sokal & Rohlf, 1981). Whenever necessary, variables were logarithmically, square root or arcsine square root transformed in order to meet the normality assumptions of *t* tests (Sokal & Rohlf, 1981). Throughout, means are given ±1 SE, tests are two-tailed and statistical significance was set at *α* ≤ 0.05.

**Results**

**Past density and distribution**

Overall, we identified 416 hobby nests or territorial pairs (repeated observations of territorial, calling individuals at the same site), corresponding to 59 historical territories: 33 inside the National Park, 20 in the Natural Park and 6 in the immediate outer surroundings of the protected area (Fig. 1). All of them seemed to be systematically occupied whenever checked between 1970 and 1999. For the protected area, this corresponded to a density of 4.6 pairs/100 km² or 7.5 pairs/100 km² if we exclude the marshland area of the park unavoidably devoid of nesting pairs because of lack of trees (Supporting Information Figure S1b). The corresponding mean nearest neighbour distance (NND) among territories was 2278 ± 241 m (range: 427–8313 m) (Fig. 1).

The density was higher in the National Park than in the Natural Park (14.1 vs. 4.1 pairs/100 km², with marshland excluded). The mean NND was significantly lower in the National Park than in the surrounding Natural Park: 1590 ± 141 m (range: 426–4414) vs. 2484 ± 480 m (range: 611–8313) (*t* = −2.16, *P* = 0.035).

**Habitat selection**

The identity of the original nest builder was known for 114 nests: 53 were originally built by ravens, 1 by Eurasian magpies *Pica Pica*, 1 by hooded eagles *Hieraaetus pennatus*, 1 by Eurasian buzzards *Buteo buteo*, 1 by goshawks and the remaining 57 by other raptors, most likely black kites. All nests and territories were located exclusively in pinewoods and were typically surrounded by wide open areas (>75% of the landscape), the latter mainly dominated by Mediterranean scrubland, grassland and wetlands (Table 1). There was a single most plausible model that incorporated two variables (Table 2): compared to random locations, hobbies selected sites closer to raven territories and with lower abundance of a potential predator, the black kite (Table 2).

**Breeding success**

On average, the hobbies of Doñana laid a clutch of 2.8 eggs on 23 June and fledged 1.13 and 2.40 young per breeding and per successful pair, respectively (Table 3). Only 58% of the eggs reached the hatching stage and only 47% of breeding pairs successfully raised chicks to fledging. Most failures happened in incubation (77%; *N* = 35 breeding attempts for which the failure stage could be ascertained). Identified ‘causes’ of failure included (a) egg predation (22 cases, including two by common genets *Genetta genetta*), (b) nestling predation (3 cases) and (c) abandonment of (cold) eggs which never hatched (7 cases). In four cases, the adult female was predated while incubating eggs (by tawny owls in 2 cases, by common genet in 1 case and by an unknown species in 1 case). Because the eggs were also broken in these adult predation events, and because 10 cases of egg predation above were also classed as ‘predated, broken eggs’, adult predation may have been more common than here reported.

All estimates of breeding performance deteriorated in drought years, significantly so for the number of fledged young per breeding pair (Mann–Whitney U test, *U* = 1109.0, *P* = 0.007) and for the percentage of successful pairs (*χ²* = 8.05, *P* = 0.006; Fig. 2). The most comprehensive measure of breeding performance (young raised per breeding pair) declined threefold with drought. Except for the number of young per successful pair, all components of breeding performance progressively deteriorated through three subsequent decades (Fig. 3).

**Diet**

The diet was strongly dominated by pallid and common swifts, followed by larks of various species (Table 4). Historical field diaries contained plenty of observations of hobbies hunting dragonflies over wetlands. These represented a poor contribution to nesting diet (Table 4), but were probably a key trophic resource for adults.

**Comparison with other European populations**

Compared to European mean values, the population exhibited a medium-high density, an average clutch size, a very low hatching success and a low number of fledged young (Table 3).

**Current population extinction**

We were unable to find any evidence of territory occupation in 2018, 2019 and 2020, despite extremely intensive search efforts. In 2019, park personnel (I. Barroso) identified a territorial pair about 3 km out of the Park border, in an area of recent Park expansion. Hobby records became already very rare after 2000, with scattered observations of territorial individuals in 2001, 2002 (at two territories), 2003, 2004 (two territories), 2006 (three territories), 2007 and 2011. The only confirmed nests with eggs or nestlings were observed in 2006 (two nests) and in 2011 (one nest).
Discussion

The protected area of Doñana used to host an important hobby population of 50 to 60 pairs, a relevant contingent for a species usually occurring at very low density. Hobbies raised their offspring on a diet dominated by swifts and likely ranged widely to hunt them, given that swifts themselves may range over vast areas (del Hoyo et al., 1999) and bred in villages that were on average 5 km and up to 12 km from hobby nests. This may explain the apparent lack of preference for specific habitats around the breeding site. Instead, interspecific interactions seemed more important for breeding-site selection: hobbies were closer than expected to ravens, whose nests they frequently used for breeding, and avoided neighbourhoods crowded with black kites. The latter is renowned as an aggressive species, capable of kleptoparasitizing food and predating adults, eggs, nestlings and fledglings of smaller raptors. It can reach extremely high densities in Doñana (locally up to over 50 pairs/km², authors’ unpubl. data) and its crowding close to wetlands (Sergio et al., 2005) may have constrained habitat availability for hobbies, which are also frequently associated with lowland wetlands throughout their range (Sergio, 2020). Interestingly, given that half of hobby nests were in platforms originally built by kites, the falcons must have faced a challenging balance between the need for areas with good availability of nesting platforms but low predator densities. In this context, the association with ravens may have also been integral to an overall antipredatory strategy: hobbies typically occupy raven nests after ravens have just fledged their young, and successful breeding by ravens could have been exploited as a cue of anti-predatory safety of the general neighbourhood. Previous studies have reported the importance of ravens as nest providers and as safety cues in other falcons (Sergio et al., 2004) and in hobbies in particular (Fyuczynski, 1991). The importance of biotic interactions for habitat selection has been shown in other raptors (review in Sergio & Hiraldo, 2008) and may be especially important in ecosystems with dense predator assemblages, such as Doñana.

Figure 1 Distribution of Eurasian hobby breeding territories (black dots) in Doñana National and Natural Park (south-western Spain) in the 1980s and 1990s. Territory locations have been moved slightly for conservation reasons. The light blue area represents the seasonally flooded marshland under maximum inundation. Dark green patches are pinewood forests, whereas sand dunes are clearly visible as sand-coloured areas along the ocean shore. The rest are open areas mainly composed of Mediterranean scrubland, grassland and farmland. The yellow line depicts the border of the protected area and the inset shows the location of Doñana in southwestern Spain.
Below, we hypothesize four main mechanisms that could have driven the extinction and discuss their likelihood in the face of the above exposed ecological knowledge available for this population. (Factor 1) Food depletion likely contributed to the extinction. For example, swifts have declined by more than 30% in Europe since 1998 (SEO/BirdLife, 2019) and are generally well adapted to anthropogenic landscapes (e.g. intensive farmland; Sergio & Bogliani, 1999, 2000), implying even more unsustainable conditions for more exigent species. (2) As an upper trophic level consumer depending on lower trophic level prey, its loss may signal the decline of other species, in turn dependent on other species, potentially amplifying the scale of the problem to a wider context than the loss of a single population. (3) Another raptor with extremely different ecological requirements, the red kite Milvus milvus, has been predicted to go extinct in Doñana over the next decade (Sergio et al., 2019, 2020), suggesting mounting, broad-level pressures affecting the whole ecosystem. (4) As a swift- and dragonfly-specialist, this species was a unique component of the Doñana raptor assemblage, leading to erosion of the Park’s functional biodiversity. Finally (5), the steep decline went on virtually unnoticed despite the local presence of many ornithologists, raptor biologists and a well-resourced Park conducting much active management for raptors (see details in Study Area section). This suggests that declines of many species could be occurring undetected in many less monitored and less resourced protected areas, and that many species may need more intensive and targeted monitoring than currently appreciated to ensure proper management oriented to their continued persistence.

Hypothesized culprits of extinction

We estimate that hobbies declined rapidly after 2000 and went extinct around 2015, with virtual extinction and only occasional records already after 2010. Thus, the extinction was rapid. These results are alarming for five reasons: (1) this falcon is not considered a particularly exigent species and is generally well adapted to anthropogenic landscapes (e.g. intensive farmland; Sergio & Bogliani, 1999, 2000), implying even more unsustainable conditions for more exigent species. (2) As an upper trophic level consumer depending on lower trophic level prey, its loss may signal the decline of other species, in turn dependent on other species, potentially amplifying the scale of the problem to a wider context than the loss of a single population. (3) Another

Table 1 Environmental variables (mean ± se) measured at 30 Eurasian hobby territories and at 30 random locations in Doñana National Park (south-western Spain)

| Variable                  | Hobby territory (N = 30) | Random location (N = 30) |
|---------------------------|-------------------------|--------------------------|
| Nearest neighbour distance | 1584.0 ± 153.2          | 1602.9 ± 150.2           |
| Distance to path          | 120.9 ± 21.0            | 76.0 ± 13.9              |
| Distance to road          | 775.6 ± 112.1           | 1069.0 ± 158.6           |
| Distance to village       | 5036.5 ± 515.2          | 5775.2 ± 363.8           |
| Distance to raven         | 1421.1 ± 283.8          | 3122.7 ± 381.2           |
| Distance to goshawk       | 2350.1 ± 243.7          | 2935.6 ± 294.2           |
| Black kites in 1 km      | 6.4 ± 2.0               | 12.3 ± 2.9               |
| % Wetland                 | 9.0 ± 1.2               | 15.2 ± 2.1               |
| % Scrubland               | 58.1 ± 1.7              | 51.8 ± 2.4               |
| % Grassland               | 4.7 ± 1.1               | 8.0 ± 1.7                |
| % Farmland                | 0.2 ± 0.2               | 0.2 ± 0.2                |
| % Woodland                | 12.0 ± 0.9              | 9.6 ± 1.5                |
| % Open                    | 77.2 ± 1.8              | 76.6 ± 2.4               |
| Habitat diversity         | 0.85 ± 0.01             | 0.86 ± 2.4               |

Univariate differences between the two samples were tested by means of t-tests. All distances were measured in metres, percentage land covers refer to a circle of 1.1-km radius centred on the hobby territory or random location (rationale in Methods) and habitat diversity was estimated through the Shannon index of habitat diversity (Krebs, 1998, Supporting Information Table S1).

Table 2 Intercept and covariate coefficients from the logistic regression GLM discriminating between 30 hobby territories and 30 random locations (Doñana National Park, south-western Spain)

| Variable                  | Estimate | SE  | chi²  | P    |
|---------------------------|----------|-----|-------|------|
| Distance to raven          | −1.33    | 0.42| 15.54 | <0.001|
| Black kites in 1 km       | −0.85    | 0.40| 6.42  | 0.011|
| Intercept                 | −0.11    | 0.31|       |      |

The model was the single most plausible model after an AIC-based model selection procedure considering all possible combinations of the covariates distance to path (m), distance to raven (m), black kites in 1 km, % scrubland and % water (see Methods).
Table 3  Density, nest spacing and breeding performance of the hobby population of Doñana National Park (south-western Spain; data from nest surveys conducted in the period 1974–2000)

| Variable                                    | N⁴  | Mean value | SE  | Range       | European mean value⁶ |
|----------------------------------------------|-----|------------|-----|-------------|-----------------------|
| Density (pairs/100 km²)                     | 53  | 4.6        | 0.6 | 4.6–7.5⁵    | 4.7                   |
| Nearest neighbour distance (km)             | 53  | 2.3        | 0.2 | 0.4–8.3     | 4.4                   |
| Laying date                               | 57  | 54.4⁴      | 1.3 | 31–80⁴      | –                     |
| Clutch size                                | 114 | 2.80       | 0.07| 1–6⁶        | 2.8                   |
| Hatching success                          | 70  | 57.5%⁵     | 5.3 | 0–100       | 86.5%                 |
| No. of young fledged per reproductive pair | 100 | 1.13       | 0.14| 0–4         | 1.66                  |
| No. of young fledged per successful pair   | 47  | 2.40       | 0.13| 0–4         | 2.26                  |
| % Successful pairs                        | 100 | 47%        | –   | 0–1         | 73.4%                 |

⁴ Number of nests.
⁵ Mean values for previous European studies taken from the review of European estimates published in Sergio et al. (2001: 194). Only studies based on more than 20 checked nests were included in the calculations.
⁶ the two values reflect the inclusion or not of the treeless area of flooded marsh depicted in Fig. 1 and in Supporting Information Figure S1b in the calculations.
⁷ Julian date: 1 = 1 May. The mean value of 54.4 corresponds to 23 June and the range of 31–80 corresponds to 31 May–19 July.
⁸ The historical record included a single case of a six-eggs clutch but none of five, suggesting caution. Clutches of five and six eggs have been previously reported from Armenia and the former USSR (reviewed in Sergio et al., 2001).
⁹ Mean percentage of eggs hatched in each of 70 nests. It corresponds to a cumulative figure of 60.7% (122 eggs hatched out of a cumulative total of 201).

Figure 2  Breeding performance of the hobby population of Doñana National and Natural Park (south-western Spain) in years of normal marsh inundation and in years of drought (1981, 1983, 1993, 1994, 1995 and 1999). Clutch size is the number of laid eggs (N for normal flooding and drought years = 89 and 24, respectively), hatching success is the mean proportion of eggs that hatched (N = 56 and 14) and breeding success is the mean proportion of pairs that raised nestlings to fledging age (N = 78 and 21). The final number of nestlings reared was expressed per breeding pair (one that laid eggs; N = 78 and 21) and per successful pair (one that successfully raised at least one nestling to fledging age; N = 42 and 14). Bars represent 1 SE.
All the above is in line with worldwide crashes in flying insect biomass, inside and outside of protected areas (e.g. Hallmann et al., 2017; van Klink et al., 2020).

Such large-scale declines in potential prey were likely linked to (Factor 2) farmland intensification and unsustainable pesticide use. Farming practices around Doñana have become extremely more intensive over the past two decades, surely entailing an increase in pesticide apportion. Three observations support a potential role of chemical contamination in the local extinction. First, pesticide contamination is known to reduce hatching rates in raptors (e.g. through eggshell thinning caused by organochlorine pollutants; Newton, 1979) and the hatching success of Doñana hobbies was dramatically low (the lowest ever recorded for the species and 30% lower than mean European levels). Second, high levels of contamination by organochlorine pesticides were found in the eggs of Doñana red kites (an all year-round local resident species) at the end of the 1990s (Gómara et al., 2008), potentially supporting a scenario of local contamination. Third, in a comprehensive screening on 18 raptor species across Spain in the 1990s, hobbies showed the highest levels of contamination by organochlorine pesticides, with levels judged to be high enough as to be harmful (Van Drooge et al., 2008). Farmland intensification in Doñana has also been associated with unsustainable, illegal water extraction, with consequent lowering of the water table, which could have increased the magnitude of drought, affecting wetland prey such as dragonflies, and thus lowering even more the already poor breeding performance of the population (Díaz-Paniagua & Aragonés, 2015; Schmidt et al., 2017).

Predation (Factor 3) could have contributed to the decline. Predators were the most frequent cause of nest failure and even imparted adult mortality, which is the most important driver of population growth in predatory vertebrates (Saether & Bakke, 2000). Avoidance of black kite concentrations further supported the idea of substantial predation pressure on this small falcon and may have displaced it into suboptimal habitats. An adult hobby appeared among the prey remains recorded at black kite nests (in 1981). In Germany and The Netherlands, hobby extinctions and substantial declines have been linked to goshawk predation (Fyuczynski, 1991; Sergio et al., 2001). In Doñana, the mature pinewoods used by hobbies for breeding exposed them to two potential adult and nest predators: goshawks and eagle owls Bubo bubo. Goshawks have increased slightly in recent decades but are not abundant, whereas eagle owls have colonized Doñana around 2000 and used mature pinewoods intensively both for nesting and foraging. Thus, the timing of local increase by eagle owls fits the timeline of hobby demise well. Unfortunately, because both goshawks and eagle owls breed much earlier than hobbies, the latter are unlikely to be detected in their diet by classical

![Figure 3](image_url) Breeding performance of the hobby population of Doñana National and Natural Park (south-western Spain) through three decades (1970s, 1980s and 1990s). Clutch size is the number of laid eggs, hatching success is the mean proportion of eggs that hatched and breeding success is the mean proportion of pairs that raised nestlings to fledging age. The final number of nestlings reared was expressed per breeding pair (one that laid eggs) and per successful pair (one that successfully raised at least one nestling to fledging age). Bars represent ± 1 SE.
study methods (e.g. the study of nest remains). Thus, although highly plausible, it is difficult to know whether predation by these species could have contributed to the extinction. Overall, the high abundance and diversity of predatory vertebrates in Doñana make it a challenging environment for smaller raptors such as hobbies or kestrels.

Finally, could climate warming (Factor 4) have contributed to the extinction? The lower breeding success during drought years suggests that the species could suffer from warming trends. Furthermore, recent climate-modelling showed a lower probability of hobby occurrence for areas with mean temperatures over 20°C during their summer breeding months (Sergio, 2020). Atlas mapping also showed a notable range shift compatible with a response to climate warming, with substantial northward expansion and a less marked retraction from the southern trailing edge of the distribution, including the Doñana region and its wider surroundings (Sergio, 2020). However, such disappearance from a wider, intensively farmed region could also be compatible with unsustainable farmland intensification and contamination. Whatever the exact mechanism, the broader-scale decline suggests that the protected area was incapable to buffer this species from the dynamics occurring over the surrounding matrix, in line with recent findings from other studies (e.g. Laurance et al., 2012; Jones et al., 2018; Pimm et al., 2018; Geldmann et al., 2019).

**Broader implications**

The here-portrayed extinction of an abundant, non-exignet falcon offers interesting reflections on the role of protected areas in modern conservation. Firstly, efficient protection will be increasingly difficult as anthropogenic pressures unavoidably grow in the areas surrounding parks. This will need strategic changes in planning to better integrate the conservation of protected areas with the management of their surrounding landscapes. Better integration will be particularly important for wide-ranging species that indirectly make protected areas more permeable to outside influences. Secondly, retaining all species currently present in a protected area will be increasingly difficult, and sometimes impossible, as climate changes and imposes losses not tied to local conditions. However, as in the case documented here, discriminating between losses caused by climate or by other anthropogenic threats will be usually difficult. Quickly ascribing species losses or declines to climate change, without proper demonstration, is becoming a common narrative among some managers and administrations. This is delicate and dangerous because it increases fatalistic attitudes and management inertia and diverts attention from other factors in need of intervention (Noss et al., 2012). For example, in our specific case, the suspicion of unsustainable pesticide use in farmed lands surrounding the Park should be thoroughly investigated and ruled out before ‘passively accepting’ a climate-driven local extinction. Obvious candidates for eco-toxicological investigation would be the swift breeding colonies in the villages surrounding the park. Third, because climate change may make species losses more common, monitoring of species trends and protected areas performance will become even more important. For example, detailed monitoring during a decline may enable better inference of potential conservation threats and more realistic management proposals (e.g. Sanz-Aguilar et al., 2015; Sergio et al., 2020), in contrast to a posteriori speculation of hypothesized extinction drivers, as unavoidably accomplished here. To date, the issue of species losses due to climate change has been mainly considered in terms of response of biodiversity coverage by a whole network of protected areas (e.g. Beale et al., 2013; Magdanga et al., 2014; Virkala et al., 2014). However, this leaves out the difficult stance that a single protected area should take when faced with a species loss that can be ascribed to climate change only with great uncertainty (as documented here). More research and reflection is required on management directions available to protected areas in such challenging scenarios.

In conclusion, we believe that our case study is representative of conditions experienced or soon to be experienced by a multitude of protected areas. Climate change and growing anthropogenic pressures in a rapidly developing world will likely make species losses increasingly common in protected areas, which will face growing difficulties in understanding drivers of declines and in performing their task. Top predatory species may be useful indicator taxa in this scenario, as they may be the first to decline or be lost from local assemblages subjected to unsustainable pressures (Bennett & Owens, 1997). In the face of such growing

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**Table 4** Diet of the hobby (cumulative percentages) in Doñana National Park (south-western Spain), based on prey remains recorded in the nest during surveys conducted between 1974 and 2000

| Species                        | N  | % by number | % by mass |
|-------------------------------|----|-------------|-----------|
| Birds                         |    |             |           |
| Pallid swift *Apus pallidus*  | 167| 78.0        | 98.8      |
| Common swift *Apus apus*      | 70 | 32.7        | 37.8      |
| Alpine swift *Tachymarptis melba* | 54 | 25.2        | 29.9      |
| Larks (Alaudidae spp.)a       | 17 | 7.9         | 8.7       |
| Other birdsb                  | 24 | 11.2        | 19.8      |
| Mammals                       |    | 1.9         | 0.7       |
| Unidentified bat              | 2  | 0.9         | 0.2       |
| Unidentified small mammal     | 2  | 0.9         | 0.5       |
| Invertebrates                 | 43 | 20.1        | 0.6       |
| Unidentified dragonfly (Odonata) | 1 | 17.8       | 0.5       |
| Unidentified beetle           | 11 | 2.3         | 0.1       |
| (Scarabaeoidea)               |    | 214         |           |

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a Includes: Eurasian skylark *Alauda arvensis* (N = 9); Thekla lark *Galend a theklae* (2); crested lark *Gal erida cristata* (1); greater short-toed lark *Calandrella brachydactyla* (1); calandra lark *Melanocorypha calandra* (1); unidentified lark (4).

b Includes: red-legged partridge *Alectoris rufa* (1); common hoopoe *Upupa epops* (1); European bee-eater *Merops apiaster* (4); Eurasian blackbird *Turdus merula* (1); woodchat shrike *Lanius senator* (1); Asian azure-winged magpie * Cyanopic a cyanus* (1); Eurasian magpie *Pica pica* (1); Eurasian tree sparrow *Passer Montanus* (1) European serin *Serinus serinus* (1); corn bunting *Emberiza calandra* (1); unidentified duck (1); unidentified wading bird (1); unidentified songbird (8).
uncertainty, we suggest that quality monitoring, increased knowledge and rapid management action will be increasingly fundamental for efficient, locally tailored conservation. However, this will require additional funding for protected areas and is in stark contrast with a worrying decline in field-based research (e.g. Ríos-Saldaña et al., 2018).

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**Supporting information**

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Figure S1.** (a) Map of the protected area of Doñana in south-western Spain. The red line outlines the inner National Park and the yellow lines the outer buffer of the Natural Park. The inset shows the location of Doñana in southwestern Spain. (b) Study areas in which hobbies were monitored. The blue sector corresponds to the seasonally inundated marshland, which is virtually devoid of trees for nesting. Thus, estimates of breeding density are given in the Results with and without the inclusion of this area. Colour codes: Orange: terrestrial sectors of the Natural Park; Yellow: terrestrial sectors of the National Park; Blue: seasonally inundated marshland.

**Table S1.** Environmental variables measured at Eurasian hobby territories and random locations in Donana National Park (south-western Spain).