

Habitat selection by Black kite breeders and floaters: Implications for conservation management of raptor floaters

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A B S T R A C T

Preserving large predators is important but challenging because these species are typically wide-ranging, select multiple habitats at different scales and often present spatial or habitat separation between the breeder and floater sectors of a population. In addition, most of our knowledge on raptor floaters' habitat requirements comes from large solitary species, whose floaters often occupy temporary settlement areas spatially separate from breeding locations. Here, we examine space and habitat use by a loosely colonial, wetland-dependent raptor, the Black kite (*Milvus migrans*), in a population where floaters co-exist with territory holders, enabling a direct comparison of their habitat preferences. The study was conducted in Doñana National Park (South-Western Spain), a seasonally drying marshland currently surrounded by intensive agriculture and rice-fields. Intensive radio-tracking revealed that breeders and floaters selected and avoided the same habitats despite a radical, four-to-eight fold difference in their home-range dimensions: all kites over-selected open habitats suitable for their aerial foraging modes and avoided woodland and farmland. These results suggest a continuum of raptor population structures ranging from solitary species whose floaters select different habitats than breeders and are concentrated in spatially separate settlement areas, to colonial and semi-social species whose floaters fully coexist with breeders with shared habitat preferences. Both extremes of this continuum will pose challenges for conservation management. In solitary species, special conservation efforts may be required to identify and manage temporary settlement areas, while in gregarious species, the larger ranges of floaters may expose them to different threats than breeders, whose occurrence and consequences may be subtle to identify.

Keywords:

Habitat selection
Black kite
Milvus migrans
Radio-tracking
Habitat restoration
Non-breeders

1. Introduction

Preserving and managing large vertebrate predators is becoming increasingly important as a way to maintain high levels of biodiversity (Estes et al., 2011), but poses special challenges for several reasons. First, these species are characterised by large home-ranges, which cannot be easily encompassed within protected areas (e.g. Newton, 1979; Clark et al., 1999; Ray et al., 2005). Second, they frequently select habitat features at multiple scales, from the micro-scale to the landscape-level (Sánchez-Zapata and Calvo, 1999; Thompson and McGarigal, 2002; Ciarniello et al., 2007), which requires broad-level management plans (e.g. Whitfield et al., 2006a). Third, they may use different habitats at different times of the year (Boal et al., 2005; Schmitz et al., 2010). Finally, the populations of large predatory vertebrates are frequently composed of a sector of territorial breeders, often concentrated in resource-rich sites, and a sector of non-breeding individuals, frequently located far away from the breeding grounds

(e.g. David Smith, 1993; Ferrer and Harte, 1997; Crabtree and Sheldon, 1999; Balbontín, 2005). The latter adds complexity to strategic management targeting long-term population persistence, especially because non-breeding animals are difficult to study due to their cryptic behaviour, differential habitat selection, spatial separation from breeders, or potential long-distanced dispersal (e.g. Zack and Stutchbury, 1992; Rohner, 1997; Whitfield et al., 2009a; Penteriani et al., 2011). As a result, there is little knowledge on the differences in habitat choices between the breeders and floaters of a population, and conservation planning is often biased to protect the habitats preferred by the breeding sector of predator populations (e.g. Real and Mañosa, 1996; Whitfield et al., 2006a). Also, most of the (scarce) available knowledge is heavily biased towards large species of solitary birds of prey, whose floaters are typically concentrated in so-called “temporary settlement areas”, where they select different habitats than breeders (Ferrer and Harte, 1997; Balbontín, 2005; Caro et al., 2011; Penteriani et al., 2011). As a result, little is known of smaller species with different social systems, such as colonial or loosely colonial species.

Because of all the above, there is a high need for further multi-scale habitat selection studies on both breeding and non-breeding

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individuals of predatory vertebrates, particularly of gregarious or semi-gregarious species. Here we provide such a study by examining the space and habitat requirements of the breeders and floaters of a semi-social raptor, the Black kite (*Milvus migrans*). In particular, we use data from a 3-year radio-tracking study on the Black kite population of Doñana National Park (South-Western Spain), one of the most renowned and biodiversity-rich reserves of Europe.

Our study system is a good model for the goals presented above due to several reasons. (1) The Black kite is a semi-gregarious raptor, which in Doñana mainly breeds in loose colonies (Sergio et al., 2005). (2) In this population, floaters coexist with breeders (Blas et al., 2009; Sergio et al., 2009, 2011a). This allows the study of habitat selection by the two status categories while controlling for differences in habitat availability, avoiding the problem of comparing the decisions by groups of individuals occupying separate areas characterised by different landscapes. (3) Doñana National Park is an island of semi-natural vegetation subject to dynamic habitat management and transformation. Outside the park, drainage of the seasonal marshes in the second half of the 20th century has generated a matrix of intensive farmland, dominated by rice fields to the north-east, whose suitability for wild life species is largely unknown. Inside the protected area, all habitats are traditionally actively managed (e.g. Fernández-Delgado, 2005). For example, large patches of forest have been recently thinned or removed, while the hydrology of the seasonal marshes that characterise the park is subjected to a recently implemented large-scale restoration program (Project “Doñana 2005”: García Novo and Marín Cabrera, 2005a), which included the restoration of various sites totalling more than 50 km² of seasonal marshland which had been originally converted to agriculture (García Novo and Marín Cabrera, 2005b; Santamaría et al., 2005; Martín-López et al., 2011). The above described habitat changes and active management inside and outside the park call for more solid knowledge of the habitat preferences of key species such as Black kites, which are the most abundant large predators in the park and which depend heavily on woodland for nesting and marshland for hunting (Sergio et al., 2011b). Understanding habitat preferences of key indicator species could be fundamental to forecast future impacts of habitat management and to implement more efficient post-intervention monitoring.

Given all the above, here we: (1) examine the home range and habitat selection of kites of different sex and status (breeders vs. floaters) and (2) propose potential management guidelines based on the obtained results.

2. Methods

2.1. Study species

The Black kite is a medium-sized, monogamous, migratory raptor. It is an opportunistic, aerial predator typical of open habitats (Viñuela and Sunyer, 1992; Blanco and Viñuela, 2004), adept at exploiting temporary situations of overabundance of relatively easy prey (Hiraldo et al., 1990). In our study population, all individuals are migratory and remain in Doñana from March to August, where they mostly breed as monogamous pairs (Sergio et al., 2007). The local breeding density can be very high (from 1 to 30 pairs/km², Sergio et al., 2005, 2011b; authors' unpublished results) and most pairs could be considered to nest within a very large, loose colony. Diet composition is very heterogeneous and dominated by wetland birds and their nestlings, crayfish, rabbits (*Oryctolagus cuniculus*) and carrion (Hiraldo et al., 1990; Viñuela and Veiga, 1997). Floaters are generally young birds (1–7 years old, Blas et al., 2009) physiologically capable of reproducing but apparently displaced from the breeding sites by older, more dom-

inant conspecifics (Sergio et al., 2009; Blas and Hiraldo, 2010; Blas et al., 2011). Sexual role division during reproduction follows the usual scheme for raptors (Newton, 1979): the male provides most of the prey for the female and offspring while the female performs most of the incubation, brooding and nest guarding.

2.2. Study area

The study was conducted in Doñana National Park, located within the estuary of the Guadalquivir river, along the coast of the Atlantic Ocean in South-Western Spain (6°12'–6°40'W, 36°48'–37°20'N). The five main macro-habitats observed in the park include: (1) seasonally drying marshland (hereafter “marshland”), (2) Mediterranean scrubland or grassland with scattered corkoaks (*Quercus suber*) (hereafter “dehesa”), (3) extensive scrubland on sandy soil (hereafter “scrubland”), a mixture of different degradation stages of autochthonous Mediterranean scrubland (Castroviejo, 1993), including patches dominated by *Pistacia lentiscus* and *Myrtus communis* or by *Halimium halimifolium*, *Ulex* spp., *Stauracanthus genistoides* and *Erica* spp.; (4) mobile sand dunes along the ocean coast, and (5) extensive forests of stone pine *Pinus pinea* and smaller woodlots dominated by Corkoaks or *Eucalyptus* spp. trees (Castroviejo, 1993). A mosaic of intensively cultivated lands and rice fields surrounds the park.

2.3. Field methods

Between 2007 and 2009 we trapped 38 Black kites by cannon-netting (Fig. 1) and equipped them with a conventional backpack transmitter (TW-3 of 15g; life expectancy=1.4 years; Biotrack Ltd., Wareham Dorset, UK), which was fitted with a Teflon harness (Kenward, 2001). The sex, status and sampling period of tracked kites are specified in Table 1. Kites were monitored every 3–4 days and all locations, obtained by triangulation, were GIS mapped through the software ArcView 3.2 (ArcView GIS, Redlands, CA, USA). In each tracking day, all marked kites were searched simultaneously while driving along a network of paved and dirt roads covering the entire park and its surroundings, thus sampling areas both close and far from nest concentrations. Also, the starting point and sequence of survey roads were varied each time, in order to avoid biasing the tracking data towards certain areas (e.g. towards nest concentrations). Using an area accumulation curve, we found that locations sampling saturation was reached for an average threshold of 40 fixes per individual and all individuals were radio-located more than 40 times.

Radio-tracking and the intensive demographic monitoring of the breeding and non-breeding sectors of the population (Sergio et al., 2009, 2011a) allowed us to determine the breeding status of all radio-tagged individuals. These included 12 breeding males, 12 breeding females and 14 floaters (eight males and six females). Breeders were defined as individuals holding a territory with a partner and building a nest. All trapped birds were sexed by molecular analysis of a blood sample (Ellegren, 1996).

2.4. GIS and statistical analysis

For each kite, we estimated the home range size and configuration through the following three indices: (1) the Minimum Convex Polygon (MCP), (2) the Kernel Density Estimator (KDE) at 95%, 75% and 50% contours, calculated with a least-squares cross-validation (LSCV) procedure and a smoothing factor (Seaman and Powell, 1996) and (3) the mean distance of all fixes from the home-range centroid (hereafter “distance to centroid”), calculated through the Animal Movement extension for ArcView (Hooge and Eichenlaub, 2000). However, to avoid reporting redundant results, for the analyses of habitat selection we only show the models based on the

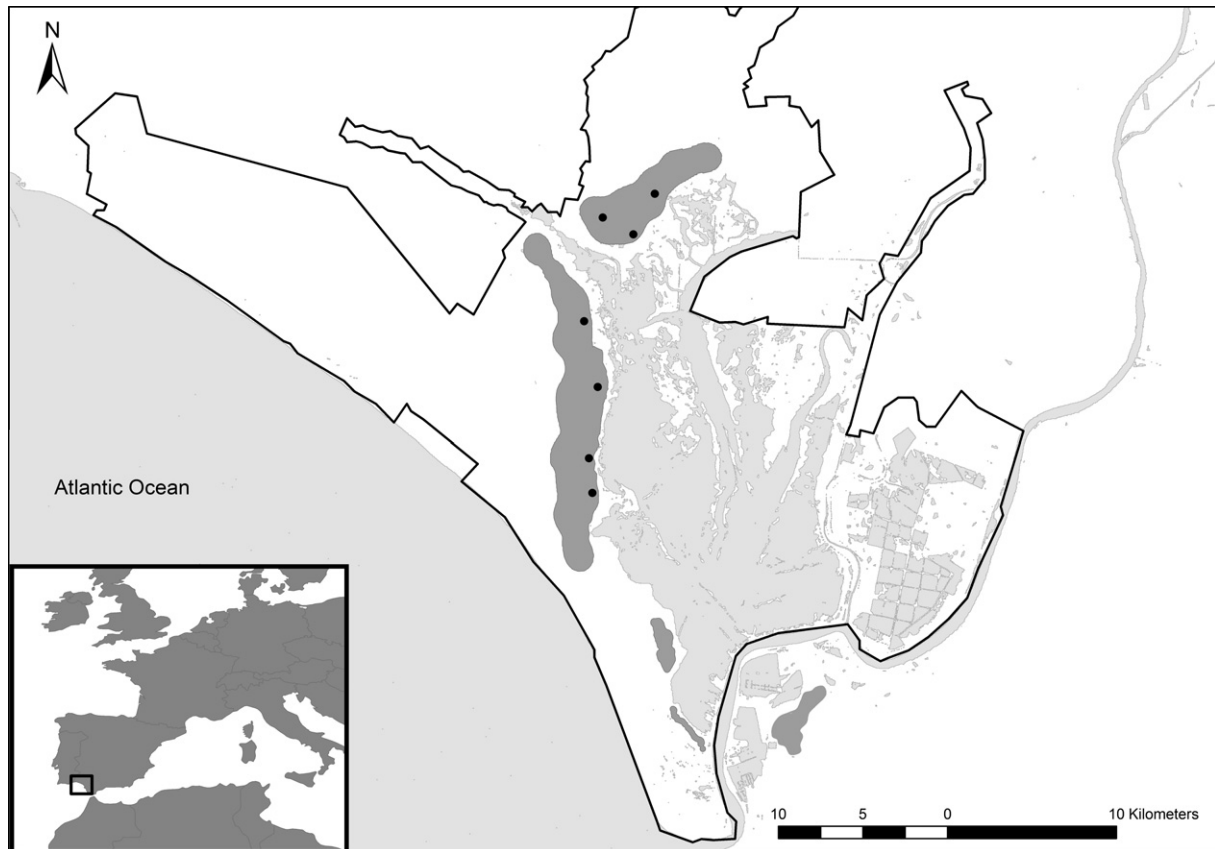


Fig. 1. Main trapping sites (circles) and areas of concentration of Blackkite nests (ingrey) around the seasonal flooded marshland of Doñana National Park (South-Western Spain) and its surroundings. The areas highlighted in grey include more than 90% of the nests used by Blackkites in any given year. The other pairs breed in single, isolated nests or in loose colonies of 2–3 nests scattered around the rest of the landscape. The continuous line represents the border of the cumulated National and Natural Park (marine portion excluded), whose location in Europe is portrayed in the inset.

Minimum Convex Polygon. Models based on Kernel estimators gave the same results (results of analysis not shown).

Habitat composition was evaluated by accessing a 1:10000 land-use map provided by the LAST-EBD group (<http://last-ebd.blogspot.com/>). Based on such map, land-uses were initially classified according to the categories listed in Table 2. However, to reduce the high frequency of zero values obtained for several infrequently used habitat types (Aebischer et al., 1993), we pooled the initial habitats into five coarser-level macro-habitats judged as potentially important for kites on the basis of accumulated knowledge on the population nesting and foraging behaviour: seasonal marshland, scrubland, dehesa, intensive farmland, and woodland.

To gain an understanding of kite ranging behaviour and habitat selection, we focused our analyses on three aspects: (1) the spatial extent and configuration of the home range (hereafter “home range analysis”); (2) the habitat composition of a whole home range and its comparison with local availability (hereafter “larger-scale habitat selection”); (3) the habitat composition around each individual radio-location and its comparison with local availability (hereafter “finer-scale habitat selection”). The first analysis focuses on the spatial requirements of different types of individuals (males vs. females, breeders vs. floaters), the second on the habitat-based selection of whole home ranges, and the third on the finer-scale selection of habitats within a home-range.

For the home range analysis, we used one way ANOVA (Lehmann and Romano, 2005) to compare the home range size and distance to centroid among breeding males, breeding females and floaters. For larger-scale habitat selection, we used a logistic regression (GLM with binomial errors; Zuur et al., 2009) to test

which combination of habitat variables discriminated between the 38 kite home ranges and 38 randomly-plotted home ranges of the same shape. The latter were generated by the following three-step procedure: (1) we plotted the centroid of all 38 kite home ranges; (2) an equal number of random points was generated through the Animal Movement extension of the GIS software (Hooge and Eichenlaub, 2000); (3) each kite home range was shifted so that its centroid would now coincide with one of the randomly plotted centroids. This generated 38 randomly plotted home ranges that maintained the same shape of the originally observed ranges, allowing us to study habitat selection while controlling for home range size.

Finally, to investigate finer-scale habitat selection, we: (1) plotted a 100-m buffer around each kite location ($n = 1980$ locations) and an equal number of randomly generated locations; (2) calculated the percentage habitat extent in each buffer using the ArcView extension Patch Analyst (Elkie et al., 1999); and (3) compared the habitat composition around kites and random locations by means of linear mixed models (LMM) where individual kite identity was fitted as a random factor (Zuur et al., 2009). The measure of 100m for the buffer was arbitrarily chosen because kites are aerial hunters that patrol large areas while typically soaring and gliding at a minimum altitude of 20–30m, thus scanning a landscape portion rather than a single point.

In all models, we added Year as a covariate to control for annual variations in ranging behaviour. Although we are aware that raptor home ranges can vary seasonally (e.g. Newton, 1979; Bosch et al., 2010), sample size limitations precluded the possibility to examine seasonal (within-year) variations. To reduce such confounding

Table 1

Sex, status (breeder vs. floater) and sampling period of 38 adult Black kites radio-tracked in Doñana National Park (South-Western Spain). All individuals were still alive when the radio-signal was lost through battery exhaustion.

Individuals	Year monitored	Sex	Status	Tracking period	Number of locations
M1-B	2007	Male	Breeder	2 May–29 July	47
M2-B	2007	Male	Breeder	11 May–23 July	69
M3-B	2007	Male	Breeder	19 April–26 July	50
M4-B	2007	Male	Breeder	20 April–16 July	48
F1-B	2007	Female	Breeder	24 April–10 July	57
F2-B	2007	Female	Breeder	13 May–19 July	53
F3-B	2007	Female	Breeder	25 April–27 July	67
M5-F	2007	Male	Floater	02 May–23 July	73
M6-F	2007	Male	Floater	21 April–26 July	55
M7-F	2007	Male	Floater	30 April–29 July	53
F4-F	2007	Female	Floater	29 April–23 July	60
F5-F	2007	Female	Floater	30 April–27 July	46
F6-F	2007	Female	Floater	30 April–26 July	51
F7-F	2007	Female	Floater	24 April–21 July	73
M8-B	2008	Male	Breeder	17 April–25 July	58
M9-B	2008	Male	Breeder	13 March–25 July	51
M10-B	2008	Male	Breeder	28 March–25 July	37
M11-B	2008	Male	Breeder	15 March–27 June	45
M12-B	2008	Male	Breeder	15 June–26 July	40
F8-B	2008	Female	Breeder	26 March–27 June	80
F9-B	2008	Female	Breeder	17 April–27 July	59
F10-B	2008	Female	Breeder	26 March–27 June	57
F11-B	2008	Female	Breeder	26 March–02 June	45
F12-B	2008	Female	Breeder	17 April–28 July	57
F13-B	2008	Female	Breeder	24 April–28 July	63
F14-B	2008	Female	Breeder	24 April–28 July	60
M13-F	2008	Male	Floater	13 April–28 July	53
M14-F	2008	Male	Floater	15 April–27 July	43
M15-F	2008	Male	Floater	28 March–23 July	38
M16-B	2009	Male	Breeder	18 March–22 July	52
M17-B	2009	Male	Breeder	21 April–15 July	44
M18-B	2009	Male	Breeder	20 March–21 July	55
F15-B	2009	Female	Breeder	7 April–15 July	45
F16-B	2009	Female	Breeder	21 March–05 June	41
M19-F	2009	Male	Floater	21 March–23 July	43
M20-F	2009	Male	Floater	7 April–21 July	47
F17-F	2009	Female	Floater	8 April–06 July	41
F18-F	2009	Female	Floater	6 April–21 July	66

Table 2

Environmental variables measured for the home ranges of 38 Black kites and 38 randomly generated home ranges. Variables were later pooled into a smaller number of descriptors used for analysis (see Methods).

Variable	Description
%Water	%Extent of water bodies excluding the seasonal marshland
%Ricepounds	%Extent of rice fields
%Farmland	%Extent of intensively managed farmland
%Dumps	%Area occupied by rubbish dumps
%Dunes	%Extent of mobile sand dunes
%Marshland	%Seasonally drying marshland
%Dehesa	%Grassland or scrubland with scattered oak trees
%Scrubland	%Mediterranean scrubland (matorral)
%Pineforest	%Extent of pinewoods
%Eucalyptus forest	%Extent of <i>Eucalyptus</i> woodland patches
%Oakwood forest	%Extent of patches of cork oak woodland
%Woodland	%Extent of total woodland excluding pine, cork oak and <i>Eucalyptus</i> forest
%Greenhouses	%Extent of strawberry greenhouses
%Urbanareas	%Extent of urban areas

factor, individuals of all age and sex categories were tracked simultaneously (Table 1). We assume that such temporal overlap prevented biases associated with seasonal changes in habitat selection. To reduce collinearity and the number of variables presented to multivariate models, we employed the method of variable reduction proposed by Green (1979) and commonly employed in habitat selection studies (e.g. Sergio et al., 2003; Zuur

et al., 2009). In this method, pairs of strongly intercorrelated variables ($r > 0.6$) were 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 ($p < 0.05$) were detected between real and random locations were included in multivariate analyses. When building GLMs and LMMs, all explanatory variables were fitted to a (maximal) model, extracted one at a time from such maximal model and the associated change in model deviance assessed by a likelihood ratio test (Zuur et al., 2009). At each step, we also calculated the AICc (Akaike Information Criterion adjusted for small sample size) and considered as the final model the one with the lowest AICc value (Burnham and Anderson, 2002). All statistics were implemented with the software R 2.9.2. (R Development Core Team, 2009) and all GLMs and LMMs were built through the *glm* and *lme* functions of the library (nlme). Before analysis, all proportions of land cover types were arcsine square root transformed to conform to a normal distribution. All means are given ± 1 SE, tests are two-tailed and statistical significance was set at $p \leq 0.05$.

3. Results

3.1. Home range analysis

The mean home range size for the pooled sample of individuals was $153.3 \pm 28.6 \text{ km}^2$ (MCP; range = 7.6–688.4 km^2 , $n = 38$). For all methods of estimation, home range size varied among individuals

Table 3

Mean estimates of home range size for male and female, breeding and floating Black kites in Doñana National Park (South-Western Spain). All ranges are measured in km distances in metres.

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	Breeding males (range)	Breeding females (range)	Floater ^a (range)	F ^b	p
Minimum Convex Polygon	80.0±13.9(23.4–164.5)	43.3±11.6(7.6–151.5)	310.2±54.9(104.8–688.4)	31.2	0.001
Kernel 50%	5.5±1.0(1.1–11.7)	2.7±0.6(0.7–9.2)	28.2±7.4(8.1–107.2)	35.1	0.001
Kernel 75%	13.4±2.9(2.3–33.6)	6.0±1.6(1.7–21.7)	83.0±21.7(20.1–326.0)	40.7	0.001
Kernel 95%	51.8±11.7(6.9–136.7)	17.9±4.2(5.0–58.0)	257.0±58.6(72.6–762.0)	39.8	0.001
Distance to centroid	2751.3±332.5(1209.0–4376.0)	1531.3±225.1(633.4–3278.5)	5738.8±554.7(3736.0–10715.5)	35.5	0.001

^a Includes both males and females; the sample size was too small for testing sexual differences in floaters.

^b F-statistic from a one-way ANOVA.

of different sex and status: ranges were consistently largest for floaters, smallest for breeding females and intermediate for breeding males (Duncan's post hoc test, $p < 0.05$; Table 3). On average, floater ranges were 4–8 times larger than those of breeders. Similarly, the mean distance of all the radio-locations of an individual from the centroid of its range was largest for floaters, intermediate for breeding males and shortest for breeding females (Duncan's post hoc test, $p < 0.05$; Table 3).

3.2. Larger scale habitat selection: whole home range level

Compared to random home ranges, those of breeding males had larger amounts of dehesa and marshland, and a lower incidence of farmland, while those of breeding females had more scrubland and less cultivation (Table 4). Finally, floater ranges had more marshland and scrubland than random ranges (Table 4).

3.3. Finer scale habitat selection: individual locations

Similar results were obtained when focusing on the habitat composition in the 100m buffers around each location (Table 5). Compared to random locations, breeding males positively selected the marshland, dehesa and scrubland, while avoiding woodland and farmland (Fig. 2). Breeding females avoided cultivated fields and positively selected the marshland, dehesa and scrubland, while floaters positively selected the marshland, dehesa and scrubland, while avoiding farmland (Fig. 2).

Table 4

Generalised linear models (with binomial errors and a logit link function) discriminating between the home ranges occupied by radio-tracked Black kites and an equal number of randomly generated ranges. Models were built separately for: (a) 12 breeding males, (b) 12 breeding females, (c) 14 non-breeding individuals (Doñana National Park, south-western Spain).

Most competitive model	Parameter estimate ± SE	t-Value	p-Value
<i>(a) Male's occupied range vs. random range (n=24)</i> ^b			
Marshland ^a	5.64±3.67	29.32	0.047
Dehesa ^a	18.55±9.85	22.29	0.008
Farmland ^a	-18.02±11.02	17.22	0.024
Intercept	9.73±5.49		
<i>(b) Female's occupied range vs. random range (n=24)</i> ^b			
Marshland ^a	1.18±3.04	33.22	0.825 [*]
Dehesa ^a	2.69±3.35	21.95	0.050
Scrubland ^a	6.57±3.86	25.78	0.006
Farmland ^a	-10.63±6.04	17.17	0.029
Intercept	4.52±3.96		
<i>(c) Floater's occupied range vs. random range (n=28)</i> ^c			
Marshland ^a	18.32±8.59	27.98	0.001
Scrubland ^a	21.90±10.07	11.90	<0.001
Intercept	18.32±7.98	38.82	

^a Proportion of each habitat in a home range (arcsin square-root transformed for analysis).

^b Includes the home ranges of 12 breeders and their 12 associated random ranges.

^c Includes the home ranges of 14 floaters and their 14 associated random ranges.

^{*} Included in the model with the lowest AICc value.

Table 5

Generalised linear models (with binomial errors and a logit link function) discriminating between the 100m buffers around the locations of radio-tracked Black kites and an equal number of randomly generated locations. Models were built separately for: (a) 12 breeding males, (b) 12 breeding females, (c) 14 non-breeding individuals (Doñana National Park, south-western Spain). In the table, n refers to the number of radio-locations.

	Parameter estimate ± SE	t-Value	p-Value
<i>(a) Male's used vs. random locations (n=1108)</i>			
Marshland ^a	0.22±0.07	-3.32	0.0009
Dehesa ^a	0.24±0.07	-3.60	0.0003
Scrubland ^a	0.22±0.07	-3.33	0.0009
Woodland ^a	-0.13±0.07	1.95	0.0509
Farmland ^a	-0.24±0.07	3.52	0.0004
Intercept	-0.69±0.10	6.87	<0.001
<i>(b) Female's used vs. random locations (n=1320)</i>			
Marshland ^a	0.24±0.03	-8.71	0.0405
Dehesa ^a	0.33±0.03	-10.59	0.0015
Scrubland ^a	0.31±0.03	-10.75	0.0038
Farmland ^a	-0.15±0.03	4.75	0.0041
Intercept	-0.80±0.04	20.94	<0.001
<i>(c) Floater's used vs. random locations (n=1532)</i>			
Marshland ^a	0.30±0.02	-12.67	<0.001
Dehesa ^a	0.07±0.03	-2.13	0.0264
Scrubland ^a	0.26±0.03	-9.29	<0.001
Farmland ^a	-0.13±0.02	5.27	0.0475
Intercept	-0.66±0.03	19.97	<0.001

^a Proportion of each habitat in a 100m buffer around each location (arcsin square-root transformed for analysis).

4. Discussion

During the first few years of life, the floaters of solitary raptors, such as many eagles, often live in so called temporary settlement areas, which can be spatially separate and often far away from breeding areas (e.g. Ferrer, 1993; Balbontín, 2005; Caro et al., 2011). As a consequence, identifying and protecting suitable settlement areas requires major study efforts and can be extremely challenging (Penteriani et al., 2005). Contrary to this pattern, our study focused on a semi-gregarious species in which floaters, which were mainly young individuals in their initial 1–7 years of life (Blas et al., 2009; Blas and Hiraldo, 2010), closely co-existed with territory holders. It is difficult to say whether such radical difference among studies was exclusively caused by the social propensity of our species, but it would be extremely interesting to test whether the same pattern is found in other species of both groups (i.e. solitary breeding vs. colonial or loosely colonial species) and in other bio-geographic regions. Independently of their cause, these results complete and extend our knowledge on the habitat and space requirements of raptor floaters, up to now heavily biased towards solitary species with spatially separate floaters and breeders sectors of a population.

Besides generalised local coexistence, the larger home ranges of floaters caused a marked ranging overlap with breeders (e.g. Fig 3

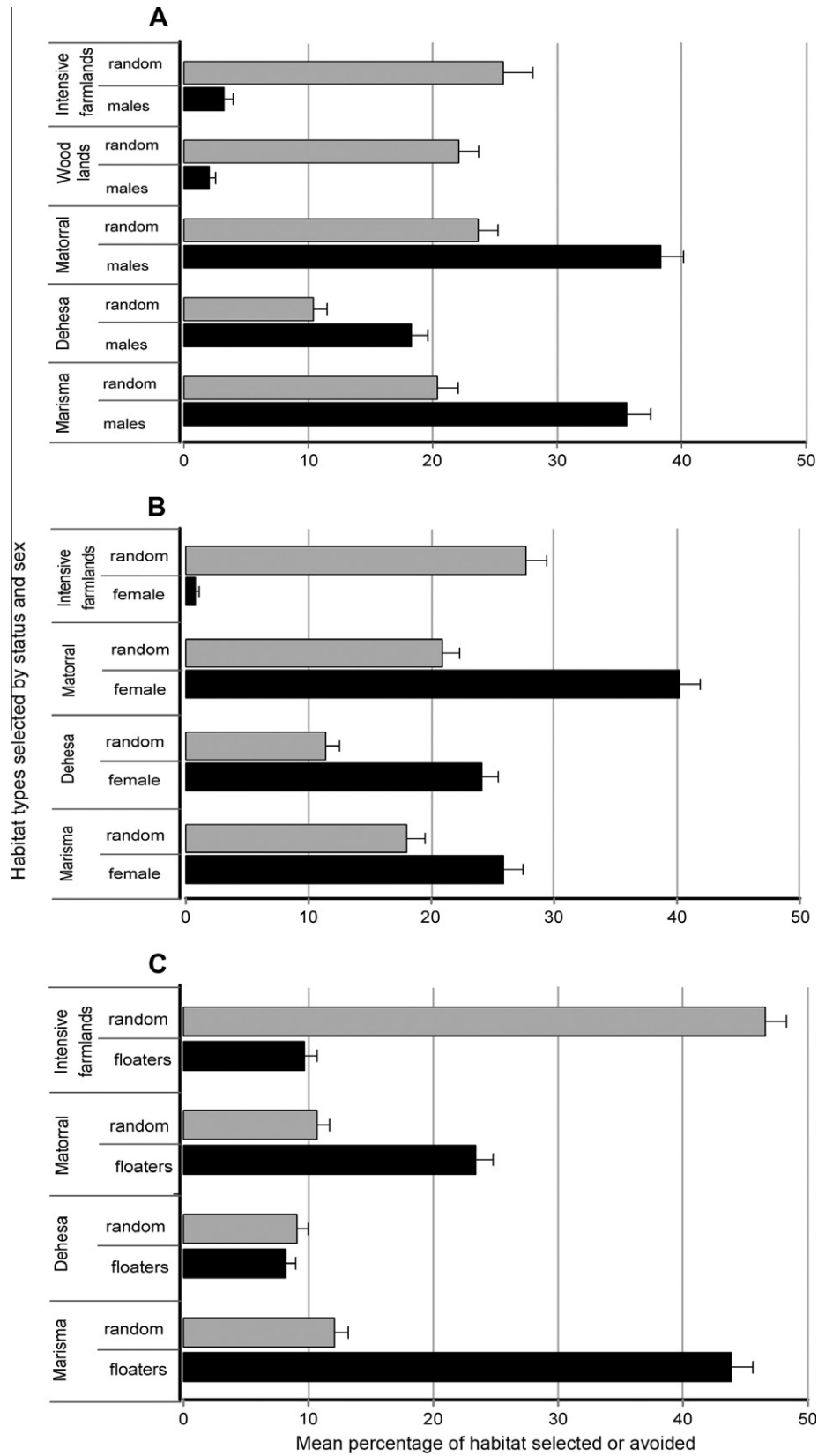


Fig.2. Meanpercentagefrequencyofhabitatsobservedaround1980radio-locationsofBlackkitesandaroundanequalnumberofrandomlygeneratedlocationsinDoñana National Park(South-WesternSpain).

andunpublishedresults).Suchextremelylargeareasusedbykite floaterswerepossiblypromotedbyacombinationofseveral factors.First,floatersarenotcentralplaceforagersandarethusfreer

tomovethanbreeders(e.g. CarreteandDonazar,2005;Guixéand Arroyo,2011).Second,floatersmayroamoverlargeareas toseek territoryvacancies, test the breeders' ability to defend their

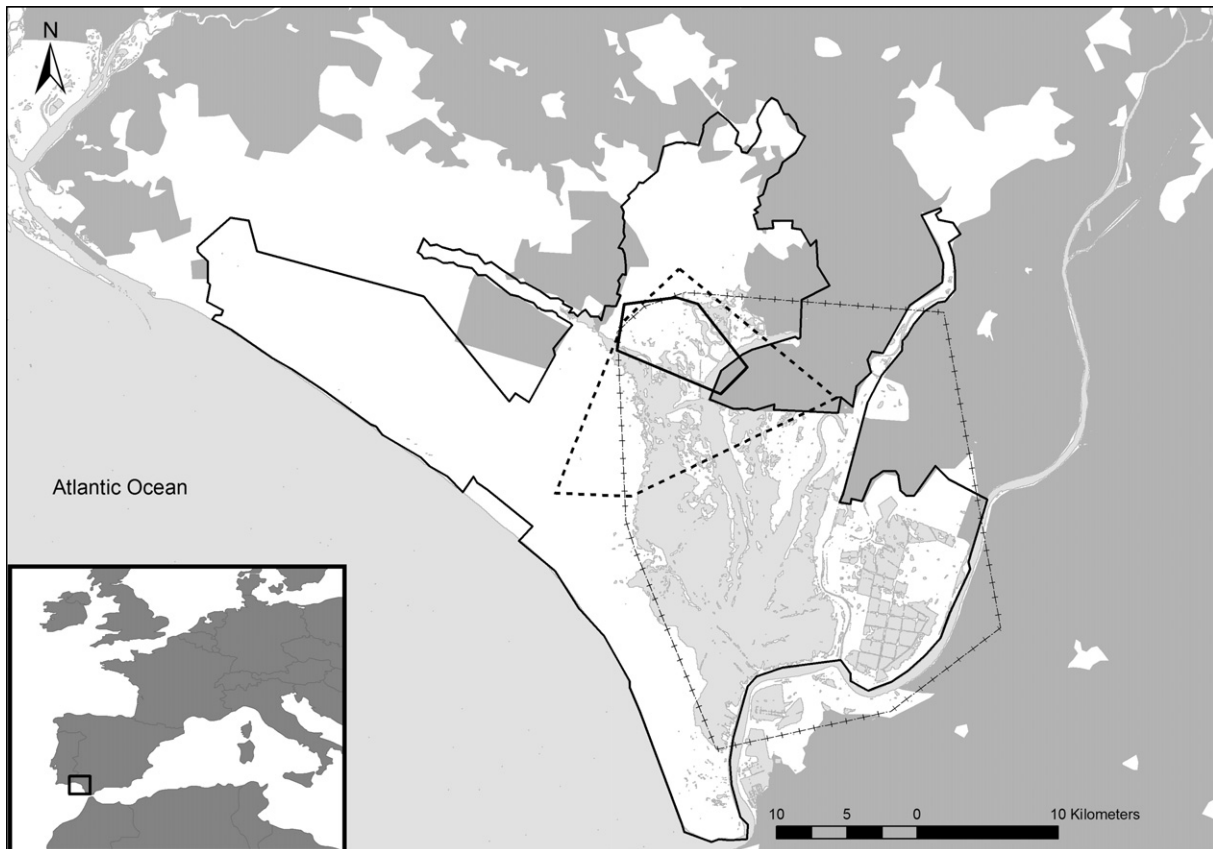


Fig. 3. Representative example of three home-ranges of Black kites of different sex and status in Doñana National Park (South-Western Spain) and its surroundings. The park location in Europe is portrayed in the inset. The solid black line represents the (smallest) home range of a breeding female, the black dotted line represents the (intermediate-sized) home range of a breeding male and the grey line with crosses represents the (largest) home range of a floater. The thin black line depicts the boundaries of the cumulated National and Natural Park (marine portion excluded). The seasonal marshland is shown in pale grey and intensive farmland in dark grey.

territories, and gain information on habitat quality for future settlement (i.e., prospecting; Sergio and Penteriani, 2005; Whitfield et al., 2009a,b; Sergio et al., 2011a). Third, floaters are on average younger and less experienced than breeders, they could thus forage less efficiently and need larger areas than breeders to gather the same daily amount of food. All these ideas are currently under study through more radio-marking.

With regard to breeding Black kites, the smaller ranges we recorded were likely the result of central place foraging and the need for territory, mate and nest guarding. The home ranges of breeding females were about half the size of males, as expected in raptors where females are usually deputed to incubation, chick brooding and nest guarding (e.g. Newton, 1979; Arroyo et al., 2009).

Whatever the differences in the amplitude of home ranges, it is interesting that individuals of all status categories basically selected and avoided the same habitats. Black kites over-selected open semi-natural habitats (marshland, dehesa and scrubland), and avoided close-structured or cultivated habitats (woodland and farmland). Such patterns were highly consistent across spatial scales of analysis, adding confidence to our results. The preference for open habitats can be explained by the aerial hunting strategies of the species and the fact that the three over-selected habitats hold important populations of the main prey species, such as waterbirds and crayfish for marshland and rabbits for mosaics of dehesa and scrubland (e.g. Hiraldo et al., 1990; Viñuela and Veiga, 1997). Besides their value in terms of prey abundance and distribution, the homogeneous selection of these habitats across individuals may be promoted by the generalist and opportunistic feeding habits of the species, which can prey upon live animals from the

size of a mosquito to a 1-kg adult rabbit, and use all sources of carrion when available (authors' personal observation).

On the other hand, despite their opportunistic diet, all kites clearly avoided agricultural habitats, mainly represented by rice fields. Such avoidance pattern was interesting given the kites' general preference for aquatic habitats (Sergio et al., 2005) and given that rice fields are inundated when the natural marshes start to dry in late spring-summer. Active avoidance by Black kites was possibly related to the very intensive agricultural practices affecting large areas around the park, which usually involve the use of large amounts of broad-spectrum pesticides and herbicides well-known to depress the populations of invertebrate species such as crayfish, as well as reptiles, amphibians, mammals and birds (Lawler, 2001; Parson et al., 2010), all of which are potential prey for kites (e.g. Hiraldo et al., 1990; Viñuela and Veiga, 1997). The fact that intensive habitat transformations and farming deteriorate habitat quality and suitability for raptor populations has been shown by numerous studies (e.g. Tella et al., 1998; Sánchez-Zapata and Calvo, 1999; Thiollay, 2006), although relationships can be complex and some species have also been shown to thrive well in human-altered landscapes (e.g. Bird et al., 1996; Whitfield et al., 2006b).

4.1. Implications for conservation

The fact that kite breeders and floaters closely coexisted and showed similar habitat preferences opens interesting possibilities for conservation strategies. Establishing habitat management guidelines that simultaneously favour individuals of different

status would be relatively straightforward, and easier than in populations with separate breeding and settlement areas (e.g. Ferrer and Harte, 1997; Balbontín, 2005). In the future, it would be interesting to test how frequently breeders and floaters show similar habitat preferences in those cases in which they happen to coexist. On the other hand, the much larger ranges of floaters implied that they used areas outside the national park more frequently than breeders (e.g. Fig. 3), making them more susceptible to human-related disturbance, thus making their management more challenging (e.g. through higher potential exposure to illegal poisoned baits placed in private game reserves that surround the national park; Sergio et al., 2005; Tenan et al., 2012; authors' unpublished results).

To date, the scanty information on habitat and range selection by breeders and floaters of a raptor population has been mainly focused on large, solitary species with disjoint settlement areas which spatially separate the two sectors of the population. Our results extend this notion to cases where breeders and floaters spatially coexist with similar habitat preferences. In both cases, preserving the floater sector of a population, which may be a major achievement to ensure long-term population persistence (Penteriani et al., 2005), may present special challenges. On one hand, for solitary species with temporary settlement areas, identifying such sites may be difficult, labour intensive and duplicate the target surface in need of management. On the other hand, for social and semi-social species, coexistence may ease the identification of local targets, but the large ranges of floaters may make them amenable to different threats that may be subtle and difficult to identify without intensive study. For example, in a population of the loosely colonial Red kite (*Milvus milvus*), floaters coexisted with breeders but their wider ranging behaviour was proposed as the cause of their higher propensity to die by poisoning and electrocution (Tavecchia et al., 2012). Similarly, in a population located close to a large rubbish dump, Black kite floaters coexisted with breeders but with a diet more dominated by refuse, which may expose them to toxic substances and pathogens (Blanco, 1997; Blanco et al., 2007). Overall, independently of coexistence or spatial separation, the few data currently available suggest that the conservation of the floater sector of raptor populations will continue to be challenging and require special, ad hoc management plans. Finally, as more studies will appear, the two alternatives of complete spatial separation with differential habitat selection and full coexistence with shared habitat preferences are likely to emerge as the two extremes of a more gradual continuum of breeders–floaters spatial relations, each situation requiring locally fine-tuned conservation action.

As for the local Black kite population of Doñana National Park, the results of the foraging habitat analyses suggest a potentially beneficial effect of the recently implemented restoration project “Doñana 2005”, which converted some 50 km² of farmland (an avoided habitat) located inside the park to seasonal marshland (a preferred habitat) (García Novo and Marín Cabrera, 2005a). Further restoration of the vast expanses of marshland which were converted to agriculture through drainage in the 1960s, and which currently surround the park, would be desirable and probably beneficial to this and other more exigent species.

Acknowledgements

We thank F.J. Chicano, J.M. Giralt, and F.G. Vilches for help in the field. We sincerely thank D. Oro, P. Whitfield and two anonymous reviewers for their very detailed and illuminating comments that greatly improved a first draft of the manuscript. Part of this study was funded by Natural Research Ltd. and research projects CGL2008-01781 and CGL2011-28103 of the Ministerio de Ciencia e Innovación, JA-58 of the Consejería de Medio Ambiente de la Jun-

ta de Andalucía and by the Excellence Projects RNM 1790, RNM 3822 and RNM 7307 of the Junta de Andalucía.

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