

Food predictability determines space use of endangered vultures: implications for management of supplementary feeding

PASCUAL LÓPEZ-LÓPEZ,¹ CLARA GARCÍA-RIPOLLÉS, AND VICENTE URIOS

Vertebrate Zoology Research Group, CIBIO Research Institute, University of Alicante, Edificio Ciencias III, Apdo. 99, E-03080 Alicante, Spain

Abstract. Understanding space use of free-living endangered animals is key to informing management decisions for conservation planning. Like most scavengers, vultures have evolved under a context of unpredictability of food resources (i.e., exploiting scattered carcasses that are intermittently available). However, the role of predictable sources of food in shaping spatial ecology of vultures has seldom been studied in detail. Here, we quantify the home range of the Egyptian Vulture (*Neophron percnopterus*), a long-lived raptor that has experienced severe population decline throughout its range and is qualified as endangered worldwide. To this end, six adults were tracked by satellite telemetry in Spain during the breeding season, from 2007 to 2012, recording 10 360 GPS locations. Using Resource Utilization Functions, we assessed the topology of the Utilization Distribution, a three-dimensional measure that shows the probability of finding an animal within the home range. Our results showed how food availability, and principally, how food predictability, determines ranging behavior of this species. Egyptian Vultures showed consistent site fidelity across years, measured as the two- and three-dimensional overlap in their home ranges. Space use varied considerably within the home range and remarkably, places located far from nesting sites were used more frequently than some areas located closer. Therefore, traditional conservation measures based on establishing restrictive rules within a fixed radius around nesting sites could be biologically meaningless if other areas within the home range are not protected too. Finally, our results emphasize the importance of anthropogenic predictable sources of food (mainly vulture restaurants) in shaping the space use of scavengers, which is in agreement with recent findings. Hence, measures aimed at ensuring food availability are essential to preserve this endangered vulture, especially in the present context of limiting carrion dumping in the field due to sanitary regulations according to European legislation.

Key words: conservation; Egyptian Vulture; food predictability; home range; kernel density estimators; *Neophron percnopterus*; resource utilization functions; satellite telemetry; spatial ecology; utilization distribution; vulture restaurants.

INTRODUCTION

Vultures have suffered a dramatic decline worldwide, particularly in Asia and Africa as a consequence of human direct persecution, indirect poisoning to kill carnivores, and by the veterinary drug diclofenac (Ogada et al. 2012). In Europe, besides direct and indirect persecution, main threats include changes in livestock husbandry practices from traditional extensive grazing to an intensive industry, and especially, shortage of food supply as a consequence of European sanitary regulations due to an outbreak of bovine spongiform encephalopathy (BSE) in 2001 (Margalida et al. 2010). These caused changes in vultures' behavior (Zuberogoi-tia et al. 2010, 2013), decreased breeding success, and have increased mortality among younger age classes (review in Donázar et al. 2009, Martínez-Abraín et al. 2012).

Understanding space use of far-ranging animals, such as vultures, is crucial for conservation planning and, especially, to inform management decisions regarding endangered species (Bograd et al. 2010, Kertson and Marzluff 2011). The combination of recent advances in “biologging” technologies (i.e., the use of miniaturized animal-attached tags for studying animal's movements, behavior, physiology and/or environment) with latest analytical techniques has allowed us to make a quantum leap in the field of movement ecology (Kernohan et al. 2001, Nathan et al. 2008, Rutz and Hays 2009). Paradoxically, despite the endangered status of most vulture species, our knowledge about ranging behavior of scavengers is still very limited. Most of our current knowledge is based on the inference from field observations of marked animals, direct observations in particular areas (e.g., breeding territories, vulture restaurants, and migratory bottlenecks), and limited spatiotemporal tracking using VHF telemetry (Donázar 1993, DeVault et al. 2004). However, there is little information from continued long-term remote-tracking of individuals by

Manuscript received 24 October 2013; accepted 3 December 2013. Corresponding Editor: R. L. Knight.

¹ E-mail: pascual.lopez@uv.es

means of satellite telemetry (Meyburg et al. 2004, García-Ripollés et al. 2010, 2011, López-López et al. 2013, Monsarrat et al. 2013, Phipps et al. 2013).

Vultures are the only obligate vertebrate scavengers and have evolved under a context of unpredictability of food resources (i.e., exploiting scattered carcasses that are intermittently available; Ruxton and Houston 2004). They provide irreplaceable ecosystem services such as waste removal, nutrient recycling, and limiting the risk of disease transmission (DeVault et al. 2003, Ogada et al. 2012). This, coupled with their rapid decline worldwide, has led them to be qualified as priority species for conservation (Directive 2009/147/EC of the European Union on the Conservation of Wild Birds). The Egyptian Vulture, *Neophron percnopterus*, could be one of the species potentially most affected by changes in cattle management regime, mainly owing to its low competitive ability against other vultures (Cortés-Avizanda et al. 2010) and its low population size (García-Ripollés and López-López 2011). Therefore, the quantification of space use and the relationship between environmental features and ranging behavior is critical to achieve a better understanding of the spatial ecology of this scavenger. Moreover, this will ultimately help to inform management actions for its conservation.

The main goals of this study were to: (1) evaluate and quantify Egyptian Vultures' home range size during the breeding season; (2) investigate the relationship between space use and external factors (i.e., environmental variables) across years and within the breeding season, with particular emphasis on how food availability, and especially, how anthropogenic predictable sources of food, are determinants of space use and shape the home range; (3) analyze the degree of repeatability (i.e., site fidelity) in the patterns of space use of individuals, both between years and within the breeding season; and finally (4) derive management recommendations for environmental assessments, for the management of anthropogenic food subsidies, and ultimately, for conservation plans of scavengers species.

METHODS

Study species

The Egyptian Vulture is a long-lived, medium-sized raptor that has experienced severe population decline throughout its range and is endangered worldwide, according to the IUCN Red List (BirdLife International 2013). Reasons for this decline include disturbance at nesting sites, direct and indirect poisoning, electrocution by power lines, and reduced food availability due to changes in traditional farming practices (BirdLife International 2013). Spain, where 1452–1556 pairs were surveyed in 2008, holds 30–45% of the European population (Del Moral 2009). Egyptian Vultures feed mainly on carrion but occasionally take small vertebrates, eggs, and even feces (Ferguson-Lees and Christie 2001). They are territorial breeders, but roost communally on large trees and cliffs placed near suitable

foraging areas, which include dump sites, vulture restaurants, and livestock farms. The European continental populations are migratory and travel from their breeding grounds to wintering areas located in the Sahel region of Africa (Ferguson-Lees and Christie 2001, García-Ripollés et al. 2010).

Data collection

To quantify Egyptian Vultures' space use, we captured six adults at two vulture restaurants located in Castellón and Guadalajara provinces, Spain, and at ad hoc artificial feeding stations located within breeding territories from 2007 to 2009 (Fig. 1). We used bow-net traps baited with giblets to capture the birds. A 45-g solar-powered GPS tag from Microwave Telemetry (Columbia, Maryland, USA) was mounted in a backpack configuration and attached using cotton ribbon, designed to ensure that the harness would fall off at the end of the tag's life. The mass of the equipment, including the harness, metal ring, and tag, was below 3% of the bird's body mass, which is within recommended limits (Kenward 2001). The GPS tags were programmed to obtain GPS fixes every two hours during the breeding season (February–September) on a 16 hours ON/8 hours OFF duty cycle (06:00–22:00 hours, Greenwich Mean Time), which coincided with vulture activity during daylight hours. Data were retrieved and managed using the Satellite Tracking and Analysis Tool (Coyne and Godley 2005).

Only locations recorded during complete breeding seasons, i.e., since the arrival in Europe from the African wintering grounds (February–March) until the onset of autumn migration (August–September), were included in this study. Therefore, we discarded the data belonging to the breeding season in which birds were trapped. Data were filtered to exclude erroneous fixes (i.e., with 0–0 coordinates). Consecutive relocations at known roosting sites were included as only one independent fix to avoid a bias toward roosting areas in space use analyses (Seaman and Powell 1996, Kenward 2001). Nocturnal movements were also excluded because Egyptian Vultures do not forage during the nighttime (López-López et al. 2013).

Field visits to each territory were also regularly conducted (three to five times per breeding season) to confirm the presence of the individuals, courtship, breeding behavior, incubation, and eventually, to record breeding success (further details about field methods are available in García-Ripollés and López-López 2006).

For the general goals of this study, data for each breeding season were divided into three periods: (1) "pre-laying period," which spanned from the arrival at breeding areas until egg laying (March–April); (2) "incubation + nestling period," which comprised 42 days of incubation (Ferguson Lees and Christie 2001) and the period in which nestlings remained in the nest just before their first flights (April to late July early August) (75 days, on average; Donazar and Ceballos

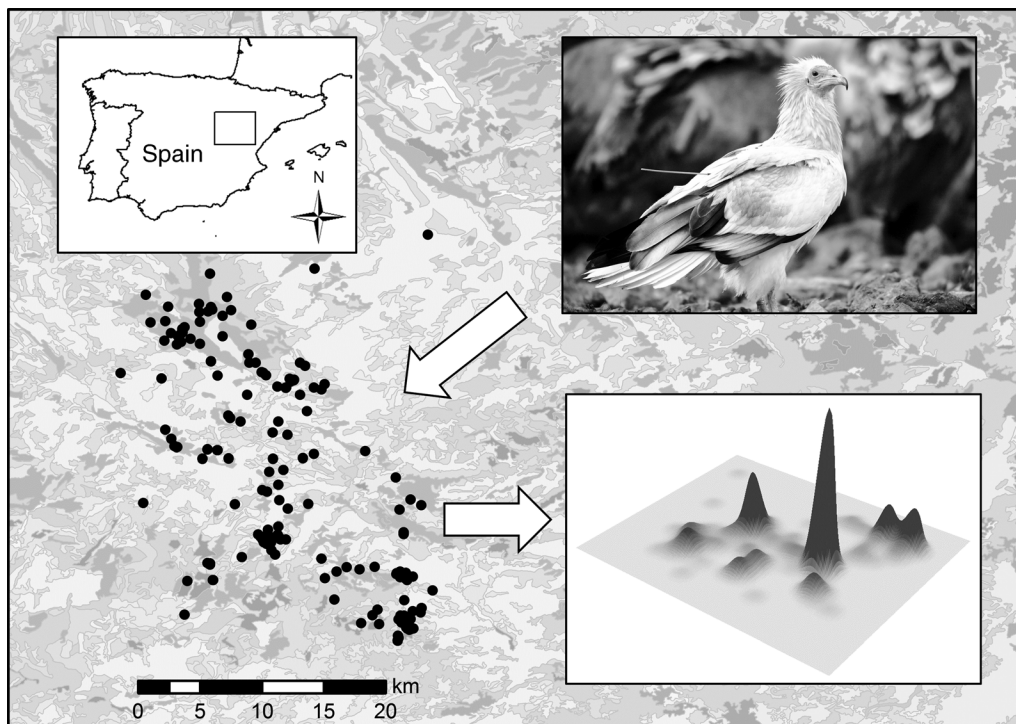


FIG. 1. Study area within the Iberian Peninsula (upper left rectangle) and flow chart of the methods used in this study. Satellite fixes (black circles, lower left) were recorded for each Egyptian Vulture (upper right; photo credit: Valentín Moreno) tracked by GPS satellite telemetry and were used for computing home range size, spatial parameters, and their corresponding three-dimensional Utilization Distribution (UD, lower right). The height of the UD indicates the relative probability of use within the home range (Marzluff et al. 2004). Resource attributes (i.e., topography, land use, population, and food availability) were sampled on a cell-by-cell basis from resource maps within the UD (e.g., in this case, Corine land cover). These attributes were related to the height of the UD by means of multiple regression analysis adjusted for spatial autocorrelation, thereby obtaining the Resource Utilization Function, RUF (Marzluff et al. 2004); see *Methods* for details). Locations and UD shown here are illustrative of a particular example.

1989); and (3) “pre-migration period”, including the dependence period of juveniles until the onset of autumn migration to African wintering grounds (August–September). Egyptian Vultures nest in caves, so when birds began the incubation, the GPS started to send irregular GPS locations and several 0–0 coordinates, a clear indication that the GPS was not directly exposed to sunlight. This circumstance, followed by an immediate field visit, allowed us to estimate the egg-laying date with an error of ± 3 days.

Space use

We quantified Egyptian Vultures’ home range by means of fixed-kernel density methods (Worton 1989, Kenward 2001). To assess different levels of space use, we computed 95%, 75%, and 50% kernel density contours using the “Animal Movement” extension for ArcView 3.2 (Hooge and Eichenlaub 2000). The area encompassed within the 95% contour represents a standard measure of the home range, whereas the 50% kernel is usually considered a good indicator of the core area of activity (Seaman and Powell 1996; e.g., Campioni et al. 2013). We also included an intermediate

measure (i.e., 75% kernel) to achieve a balance between the entire home range and the areas most used. We used the least squares cross validation method (LSCV) to calculate the smoothing parameter (Silverman 1986), which produces an objective and accurate estimate of home range size (Silverman 1986, Seaman and Powell 1996). The combination of kernel density estimators through location-based kernels and LSCV offers an optimal combination of ecological and statistical validity (Cumming and Cornélis 2012). Additionally, we also calculated the “overall” home range as the minimum convex polygon (MCP) encompassing all relocations obtained for each bird (Worton 1989). This estimate, although it usually tends to overestimate the extent of the “true” home range (Seaman et al. 1999), was computed to facilitate comparisons with other studies and regions. Importantly, a preliminary analysis showed that there was no significant correlation between the four different measures of home range size (MCP and kernels 95%, 75%, and 50%) and the number of relocations obtained per individual (Appendix B: Table B1). This preliminary test of the effect of sample size on the home range size is critical because it allows the ruling

out of possible bias in the estimation of space use due to individual variability (Kernohan et al. 2001).

Spatial parameters

We calculated the average spider distance (SD) and the eccentricity (ECC) of home ranges, which both represent a measure of spread of the ranging area. SD is a linear indicator of the home range size and was calculated as the average distance from the arithmetic center of all relocations (ACL) to each particular relocation (Hooge and Eichenlaub 2000). The eccentricity of home ranges was calculated as the distance from the nest used in each particular year to the ACL, and was used to assess the extent to which the breeding area was centered on the home range (Bosch et al. 2010). Like measures of home range, spatial parameters did not correlate with the number of relocations per animal (Table B1, Appendix B).

Resource utilization functions analysis

Traditional resource selection analyses have been grounded in the comparison of resource use vs. resource availability (Manly et al. 2002). Resource use can be easily quantified as the number of locations recorded in each resource class, or as the proportional occurrence of a resource within home range (Marzluff et al. 2004). However, obtaining an adequate measure of resource “availability” becomes a problematic question (Thomas and Taylor 1990, Millsaugh et al. 2006). To overcome this problem, Marzluff et al. (2004) proposed an alternative, straightforward method based on relating resources to a probabilistic measure of space use, the so-called utilization distribution (UD). Basically, the UD is a probability density function obtained through kernel density analysis that shows the probability of finding an animal within the home range as a function of relocation points (Silverman 1986, Worton 1987, Kernohan et al. 2001). Therefore, we obtained the UD for the combination of each individual–year (i.e., overall breeding season, $N = 18$; e.g., #75657–2009) as well as for each individual–period–year ($N = 54$; e.g., #75657–pre-laying–2009) using the “Animal Movement” extension for ArcView 3.2 (Hooge and Eichenlaub 2000). The UD displays a three-dimensional measure of space use across the home range in which the height of the UD represents the probability of use at each pixel (Millsaugh et al. 2006); see Fig. 1. Then, following Marzluff et al. (2004), we related space use with resource use using resource utilization functions implemented in the “ruf” package (Handcock 2012) for R version 2.15.3 (R Core Team 2013). To that end, we sampled a set of environmental variables (i.e., resources) at each pixel of the UD and used multiple regression analysis to relate the UD height to these environmental predictor variables (Marzluff et al. 2004). Pixel size was determined by the smallest pixel size of the environmental variables (80×80 m), thereby increasing spatial resolution to the limit. The spatial extent of space use

was defined as the 99% fixed-kernel home range boundary (Marzluff et al. 2004, Kertson and Marzluff 2009). One of the main advantages of the RUF method is that it accounts for spatial autocorrelation by incorporating a Matern correlation function (Handcock and Stein 1993, Marzluff et al. 2004). The importance of each resource to variations in the UD (i.e., the measure of resource use) was indicated by the magnitude of the standardized coefficients of the RUFs (Marzluff et al. 2004). A complete review of the basics and a discussion of the pros and cons of RUFs can be found in Marzluff et al. (2004), Millsaugh et al. (2006), and Hooten et al. (2013).

Environmental variables

To extract landscape metrics and relate them to the measures of space use, we first created a sampling point grid that extended across the UD. This was done with the “Hawth Tools” extension (Beyer 2004) for ArcMap 9.2 (ESRI 2006). The UD was first sampled to extract the values of space use (i.e., the height of the UD). Then, four sets of environmental variables were measured: topography, land use, population, and food availability. We avoided sampling a large number of resources to prevent multicollinearity among predictor variables and inclusion of resources that could be biologically meaningless (Mac Nally 2000). Topographic variables included the measurement of the altitude of each pixel of the sampling grid through a digital elevation model (DEM) obtained from the Shuttle Radar Topography Mission with a resolution of 3-arc seconds (*available online*).² We also calculated the aspect, which was derived from the DEM and was categorized into five main classes (1, North; 2, East; 3, South; 4, West; 5, flat areas). The land cover layer was provided by the Corine 2000 Land Cover program (*available online*).³ Corine 2000 is divided into 44 land cover classes (i.e., third-level CORINE codes). We grouped them into four main categories: artificial surfaces (ART, codes 111–142), agricultural areas (AGR, 211–244), forests and semi-natural areas (FOR, 311–335), and wetlands, water bodies, and rivers (WAT, 411–523). The full Corine land cover legend is *available online* through the European Environmental Agency.⁴ Human population was obtained from the Spanish Statistical Office corresponding to the census conducted in 2011 (data *available online*).⁵ Population density was computed in “Spatial Analyst tools” of ArcMap joining the population database with a point shapefile including the 8117 municipalities of Spain. Finally, eight resource levels of food availability were used in the analyses. Seven resources, including the number of horses, goats, sheep, cows, pigs, rabbits, and

² <http://srtm.csi.cgiar.org/>

³ <http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2000-raster-2>

⁴ <http://www.eea.europa.eu/>

⁵ <http://www.ine.es/>

poultry per municipality were obtained from the publicly available Agricultural Survey carried out in Spain in 2009 (*available online*).⁶ Finally, we incorporated an environmental variable including the presence/absence of predictable sources of food within the area encompassed by the full extension of all home ranges. This resource level included supplementary feeding places (i.e., vulture restaurants managed by the administration), dumping sites, poultry waste treatment plants, and cattle pens where cattle give birth their young. This layer was created and integrated into a raster data set by combining information from different Spanish regional environmental administrations and specific fieldwork conducted throughout the study period. All samplings of resources were computed in Geospatial Modelling Environment software (Beyer 2012).

Site fidelity

To quantify site fidelity of individuals across years and between periods of the breeding season, we calculated the two- and three-dimensional home range overlap (Kernohan et al. 2001) in ArcMap following Kertson and Marzluff (2009). Two-dimensional overlap provides a basic measure of site fidelity, regardless of habitat use within the home range (Fieberg and Kochanny 2005). Furthermore, three-dimensional overlap takes into account differential probabilities of space use and quantifies site fidelity by means of the UD (Fieberg and Kochanny 2005). Further details about specific formulae used for this analysis are available in Appendix A. In both cases, site fidelity was tested at the individual level (i.e., within individuals). Between-individual overlap of home ranges was not computed. Measures of two- and three-dimensional overlap are given as percentage \pm standard deviation and range.

Statistical analysis

Space use and spatial parameters were analyzed considering two temporal scales: (1) an “overall timescale” including each complete breeding season and (2) a “seasonal timescale” divided into “pre-laying,” “incubation + nestling,” and “pre-migration” periods, separately (for a similar approach, see Campioni et al. 2003). The overall scale allowed us to provide a general estimation of Egyptian Vultures’ spatial ecology and the seasonal scale enabled us to account for potential variations in space use within the breeding period.

First, we used the Shapiro-Wilk normality test to determine whether measures of home range size and spatial parameters were normally distributed. Because these variables did not follow a normal distribution, descriptive results are given in median \pm interquartile range (Gotelli and Ellison 2004). Next, because we had repeated measures for the same individual between and within years, we analyzed overall and seasonal differ-

ences in home range size, spatial parameters, standardized RUF coefficients, and site fidelity by means of linear mixed models, LMMs (Zuur et al. 2009). Differences between sexes were not tested due to limited sample size. The variables “seasonal period” and “year” were included as fixed effects and the “individual” was incorporated as a random effect. In order to find the best model structure, we followed the top-down strategy suggested by Zuur et al. (2009). Initially, we fitted a full factorial model (“beyond optimal model” sensu Zuur et al. 2009), and then we tried different models, varying the structure of fixed effects. These models were compared using the maximum likelihood estimation. Finally, having selected the best structure of fixed effects, we presented the best model using the restricted maximum likelihood estimation (Zuur et al. 2009). Models were validated by checking for homoscedasticity and normality of the residuals. To that end, relevant model diagnostic graphs were computed (residuals against fitted values, residuals against each explanatory variable, histogram of residuals, and normality Q–Q [quantile–quantile] plots; Zuur et al. 2009). When required, variables were previously log-transformed to meet the assumptions of LMMs. For models including individual as the random term, we reported the intra-class correlation coefficient (ICC), which measures the correlation between observations from the same individual and can be interpreted as a measure of consistency of the results (Bartko 1966). It was computed as $ICC = d^2 / (d^2 + \sigma^2)$, where d^2 is the covariance between any two observations for the same individual and its variance is $d^2 + \sigma^2$ (Zuur et al. 2009). Thus, higher ICC values indicate higher evenness among observations of the same individual. Moreover, we also reported a generalized R^2 for the random effect, calculated as the squared correlation between the fitted values of the model and the observed values of the data (Zheng and Agresti 2000). This value provides information about the amount of variation in the data explained by the random effect (i.e., between-individual variation); see Campioni et al. (2013). Computations were run with the “nlme” extension for R (Pinheiro et al. 2013).

We compared individual standardized RUF coefficients in order to rank resource use at both overall and seasonal scales. Relative importance of resources was evaluated by the magnitude (i.e., positive or negative sign) of the standardized RUF coefficients (Marzluff et al. 2004, Millspaugh et al. 2006). To test for consistency in selection of resource use at the population level, we tested the null hypothesis that the average β was zero (see Marzluff et al. [2004] for a complete description of this method). In addition, for the combination of each individual–period–year–resource category, we ranked the models including topography, land use, population, and food availability (including food predictability) resources by means of the Akaike information criterion (Burnham and Anderson 2002). Statistical analyses were

⁶ <http://www.ine.es/jaxi/menu.do?type=pcaxis&path=%2Ft01%2Fp042/E01&file=inebase&L=1>

TABLE 1. Home range size and spatial parameters (median with IQR in parentheses) of six adult Egyptian Vultures (*Neophron percnopterus*) tracked by GPS satellite telemetry in Spain over different periods.

Parameter and units	Pre-laying	Incubation + nestling	Pre-migration	Overall breeding season
MCP (km ²)	272.9 (170.6–1701.8)	582.6 (435.9–741.7)	526.4 (370.0–1997.3)	1257.0 (745.2–3954.4)
K95% (km ²)	262.5 (205.1–2313.8)	210.7 (125.4–254.8)	303.9 (131.3–2708.3)	253.3 (201.7–1669.9)
K75% (km ²)	143.6 (75.0–1171.5)	51.4 (22.3–83.3)	76.3 (47.2–1037.0)	101.2 (62.9–660.6)
K50% (km ²)	72.8 (43.2–649.9)	15.9 (11.9–33.5)	37.4 (26.3–555.5)	46.6 (26.4–343.7)
SD (m)	13 489.9 (8723.4–45 118.2)	8219.8 (7037.8–14 038.9)	11 144.4 (8512.7–36 675.9)	15 453.6 (12 098.2–30 980.1)
ECC (m)	17 435.2 (7177.5–26 750.3)	4828.0 (3471.4–9420.2)	7499.2 (4810.4–20 795.2)	10 400.8 (7627.3–14 731.0)

Notes: Abbreviations are IQR, interquartile range; MCP, minimum convex polygon; K, fixed-kernel density; SD, spider distance; ECC, eccentricity. Surface units (MCP and kernels) are expressed in square kilometers, and distance units (SD and ECC) in meters. In all cases, $N = 18$ (i.e., six individuals per three periods and 18 breeding seasons overall).

performed using STATISTICA version 10.0 (StatSoft 2010). Statistical significance was set at $P < 0.05$.

RESULTS

Overall, 10 360 valid GPS fixes were used for analyses, with a mean \pm SD of 1727 ± 856 relocations/bird (range 643–2689). All birds were territorial breeders according to fieldwork. One bird (transmitter code #75657) was tracked during five consecutive breeding seasons (2008–2012), three individuals (#80420, #89730, and #89731) were tracked during three breeding seasons (2010–2012), and two birds (#75659 and #80419) were tracked during two breeding seasons (2009–2010 and 2010–2011). According to molecular sexing, two birds were males (#80420 and #89731) and four birds were females (#75657, #75659, #80419, and #89730).

Home range size

Descriptive values of home range size and spatial parameters are available in Table 1. At the overall timescale, median size of home range areas ranged from 47 km² (core area) to 101 km² (kernel 75%), 253 km² (kernel 95%), and 1257 km² (MCP). At this scale, home range size and spatial parameters did not show interannual variations (i.e., the variable “year” was not included in the best LMMs), thus showing evenness in ranging behavior across years. At the seasonal timescale, home range sizes according to kernel 95% (K95), kernel 75% (K75), and kernel 50% (K50) were significantly lower during the “incubation + nestling” period (Fig. 2). The MCP size did not vary among periods. Moreover, we observed high intra-individual consistency in home range size ($ICC_{MCP} = 0.36$; $ICC_{K95} = 0.42$; $ICC_{K75} = 0.36$; $ICC_{K50} = 0.29$) and moderate levels of between-individual variation ($R^2_{MCP} = 0.55$; $R^2_{K95} = 0.65$; $R^2_{K75} = 0.64$; $R^2_{K50} = 0.60$).

Similar results were observed for spatial parameters. The measures of SD and ECC were significantly lower during the incubation + nestling period in comparison with the other two periods. Again, there was large intra-

individual consistency in spatial parameters ($ICC_{SD} = 0.39$; $ICC_{ECC} = 0.26$) and intermediate levels of between-individual variation ($R^2_{SD} = 0.51$; $R^2_{ECC} = 0.48$). In all cases, validation results showed nonsignificant deviation of residuals from a normal distribution ($P > 0.05$ in all Shapiro-Wilk tests). Model validation graphs of LMMs are available in Appendix B: Figs. B1–B8). Remarkably, all birds’ home ranges were eccentric both at overall and at seasonal timescales, indicating that breeding sites were not located in the center of the home range (Table 1).

Predictors of space use

According to model ranking for the combination of each individual–period–year–resource category, the RUF analysis showed that the best predictors of space use at the individual level were those models including food variables, which were ranked first in 75.00% of cases. Models including population, topography, and land-use predictors were ranked first in 15.28%, 5.56%, and 4.69% of cases, respectively (Fig. 3).

At the population level, the results of RUFs showed that Egyptian Vultures had increased space use in areas within the home range where food availability was higher, especially during the incubation + nestling period (Table 2). Particularly, in this period, Egyptian Vultures preferred areas with high density of sheep and poultry and avoided areas with high concentrations of horses, cows, and pigs. During the pre-laying period, Egyptian Vultures avoided areas of higher altitude, and during the incubation + nestling period, vultures decreased space use in southern-oriented areas. Importantly, the occurrence of predictable sources of food was the only predictor of space use that was positively selected in all three seasons (pre-laying, $P = 0.002$; incubation + nestling, $P = 0.002$; pre-migration, $P = 0.014$; Table 2). These results showed high consistency at the population level, thus showing that food predictability plays a key role in shaping the UD for Egyptian Vultures.

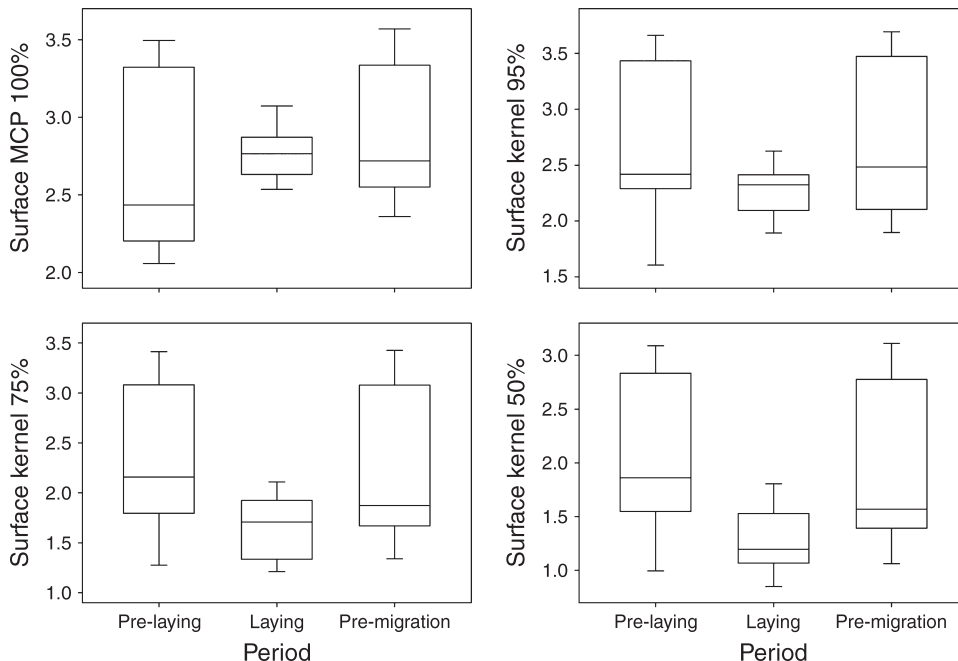


FIG. 2. Boxplots of log-transformed home range size of adult Egyptian Vultures (*Neophron percnopterus*) satellite-tracked in Spain. Home range was quantified by means of the minimum convex polygon (MCP) and fixed-kernel density methods (see *Methods: Space use* for computational details). Horizontal lines show the median, box ends are the 25th and 75th percentiles, and whiskers show 5th and 95th percentiles. Pre-laying spanned arrival at breeding areas until egg laying (March–April); laying (incubation + nestling period) included 42 days of incubation and ~75 days in which nestlings remained in the nest just before their first flights (April to late-July or early August); and pre-migration was the period from juvenile dependence until the onset of autumn migration to African wintering grounds (August–September). Home range size was significantly lower during the incubation + nestling period (except for MCP, encompassing all relocations obtained for each bird). See *Results: Home range size* for details.

When standardized RUF coefficients were compared individually among seasons, results of LMMs showed that Egyptian Vultures showed a clear preference for areas where predictable food resources and sheep density were higher (for food predictability, model estimate ± SE = 3.869 ± 1.652, *P* = 0.019; for sheep, model estimate ± SE = 4.001 ± 1.652, *P* = 0.016). The other standardized RUF coefficients did not show differences at the seasonal timescale (Appendix B: Table B2). At the overall timescale, LMMs did not converge to a significant model, thus indicating that no relevant differences in measures of space use were detected across years.

Site fidelity

In relation to site fidelity, Egyptian Vultures showed a high level of two-dimensional home range overlap at the individual level across years and among periods of the breeding season. The percentage of overlap among seasonal periods (mean ± SD) was 68.02% ± 25.53% (range 0.03–100%, *N* = 126) and home range overlap within individuals across years was 72.76% ± 21.97% (range 4.21–100%; *N* = 42). No differences were observed in home range overlap either among seasonal periods (*SEAS*) or among years (*YR*) (all *P* > 0.05),

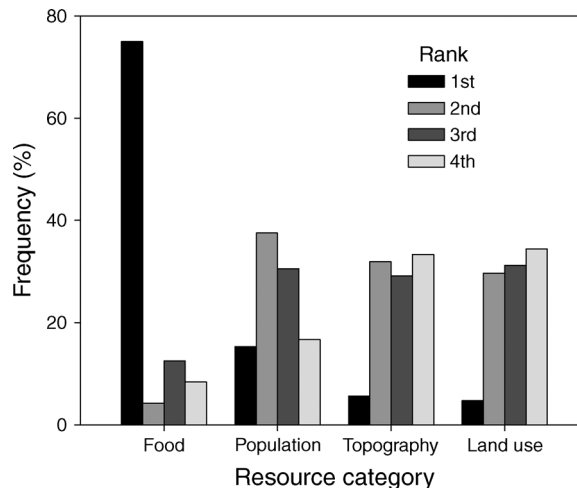


FIG. 3. Model rankings for each resource category according to Akaike Information Criterion. Differences in AIC (i.e., ΔAIC) were computed for the combination of each individual–period–year–resource category (*N* = 288 models). For example, models including the resource category “food” were ranked first in 75% of cases, 4% of cases in second place, 13% in third place, and 8% in fourth place.

TABLE 2. Estimates of standardized RUF (resource utilization function) coefficients (β , mean with 95% confidence limits in parentheses) and P values for six adult Egyptian Vultures tracked by GPS satellite telemetry in Spain over different periods.

Model and resource	Pre-laying		Incubation + nestling		Pre-migration		Overall breeding season	
	Standardized β	P	Standardized β	P	Standardized β	P	Standardized β	P
Topography	-0.318 (-0.609, -0.027)	0.033	-0.302 (-0.585, -0.019)	0.037	0.034 (-0.291, 0.360)	0.835	-0.070 (-0.191, 0.050)	0.247
ALT	-1.207 (-2.290, -0.124)	0.031	-0.777 (-1.907, 0.353)	0.165	0.183 (-1.179, 1.545)	0.780	-0.240 (-0.746, 0.265)	0.330
ASP1	-0.063 (-0.230, 0.104)	0.436	-0.246 (-0.515, 0.023)	0.071	0.023 (-0.085, 0.130)	0.662	0.013 (-0.033, 0.058)	0.564
ASP2	-0.054 (-0.275, 0.167)	0.613	-0.076 (-0.316, 0.164)	0.513	0.013 (-0.147, 0.174)	0.862	-0.024 (-0.052, 0.004)	0.090
ASP3	0.053 (-0.178, 0.284)	0.632	-0.109 (-0.210, -0.008)	0.036	-0.083 (-0.363, 0.197)	0.541	-0.030 (-0.076, 0.016)	0.185
Land use	-1.971 (-3.904, -0.037)	0.046	-0.721 (-1.778, 0.335)	0.174	0.083 (-0.721, 0.888)	0.835	-0.679 (-1.623, 0.265)	0.153
AGR	-1.760 (-4.148, 0.628)	0.137	-0.696 (-2.086, 0.693)	0.302	-0.184 (-1.195, 0.828)	0.706	-0.606 (-1.867, 0.655)	0.322
FOR	-2.182 (-5.521, 1.157)	0.184	-0.746 (-2.509, 1.016)	0.381	0.350 (-1.005, 1.705)	0.592	-0.752 (-2.312, 0.807)	0.320
Population, POP	1.038 (-1.270, 3.347)	0.356	0.315 (-1.270, 1.901)	0.680	-0.047 (-0.774, 0.681)	0.893	0.406 (-0.523, 1.335)	0.369
Food	-0.160 (-2.501, 2.180)	0.892	-0.189 (-1.367, 0.989)	0.752	-0.192 (-2.102, 1.717)	0.842	0.082 (-0.662, 0.826)	0.828
HOR	-3.661 (-8.351, 1.029)	0.118	-2.005 (-3.686, -0.324)	0.022	-0.094 (-2.738, 2.549)	0.941	0.205 (-0.182, 0.592)	0.279
GOAT	-9.168 (-19.409, 1.072)	0.076	-3.487 (-8.580, 1.605)	0.167	3.729 (-6.380, 13.838)	0.447	-2.528 (-6.429, 1.372)	0.189
SHEEP	5.998 (-2.870, 14.866)	0.172	3.272 (0.117, 6.428)	0.043	0.135 (-2.980, 3.250)	0.928	0.601 (-0.775, 1.976)	0.370
COWS	-5.566 (-12.074, 0.941)	0.089	-4.527 (-8.641, -0.414)	0.033	-2.209 (-7.672, 3.254)	0.405	-1.434 (-4.306, 1.438)	0.307
PIGS	1.176 (-2.867, 5.219)	0.547	-1.915 (-3.798, -0.032)	0.047	1.304 (-1.666, 4.275)	0.367	0.066 (-0.617, 0.749)	0.840
RABB	3.937 (-4.163, 12.037)	0.320	0.516 (-3.485, 4.516)	0.789	-5.312 (-14.791, 4.167)	0.253	1.966 (-0.702, 4.634)	0.138
POULT	1.705 (-3.872, 7.283)	0.527	3.370 (0.445, 6.294)	0.026	-0.541 (-4.732, 3.649)	0.788	0.998 (-1.157, 3.153)	0.342
PRED	4.296 (1.844, 6.749)	0.002	3.265 (1.372, 5.158)	0.002	1.449 (0.327, 2.571)	0.014	0.780 (-0.215, 1.775)	0.116

Notes: Abbreviations are ALT, altitude; ASP, aspect; AGR, agricultural areas; FOR, forests and seminatural areas; POP, human population density; HOR, horses; RABB, rabbits; POUL, poultry; PRED, predictable sources of food. Relative importance of resources is indicated by the magnitude (positive or negative) of mean standardized β (Marzluff et al. 2004). Consistency in selection at the population level is indicated by significance of β . Significant P values (testing the null hypothesis that the average $\beta = 0$; see Marzluff et al. 2004) are in boldface.

mainly due to important intra-individual variation in home range overlap in the intra-class correlation coefficient ($ICC_{SEAS} = 0.100$; $ICC_{YR} = 0.106$) and low levels of between-individual variation ($R^2_{SEAS} = 0.135$; $R^2_{YR} = 0.168$).

Considering the UD, the percentage of three-dimensional overlap among periods was $55.13\% \pm 16.10\%$ (range 15.81–81.91%, $N = 63$) and UD overlap across years was $67.72\% \pm 7.5\%$ (range 45.19–76.54%; $N = 21$). Significant differences were found in the degree of overlap at the seasonal timescale, which was higher during the incubation + nestling period (incubation + nestling, model estimate \pm SE = 0.129 ± 0.048 , $P = 0.009$). Between-individual variation in UD overlap was low ($R^2_{SEAS} = 0.113$). At the overall timescale, no differences were found in the degree of UD overlap across years. Intra-individual consistency in UD overlap

was high ($ICC_{YR} = 0.717$) and between-individual variation was moderate ($R^2_{YR} = 0.619$).

DISCUSSION

The amount of information available about animal movement is increasing exponentially, allowing for rapid advances in our understanding of spatial ecology of organisms (Cooke et al. 2004). We are now able to answer old questions (i.e., when, where, and how far animals move during their life) with novel information, by quantifying animals' home ranges, obtaining probabilistic measures of space use, and, ultimately, linking them with resource selection (Silverman 1986, Worton 1989, Kernohan et al. 2001, Marzluff et al. 2004). To the best of our knowledge, here we have provided the first quantitative assessment of the home range size of the Egyptian Vulture by means of GPS satellite telemetry. Our results showed greater home range size, as

calculated as MCPs or as according to fixed-kernel density estimators, than that reported in previous works. In fact, explicit works quantifying Egyptian Vulture's home range were lacking and data with which to compare our figures were usually immersed in other works about other aspects of the basic ecology of Egyptian Vultures. For example, home range size of a territorial adult tracked by radio-tracking in Spain was estimated as 21 km² (Ceballos and Donazar 1988) and 10–15 km² in a similar study conducted in Israel with 10 pairs and two trios (Levy 1990). Donazar (1993) reported a core area size between 0.07 and 0.37 km². Home range size of two nonbreeding adults ranged between 95 and 523 km² and was estimated at 40 km² for a nonbreeding immature (Donazar 1993). Differences between our figures and those provided by previous studies are easily accounted for by differences in the tracking methods, indicating that visual observation and radio-tracking tend to underestimate measures of home range size (Kenward 2001). Other authors estimated core area and home range size based on a circle with 1 km (3.14 km²) and 8 km (~200 km²) radii from the nest, respectively (Carrete et al. 2007), although these measures were set arbitrarily. The lack of accurate measures of Egyptian Vulture's home range could be explained by the difficulty in capturing adult birds. Hitherto, the majority of Egyptian Vultures marked have been nestlings, which usually remain in the floater population, with most of them in Africa (P. López-López, C. García-Ripollés, and V. Urios, *unpublished data*) until sexual maturity is attained, approximately at the age of five years (Grande et al. 2009).

Our results showed that home range size and spatial parameters did not vary across years, thus demonstrating repeatability in ranging behavior regardless of possible annual variations in ecological conditions. In contrast, home range was larger during the pre-laying and pre-migration periods than during the incubation + nestling period. All birds exhibited this common pattern, regardless of individual variations in the absolute size of their home ranges. Spider distances showed that birds reduced their foraging movements during the period in which they were more linked to the nest, probably to defend their territory and to avoid predation of their chicks by other raptors (Newton 1979). Interestingly, our results showed that Egyptian Vultures' home ranges were eccentric; that is, territories were not centered in the nest site. This has important implications from both an ecological and a conservation point of view. Ecologically, the main determinant of home range shape (i.e., according to the kernels' topology) was the spatial distribution of predictable sources of food. Similar results were described by Ceballos and Donazar (1988), who found that maximum distances traveled by a marked individual were determined by how far from its nesting site vulture restaurants were. Similar results have also been reported for the Eurasian Griffon Vulture *Gyps fulvus* (García-Ripollés et al. 2011,

Monsarrat et al. 2013). Remarkably, our results showed that, for all birds, places far from nesting sites (i.e., 20–30 km away) were used more frequently (i.e., had higher UD values) than some closer areas (e.g., <5 km away). This challenges common approaches in conservation that are based on the assessments of potential threats within a pre-fixed radius around nesting sites, which is set arbitrarily by researchers or by environmental authorities (Jennrich and Turner 1969). In fact, large-scale conservation assessments, analyses of habitat preferences, demographic analyses, and evaluations of extinction risk were based on this approach, although in most cases they lacked biological justification (e.g., Carrete et al. 2007, 2009, Grande et al. 2009). Therefore, although the "precautionary principle" could be argued for this practice (thereby at least part of the core area of activity is included), we urge that environmental risk assessments, conservation planning, and studies of resource selection should incorporate spatially explicit information and should be evaluated case by case, taking into account ranging behavior of the target species rather than relying on a fixed radius around nesting sites, which may miss additional areas of importance within the home range.

According to the RUF analysis, the best predictor of Egyptian Vulture space use at the individual level was the availability of food resources. This result was consistent both across years and within seasonal periods, with all individuals showing a similar pattern. Interestingly, at the population level, our results emphasized the importance of predictable sources of food in shaping the space use of this scavenger. Predictable sources of food included mainly vulture restaurants and, to a lesser degree, other places such as traditional dump sites, slaughterhouses, poultry waste treatment plants, and cattle pens where cattle are temporarily housed and give birth their offspring. In fact, Egyptian Vultures made long displacements daily or every two to three days to these places (in some cases up to 250 km outward-and-return), where they could easily fulfil feeding requirements. In the light of the ongoing debate about the advantages and shortcomings of supplementary feeding for vultures (Deygout et al. 2009, Donazar et al. 2009, Cortés-Avizanda et al. 2010, Dupont et al. 2012), our results highlight the importance of predictable sources of food in the trophic ecology and, consequently, in the preservation of this endangered scavenger. In addition, our findings also have an important conservation implication because predictable sources of food are potential predictors of the space use of scavengers (García-Ripollés et al. 2011, Monsarrat et al. 2013, Phipps et al. 2013). Therefore, managers could take advantage of this information and anticipate potential impacts of the construction of man-made structures (e.g., wind farms, power lines, and so forth) close to, or in the way of, these predictable sources of food. Conversely, managers can plan in advance the best location for vulture restaurants.

The magnitude of resource use by Egyptian Vultures varied between seasonal periods. Vultures increased space use in areas where food predictability was higher, especially during the pre-laying and pre-migration periods, probably to fulfil energy requirements after and before migration (García-Ripollés et al. 2010, López-López et al. 2013). Egyptian Vultures are territorial breeders, but show an important social behavior at these predictable sources of food, roosting communally nearby (Cortés-Avizanda et al. 2011). According to our fieldwork, in all cases communal roosting places were associated with predictable sources of food, particularly vulture restaurants. Communal roosting places play a key role in pair bonding, allowing the establishment of social relationships, and as information centers, where Egyptian Vultures could take advantage of a crowding effect (Cortés-Avizanda et al. 2011).

Conservation implications

Egyptian Vultures showed high levels of site fidelity according to both two- and three-dimensional overlap in their home range across years and among periods of the breeding season. A high degree of repeatability in space use indicates that ranging behavior does not change significantly over time; a similar pattern has also been reported for other raptors (Campioni et al. 2013). This is positive from the conservation point of view because it allows for the establishment of effective, long-term conservation measures if ecological conditions are not to change.

Like most scavengers, Egyptian Vultures are human-subsidized species nowadays, particularly in Europe (Deygout et al. 2009, Oro et al. 2013). Vulture restaurants are an essential conservation technique to preserve populations of endangered scavengers, always under adequate sanitary guarantees and with a controlled carrion disposal (Dupont et al. 2012). From an academic point of view, it is easily arguable that supplementary feeding management should mimic natural conditions, based on numerous “light” feeding stations supplemented with low quantities of food, thus simulating low predictability in food resources as it occurs in natural conditions (Cortés-Avizanda et al. 2010, 2012, Monsarrat et al. 2013). Policies to favor population recovery of wild herbivores and the authorization of the abandonment of livestock carcasses in the field can also be advocated to help to maintain populations of avian scavengers (Margalida et al. 2010). Notwithstanding, we consider that taking into account the current framework of highly subsidized cattle-raising in Europe, especially by the Common Agricultural Policy of the European Union (*available online*),⁷ the lack of generational turnover in cattle farmers, and the continuous process of abandonment of

traditional pastoralism (Bernués et al. 2011), conservation planning of endangered species should meet reality and be more pragmatic. Recent findings have shown that predictable anthropogenic food subsidies may help to increase population numbers of endangered species through reduction in the variance of demographic parameters (Oro et al. 2013). Predictable sources of food buffer the influence of environmental stochasticity (Cortés-Avizanda et al. 2012, López-López et al. 2013), thus increasing the time to extinction (Oro et al. 2013). Considering the key role of vulture restaurants in the space use of Egyptian Vultures, we advocate to keep them functioning to facilitate population increase of the Egyptian Vulture at least to a better conservation status.

ACKNOWLEDGMENTS

We thank L. Bolonio, J. De Lucas, V. García, R. Ibáñez, M. Nieto, and Á. Vela for their help during fieldwork. J. Marzluff, J. Zabala, and L. M. Carrascal gave important methodological and statistical advice. P. López-López is supported by a “Juan de la Cierva” postdoctoral grant of the Spanish Ministry of Economy and Competitiveness (reference JCI-2011-09588). The authors declare that they have no conflict of interest. This paper complies with the current laws in Spain.

LITERATURE CITED

- Bartko, J. J. 1966. The intraclass correlation coefficient as a measure of reliability. *Psychological Reports* 19:3–11.
- Bernués, A., R. Ruiz, A. Olaizola, D. Villalba, and I. Casasús. 2011. Sustainability of pasture-based livestock farming systems in the European Mediterranean context: Synergies and trade-offs. *Livestock Science* 139:44–57.
- Beyer, H. L. 2004. Hawth's analysis tools for ArcGIS. <http://www.spatial ecology.com/htools>
- Beyer, H. L. 2012. Geospatial modelling environment. Version 0.7.2.0. <http://www.spatial ecology.com/gme>
- BirdLife International. 2013. Species factsheet: *Neophron percnopterus*. <http://www.birdlife.org/datazone/dzstage/speciesfactsheet.php?id=3371>
- Bograd, S. J., B. A. Block, D. P. Costa, and B. J. Godley. 2010. Blogging technologies: new tools for conservation. *Introduction. Endangered Species Research* 10:1–7.
- Bosch, R., J. Real, A. Tintó, E. L. Zozaya, and C. Castell. 2010. Home-ranges and patterns of spatial use in territorial Bonelli's Eagles *Aquila fasciata*. *Ibis* 152:105–117.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach, Second edition. Springer, New York, New York, USA.
- Campioni, L., M. M. Delgado, R. Lourenço, G. Bastianelli, N. Fernández, and V. Penteriani. 2013. Individual and spatio-temporal variations in the home range behaviour of a long-lived, territorial species. *Oecologia* 172:371–385.
- Carrete, M., J. M. Grande, J. L. Tella, J. A. Sánchez-Zapata, J. A. Donazar, R. Díaz-Delgado, and A. Romo. 2007. Habitat, human pressure, and social behavior: partialling out factors affecting large-scale territory extinction in an endangered vulture. *Biological Conservation* 136:143–154.
- Carrete, M., J. A. Sánchez-Zapata, J. R. Benítez, M. Lobón, and J. A. Donazar. 2009. Large scale risk-assessment of wind-farms on population viability of a globally endangered long-lived raptor. *Biological Conservation* 142:2954–2961.
- Ceballos, O., and J. A. Donazar. 1988. Actividad, uso del espacio y cuidado parental de una pareja de alimocho (*Neophron percnopterus*) durante el periodo de dependencia de los pollos. *Ecología* 2:275–291.

⁷ http://europa.eu/pol/agr/index_en.htm

- Cooke, S. J., S. G. Hinch, M. Wikelski, R. D. Andrews, L. J. Kuchel, T. G. Wolcott, and P. J. Butler. 2004. Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology and Evolution* 19:334–343.
- Cortés-Avizanda, A., P. Almaraz, M. Carrete, J. A. Sánchez-Zapata, A. Delgado, F. Hiraldo, and J. A. Donazar. 2011. Spatial heterogeneity in resource distribution promotes facultative sociality in two trans-Saharan migratory birds. *PLoS ONE* 6:e21016.
- Cortés-Avizanda, A., M. Carrete, and J. A. Donazar. 2010. Managing supplementary feeding for avian scavengers: guidelines for optimal design using ecological criteria. *Biological Conservation* 143:1707–1715.
- Cortés-Avizanda, A., R. Jovani, M. Carrete, and J. A. Donazar. 2012. Resource unpredictability promotes species diversity and coexistence in an avian scavenger guild: a field experiment. *Ecology* 93:2570–2579.
- Coyne, M. S., and B. J. Godley. 2005. Satellite tracking and analysis tool (STAT): an integrated system for archiving, analyzing and mapping animal tracking data. *Marine Ecology Progress Series* 301:1–7.
- Cumming, G. S., and D. Cornélis. 2012. Quantitative comparison and selection of home range metrics for telemetry data. *Diversity and Distributions* 18:1057–1065.
- Del Moral, J. C., editor. 2009. El alimoche común en España. Población reproductora en 2008 y método de censo. SEO/BirdLife, Madrid, Spain. http://www.seo.org/wp-content/uploads/2012/04/31_alimoche.pdf
- DeVault, T. L., B. D. Reinhart, I. L. Brisbin, Jr., and O. E. Rhodes, Jr. 2004. Home ranges of sympatric Black and Turkey Vultures in South Carolina. *Condor* 106:706–711.
- DeVault, T. L., O. E. Rhodes, and J. A. Shivik. 2003. Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. *Oikos* 102:225–234.
- Deygout, C., A. Gault, F. Sarrazin, and C. Bessa-Gomes. 2009. Modeling the impact of feeding stations on vulture scavenging service efficiency. *Ecological Modelling* 220:1826–1835.
- Donazar, J. A. 1993. Los buitres ibéricos. *Biología y conservación*. J. M. Reyero, editor. Ediciones de la Naturaleza, Madrid, Spain.
- Donazar, J. A., and O. Ceballos. 1989. Growth rates of nestling Egyptian Vultures *Neophron percnopterus* in relation to brood size, hatching order and environmental factors. *Ardea* 77:217–226.
- Donazar, J. A., A. Margalida, and D. Campión. 2009. Vultures, feeding stations and sanitary legislation: a conflict and its consequences from the perspective of conservation biology. *Munibe* 29 (Suppl.). Sociedad de Ciencias Aranzadi, Donostia, Spain.
- Dupont, H., J. B. Mihoub, S. Bobbe, and F. Sarrazin. 2012. Modelling carcass disposal practices: implications for the management of an ecological service provided by vultures. *Journal of Applied Ecology* 49:404–411.
- ESRI. 2006. ArcMap 9.2 of ArcGIS. Environmental Systems Research Institute, Redlands, California, USA. <http://www.esri.com/>
- Ferguson-Lees, J., and D. A. Christie. 2001. *Raptors: birds of prey of the world*. A. and C. Black Publishers, London, UK.
- Fieberg, J., and C. O. Kochanny. 2005. Quantifying home-range overlap: the importance of the utilization distribution. *Journal of Wildlife Management* 69:1346–1359.
- García-Ripollés, C., and P. López-López. 2006. Population size and breeding performance of Egyptian Vulture (*Neophron percnopterus*) in eastern Iberian Peninsula. *Journal of Raptor Research* 40:217–221.
- García-Ripollés, C., and P. López-López. 2011. Integrating effects of supplementary feeding, poisoning, pollutant ingestion and wind farms of two vulture species in Spain using a population viability analysis. *Journal of Ornithology* 152:879–888.
- García-Ripollés, C., P. López-López, and V. Urios. 2010. First description of migration and wintering of adult Egyptian vultures *Neophron percnopterus* tracked by GPS satellite telemetry. *Bird Study* 57:261–265.
- García-Ripollés, C., P. López-López, and V. Urios. 2011. Ranging behaviour of non-breeding Eurasian Griffon Vultures *Gyps fulvus*: a GPS-telemetry study. *Acta Ornithologica* 46:127–134.
- Gotelli, N. J., and A. M. Ellison. 2004. *A primer of ecological statistics*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Grande, J. M., D. Serrano, G. Tavecchia, M. Carrete, O. Ceballos, R. Díaz-Delgado, J. L. Tella, and J. A. Donazar. 2009. Survival in a long-lived territorial migrant: effects of life-history traits and ecological conditions in wintering and breeding areas. *Oikos* 118:580–590.
- Handcock, M. S. 2012. Estimates of the resource utilization function. Version 1.5-2. <http://www.stat.ucla.edu/~handcock/ruf/>
- Handcock, M. S., and M. L. Stein. 1993. A Bayesian analysis of kriging. *Technometrics* 35:403–410.
- Hooge, P. N., and B. Eichenlaub. 2000. Animal movement extension to ArcView, Version 2.0. Alaska Science Center, Biological Science Office, U.S. Geological Survey, Anchorage, Alaska, USA. [http://alaska.usgs.gov/science/biology/spatial/gistools/index.php#animal movement](http://alaska.usgs.gov/science/biology/spatial/gistools/index.php#animal%20movement)
- Hooten, M. B., E. M. Hanks, D. S. Johnson, and M. W. Allredge. 2013. Reconciling resource utilization and resource selection functions. *Journal of Animal Ecology* 82:1146–1154.
- Jennrich, R. I., and F. B. Turner. 1969. Measurement of a non-circular home range. *Journal of Theoretical Biology* 22:227–237.
- Kenward, R. E. 2001. *A manual for wildlife radio tagging*. Academic Press, London, UK.
- Kernohan, B. J., R. A. Gitzen, and J. J. Millsbaugh. 2001. Analysis of animal space use and movements. Pages 125–166 in J. J. Millsbaugh and J. M. Marzluff, editors. *Radio-tracking and animal populations*. Academic Press, San Diego, California, USA.
- Kertson, B. N., and J. M. Marzluff. 2009. Animal movement, home range, and resource utilization function (ruf) analysis in ArcMap 9.3. School of Forest Resources, University of Washington, Seattle, Washington, USA.
- Kertson, B. N., and J. M. Marzluff. 2011. Improving studies of resource selection by understanding resource use. *Environmental Conservation* 38:18–27.
- Levy, N. 1990. *Biology, population dynamics and ecology of the Egyptian vultures, Neophron percnopterus, in Israel*. Thesis. Tel Aviv University, Tel Aviv, Israel.
- López-López, P., J. Benavent-Corai, C. García-Ripollés, and V. Urios. 2013. Scavengers on the move: behavioural changes in foraging search patterns during the annual cycle. *PLoS ONE* 8(1):e54352.
- Mac Nally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between—and reconciliation of—‘predictive’ and ‘explanatory’ models. *Biodiversity and Conservation* 9:655–671.
- Manly, B. F. J., L. L. McDonald, D. Thomas, T. L. McDonald, and W. P. Erickson. 2002. *Resource selection by animals: statistical design and analysis for field studies*. Second edition. Kluwer Academic, Boston, Massachusetts, USA.
- Margalida, A., J. A. Donazar, M. Carrete, and J. A. Sánchez-Zapata. 2010. Sanitary versus environmental policies: fitting together two pieces of the puzzle of European vulture conservation. *Journal of Applied Ecology* 47:931–935.
- Martínez-Abraín, A., G. Tavecchia, H. M. Regan, J. Jiménez, M. Surroca, and D. Oro. 2012. Effects of wind farms and food scarcity on a large scavenging bird species following an epidemic of bovine spongiform encephalopathy. *Journal of Applied Ecology* 49:109–117.

- Marzluff, J. M., J. J. Millsbaugh, P. Hurvitz, and M. S. Handcock. 2004. Relating resources to a probabilistic measure of space use: forest fragments and Steller's Jays. *Ecology* 85:1411–1427.
- Meyburg, B.-U., M. Gallardo, C. Meyburg, and E. Dimitrova. 2004. Migrations and sojourn in Africa of Egyptian vultures (*Neophron percnopterus*) tracked by satellite. *Journal of Ornithology* 145:273–280.
- Millsbaugh, J. J., R. M. Nielson, L. McDonald, J. M. Marzluff, R. A. Gitzen, C. D. Rittenhouse, M. W. Hubbard, and S. L. Sheriff. 2006. Analysis of resource selection using utilization distributions. *Journal of Wildlife Management* 70:384–395.
- Monsarrat, S., S. Benhamou, F. Sarrazin, C. Bessa-Gomes, W. Bouten, and O. Duriez. 2013. How predictability of feeding patches affects home range and foraging habitat selection in avian social scavengers. *PLoS ONE* 8:e53077.
- Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences USA* 105:19052–19059.
- Newton, I. 1979. Population ecology of raptors. T. and A. D. Poyser, London, UK.
- Ogada, D. L., F. Keesing, and M. Z. Virani. 2012. Dropping dead: causes and consequences of vulture population declines worldwide. *Annals of the New York Academy of Sciences* 1249:57–71.
- Ogada, D. L., M. E. Torchin, M. F. Kinnaird, and V. O. Ezenwa. 2012. Effects of vulture declines on facultative scavengers and potential implications for mammalian disease transmission. *Conservation Biology* 26:453–460.
- Oro, D., M. Genovart, G. Tavecchia, M. S. Fowler, and A. Martínez-Abrain. 2013. Ecological and evolutionary implications of food subsidies from humans. *Ecology Letters* 16:1501–1514.
- Phipps, W. L., S. G. Willis, K. Wolter, and V. Naidoo. 2013. Foraging ranges of immature African White-Backed Vultures (*Gyps africanus*) and their use of protected areas in southern Africa. *PLoS ONE* 8:e52813.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Development Core Team. 2013. nlme: linear and nonlinear mixed effects models. R package version 3.1–109. <http://cran.r-project.org/web/packages/nlme/index.html>
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Rutz, C., and G. C. Hays. 2009. New frontiers in biologging science. *Biology Letters* 5:289–292.
- Ruxton, G. D., and D. C. Houston. 2004. Obligate vertebrate scavengers must be large soaring fliers. *Journal of Theoretical Biology* 228:431–436.
- Seaman, D. E., J. J. Millsbaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739–747.
- Seaman, D. E., and R. A. Powell. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* 77:2075–2085.
- Silverman, B. W. 1986. Density estimation for statistics and data analysis. Chapman and Hall, London, UK.
- StatSoft. 2010. STATISTICA version 10.0. StatSoft, Tulsa, Oklahoma, USA.
- Thomas, D. L., and E. J. Taylor. 1990. Study designs and tests for comparing resource use and availability. *Journal of Wildlife Management* 54:322–330.
- Worton, B. J. 1987. A review of models of home range for animal movement. *Ecological Modelling* 38:277–298.
- Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home range studies. *Ecology* 70:164–168.
- Zheng, B., and A. Agresti. 2000. Summarizing the predicted power of a generalized linear model. *Statistics in Medicine* 19:1771–1781.
- Zuberogoitia, I., J. A. González-Oreja, J. E. Martínez, J. Zabala, I. Gómez, and P. López-López. 2013. Foraging movements of Eurasian griffon vultures (*Gyps fulvus*): implications for supplementary feeding management. *European Journal of Wildlife Research* 59:421–429.
- Zuberogoitia, I., J. E. Martínez, A. Margalida, I. Gómez, A. Azkona, and J. A. Martínez. 2010. Reduced food availability induces behavioural changes in Griffon Vulture *Gyps fulvus*. *Ornis Fennica* 87:52–60.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, New York, USA.

SUPPLEMENTAL MATERIAL

Appendix A

Computation of two- and three-dimensional overlap in home ranges ([Ecological Archives A024-055-A1](#)).

Appendix B

Correlation test between measures of home range size, spatial parameters, and the number of relocations obtained per individual; LMM for the standardized RUF coefficients; and model validation graphs for the LMMs of the home range area ([Ecological Archives A024-055-A2](#)).