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BIODIVERSITY RESEARCH

Spatially explicit estimation of occupancy, detection probability and survey effort needed to inform conservation planning

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ABSTRACT

Aim It is increasingly recognized the importance of accounting for imperfect detection in species distribution modelling and conservation planning. However, the integration of detectability into a spatially explicit frame has received little attention. We aim (1) to show how to develop distribution maps of both detection probability and survey effort required to reliably determine a species presence/absence and (2) to increase awareness of the spatial variation of detection error inherent in studies of species occurrence.

Location North-western Spain.

Methods We registered the presence/absence of the endangered Egyptian vulture (*Neophron percnopterus*) in 213 surveys performed in 40 of 104 territories once known to be occupied. We model simultaneously both detection probability and occurrence, using site occupancy modelling. With the resulting regression equations, we developed distribution maps of both detection probability and required sampling effort throughout the area.

Results Of the studied territories, 72.5% were detected as occupied, but after accounting for imperfect detection, the proportion of sites truly occupied was 79%. Detectability decreased in territories with higher topographical irregularity and increased with both the time of day of the survey and the progress of the season. Spatial distribution of detectability showed a mainly north–south gradient following the distribution of slope in the area. The likelihood of occupancy increased with rockier, less forested surface and less topographical irregularity within the territory. A minimum of five surveys, on average, are needed to assess, with 95% probability, the occupancy status of a site, ranging from ≤ 3 to > 24 visits/territory depending on survey- and site-specific features.

Main conclusions Accounting for detectability and its sources of variation allows us to elaborate distribution maps of detectability-based survey effort. These maps are useful tools to reliably assess (e.g. with 95% probability) occupancy status throughout a landscape and provide guidance for species conservation planning.

Keywords
Detection probability, monitoring programmes, *Neophron percnopterus*, presence–absence, site occupancy modelling, species distribution models.

INTRODUCTION

The monitoring of plant and animal populations is a widespread, core activity in ecological conservation (Marsh & Trenham, 2008). It consists of gathering information regarding system state variable(s) to gain knowledge about the state and dynamics of the monitored system (Yoccoz *et al.*, 2001). When linked to adaptive management (Nichols & Williams, 2006; Lindenmayer & Likens, 2009), monitoring allows researchers to reliably assess population trends, distributions and species richness, mainly to assist in management and conservation decisions (Yoccoz *et al.*, 2001). A relevant application of monitoring is that of the World Conservation Union (IUCN), which estimates the threat level for species through either the degree of population decline or the size of the area of occupancy, the extent of occurrence or their changes over time

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(IUCN, 2001). The occupied area or fraction of sites where a species is present (i.e. occupancy) is one of the state variables that is being increasingly used in monitoring programmes to characterize the status and trends of a large number of different species (e.g. MacKenzie & Royle, 2005; Pellet & Schmidt, 2005; MacKenzie *et al.*, 2006).

Traditionally, occupancy has been estimated by assuming perfect detection of species (Rota *et al.*, 2009), i.e., if a species occurs at a site, it will be detected. However, as various studies have recognized (e.g. Royle *et al.*, 2005; Kéry & Schmid, 2006; MacKenzie *et al.*, 2006), non-detection of species in occupied sites (i.e. false absence or false negative) is unavoidable during fieldwork. False absences can be interpreted as real absences or extinctions, with negative consequences for management and conservation planning (MacKenzie *et al.*, 2006; Rondinini *et al.*, 2006). For example, it can lead to an overestimation of extinction rates, misidentification of extinction-related factors (Kéry *et al.*, 2006), distorted estimates of covariate relationships (Gu & Swihart, 2004), areas for conservation action smaller than required (Rondinini *et al.*, 2006) and poor species distribution models (Lobo *et al.*, 2010), all of which can result in a misallocation of limited conservation resources (Wintle *et al.*, 2004). Therefore, comparing species distributions or occurrence over space or time, without accounting for detection probability, is problematic as long as it confounds species distribution with sampling effort or detection (Conroy & Carroll, 2009; Kéry *et al.*, 2010; Rota *et al.*, 2011).

The modelling approach of MacKenzie *et al.* (2002) is the most flexible among the methods available (MacKenzie & Royle, 2005) to model occupancy while accounting for imperfect detection, and it has been used successfully for various species (MacKenzie *et al.*, 2002, 2006; Pellet & Schmidt, 2005; Bailey *et al.*, 2007; Henneman *et al.*, 2007). This method allows the estimation of the parameters of occupancy and detection probability as well as the factors affecting them. Detectability also allows the estimation of the survey effort needed to infer absence in an unoccupied site or to ensure detection in an occupied one. However, spatial extrapolation of these resulting detectability–environment relationships (and survey effort needed) over unmeasured locations has not been done explicitly. The estimation and spatially explicit visual projection of both detectability and required sampling effort across a landscape could improve spatial inference and prediction of species distribution maps and assist in improving the design of monitoring programmes and conservation planning. This issue can be particularly relevant for endangered species requiring adaptive monitoring programmes to achieve specific conservation targets. Here we develop distribution maps of detectability-based effort using as study model to a threatened, territorial elusive species, the Egyptian vulture (*Neophron percnopterus* L.).

Egyptian vulture is a migrant scavenger classified as endangered by IUCN (BirdLife International, 2008). The species populations have suffered a recent and extremely rapid decline in India (Cuthbert *et al.*, 2006) and long-term declines throughout its European and African ranges (BirdLife International, 2008). Spain holds the most important population in Europe, comprising approximately 80% of the breeding population (Del Moral & Martí, 2002). Since the late 1980s, three broad-scale monitoring programmes of the species have been undertaken every 8–12 years in Spain, covering around 1200–1500 territories in each census (Perea *et al.*, 1990; Del Moral & Martí, 2002; Del Moral, 2009). From these censuses, negative trends for the vulture have been inferred (i.e. 25% of territories were unoccupied or ‘lost’ between 1987 and 2000, and there was a sharp decrease in many regions between 2000 and 2008; Del Moral & Martí, 2002; Del Moral, 2009). The large amount of vacant territories observed contrasts with the total number of national occupied territories, which has steadily increased between 1987 and 2008 (Del Moral, 2009). Although this increase could be an artefact of better survey techniques (Donázar, 2004), the detection probability of this vulture has not yet been estimated, and thus the effects of changes in population, detectability, and sampling effort over space and time are expected to be confounded, which could explain some of the discrepancies observed in the Egyptian vulture’s population trends in Spain.

Our specific aims were to (1) estimate the true fraction of occupied territories (occupancy) of the Egyptian vulture after accounting for imperfect detection, (2) identify separately the factors explaining the probability of detecting a vulture in a territory from those covariates influencing the probability of site occupancy, (3) develop spatially explicit predictive maps of both detectability and sampling effort requirements to reliably infer the occupancy state of a site and (4) develop recommendations to improve the design of species surveys, i.e., when and how many surveys are needed to improve monitoring programmes.

METHODS

Study area

The study area covers 7000 km^2 on the south slope of the Cantabrian Mountains, in north-western Spain (León and Palencia provinces; Fig. 1). This area has two climatic regions, the Temperate and Mediterranean regions, running east to west. The Temperate region extends over most of the study area, ranging between 390–2648 m above sea level (i.e. a.s.l.). Here, the landscape consists of a wide variety of habitats, from oak and beech woodlands and pastures mainly devoted to cattle and horse rearing (Junta de Castilla y León, 2003). The Mediterranean climate extends over a small area in the south. Here, the topography becomes progressively flatter with altitudes around 1000 m a.s.l. (Fig. 1). The landscape is dominated by crops and scrublands with scarce pastures and oak forests; livestock consists mainly of sheep (Jubete, 1997). Throughout the study area rocky cliffs, principally of limestone, are common (see Mateo-Tomás & Olea, 2009 for more details of the study area).

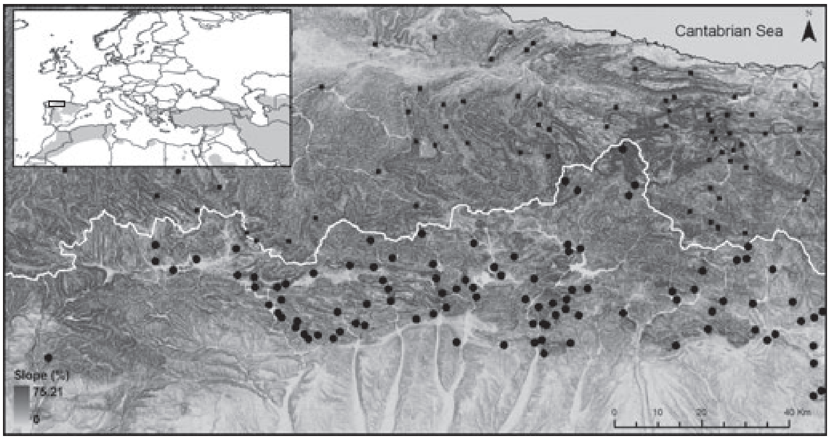

Figure 1 The map shows the 104 territories once known to be occupied by the Egyptian vulture in the study area (i.e. large, filled circles). Squares represent unmonitored territories lying on the north slope of the Cantabrian Mountains. The white line running E–W shows the northern border of the study area. Points are centred at the last nest known or at the most suitable cliff for nesting. The shaded surface in the inset represents the distribution of the species in the western Palaearctic, with the black rectangle indicating the location of the study area.

Study species

The Egyptian vulture is a cliff-nesting, medium-sized scavenger distributed from the Mediterranean countries to India and South Africa. In Spain, the species occupies very different habitats from plains to middle and high mountains (Donázar, 1993). The breeding pairs arrive from their winter grounds in Africa in early March and remain on the territories until mid-September. During this period, they rear 1 or 2 chicks. The nest is generally used year after year, and the nesting territory is actively defended by its occupants (Mateo & Olea, 2007), especially within 1 km around the nest site (Donázar, 1993). The Egyptian vulture is not a very active species: it spends less time than other vultures looking for food, spending most of the day roosting within their territories or feeding areas (Elosegui, 1989). The parents bring food to the nest at a mean rate of only two times per day (Ceballos & Donázar, 1988). During breeding, it is a very secretive species, with the adults being extremely cautious when they approach the nest (Zuberogoitia *et al.*, 2008). Adults attending a nest are difficult to observe because of the fact that nests are usually built in caves (Ceballos & Donázar, 1988; Mateo-Tomás & Olea, 2009).

Field methods

We located 104 historic territories or places likely to be occupied by the Egyptian vulture in the study area (Fig. 1). This information was obtained from revision of previous censuses (Perea *et al.*, 1990; Del Moral & Martí, 2002; F. Jubete (Fundación Global Nature) & J. Placer, pers. comm. (2nd Egyptian Vulture National Census, SEO/BirdLife)), interviews with local shepherds, and field surveys conducted during the 2005–2007 breeding seasons (Mateo-Tomás & Olea, 2009). We defined a sampling unit, or 'site', as a territory potentially occupied by an Egyptian vulture breeding pair, i.e., sites once known to be occupied or to have shown some evidence of possible occupancy. Therefore, our study population is defined by pre-existing knowledge of the potential occupancy state (MacKenzie & Royle, 2005). Although it is preferable to estimate parameters from an unknown population, the population formed by sites known to be occupied was our population of interest (MacKenzie & Royle, 2005). For an endangered species (i.e. suspected to be in decline), the proportion of once-occupied sites that truly remain occupied today is of great interest for management and conservation. Every possible territory was plotted using ArcGIS 9.2 (Environmental Systems Research Institute Inc., Redlands, California, US), taking as the centre the known or most suitable nesting cliff. Selection of the suitable nesting cliffs was based on previous experience with species habitat selection (Mateo-Tomás & Olea, 2009, 2010). The site consisted of a circular plot of an approximately 2.5-km radius with the centre in the known (or suspected) nesting cliff. The 2.5-km distance was half the average nearest-neighbour distance (i.e. NND/2) between territories in the study area (Mateo-Tomás & Olea, 2009; see also Sára & Di Vittorio, 2003 for other areas) and the scale at which relationships of presence of Egyptian vulture with habitat variables were stronger (Mateo-Tomás & Olea, 2009, 2010). Of the total number of territories or sites (i.e. 104), two expert observers visited a random sample of 40 in 2007 (38% of the total number of potential territories; Fig. 1, Appendix S1 in Supporting Information). Observer one carried out 141 visits and observer two 72. Visits ranged from the first week of March until the second week of September totalling 19 sampling occasions. Surveys were adequately distributed throughout the breeding period. All of the surveys took place on days with good visibility. Every survey consisted of an inspection, from vantage points, of one relatively high portion of the territory for up to 20 min or until detection occurred within 20 min. This time window can be a reasonable survey effort for detection while enabling an observer to visit various territories within a day in accordance with the often limited budget for this type of survey (Del Moral, 2009). The observation points were placed close (*c.* 300–1000 m) to the known or potential nesting cliffs. Inspection consisted of the observation, with binoculars and 20–60× telescopes, of the landscape and cliffs looking for the species, i.e., the presence of adults or fledglings. Short displacements (up to 1 km) were carried out when necessary to improve visibility. There was usually a relatively wide visibility around the observation point (mean radius ± SE: 1700 m ± 633.3, $n = 40$) as calculated by the Viewshed utility of ArcGIS 9.2.

Data analysis

We estimated the probability that a site is occupied (ψ) by the Egyptian vulture, as well as the probability of detecting the species at an occupied site (p), in accordance with the method described by MacKenzie *et al.* (2002, 2006) and implemented in the PRESENCE software (Hines, 2006). This method is similar to the closed-population, mark–recapture model and assumes that (1) occupancy status at each site does not change within a season, i.e., sites are 'closed' to changes in occupancy, and thus, neither colonizations nor extinctions occur (MacKenzie *et al.*, 2006; see also Discussion); (2) the probability of detecting the species at a site is independent of the probability of detecting the species at all other sites; and (3) species are not falsely detected (MacKenzie *et al.*, 2002).

To minimize violations in the closure assumption, we truncated the data set to include surveys between first and last detection (exclusive) of the species (see MacKenzie *et al.*, 2002). Although the first detection in our study area occurred on 2 March, we considered 16 March as the first valid visit, to ensure the presence of the species in all of the occupied territories; 16 March was eleven days later than the mean date of the arrival of Egyptian vultures recorded in the study area over the last 5 years (5 March, authors, pers. obs.; B. Palacios, Parque Nacional Picos de Europa, unpubl. data). The last survey considered was conducted on 6 September, well before migration (i.e. mid-September; Elosegui, 1989). The final data set consisted of 213 visits to 40 territories (mean = 5.38 times/territory, median = 5.0, range = 3–14). The study period from 16 March to 6 September was divided into 19 periods of around 10 days each (i.e., 19 sampling occasions). Not all the territories were visited in each sampling occasion (Appendix S2 in Supporting Information). There was a large number of missing observations in the final data set (72%; i.e., 547 missing observations from a total of 760 potential surveys: 40 territories x 19 sampling occasions). A missing observation was any sampling occasion between 16 March and 6 September on which a territory was not sampled. This kind of models is robust with respect to missing observations (MacKenzie *et al.*, 2006; see, for example, MacKenzie *et al.*, 2002 for modelling with *c.* 90% missing observations).

Covariates can be incorporated in the logit models for modelling detection and occupancy probability (MacKenzie *et al.*, 2002, 2006). Occupancy probability may be modelled as a function of site-specific covariates, whereas detection probability may be modelled as a function of either site-specific or survey-specific covariates (Bailey *et al.*, 2007). We noted survey-specific characteristics, which were included as covariates: day of the year (DAY), time of the visit (TIME) and observer (OBSERVER) (see Table 1 for explanations). DAY and TIME were considered continuous variables. Based on previous studies (Mateo-Tomás & Olea, 2009, 2010), we also measured several site-specific habitat and topographical features within plots of a 2.5-km radius centred at the known (or suspected) nesting cliff (see above; Table 1). We measured these variables on the spot or from aerial photographs and detailed maps of the study area, validating them through field observations when necessary. The site-specific variables were percentage of surface covered by rocky terrain (ROCKY), percentage of surface covered by open land (OPENLAND), percentage of surface covered by forest (FOREST), and topographical irregularity (SLOPE) (see Table 1 for explanations). The first three variables do not add up to 100%. Although other variables could influence occupancy on a smaller scale (Mateo-Tomás & Olea, 2009), we intended to use landscape-scale covariates in a GIS and, thus, allow them to be used easily by wildlife managers. Because topographical irregularity could also influence detectability of the species (Table 1), we included this covariate in the detectability models, too. The continuous variables were normalized. Following the MacKenzie *et al.*, 2002 method, we used the following simultaneous logit models to model the detection probability at site i and sampling occasion t:

$$\begin{aligned}\mathrm{logit}(p_{it}) = {} & \beta_{0i} + \beta_1\mathrm{DAY}_{it} + \beta_2\mathrm{TIME}_{it} + \beta_3\mathrm{OBSERVER}_{it} \\ & + \beta_4\mathrm{SLOPE}_i \end{aligned} \tag{1}$$

and for occupancy probability:

$$\begin{aligned}\mathrm{logit}(\psi_i) = {} & \alpha_0 + \alpha_1\mathrm{ROCKY}_i + \alpha_2\mathrm{FOREST}_i + \alpha_3\mathrm{OPENLAND}_i \\ & + \alpha_4\mathrm{SLOPE}_i \end{aligned} \tag{2}$$

Some relationships of the covariates with occupancy and detection probability could also be nonlinear. The eight covariates used for occupancy and detectability plus their nonlinear relationships (except OBSERVER) yielded 15 possible covariates and 2^{15} candidate models. To reduce this high number of possible models, we first compared models with linear and nonlinear covariates. Models with nonlinear variables (second-order polynomial) were no better (AIC-based) than those with linear variables, so thereafter, only linear variables were considered. We did not perform model selection on both occupancy and detection probability simultaneously. We first fit a general model for detectability (i.e., the four survey-specific covariates were always included) and fit all possible models for occupancy (see MacKenzie *et al.*, 2006 p. 115 for a similar approach). The 16 resulting models were ranked using the Akaike's information criterion (AICc) and the Akaike weight of each model (ω_m), estimated in accordance with Burnham & Anderson (2002). All possible models of detectability were fitted to each of the five best occupancy models (i.e. < 2 AIC units from the top-ranked model), yielding 80 (5*16) candidate models. The model $\psi(.)\ p(.)$ was also added. These models were ranked according to AICc, and a 95% confidence set of models was constructed by starting

Table 1 Covariates considered in detectability and occupancy models.

Variable	Definition	Hypotheses
Detectability		
Observer	Person who makes the visit (1) or (2).	Some differences in skill of detection of the species could occur between observers.
Day	Date when survey was carried out; Julian day.	Detection probability can vary through the breeding season. This variable allows for the possibility of within-season variation in detection probability.
Time	Period of the day when the visit takes place considering five equal periods: early morning (1), late morning (2), midday (3), afternoon (4) and evening (5).	Detection probability can vary through the day. This variable allow for the possibility of within-day variation in detection probability.
Slope	Mean slope within a radius of 2.5 km around the potential nesting cliff (in degrees).	Sites with lager/lower topographical irregularity could reduce/increase the detection probability because of greater/smaller surface to looking for by observer.
Occupancy		
Rocky	Percentage surface covered by rocky within a radius of 2.5 km with centre in the potential nesting cliff.	Surface of rocky is a proxy of cliffs and could influence occupancy probability or persistence of the territory (Mateo-Tomás & Olea, 2009, 2010).
Openland	Percentage of surface covered by openland (pastures, rocky and small shrubs) within a radius of 2.5 km around the potential nesting cliff.	Openland facilitates foraging, acquisition of food and positively affects probability of occupancy.
Forest	Percentage of surface covered by forest and high shrubs within a radius of 2.5 km around the potential nesting cliff.	Dense vegetation makes foraging more difficult, negatively affecting probability of occupancy.
Slope	Mean slope within a radius of 2.5 km around the potential nesting cliff (in degrees).	Irregular topography makes foraging more difficult and energetically expensive, negatively affecting probability of occupancy.

with the highest Akaike weight and adding the model with the next highest weight until the cumulative sum of weights exceeded 0.95 (Burnham & Anderson, 2002). Because non-model was much better than the others (i.e. $\omega_m > 0.9$), multimodel inference was used by undertaking a model averaging approach. The coefficients of each variable in the model were estimated from all models within the 95% probability, weighted by ω_m (i.e. $\Sigma\omega_m = 0.95$), thus obtaining unconditional coefficients on a single model (Burnham & Anderson, 2002). The averaged model was used for inference. To determine the relative contribution of each variable, we calculated its Akaike weight. The Akaike weight for each variable (ω_i) was calculated by summing, from the set of models within the 95% probability, the weights of those containing the variable. The variables with the highest weight ($\Sigma\omega_m$) are more important relative to the others. The multimodel inference and Akaike weights of the variables were computed in a spreadsheet. The model fit was assessed by the MacKenzie-Bailey goodness-of-fit test (MacKenzie & Bailey, 2004), which is based on parametric bootstrapping.

Absence probability

The probability P_n of detecting a species at least once after n repeated visits (or surveys) to an occupied site is given by

$$P_n = 1 - (1 - P)^n \quad (3)$$

where P is the per-visit detection probability of the species (MacKenzie & Royle, 2005; Kéry *et al.*, 2006). Therefore, $(1 - P)^n$ is the probability of not detecting the species, if present, after n visits. From here, we calculated the minimum number of visits necessary ($N_{\min}$) to be 95% certain that the species is truly absent from a site (Kéry, 2002; Pellet & Schmidt, 2005): $N_{\min} = \log(0.05)/\log(1 - P)$.

Predictive maps

We used the averaged model (i.e. $\Sigma\omega_m = 0.95$; see above) to elaborate 90-m resolution predictive maps using ArcGIS 9.2 (Environmental Systems Research Institute Inc.). Extrapolation of the resulting regression equation allowed us to predict the detection probability and sampling effort needed to correctly classify a territory with 95% probability across the space in locations unmeasured on the ground. Each predictive map was created for each stage of the breeding period, using the middle date within each period (i.e. courtship: day 97, incubation: day 143, nestling: day 188, post-fledgling: day 232). We show only the courtship period (others periods are available in Appendix S3 in Supporting Information).

RESULTS

The Egyptian vulture was detected in 29 of 40 sites (0.725). This value is the proportion of sites used by the species without account for detectability. However, after accounting for detectability, the estimated proportion of occupied sites was higher, 0.769 (SE: 0.076) (31 occupied sites) for the model $\psi(.)$ $p(.)$ and 0.775–0832 (SE: 0.09–0.11) (31–33 occupied sites) for the best models (i.e. < 2AIC units from the top-ranked model; Table 2). The averaged model ($\Sigma\omega_m = 0.95$) estimated a proportion of occupied sites of 0.788 (SE: 0.097) (32 occupied sites). A greater ROCKY surface (weight = 83%, $\beta = 1.670$, SE: 1.078) and lower SLOPE (weight = 51%, $\beta = -0.653$, SE: 0.402) within 2.5-km radius around the known or suitable nesting cliff increased the occupancy probability of the Egyptian vulture, according to the top-ranked model ($\omega_m = 0.103$). The averaged model also showed that FOREST (weight = 44%, $\beta = -0.382$, SE: 0.394) negatively influenced occupancy.

The detectability of the Egyptian vulture in the territories was 0.516 (SE: 0.041), according to the model $\psi(.)$ $p(.)$. This detectability varied 18% among the best models: 0.405–0.491(SE: 0.057–0.089). The detectability estimated by the averaged model ($\Sigma\omega_m = 0.95$) was 0.453 (SE: 0.069). Detectability decreased with increasing SLOPE (weight = 98%, $\beta = -0.660$, SE: 0.226; Fig. 2a) and increased with both TIME (84%, $\beta = 0.0531$, SE: 0.441; Fig. 2a) and the progress of the season (DAY, weight = 31%, $\beta = 0.145$, SE: 0.131) (Fig. 2b). The observer had a slight influence on detection of the species (weight: 26%, $\beta = -0.107$, SE: 0.357). Spatial distribution of detectability (Fig. 4) shows a mainly north–south gradient according to the distribution of slope in the study area (Fig. 1).

Neither the global model ψ(ROCKY + SLOPE + FOREST), p(SLOPE + TIME + DAY + OBSERVER) from the candidate set nor the best model ψ(ROCKY + SLOPE), p(SLOPE) indicated any evidence of lack of fit, as assessed by 1000 bootstrap samples ($\chi^2 = 470.3$, $P = 0.73$, $\hat{c} = 0.88$ and $\chi^2 = 547.1$, $P = 0.64$, $\hat{c} = 0.86$, respectively).

False absence probability and sampling effort

The detectability estimated by the averaged model ($P = 0.453$) and the mean number of visits per territory from our study (5.4) allow us to estimate the expected probability of not detecting the Egyptian vulture at an occupied territory (i.e. the false absence probability). It was calculated as $(1 - 0.453)^{5.4} = 0.038$, that is, the Egyptian vulture would not be detected *c.* 4 times in 100 occupied territories.

Applying the detectability estimated by the averaged model (0.453) yields a minimum of five visits (4.97, ±SE: 4.05–6.19) required to be 95% certain that an average territory of the Egyptian vulture is truly unoccupied. However, this minimum number of surveys varied with survey- and site-specific characteristics (Fig. 3) throughout the study area (Fig. 4). The number of unsuccessful visits that are required before a site can be assumed unoccupied, with a 95% probability, increased considerably with the territory relief (SLOPE) and slightly decreased with the progress of the season (DAY) (Fig. 3 and 4; see also Fig. 1). Note that similarly this required survey effort that we estimated is exactly the same as and, thus, applicable to a 95% probability of detecting the species at least once after k surveys are made at an occupied site, i.e. $1 - (1 - P)^k$.

DISCUSSION

A reliable estimation of species occurrence is crucial for researchers and wildlife managers (MacKenzie *et al.*, 2006). In our study, the Egyptian vulture was detected in less than one-half (0.45) of the surveys performed at occupied sites, indicating that this species requires several repeated surveys to reliably assign a site occupancy status. The vulture was detected in 72.5% of sampled sites, but estimates showed that the proportion of sites truly occupied was 79%, after accounting for imperfect detection. After this correction, there were 31–32 (±SE: 28–35) occupied territories among 40 surveyed sites, and thus there should be 82 (±SE: 72–92) occupied territories for the entire population (i.e., sites once known to be occupied, $N = 104$ sites). This suggests that in our study area, a large fraction of sites once known to be occupied by the Egyptian vulture could have become unoccupied (extinct) over the last about 20 years. In fact, up to 14 territories were known to have been abandoned between

Table 2 Summary of the best models (up to 2AICc units from the top-ranked model) obtained in the model selection procedure for estimating occupancy and detectability in the Egyptian vulture. Model AICc values, the relative difference in AICc units compared with the top-ranked model (ΔAIC), AIC model weights (ω_m), twice the negative log-likelihood (-2ℓ), estimates of occupancy rates ψ(±SE) and detectability p(±SE) and *pseudo-*R^{2*} are shown. Estimates of occupancy and detectability of the averaged model ($\Sigma\omega_m = 0.95$) are shown.

Ranking	Model	AICc	ΔAIC	-2ℓ	ω_m	$\hat{\psi}$ (SE)	p(SE)	*Pseudo-*R^2
1	ψ(ROCKY + SLOPE), p(SLOPE)	266.6	0.00	256.4	0.11	0.78 (0.09)	0.49 (0.05)	0.082
2	ψ(ROCKY + SLOPE), p(SLOPE + TIME)	267.4	0.75	255.0	0.07	0.78 (0.10)	0.41 (0.09)	0.090
3	ψ(ROCKY), p(SLOPE)	267.6	0.91	259.4	0.07	0.82 (0.09)	0.48 (0.05)	0.067
4	ψ(FOREST), p(SLOPE)	268.2	1.54	260.0	0.05	0.83 (0.10)	0.48 (0.05)	0.065
5	ψ (ROCKY), p(SLOPE + TIME)	268.3	1.63	258.0	0.05	0.82 (0.10)	0.41 (0.09)	0.076
6	ψ(ROCKY + FOREST), p(SLOPE)	268.4	1.78	258.1	0.04	0.82 (0.10)	0.48 (0.05)	0.075
7	ψ(ROCKY + SLOPE), p(SLOPE + DAY)	268.7	2.06	256.3	0.04	0.78 (0.09)	0.49 (0.06)	0.086
64	$\psi(.)$, $p(.)$	279.9	13.2	275.8	0.0001	0.77 (0.08)	0.52 (0.04)	
	Averaged model				0.95	0.79 (0.10)	0.45 (0.07)	

*Adjusted McFadden $R^2 = 1 - (\log L(m_1) - k - 1)/(\log L(m_0) - 1)$, where Log$L(m_1)$ and Log$L$ (m_o) is the log-likelihood of the fitted model and null (intercept only) respectively; k is the number of covariates.

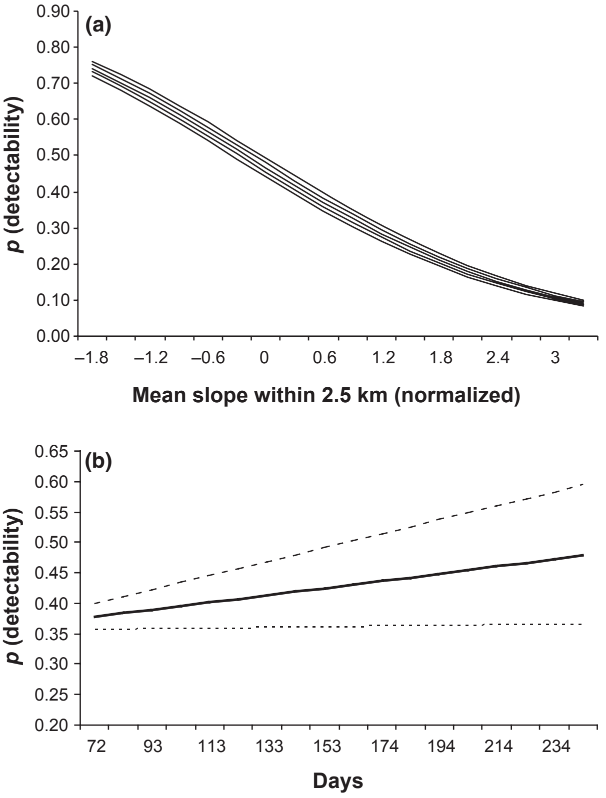

Figure 2 (a) Effect of the topographical irregularity (i.e. mean slope) within a 2.5-km radius around known or suitable nesting cliffs on the probability of detecting the Egyptian vulture at various times (different lines, from bottom to top: early morning, late morning, midday, afternoon, evening). The variable SLOPE is normalized (i.e. mean = 0). The estimation of the detection probability is based on the averaged model, ψ(ROCKY + SLOPE + FOREST), *p*(SLOPE + TIME + DAY + OBSERVER). Day was fit at its mean value (i.e. 158, middle of the breeding season, 9th June). (b) Increase in the detection probability (±1 SE) of the Egyptian vulture throughout the breeding season (1 = 1st January; 72 = 13th March, 244 = 6th September). The estimation of the detection probability is based on the averaged model.

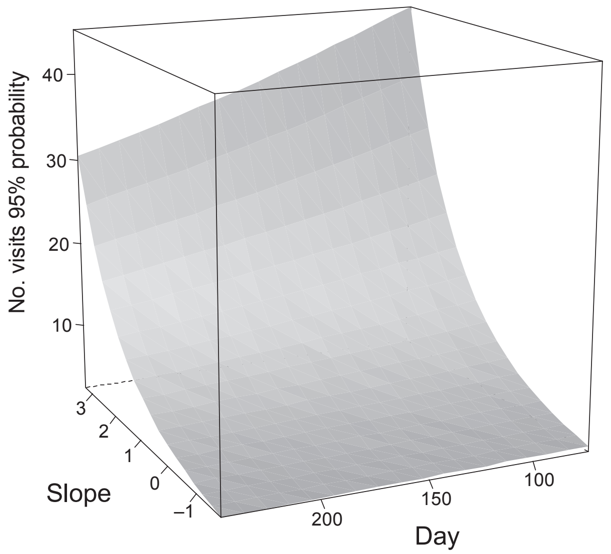

Figure 3 Minimum number of visits necessary to correctly assess (i.e. with 95% probability) the absence of the Egyptian vulture in a territory according to the topographical irregularity within a 2.5-km radius around the potential nesting cliff (i.e. SLOPE) and the day of the survey (i.e. DAY). The variable SLOPE is normalized (mean = 0). DAY indicates days beginning with 1 January. The estimation of the number of visits was based on the detectability ($p = 0.453$) obtained by the averaged model.

1997–1999 and 2005–2007 in our study area (Mateo-Tomás *et al.*, 2010). However, to reliably estimate the fraction of sites becoming unoccupied (extinct), it would be necessary to have more study years and know the species occupancy dynamics (i.e. extinction and colonization rates; MacKenzie *et al.*, 2006).

The statistical models showed that the Egyptian vulture tended to occupy (remain in) those sites with a greater relative rocky surface and less forest, with little topographical irregularity within 2.5-km radius around known or suitable nest cliffs. These occupancy-related factors found here are consistent with those found in previous studies (Carrete *et al.*, 2007; Mateo-Tomás & Olea, 2009) and with the hypotheses posed (Table 1). 'Rocky surface' is a proxy of 'cliffs' and, thus, could influence occupancy probability or persistence of the territory (Mateo-Tomás & Olea, 2010), while irregular topography and forest cover make foraging more difficult and expensive in terms of energy, negatively affecting breeding habitat selection and, thus, occupancy.

Detection probability

The detectability of the Egyptian vulture was affected by both survey-specific and territory-specific factors. The probability of detection increased monotonically with the progress of the season, with the highest detection probability occurring towards the end of the breeding period (Fig. 2b), when nestlings or fledglings are in or around the nests. During this time, fledglings often lean out of the caves and undertake their first flights, corresponding to a phase of low risk of breeding failure with slightly less careful behaviour by the familiar group (Newton, 1979; pers. obs.), making detection more likely. Detection also increased throughout the day, with the highest detection occurring at the end of the day, when the adults return to the nesting cliffs for resting or roosting (Elosegui, 1989; Del Moral, 2009). Territories in areas with high topographical irregularity had lower detection probability. Sites with softer relief offer better access and allow easier observation, as there are, generally, fewer places for vultures to nest or rest, making detection easier.

Spatial distribution of detectability/effort and conservation

The knowledge of the sampling effort needed to reliably determine a species occurrence is crucial for the design of ecological studies and monitoring programmes. If the survey

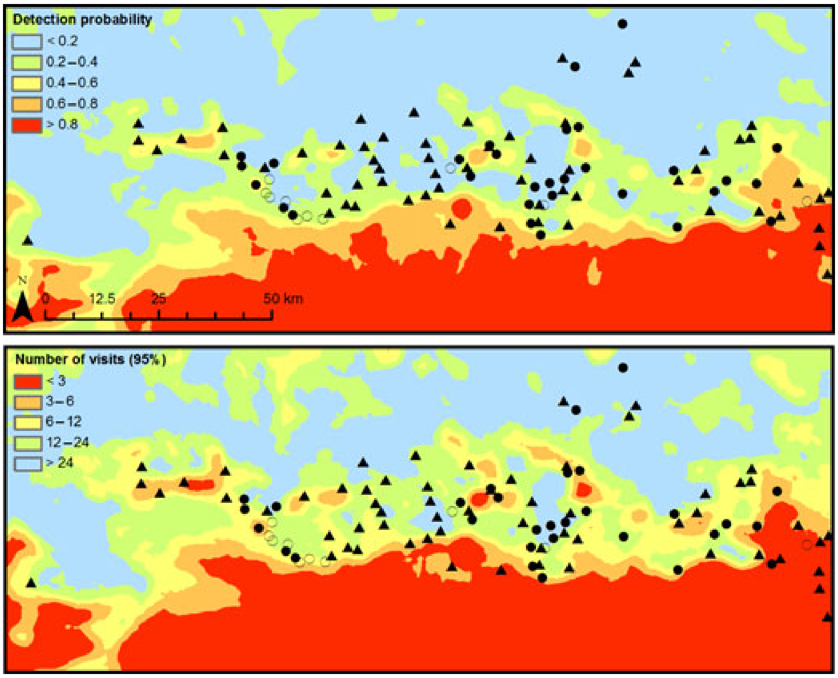

Figure 4 Predictive map of the study area (i.e. north-western Spain) representing the detection probability and survey effort needed to be 95% certain that a site is truly unoccupied by the Egyptian vulture as a function of the characteristics of the landscape (topographical irregularity) during the courtship stage of the breeding period. The predictions are based on the averaged logistic regression model. Note that the survey effort needed is also applicable in the case of occupied sites to determine the 95% probability of detecting the species at least once after *k* surveys (i.e. effort needed). Circles indicate the territories surveyed, open circles indicate sites where the species was non-detected, filled circles indicate sites with at least 1 detection and triangles indicate non-surveyed sites.

effort needed is unknown or misled, the sites occupied by a species can be overlooked, which reduces the possibility that the species will receive proper management, increasing the risk of local extinction (Kéry, 2002). Our study population requires a minimum of five surveys to be 95% certain that an average territory of the Egyptian vulture is truly unoccupied (note that the number of surveys varies depending on territory/visit-specific characteristics, Figs 3 and 4). Similarly, five surveys, on average, would be needed to achieve a 95% probability of detecting the species at least once in an occupied site (see Figs 3 and 4 for site-specific effort). A lower number of surveys per territory, on average, (i.e. with 1–4 surveys) would leave undetected between 9% and 54% of sites that are truly occupied in our study area. For example, applying the 2.4 surveys/territory performed, on average, in the Egyptian Vulture National Census (Del Moral & Martí, 2002) would leave undetected 23.5% of occupied territories, i.e., nine territories for the studied sample and 24 for the whole studied area. It is important to realize that a detection error of around of 20% could lead to a miss-classification of the threat level for any species (i.e. it could change a species threat status from ‘vulnerable’ to ‘endangered’ under IUCN criteria). Therefore, the Egyptian Vulture National Census needs appraisal and modification. Our study could assist in the design of surveys of this endangered species (Figs 3 and 4). But more important, our study highlights that predictive maps of detection probability and sampling effort can be of great value for researchers and wildlife managers working with territorial (elusive) species. Illustratively, the map of Fig. 4 shows spatially explicit information regarding the number of surveys that is necessary to infer absence at any site with a 95% probability in accordance with the territory characteristics and stage of the breeding period when the survey is conducted (see Appendix S3). It allows researchers or wildlife managers to predict the sampling effort needed in both already-known sites and in those unmeasured sites, facilitating the design of field studies and monitoring programmes. Moreover, knowing the degree of evidence necessary to say that a site is unoccupied by a species (extinction) is relevant in management and conservation planning (Kéry, 2002; Rondinini *et al.*, 2006). Our study can reliably provide this information to wildlife managers, who should demand sufficient evidence (with at least 95% probability) that a site is ‘truly’ unoccupied by the species (Kéry, 2002) before authorizing, for example, climbing paths, quarries, and other human activities that are known to affect in the case of the Egyptian vulture (Zuberogoitia *et al.*, 2008). Providing reliable information on species absences can also reduce the false negative rate of occurrence data, improving the efficiency of selected areas for conservation action (Rondinini *et al.*, 2006). Our approach, i.e., the development of distribution maps of detectability-based effort can be applicable to other species (including plants, Kéry, 2004) in which information of several visits per site is available or feasible to collect.

Potential sources of bias

A potential source of bias in the approach addressed here, and in general in this type of studies, would be a violation of the assumption of closure, i.e., no occupancy change between surveys (MacKenzie *et al.*, 2006; Rota *et al.*, 2009). The extent to which unsuccessful pairs of Egyptian vultures may abandon the territory during a season (Del Moral, 2009), thus inducing bias in estimating detectability and occupancy, is unknown. The problem of lack of model fit occurs when there are violations of the assumptions of the model or an inappropriate model structure (i.e. covariates that were not considered or were inadequately modelled; MacKenzie & Bailey, 2004). However, our models showed no evidence of lack of fit, as assessed by the MacKenzie-Bailey goodness-of-fit test. This suggests that the assumption of closure was not problematic in our study system. Moreover, the assumption of closure can be relaxed, considering that any occupancy change occurs completely at random (MacKenzie *et al.*, 2006).

Because our study is based on a single year, the potential between-year variation should be assessed (MacKenzie *et al.*, 2003). We standardized the duration of surveys up to 20 min (around 90% of detections occur within 20 min of duration of the visit; authors, unpubl. data). Nevertheless, a very long survey increases the cost and reduces the number of sites to visit. Future studies could assess the optimal survey duration that will adequately balance detection and sampling effort. Our population of interest was formed by all of the historic sites that were once known to be occupied by the Egyptian vulture. Therefore, the generalization from our study sample is to the population of interest (i.e. sites known to be occupied) but not to the entire area. Nonetheless, the many years of study with this species (from 1987) suggest that both population types, i.e., the known (historic) and the population of the entire area are very similar. This is owing to the fact that censuses have always been conducted by prospecting all of the sites that were, by their characteristics, likely to be occupied by the species (Perea *et al.*, 1990; Del Moral & Martí, 2002; Mateo-Tomás & Olea, 2009). To determine the occupancy rate in the entire area, a grid-based approach may be adopted. Because a territory is not a sampling unit naturally defined, the area might be divided into squares, and then a fraction drawn from the total of squares can be visited multiple times (MacKenzie & Royle, 2005).

Finally, we suggest that our approach, through developing distribution maps of detectability-based effort, may be also useful in improving species distribution models (i.e. SDMs) through providing reliable information about the collection of (pseudo)absence data. Because methodological absences can lead to poor SDMs (Gu & Swihart, 2004; Lobo *et al.*, 2010), the required and performed survey effort may be compared (e.g. via estimation or effort-based maps). For example, if there are sites in which the survey effort needed is close to the performed effort, then these sites are expected to provide high-quality, evidence-based documentation of absences. On the contrary, if the survey effort needed is much higher than the performed effort, then those sites are expected to yield absence documentation of poor quality, making them less adequate to be selected. Maps of detectability-based effort, along with additional information/survey strategies, could become a useful tool in the design of studies, monitoring and conservation planning for (threatened) species.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Selection of sites to survey.

Appendix S2 Distribution of the visits performed to each territory during the monitoring period.

Appendix S3 Predictive maps of detection probability and sampling effort for each stage of the breeding period.

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