

Preservation of wide-ranging top predators by site-protection: Black and red kites in Doñana National Park

Fabrizio Sergio ^{a,*}, Julio Blas ^b, Manuela Forero ^a, Néstor Fernández ^{a,c},
José Antonio Donázar ^a, Fernando Hiraldo ^a

^a Department of Applied Biology, Estación Biológica de Doñana, C.S.I.C., Avda de María Luisa s/n., Pabellón del Perú, Apdo 1056, 41013 Seville, Spain

^b Department of Biology, University of Saskatchewan, Canada S7N5E2

^c Department of Ecological Modelling, UFZ – Centre for Environmental Research, Permoserstrasse 15, D-04301 Leipzig, Germany

Received 25 August 2004

Available online 14 April 2005

Abstract

We used data from a long-term study on two medium-sized generalist predators, the black kite (*Milvus migrans*) and the red kite (*Milvus milvus*), to illustrate the complexity of managing wide-ranging top predators by site-protection. The study was conducted between 1989 and 2000 in the Reserva Biológica de Doñana, located at the core of Doñana National Park. Both species occurred at high density and showed high productivity. Black kites were slightly increasing, and red kites showed a non-significant trend. The main cause of breeding failure was nest predation, mainly by mammalian predators, most likely Iberian lynx (*Lynx pardinus*) or common genet (*Genetta genetta*). The main cause of mortality was illegal poisoning, which sharply increased in the late 1990s. Nest-site selection models showed that: (1) black kites selected areas near the seasonal marshes, rich in their main prey species and (2) red kites selected areas rich in marshland and far from the park border, possibly in response to illegal poisoning episodes. Productivity was positively related to the availability of marshland and of open terrestrial habitats for black and red kites, respectively, and negatively related for both species to the density of black kites within 200 m of the nest. Our results showed that: (1) intraguild predation and competition among predators make outcomes of interspecific interactions extremely complex, leading to unpredictable side-effects of priority actions targeting one species at a time and (2) though the park was fenced and patrolled by wardens, the wide ranging behaviour of the two species made park borders permeable to negative human pressures, such as poisoning, leading to extreme edge effects and absence of a true, safe core of the park. Park management needs to be better integrated with its regional socio-economic and cultural context. Education programmes against illegal poisoning should be urgently promoted.

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Keywords: Black kite; Conflict; Doñana National Park; Habitat selection; Intraguild predation; *Milvus migrans*; *Milvus milvus*; Nest-site selection; Red kite; Reserve preservation; Top predators conservation; Top vertebrate predators

1. Introduction

The main role of a reserve should be to promote biodiversity conservation (e.g., Wright, 1996; Norris and

Pain, 2002; Bojórquez et al., 2004). However, managing parks to preserve simultaneously all species is likely to be difficult, given the frequent differences among species in habitat requirements and predatory or competitive interactions (Sutherland, 1998). For example, management actions favouring one species may indirectly disavour its subordinate competitor (Keddy, 2001). Such problems are likely to be exaggerated when dealing with

* Corresponding author. Tel.: +34 954 232340.

E-mail address: fsergio@esd.csic.es (F. Sergio).

vertebrate top predators. These species are unanimously considered difficult to preserve through site-protection because of their wide-ranging behaviour and large area-requirements (e.g., Newton, 1979; Gittleman et al., 2001), which make most reserves too small to sustain viable populations. Furthermore, recent evidence suggests that subtle competitive and predatory interactions may be more pervasive in predator communities than previously thought (Palomares et al., 1996; Palomares and Caro, 1999; Fielding et al., 2003; Sergio et al., 2003a, 2004), leading to conflicts between management guidelines targeting different species.

Here, we use data from a 12 years study on two vulnerable raptor species to illustrate the difficulties involved in managing a predator community within a national park. In particular, for both species we assess their conservation status, population trends, spatial distribution, mortality factors, habitat relationships and interspecific interactions with other competitor and predator species. We then discuss the implications of such results in terms of prioritisation of park management actions. The study was conducted in Doñana National Park (south-western Spain), which holds some of the highest biological diversity of Europe (Fernández-Delgado, 1997) and which is world-renowned for its dense predator populations, including 16 breeding species of birds of prey and eight species of carnivores (Valverde, 1967). The park also hosts important populations of some of the most endangered predators of the world, such as the Spanish imperial eagle (*Aquila adalberti*) and the Iberian lynx (*Lynx pardinus*), which may in turn prey on other predators (Palomares et al., 1996; Forero et al., 1999; Ferrer, 2001), leading to potential conflict between the management actions required for species with different degrees of vulnerability and abundance.

1.1. Model species

Our study focused on two medium sized raptors, the black kite (*Milvus migrans*) and the red kite (*Milvus milvus*). During breeding, both species usually defend a small territory of 100–200 m around the nest and forage communally over the surrounding areas. The black kite is a loosely colonial, opportunistic predator usually associated in Europe with wetland habitats (Sergio et al., 2003b). Though locally abundant, its European populations have undergone a large decline (Viñuela and Sunyer, 1994; Sergio et al., 2003c) and are now concentrated in Spain, France and Switzerland (Bijlsma, 1997). In Doñana, the species occurs at high density with a diet dominated by wetland prey species (Hiraldo et al., 1990; Veiga and Hiraldo, 1990; Forero et al., 1999), apart from a relatively small area of the park where the rabbit (*Oryctolagus cuniculus*) can be an important additional prey (Viñuela and Veiga, 1992; Viñuela et al., 1994).

The red kite is a generalist predator with a range mainly restricted to Europe. In Spain, which holds most of the European wintering population and about 22% of the European breeding population (Nicolai, 1997; Viñuela et al., 1999), red kites are usually associated with medium-low elevation, extensively farmed areas, avoiding excessively rainy or arid climatic zones (Seoane et al., 2003). In most of Europe, the species has recently suffered a rapid and enormous decline, mainly associated with rodenticide poisoning and persecution (Villafuerte et al., 1998; Viñuela et al., 1999; BirdLife International/European Bird Census Council, 2000). Doñana National Park hosts a relatively small but dense population with a generalist diet dominated by lagomorphs and waterbird carcasses in the winter and by lagomorphs, small mammals, water birds and reptiles in the breeding season (Blanco et al., 1987, 1990; Veiga and Hiraldo, 1990; Heredia et al., 1991). In this and other areas, red kites have often been suggested to suffer from competition with black kites (e.g., Heredia et al., 1991; Viñuela et al., 1999) but the hypothesis has never been explicitly tested. Given the precarious European conservation status of both black and red kites, it is considered extremely urgent to provide adequate conservation guidelines within protected areas, which may act as potential sources of colonizers for depleted populations elsewhere (e.g., those subject to human persecution, once this is relieved).

2. Study area

Kites were surveyed between 1989 and 2000 in the Reserva Biológica de Doñana (RBD, 37°10'N, 6°21'W), a 62 km² plot located within Doñana National Park. Elevation ranged between 0 and 32 m a.s.l. The plot included four main habitat types: (1) the marisma, a seasonal marsh, usually flooded during winter and progressively drying during the spring-summer; (2) scrubland, a mixture of different degradation stages of autochthonous Mediterranean scrubland (Castroviejo, 1993), including patches of tall shrubs (>1.5 m tall), mainly *Pistacea lentiscus*, *Myrtus communis* and *Erica* spp. and patches of short shrubs (<1.5 m), mainly *Halimium halimifolium*, *Ulex* spp., *Stauracanthus genistoides* and *Erica* spp; (3) sparse grassland with ferns, mainly located at the interface between Mediterranean scrubland and the marisma; and (4) mobile sand dunes along the sea shore. Mature trees are mainly present as stone pine (*Pinus pinea*) plantations scattered throughout the reserve and as isolated or small clumps of cork oaks (*Quercus suber*) mainly located near the shore of the marisma. Climate is Mediterranean sub-humid with mild, wet winters and hot, dry summers, and a mean annual precipitation of circa 600 mm (Fernández et al., 2003).

3. Methods

3.1. Field surveys and nest checks

Kite territories were censused by looking at territorial displays, nest material transfers and presence of birds perched in or near a nest in February–April, during the pre-incubation period of both species. A very high number of individuals were marked with PVC colour rings, as part of a long-term demographic study (e.g., Forero et al., 1999, 2002). Thus, when two active nests were near each other, maximum effort was placed in identifying the individuals using them, so as to exclude the possibility that they were alternative nests of the same pair. Whenever possible, nest contents were checked three times: first during incubation to assess clutch size, second just after hatching to estimate hatching success and brood size, and third when the nestlings were 40–45 days old to record the number of reared young (nestlings fledge at about 48 days old in the black kite and 55 days old in the red kite, Bustamante and Hiraldo, 1993).

Most nests were actually inspected every few days, which frequently allowed the identification of the proximate causes of egg or chick loss. A nest was classified as predated when we found: (1) remains of eggs with the beak or teeth marks of the predator or (2) remains of plucked chicks. Cases potentially ascribed to cainism (death of one chick subsequently fed to other nestlings) were not included among the predation events. Predation was classified as by mammals when there were claw marks on the trunk of the nesting tree and when we found fur or a common genet (*Genetta genetta*) latrine in a predated nest or on the same tree of a predated nest. Cause of failure was classified as poisoning when we found intact dead adults inside or below the nest: based on post-mortem, chemical analyses, such cases are invariably caused by poisoning (details in Hernández et al., 2001; Blas, 2002). Of course, the latter cause of failure was likely to be underestimated, because poisoned adults may die far away from the nest.

During kite censuses and subsequent nest checks, maximum effort was placed into mapping the nest locations of other potential avian competitor and predator species, including: common buzzard (*Buteo buteo*), Spanish imperial eagle, booted eagle (*Hieraetus pennatus*), and raven (*Corvus corax*). In the 1990s, Spain was afflicted by a large-scale increase in the occurrence of illegal poisoning (e.g., Sánchez and Roig, 2001), particularly in its southern portion (Hernández et al., 2001). Because kites are extremely vulnerable to poisoned baits (Villafuerte et al., 1998; Viñuela et al., 1999), we collected all available data on kites poisoned in Doñana and subsequently given to raptor rehabilitation centres or to local authorities during the study period.

3.2. Statistical and GIS analyses

We used ANOVA and the Spearman correlation coefficient to test for among-years differences in mean productivity and for directional population trends (Sokal and Rohlf, 1981). We employed logistic regression (Tabachnick and Fidell, 1996) with a backward stepwise procedure to analyse the environmental and biotic factors (Table 1) discriminating between kite nests and an equal number of random locations. For black kites, because density varied significantly among years, we used data from the nest census of 1998, when density was nearest to its long-term mean (density-dependent habitat selection will be analysed elsewhere). Of the 94 available nests, we randomly selected 50 to use for model building and employed the remaining 44 for model validation (Fielding and Haworth, 1995). For red kites, we identified 34 territories occupied at least once during the study and randomly selected one nest used within each territory, so as to avoid pseudoreplication. Model validation was performed on 20 random locations and 20 nests, each one from a different territory, located outside the study area but within Doñana National Park. All random locations were generated by means of the extension “Animal Movement” of the GIS software ArcView 3.2 (Hooge and Eichenlaub, 1997). Because in our area kites nested only on trees at least 7–8 m tall, we mapped the availability of such trees in the field by means of a GPS, entered them in a GIS and forced random locations to be plotted within such potentially suitable trees. We also enforced that the minimum distance between neighbouring random locations would be the same as the observed minimum nearest neighbour kite distance, so as to take into account potential minimum thresholds of intraspecific territoriality. The variables of Table 1 were measured after entering the nests of kites and other species in a GIS and by accessing a fine-scale GIS land-use map, constructed by digitising 1:15,000 colour-infrared aerial photographs dated 12 June 1998 (details in Fernández et al., 2003). The variables were chosen so as to measure: (1) the characteristics of the nest-site and its immediate surroundings (within a radius of 200 m of the nest), (2) the distance to potential hunting grounds or to sources of human disturbance, (3) the distance to potential competitor and predator species, and (4) the structure and composition of the landscape within 1 and 2 km of the nest. The latter measures were chosen on the basis of telemetry data previously collected in Doñana and on the basis of previously published nest-site selection studies on the same species (e.g., Heredia et al., 1991; Newton et al., 1996; Ortlieb, 1998; Sergio et al., 2003d; and unpublished telemetry data). Larger circular buffers were not considered because they would have caused excessive spatial overlap among the circles.

Table 1
Variables measured at black and red kite nests and random sites

Variable	Description
<i>Nest area-level</i>	
<i>Characteristics of the nest and its immediate surroundings</i>	
Tree species	1 = cork oak; 2 = stone pine
% low shrubs 200 m	% of low shrubs (<1.5 m tall) within 200 m of the nest
% tall shrubs 200 m	% of tall shrubs (>1.5 m tall) within 200 m of the nest
% pasture 200 m	% of pasture within 200 m of the nest
% woodland 200 m	% of woodland within 200 m of the nest
% marisma 200 m	% of marisma within 200 m of the nest
% sand dunes 200 m	% of sand dunes within 200 m of the nest
Black kite nests 200 m	Number of black kite nests within 200 m of the nest
Red kite nests 200 m	Number of red kite nests within 200 m of the nest
Competitor + predator 200 m ^a	Number of nests of competitor or predator species ^a within 200 m of the nest
<i>Distance variables</i>	
<i>Distance to conspecifics, heterospecifics and sources of human disturbance</i>	
Distance to black kite (m)	Distance to the nearest black kite nest
Distance to red kite (m)	Distance to the nearest red kite nest
Distance to <i>S. imperial eagle</i> (m)	Distance to the nearest Spanish imperial eagle nest
Distance to booted eagle (m)	Distance to the nearest booted eagle nest
Distance to buzzard (m)	Distance to the nearest common buzzard nest
Distance to raven (m)	Distance to the nearest raven nest
Distance to path (m)	Distance to the nearest path
Distance to dirt road (m)	Distance to the nearest dirt road
Distance to building (m)	Distance to the nearest inhabited building
Distance to village (m)	Distance to the nearest village or town
Distance to Doñana border (m)	Distance to the border of Doñana National Park
Distance to marisma (m)	Distance to the marisma
<i>Landscape-level</i>	
<i>Landscape structure and composition within 1 and 2 km of the nest</i>	
Black kite nests 1 km	Number of black kite nests within 1 km of the nest
Red kite nests 1 km	Number of red kite nests within 1 km of the nest
Competitor + predator 1 km ^a	Number of nests of avian competitor or predator species ^a within 1 km of the nest
Kleptoparasites	Number of black kite nests on a transect 200 m wide joining the nest to the marisma
Kleptoparasites + red kites	Number of black and red kite nests on a transect 200 m wide joining the nest to the marisma
% low shrubs 1 and 2 km ^b	% of low shrubs (<1.5 m tall) within 1 and 2 km of the nest
% tall shrubs 1 and 2 km ^b	% of tall shrubs (>1.5 m tall) within 1 and 2 km of the nest
% pasture 1 and 2 km ^b	% of pasture within 1 and 2 km of the nest
% open terrestrial	% of low shrubs + pastures within 1 and 2 km of the nest
% woodland 1 and 2 km ^b	% of woodland within 1 and 2 km of the nest
% marisma 1 and 2 km ^b	% of marisma within 1 and 2 km of the nest
% total water 1 and 2 km ^b	% of marisma + other water bodies within 1 and 2 km of the nest
% sand dunes 1 and 2 km ^b	% of sand dunes within 1 and 2 km of the nest
Habitat diversity	Shannon index ^c of habitat diversity (Krebs, 1998)

^a Includes: black kites, red kites, Spanish imperial eagles, booted eagles, common buzzards and ravens.

^b Measured both within 1 km and within 2 km of the nest.

^c Calculated as: $\sum(p \log_e p)$, where p is the proportion of each habitat type.

To reduce collinearity and the number of variables presented to logistic models, we employed the method of variable reduction proposed by Green (1979) and commonly employed in habitat selection studies (e.g., Sergio and Bogliani, 2000; Sergio et al., 2003d and references therein). 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 significant univariate differences ($P < 0.1$) were detected between nests and random locations were included in multivariate analyses.

To gain a deeper understanding of kites habitat quality and to test whether the observed habitat

choices were adaptive (e.g., Clark and Schutler, 1999; Sergio et al., 2003c,d), we used multiple regression (Sokal and Rohlf, 1981) to relate breeding success to the same set of variables presented to the habitat selection logistic models. For red kites, because we pooled data from different years and because productivity varied significantly among years, we expressed it as a deviation from the yearly mean of fledged young, following Perrins and Jones (1974) and Schiek and Hanon (1992).

In all analyses, logistic regression models were run through a standard and also through a generalized linear model procedure (GLM, software GLIM 4); we then retained the model with the highest predictive power. GLM modelling procedures follow

Table 2
Density and productivity of black kite and red kite populations in Europe in the 1980s and 1990s

Area (period)	Density (n) ^a	n ^b	Clutch size	Hatching success (n) ^c	Breeding success (%) ^d	Mean No of young fledged per			Reference
						Territorial pair	Breeding pair	Successful pair	
<i>Black kite</i>									
Matas Gordas, S (1992–2000)	1008.3 (121)	515	2.12	70.3 (232)	44	0.61	0.85	1.46	Authors' unpublished data ^e
RBD, S (1989–2000)	150.7 (93)	1059	2.02	67.4 (416)	41	0.59	0.71	1.43	This study
Lake Lugano, I (1992–2003)	29.4 (38)	365	2.30	74.0 (88)	50	0.90	1.24	1.80	F. Sergio (unpublished data)
Lake Maggiore, I (1996–2000)	24.0 (13)	30	–	–	50	0.87	–	1.73	Sergio et al. (2003c)
Lake Como, I (1996–2000)	47.3 (19)	40	–	–	48	0.75	–	1.58	Sergio et al. (2003c)
Lake Iseo, I (1996–2000)	35.2 (27)	48	–	–	38	0.48	–	1.10	Sergio et al. (2003c)
Lake Idro, I (1997–2001)	66.5 (27)	37	–	–	59	1.05	–	1.63	F. Sergio (unpublished data)
Lake Garda, I (1997–2000)	14.9 (16)	18	–	–	44	0.83	–	2.14	Sergio et al. (2003c)
Sarca Valley, I (1997–2003)	13.1 (21)	88	–	–	40	0.63	–	1.62	F. Sergio (unpublished data)
Castelporziano, I (1991–1992)	33.3 (16)	–	–	–	–	–	–	–	De Giacomo et al. (1993)
Lac Lemán, CH (1975–1990)	100.6 (319)	165	2.25	–	–	–	2.02	–	Henrioux and Henrioux (1995)
Brandenburg, G (1987–1990)	7.5 (19)	90	–	–	–	–	1.90	2.60	Lohmann (1989) ^f
Sachsen, G (1986–1990)	5.3 (40)	87	2.63	–	–	–	–	2.39	Schömbrodt and Tauchnitz (1991) ^f
Sachsen, G (1988–1994)	3.5 (57)	–	–	–	–	–	–	–	Mammen (1995) ^f
Hakel, G (1982–1991)	–	166	–	–	72	–	1.43	1.99	Stubbe and Zörner (1993) ^f
Odertal, P (1988–1992)	–	51	–	–	–	–	1.20	2.03	Adamski (1992) ^f
<i>Red kite</i>									
Welsh uplands, W (1986–1993)	3.5 (113)	675	2.39	–	45	0.64	0.82	1.44	Newton et al. (1994)
RBD, S (1989–2000)	31.9 (20)	208	2.33	55.0 (93)	40	0.62	0.76	1.55	This study
Monti Tofa, I (1981–1987)	1.9 (5)	13	1.92	56.0 (13)	46	–	0.77	1.67	Arcà (1989)
Harz Mountains, G (1991)	48.7 (730)	–	–	–	–	–	–	–	Nicolai (1997)
Corsica, F (1980s)	–	22	2.82	–	–	–	1.27	1.94	Patrimonio (1990) ^g

W, Wales; S, Spain; F, France; I, Italy; CH, Switzerland; G, Germany; P, Poland.

^a Median number of pairs/100 km² during the study period.

^b Number of pairs checked for reproduction.

^c Percentage of eggs which hatched (*n*, number of clutches).

^d Percentage of territorial pairs that raised at least one chick to fledging.

^e Additional data for the period 1987–1989 available in Viñuela et al. (1994).

^f In Ortlieb (1998).

^g In Evans and Pienkowski (1991).

Crawley (1993): all explanatory variables were fitted to the model, extracted one at a time from such maximal model and the associated change in model deviance assessed by an F-test for multiple regression (GLM model with normal errors and an identity link function) or a χ^2 test for logistic regression (GLM model with binomial errors and a logit link function).

In all analyses, each territory is used only once to avoid pseudoreplication, means are given ± 1 SE, tests are two-tailed, and statistical significance was set at $\alpha \leq 0.05$. When multiple tests were performed on the same data set, the sequential Bonferroni correction was used to adjust the significance level (Rice, 1989).

4. Results

4.1. Density, productivity, causes of breeding failure and population trends

Black kite density was high compared to other populations, with on average 151 pairs/100 km² (Table 2). It fluctuated through the years, with an overall increasing trend ($r_s = 0.61$, $n = 12$, $P = 0.035$, Fig. 1). Red kite density was on average 38 pairs/100 km², it was moderate to high compared to other European populations (Table 3) and showed a non-significant trend ($r_s = -0.31$, $n = 12$, $P = 0.33$, Fig. 1).

Estimates of productivity were comparable or higher than those reported for other European populations (Table 2) and varied among years for both species (e.g., for the mean number of fledged young per territorial pair: black kites: $F_{11,1047} = 9.05$, $P < 0.0001$; red kites: $F_{11,196} = 3.37$, $P < 0.001$). None of the productivity estimates showed any clear directional trend through the years (all $r_s < 0.25$, $P > 0.43$). For both species, predation was the main cause of breeding failure. Most of the predation events were caused by mammalian predators, most likely Iberian lynx or common genet (Table 3). Finally, poisoning incidents were detected for both species throughout the 1990s, with a sharp increase in 1999–2000 (Fig. 2).

4.2. Nest-site selection

Distance to the marisma was the only variable retained by the logistic model discriminating between black kite nests and random locations (Tables 4 and

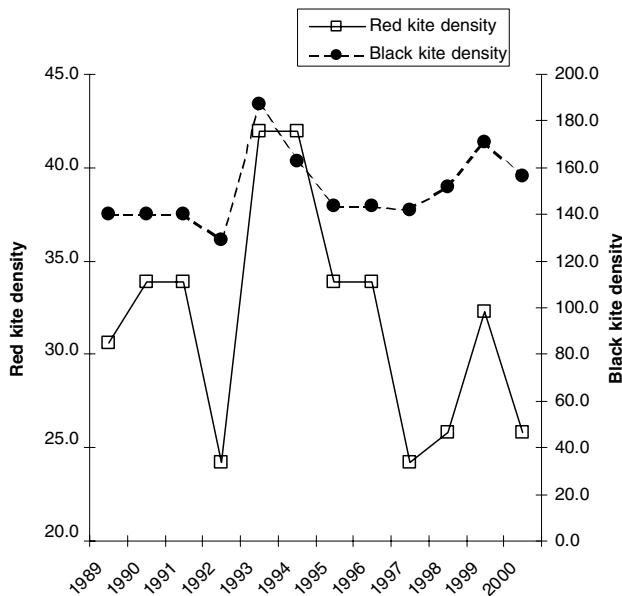


Fig. 1. Density (territorial pairs/100 km²) of black and red kites in the Reserva Biológica de Doñana (Doñana National Park, south-western Spain, 1989–2000).

Table 3

Causes and timing of breeding failure by black and red kites in Doñana National Park (1989–2000)

Variable	Black kites (<i>n</i> = 325 failures)	Red kites (<i>n</i> = 77 failures)
% occurred during incubation (<i>n</i>)	58.7 (196)	55.6 (54)
% occurred during chick rearing (<i>n</i>)	41.3 (196)	44.4 (54)
% caused by predation	49.2	44.2
% caused by nest abandonment or infertile eggs	9.5	3.9
% caused by nest collapse	5.8	7.8
% caused by poisoning	1.8	5.2
% caused by take-over of the nest by booted eagles	1.5	1.3
% by unknown causes	32.0	37.7
% of the predation events caused by mammalian predators ^a (<i>n</i>)	40.6 ^a (160)	61.8 ^a (34)

Sample size is reported in parenthesis when different from the one specified in the column-headings.

^a In most of the remaining cases the identity of the predator could not be ascertained and could still include mammalian predators. The presented percentages are thus minimum estimates of mammalian predation.

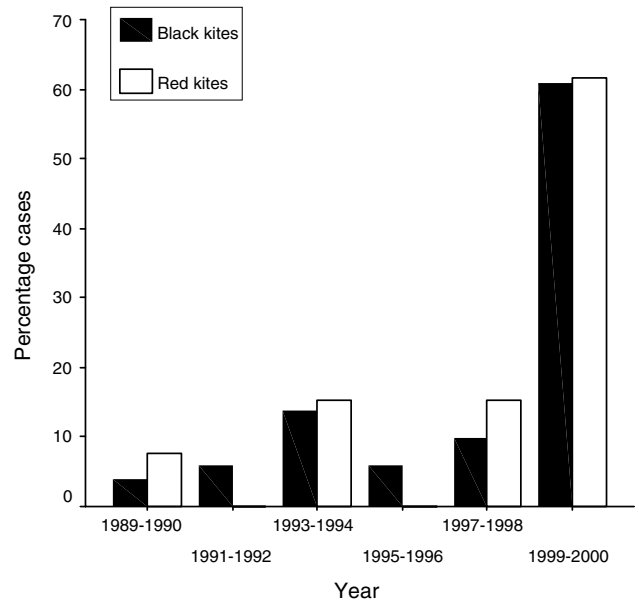


Fig. 2. Mortality by illegal poisoning of black kites ($n = 51$) and red kites ($n = 13$) in Doñana National Park (south-western Spain) between 1989 and 2000.

5(a)). The model correctly re-classified 80% of the 50 kite nests and 88% of the 50 random locations. Model validation showed that the model was robust: it correctly classified 80% of 44 black kite nests and 89% of 44 random locations not used for model building.

Table 4
Environmental variables measured at kite nests and random locations (Doñana National Park, Spain)

Variable	Black kite nests ($n = 50$)	Random locations ($n = 50$)	Red kite nests ($n = 34$)	Random locations ($n = 34$)
Tree species ^a	72.0*	12.0	67.6*	14.7
% low shrubs 200 m	33.6 ± 1.4*	26.1 ± 1.8	39.6 ± 4.2	30.9 ± 4.1
% tall shrubs 200 m	16.3 ± 1.1***	23.0 ± 1.1	16.6 ± 3.2	22.4 ± 4.3
% pasture 200 m	5.4 ± 0.6***	1.5 ± 0.4	6.2 ± 2.1**	0.1 ± 0.1
% woodland 200 m	4.1 ± 0.8***	16.6 ± 1.7	17.5 ± 5.0	33.3 ± 5.4
% marisma 200 m	24.0 ± 2.3***	4.1 ± 1.6	3.4 ± 1.8	1.0 ± 1.0
% sand dunes 200 m	2.2 ± 0.9***	10.9 ± 1.3	0.6 ± 0.6	3.6 ± 1.4
Black kite nests 200 m	1.68 ± 0.25**	0.84 ± 0.28	1.21 ± 0.29†	0.68 ± 0.31
Red kite nests 200 m	0.34 ± 0.07*	0.10 ± 0.04	0.03 ± 0.03	0.09 ± 0.05
Competitor + predator 200 m	2.28 ± 0.33	1.20 ± 0.34	1.50 ± 0.31	0.97 ± 0.33
Distance to black kite	205.3 ± 33.4***	270.0 ± 44.1	233.5 ± 59.0	422.0 ± 54.3
Distance to red kite	471.2 ± 73.0***	1517.9 ± 112.2	799.5 ± 88.2	475.0 ± 57.7
Distance to imperial eagle	1800.7 ± 128.2***	2854.6 ± 140.6	2000.3 ± 181.7*	2886.9 ± 182.7
Distance to booted eagle	1961.6 ± 238.6***	1341.4 ± 201.8	933.1 ± 161.4	1595.7 ± 245.5
Distance to buzzard	999.6 ± 67.8***	1561.6 ± 81.7	1804.2 ± 252.5	1585.9 ± 214.7
Distance to raven	2151.5 ± 154.7***	1178.9 ± 138.5	2025.8 ± 187.6	1566.6 ± 198.1
Distance to path	94.6 ± 17.3	154.2 ± 20.7	92.1 ± 15.5	142.6 ± 32.4
Distance to dirt road	47.8 ± 6.1*	111.5 ± 15.2	75.3 ± 15.0	102.6 ± 19.6
Distance to building	2311.9 ± 221.3	2460.2 ± 191	2634.1 ± 265.4	2228.9 ± 244.4
Distance to village	6882.5 ± 241.8***	3459.4 ± 339.4	6356.0 ± 362.4***	3269.3 ± 400.0
Distance to Doñana border	6208.9 ± 214.6***	3104.9 ± 304.6	5737.9 ± 312.9***	2937.2 ± 364.8
Distance to marisma	1260.5 ± 212.5**	4526 ± 295.8	1933.1 ± 345.5***	4696.2 ± 357.4
Black kite nests 1 km	16.24 ± 1.26***	6.04 ± 0.85	10.44 ± 1.34	4.97 ± 0.94
Red kite nests 1 km	0.50 ± 0.15***	2.46 ± 0.19	1.50 ± 0.25	0.88 ± 0.15
Competitor + predator 1 km	18.54 ± 1.29***	10.30 ± 0.89	13.41 ± 1.59	7.62 ± 1.12
Kleptoparasites	4.66 ± 0.63	5.30 ± 0.59	3.29 ± 0.48	5.65 ± 0.47
Kleptoparasites + red kites	5.46 ± 0.70	6.32 ± 0.63	3.65 ± 0.52*	6.62 ± 0.51
% low shrubs 1 km	41.0 ± 1.8***	29.2 ± 2.0	41.7 ± 2.2*	29.5 ± 2.6
% tall shrubs 1 km	14.8 ± 1.5	18.1 ± 1.6	17.4 ± 2.0	22.1 ± 2.1
% pasture 1 km	7.5 ± 0.9***	1.8 ± 0.7	5.7 ± 1.2***	0.9 ± 0.3
% open terrestrial 1 km	48.6 ± 2.1***	30.9 ± 2.2	47.4 ± 2.4***	30.4 ± 2.8
% woodland 1 km	4.4 ± 1.0***	20.3 ± 2	9.0 ± 2.6***	21.9 ± 2.5
% marisma 1 km	14.8 ± 2.3***	2.6 ± 1.2	11.5 ± 2.8*	1.4 ± 1.3
% total water 1 km	16.3 ± 2.2*	7.6 ± 1.2	13.2 ± 2.7	5.8 ± 1.4
% sand dunes 1 km	2.9 ± 1.3***	14.6 ± 2.2	1.5 ± 1.1*	10.8 ± 2.3
% low shrubs 2 km	39.1 ± 3.7	33.0 ± 3.6	37.1 ± 2.1	27.7 ± 2.4
% tall shrubs 2 km	11.8 ± 2.2	15.4 ± 3.3	17.4 ± 1.5*	23.6 ± 1.4
% pasture 2 km	9.2 ± 2.1*	1.9 ± 0.9	4.7 ± 0.6***	1.3 ± 0.4
% open terrestrial 2 km	48.3 ± 3.8	34.8 ± 3.8	41.8 ± 2.3**	28.9 ± 2.7
% woodland 2 km	14.8 ± 3.7*	32.6 ± 4.4	8.2 ± 2.0**	18.2 ± 2.1
% marisma 2 km	3.7 ± 1.6	0.4 ± 0.4	17.5 ± 3.1***	2.2 ± 1.4
% total water 2 km	5.2 ± 1.7	5.7 ± 1.5	19.7 ± 2.9	6.2 ± 1.5
% sand dunes 2 km	0.7 ± 0.7	9.5 ± 2.0	1.4 ± 0.8	9.4 ± 1.5
Habitat diversity	0.75 ± 0.01	0.80 ± 0.1	0.75 ± 0.01	0.80 ± 0.01

Univariate differences between the two samples were tested by means of t tests.

^a % nests on oaks. Difference tested by means of a χ^2 test on the count data.

† 0.05 < P < 0.1.

* P < 0.05.

** P < 0.01.

*** P < 0.001.

Two variables were retained by the logistic regression discriminating between red kite nests and random locations: the distance to the border of the National Park and the percentage area of marisma within 2 km of the nest (Tables 4 and 5(b)). The model correctly re-classified 85% of the red kite nests and 82% of the random locations. When validated on the independent data set, the model correctly classified 90% of 20 red kite nests and 75% of 20 random locations.

4.3. Factors affecting productivity

In a multiple regression model, the mean number of young raised by black kites was positively related to the amount of marisma within 1 km of the nest and negatively related to the number of conspecifics within 200 m of the nest (Table 5(c)). Red kite productivity was positively related to the amount of open terrestrial habitats within 2 km of the nest and negatively related to

Table 5
Effect of environmental and biotic variables on nest-site selection and productivity (number of young fledged) of black and red kites in Doñana National Park, Spain

Variable	Parameter estimate \pm SE	<i>t</i>	<i>P</i>	% deviance explained
<i>(a) Effect on: black kite nest site selection (n = 100)^a</i>				
Distance to marisma ^b	-1.40 \pm 0.27	5.2 ^c	<0.0001	33.3
Constant	10.45 \pm 2.06	–	–	
<i>(b) Effect on: red kite nest-site selection (n = 78)</i>				
% marisma 2 km ^e	4.12 \pm 1.50	7.4 ^f	<0.01	54.4 ^d
Distance to Doñana border	0.001 \pm 0.0002	11.0 ^f	<0.0001	
Constant	-3.04 \pm 0.83	–	–	
<i>(c) Effect on: black kite productivity (n = 83)^{b,g}</i>				
Black kite nests 200 m	-0.15 \pm 0.05	3.0	<0.01	25.3
% total water 1 km ^e	0.86 \pm 0.40	2.2	<0.05	
Constant	1.65 \pm 0.19	–	–	
<i>(d) Effect on: red kite productivity (n = 34)^{b,g}</i>				
Black kite nests 200 m ^b	-0.33 \pm 0.15	2.3	<0.05	28.5
% open terrestrial 2 km ^e	1.32 \pm 0.64	2.1	<0.05	
Constant	-0.20 \pm 0.47	–	–	

^a GLM logistic regression with binomial errors and a logit link function (Crawley, 1993).

^b Variable log_e-transformed.

^c Tested by means of a χ^2 test.

^d Nagelkerke R^2 (Norusis, 1993).

^e Variable converted to a proportion and arcsin square-root transformed.

^f Tested by means of the Wald statistic (Norusis, 1993).

^g GLM linear regression with normal errors and an identity link function (Crawley, 1993).

the number of black kite pairs within 200 m of the nest (Table 5(d)).

5. Discussion

Both species showed a high density and productivity, but were not free from potential conservation problems, such as illegal poisoning, and high rates of competition and nest predation. For black kites, our results confirmed the strong association of this species with freshwater habitats (Forero, 1998; Sergio et al., 2003b,c,d), whose availability simultaneously affected nest-site selection and breeding performance. On the other hand, nesting preferentially near the marisma implied some costs: first, black kite density was extremely high near the shore, leading to high opportunities for interference competition, kleptoparasitism, and intra-specific predation (e.g., Veiga and Hiraldo, 1990; Jones and Manéz, 1990; Sunyer, 1998), which may explain the negative effect of conspecific density near the nest on productivity. Second, because of its relatively high rabbit availability (Moreno and Villafuerte, 1995), the diverse area of scrubland and grassland near the marisma was also positively selected by the Iberian lynx (Palomares et al., 2001; Fernández et al., 2003), which may in turn prey on kite nests, possibly explaining the high nest predation rates observed. The latter were probably further promoted by the crash of the local rabbit population, the main lynx prey, at the beginning of our study (Villafuerte et al., 1995).

Like black kites, red kites also selected areas with a high availability of the seasonal marshlands. This may seem surprising at first sight because: (1) red kites are usually associated with extensive farmland and pastures (e.g., Newton et al., 1996; Seoane et al., 2003), as further confirmed by the positive relationship between productivity and the availability of pasture and low scrubland in our study and (2) in Doñana, the diet of breeding red kites is more dominated by terrestrial prey than the diet of black kites (Veiga and Hiraldo, 1990). However, breeding red kites are year-round residents in Doñana and their diet is strongly dominated by carcasses of water birds in the winter (Heredia et al., 1991). Furthermore, wetland species still represent more than 20% of the prey items during the breeding period, and terrestrial habitats near the marisma are rich in rabbits (see above), the main prey of red kites during the breeding period (Delibes and García, 1984; Veiga and Hiraldo, 1990). Whatever its cause, the selection of areas near the marisma by red kites may have exacerbated the competition and risk of nest predation by black kites, which may explain the negative effect of local black kite density on red kite productivity.

Finally, red kites avoided areas near the border of the park. Because the park is fenced, and because poachers are mainly interested in ungulates (Revilla et al., 2001), the most likely explanation for this result is that: (1) kites perceived areas near the park border as dangerous and avoided them and/or (2) kites closer to the border were subject to a higher mortality rate by illegal poisoning, resulting in the progressive abandonment of territories

near the border and apparent selection for areas far from it. Whatever the mechanism involved, such result confirm earlier findings of consistent, negative edge-effects linked to illegal persecution in Doñana National Park (e.g., Forero, 1998; Revilla et al., 2001).

5.1. Conservation of top predators by site protection: problems and implications

Our study illustrates two classical problems associated with the management of top predators within a reserve: edge-effects and conflicts among management plans for different species. Firstly, even if a park is fenced, this does not imply that it is free from negative human pressures (Janzen, 1986). Even assuming that poisoned baits were never placed inside the park, the wide ranging behaviour of kites would easily expose them to baits located outside the park. Such behaviour makes park borders functionally permeable to negative human pressures. Furthermore, the fact that poisoning affected pairs nesting in the RBD, which is located at the core of the park, suggested that there was no safe core of the park, at least for such wide-ranging species and despite the relatively large size of the park (~1100 km²). In southern Spain, where game hunting is a popular activity generating considerable income, predator control is a common management practice, and unfortunately it often includes illegal predator poisoning, that seems to be deeply rooted in the local culture and has never been fully eradicated, even increasing in recent years (e.g., Villafuerte et al., 1998; Hernández et al., 2001; Viñuela and Villafuerte, 2004). Given that increasing the area of a park is frequently a difficult or unfeasible alternative, this illustrates once more the importance of integrating park management with its wider, socio-economic and cultural context (e.g., Ghimire and Pimbert, 1997; Wynne, 1998). Management strategies inside the park cannot be independent from human activities in its surroundings (Wells and Brandon, 1992). Such problems are likely to be exacerbated when dealing with the management of wide-ranging species.

Secondly, our results show how some top predators may limit the productivity of other top predators through competition and intraguild predation. Doñana National Park is world famous for its dense predator community and is actively managed to increase the populations of some endangered predatory species by enhancing nest-site availability and prey supplies (e.g., Ferrer and Hiraldo, 1991; Moreno and Villafuerte, 1995; Travaini et al., 1996). While favouring some species, this may indirectly disfavour others in ways that are difficult to predict. For example, high black kite density near the marisma may limit red kite populations. Because red kites are currently more endangered than black kites (Viñuela et al., 1999), this may generate conflict between conservation priorities for the two species. It has even

been previously proposed the culling of black kites to favour red kites (Viñuela et al., 1999), but this may be ethically questionable within a national park and given the vulnerable European status of black kites.

Along the same line, kite nests were subject to high mammalian predation pressure, compared to data from other medium-sized raptors (e.g., Newton, 1979). In most cases it was likely caused by Iberian lynx or common genet, but it was often difficult to discriminate between the two. If lynx were the major predator, much management is currently devoted to enhance the populations of this globally endangered species (Travaini et al., 1996), which could indirectly boost future predation rates at kite nests, especially in years of low rabbit abundance, such as those in which our study was conducted. However, if common genet were the main predator, an increase in lynx density could indirectly favour kites by reducing genet populations through intraguild predation (Palomares et al., 1996). This reinforces the idea of the complexity of predicting the side-effects of current management actions on non-target species, and further highlights the difficulty of managing one species at a time, especially within a dense predator community.

5.2. Conservation guidelines

The highly productive areas near the marisma host an extremely dense predator community and should thus be the primary focus of conservation management. Illegal poisoning is often difficult to eradicate and is probably better tackled through long-term programmes of education of local human communities, some of which are already underway. In the meanwhile, patrolling operations by park staff could focus more on the border of the park, ideally including the areas outside the border.

The current plans of scrubland management aimed at enhancing rabbit populations in inland areas (Moreno and Villafuerte, 1995) may favour red kites by relieving competition with black kites. However, mammalian predation on raptor nests should be intensively monitored, especially in years of low rabbit density, to assess its role as a potential limiting factor for raptor populations. Finally, protection of vulnerable species such as kites inside the park should be integrated with a strategic management plan which includes actions targeting the populations in the surroundings of the park and in the wider region. For kites, such populations are currently fully left to themselves and steeply declining (e.g., Forero, 1998).

Acknowledgements

We thank L. Marchesi, J. viñuela, P. Whitfield and an anonymous reviewer for comments on a previous draft

of the manuscript and F.G. Vilches, G. García, S. Cabezas, A. Sánchez and A.M. Guerrero for help in the field. F.S. was supported by a grant of the European Community-Access to Research Infrastructure action of the Improving Human Potential Programme in Doñana Biological Station. J.B. was supported by a post-doctoral fellowship from the Spanish Ministerio de Educación Cultura y Deporte.

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