Occurrence vs abundance models. Differences between species with varying aggregation patterns

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Abstract

Predicting distribution has become a fundamental component in conservation or wildlife management. Modelling is increasingly used to identify important areas (e.g. those areas more suitable for a species or more likely to hold high densities). Models often use presence/absence rather than abundance data, partly because measuring abundance is more difficult than measuring presence. We aimed to test if the relationship between occurrence models and predicted abundance varied for two sibling species that differ in the level of nest aggregation: the Montagu’s harrier (a semi-colonial raptor species) and the hen harrier (more territorial). We modelled presence/absence distribution and the number of pairs of each species with GLM and large-scale environmental variables, and compared predicted results of both sets of models. In the case of the hen harrier, predictions of the presence/absence model reliably identified areas with highest densities for the species. In contrast, in the Montagu’s harrier, there were large apparently favourable areas where predicted breeding density was low. Our results indicate that breeding system is likely to shape the relationship between presence/absence vs density models. In species that are randomly or evenly spaced, even if spatial variations in density occur, using results of presence/absence models is likely to be adequate for population monitoring. In contrast, in the case of semi-colonial species, it is necessary to take into account both occurrence and abundance models to identify areas of conservation importance or concern. There are a considerable number of birds which are semi-colonial or aggregated species, thus these results have general implications.

Keywords: Circus pygargus, Circus cyaneus, favourability function, hen harrier, Montagu’s harrier, predictive models.
1. Introduction

The relationship between geographic distribution of species and abundance, and the patterns and environmental conditions which determine them, is a central theme of ecology and conservation (Brown, 1984; Nielsen et al., 2005). At a macroecological level, species atlases are normally used as indicators of species distribution, but they have the drawback that they can be biased depending on survey effort (Estrada et al., 2008). Spatial models are normally used to attenuate this problem by providing potential distribution of species, which do not depend so much on the survey effort (Wilson et al., 2005; also in new generation atlases, e.g., Herrando et al., 2011).

Predicting distribution has thus become a fundamental component in disciplines such as conservation or wildlife management, and in the assessment of the impact of climate change (Carvalho et al., 2011; Estrada et al., 2010; Marini et al., 2010; Real et al., 2010).

For example, it may be relevant to identify important areas for species of conservation concern to concentrate conservation efforts there, or to assess how current distribution of protected areas fits with the species distribution. These important areas (e.g. those areas more suitable for the species, or more likely to hold high densities) are sometimes identified based on existing information (i.e. local censuses), but other times they are identified through modelling (Beresford et al., 2011; Coetzee et al., 2009; Estrada et al., 2011; Greve et al., 2011; Marini et al., 2010). Many of those models use presence/absence data rather than abundance data (e.g. Coetzee et al., 2009; Estrada et al., 2011; Marini et al., 2010; Rodríguez-Estrella, 2007), partly because measuring abundance is always more difficult than measuring presence and in a wide number of species comparable data on spatial variation in abundance is lacking. Results of presence/absence (P/A) models are sometimes considered as indicators of variations of
species abundance, as higher probability of occurrence may correlate with higher
number of individuals (Greaves et al., 2006; Sarà, 2008). The latter falls from the fact
that occurrence simply denotes that abundance at a site is greater than zero (Royle et al.,
2005), and thus from the hypotheses that P/A data follow an abundance-related
detection probability (Barbosa et al., 2009). Additionally, occurrence models reflect
habitat or environmental suitability (Jiménez-Valverde et al., 2009), and more
individuals are supposed to inhabit most suitable areas.

Being able to evaluate if P/A models can be reliably considered indicators of abundance
may thus be very useful. Overall, there are not numerous studies concerning the
presence/abundance relationship, and of those some have obtained a significant positive
correlation between suitability for the species and abundance (Coudun and Gégout,
2007; He and Gaston, 2003; Royle et al., 2005; Real et al., 2009) whereas others have
not found such association (Jiménez-Valverde et al., 2009; Nielsen et al., 2005; Pearce
and Ferrier, 2001). The general idea of these studies is that we can not assume that
occurrence models will always reflect species abundance. But the question is still
unresolved and it would be interesting to analyze in which cases this relationship is
valid, and where conclusions based on P/A models may be sufficient to identify
important areas for certain species.

In particular, bird species have a variety of breeding systems that strongly affect their
spatial distribution, thus spatial behaviour may modify the relationship between
occurrence and density. One could hypothesize that in species where nests are evenly or
randomly distributed (such as territorial species) both parameters are highly correlated,
whereas in semi-colonial species (where local breeding numbers may depend on social
parameters beyond the distribution of suitable habitat, Cornulier and Bretagnolle, 2006)
the relationship between occurrence and abundance may be weaker.
The Montagu’s harrier *Circus pygargus* and the hen harrier *Circus cyaneus* are two ground-nesting raptors listed on Annex 1 of the Birds Directive (Council Directive 2009/147/EC on the Conservation of Wild Birds). The Montagu’s harrier is considered vulnerable in the Iberian Peninsula, the stronghold of the Western European population (Arroyo and García, 2008). Similarly, the hen harrier is considered vulnerable within Spain, although the proportion of the Spanish population among European numbers is smaller than for the other species (Arroyo and García, 2008). Both species are extremely similar concerning their ecological requirements: they have similar diets, both nest on the ground and use the same breeding habitats (Arroyo and García, 2008; García and Arroyo, 2005; Millon et al., 2002). Regarding their breeding behaviour, the Montagu’s harrier is a semi-colonial species which presents clumped distribution of nests (groups of 2 to > 40 pairs) (Arroyo, 1995; Cornulier and Bretagnolle, 2006). On the other hand, the hen harrier is considered to be more territorial than the Montagu’s harrier (Arroyo and García, 2008; García and Arroyo, 2002), although breeding densities may vary strongly spatially and some clumping of nests at larger scales have been observed (Cornulier, 2005).

Our objective in this study was to test if occurrence models reflect predicted abundance for the two harrier species, or if, in contrast, there are differences between the species in relation to their level of nest aggregation. We discuss the relevance of the important areas identified with one, the other or combined methods.

2. **Methods**

2.1 **Distribution models**
The most recent atlas for breeding birds in Spain was compiled in 2003 by the Spanish Society of Ornithology (SEO/Birdlife) (Martí and del Moral, 2003) and it indicates presence or absence of breeding pairs of each species in each 10 km x 10 km UTM cell. Additionally, in 2006 SEO/Birdlife coordinated a national census of breeding Montagu’s and hen harriers in Spain (Arroyo and García, 2008), sampling random 100 km² UTM cells within the area of presence according to the atlas, and estimating the minimum and maximum number of pairs of both species in each UTM cell. The minimum number of pairs consisted on birds observed at the nest or with breeding behaviour (feeding passes between male and female, nest material transport, etc.), while the maximum number considered also pairs with possible breeding (males or females observed in the area but no specific breeding behaviour). The protocol indicated a minimum of three visits to each UTM cell at different times of the breeding cycles, each lasting at least 3 hours. However, number of visits per cell varied among regions. Maximum and minimum numbers calculated per cell were corrected for the number of visits, which were found to influence total number of nests detected in a cell (Arroyo and García, 2008). Therefore, the variable used for abundance analyses includes some degree of correction for imperfect detection (Kéry et al., 2010), but it is likely that the atlas data includes some non-quantified detection errors. The atlas presents combined information collected (non systematically) over several years (with some repeated observations of different areas), and a “presence” indicates a cell where breeding was observed at least once, whereas “absence” indicates a cell where breeding has never been observed.

We modelled the distributions of both species in Spain in relation to large-scale environmental conditions, mainly related to topography, climate, land use and human presence (Table 1). The digital procedure performed to obtain the variables was carried
out by the Biogeography, Diversity and Conservation Research Team of the University of Málaga (Spain) and are detailed in Estrada et al. (2008). We fitted two models for each species, i.e., a breeding P/A model with data from the atlas and a breeding density model with data from the census. The P/A model was carried out using data from 5167 cells (covering the whole of peninsular Spain); for the breeding density model, data used were 1220 cells (the extension of the census), but then this model was evaluated on the complete set of Spanish UTM cells (n=5167). In order to be conservative, we selected the minimum number of pairs of each species as the response variable in the breeding density models. Both models were calibrated on a 75% random sample of the original data and predictive accuracy was evaluated on the remaining 25% of the data (Araújo et al., 2005).

The P/A model was calculated as follows. By performing logistic regression of each species presence/absence on each variable separately we selected a subset of variables significantly related to each species’ distribution. To control for the increase in type I error due to multiple testing (Benjamini and Hochberg, 1995; García, 2003), we controlled the false discovery rate (FDR) using the procedure proposed by Benjamini and Hochberg (1995), only accepting the variables that were significant under a FDR of \( q < 0.05 \). Then we performed forward–backward stepwise multiple logistic regression of presence/absence data on the subset of significant predictor variables. Finally we applied the favourability function proposed by Real et al. (2006) on the predicted values of logistic regression, thus converting logistic probabilities \( P \) into favourability \( F \) values.

The logistic regression model has the form

\[
P = \frac{e^y}{1 + e^y}
\]
In the favourability function the effect of prevalence is removed from the logit function \( y \). \( F \) can be obtained directly from probabilities of logistic regression \( (P) \) in the following way (Real et al., 2006):

\[
F = \frac{e^y}{\frac{n_1}{n_0} + e^y} = \frac{P}{\frac{n_1}{n_0} + \frac{P}{(1 - P)}}
\]

\( F \) is a logistic function with values between 0 and 1. Whereas \( P \)-values for different species are not comparable because of the different prevalence of each species, \( F \)-values are directly equivalent, and the models are then levelled to the same threshold of favourability and can be compared and combined directly. The output value of \( F = 0.5 \) will always correspond to the same neutral environmental threshold for all species, whatever the proportion of presences in the sample. Favourability values higher than 0.5 correspond to areas where the probability of presence is higher than that expected according to prevalence (i.e., higher than that expected by chance), and the opposite occurs in areas with favourability below 0.5. Furthermore, the favourability value for a species in a cell can be interpreted as the grade of membership of the cell to the fuzzy set of cells that are favourable for the species. This fact allows the use of concepts and operations of fuzzy logic to the resulting spatial analysis of the species. Additional details on the favourability function can be found in Real et al. (2006).

We assessed the discrimination power of the P/A models with the validation dataset (25% of data) by estimating the sensitivity, specificity, and their Correct Classification Rate (CCR), using the favourability value of \( F = 0.5 \) as classification threshold, and the Area Under the Curve (AUC) of the Receiver Operating Characteristic, which is independent of any favourability threshold (Hosmer and Lemeshow, 2000).
For the breeding density model, we fitted a Poisson GLM with log link (Yen et al., 2004) to the minimum numbers of pairs on each variable separately, and then proceeded analogously as in the P/A model to control for the FDR. We then performed forward–backward stepwise GLM (according to AIC) fitted to a Poisson distribution of the minimum number of pairs on the subset of significant predictor variables, to identify factors affecting species abundance. In case any non-significant variables remained in a model after this procedure, the model was further updated by removing them step by step, starting with the least significant variable (Barbosa and Real, 2010; Crawley, 2007); we finally accepted the parsimonious model thus calculated provided that the difference between the AIC score of the resultant model and the first model was less than two units (Burnham and Anderson, 2002).

We assessed if Poisson models were affected by overdispersion. The dispersion parameter is the quotient between the residual deviance and the degrees of freedom. It is supposed to be equal to 1 under the Poisson model (i.e. the mean is equal to the variance) but dispersion levels between 0.5 and 1.5 are frequently accepted (Zuur et al., 2009). When a Poisson distribution was fitted to the observed counts of Montagu’s harrier we obtained overdispersion (3.7). When count data are not Poisson-distributed, a good candidate distribution where the variance-mean ratio is greater than 1 is the negative binomial distribution (Crawley, 2007, p.538). The meaning of the variance being greater than the mean is that the population is more clumped or aggregated than random, as Poisson distribution assumes that occurrences are randomly distributed (Dytham, 1999). The Montagu’s harrier is a semi-colonial species with clumped distribution of nests, so it is logical that the number of pairs of this species had to be modelled with a negative binomial distribution.
As with the P/A models, density models were calibrated using 75% of the data, and were validated with the remaining 25% of the data by performing Spearman correlations between results from the model and the raw abundance data from the validating data set. We used Spearman correlations because model outputs had non-normal frequency distributions. We also present the explained proportion of the deviance of the models. Models were performed in SPSS and R.

2.2 Combination of the models

We computed Spearman correlations between the P/A model and the breeding density model. With the intention of knowing how each model performed in predicting the other dataset, we calculated the AUC and Spearman correlations between the abundance model results (calculated with the training data set) and the raw presence/absence data from the remaining 25% data. Analogously, we performed correlations between the P/A model results (calculated with the training data set) and the raw abundance data from the remaining 25% of data.

In order to know the degree with which the P/A model was spatially coincident with the breeding density model, we performed and mapped different combinations between the predicted values of both models for each species. These combinations were the intersection and the subtraction. The favourability model (presence/absence) values range between 0 and 1. We rescaled the breeding density model results dividing the values in each cell by the maximum value predicted by the model, thus obtaining predicted abundance also scaled between 0 and 1. The intersection represents the areas that are simultaneously favourable for a set of criteria, and is computed in each locality as the minimum value of both models. In our case, the biological meaning of the
intersection between the favourability model and the breeding density model represents the areas that are simultaneously important for the presence of the species as a breeder and for holding high breeding numbers. The subtraction of both models highlights the areas where there are higher discrepancies between both models, and is calculated by subtracting favourability values minus scaled predicted densities.

3. Results

3.1 Favourability and breeding density models for both species

We obtained the most favourable areas (Fig. 1a and Fig. 2a) and the estimated abundance (Fig. 1b and Fig. 2b) of each species in peninsular Spain. Tables 2 and 3 show the environmental variables that affect their distributions.

Most favourable areas for Montagu’s harrier were principally located in the Western part of the country (Fig. 1a), with variables related to land use and spatial situation among the first to form part of the model and the ones which define the distribution of the species at a wide scale (Table 2). The favourability model presented an excellent discrimination capacity according to Hosmer and Lemeshow (2000) (AUC: 0.835, sensitivity: 0.79, specificity: 0.757, CCR: 0.773).

Highest predicted densities, after applying a negative binomial distribution, occurred in the Southwestern part of the country and in some places of the Mediterranean coast (Fig. 1b); the most important variables associated with higher densities at a wide scale were climatic instability, low permeability and lowlands (Table 2). The correlation between predicted values and the raw abundance data of the validation dataset was significant (rho=0.445, p<0.001) and the explained proportion of the deviance of the model was 31.2%.
Hen harrier’s favourability areas were concentrated in the Northern half of Spain (Fig. 2a), being primarily influenced at a macroecological scale by the spatial location, the existence of broad valleys and water availability (Table 3). The favourability model for this species presented also an outstanding discrimination capacity according to Hosmer and Lemeshow (2000) (AUC: 0.901, sensitivity: 0.831, specificity: 0.794, CCR: 0.799).

Breeding density of hen harrier fitted a Poisson distribution (dispersion parameter=0.6). Higher predicted density for this species occurred in Northern Spain (Fig. 2b), in areas with low insolation and low climatic stability (Table 3). The correlation between predicted values of the Poisson GLM and the raw abundance data of the validation dataset was significant (rho=0.444, p<0.001) and the explained proportion of the deviance of the model was 54.1%.

3.2 Coincidences between the P/A models and the breeding density models

Fig. 1c and Fig. 2c show the intersection between the favourability model and the breeding density model for the two species. Intersection values for Montagu’s harrier were lower than for the hen harrier, but were more widely distributed.

Results of the subtraction of the P/A model and the abundance model are shown in Fig. 1d and Fig. 2d. Dark colours highlight areas where favourability is higher than density, and the opposite occurs with light colours. Neutral grey identifies coincidence between both models. In the case of hen harrier, areas with high density were located within high favourability areas (Fig. 2d). In the case of Montagu’s harrier, there were large areas where scaled density was much lower than favourability (in the North-West part of the country, Fig. 1d), and some local areas where scaled density was higher than
favourability (along the Mediterranean coast and in the South-West part of the country, Fig. 1d).

As can be deducted from Fig. 1 and Fig. 2, Spearman correlations between the P/A model and the breeding density model were low for the Montagu’s harrier (rho=0.219, p<0.001) and high for the hen harrier (rho=0.848, p<0.001). Analogously, the relationship between the abundance model results and the raw presence/absence data in the 25% validating data set was low for the Montagu’s harrier (AUC=0.611; Spearman rho=0.192, p<0.001) and high for the hen harrier (AUC=0.866; Spearman rho=0.437, p<0.001). Finally, the correlation between the P/A model results and the raw abundance data in the 25% validating data set was 0.207 (p<0.001) for the former and 0.444 (p<0.001) for the latter.

4. Discussion

4.1 Variables affecting distribution and abundance of harriers in Spain

Our results highlight the environmental variables that are more likely to have a relationship with both harrier species in Spain at a large scale. It is important to remember that since GLM models assume perfect detection, and that it is likely not to be the case, results obtained may be biased (Kéry et al., 2010). Additionally, our models do not include food abundance, which is likely to influence breeding density (Millon et al., 2008) and thus potentially occurrence. Inclusion of this variable would reduce the percentage of unexplained deviance, but would probably change only slightly the shape of the spatial predictions obtained in this study, because food abundance is likely to have a strong significance at more local scales, whereas the environmental variables
included in this study shape macroecological distributions in these species (Anderson et al. 2009; García and Arroyo, 2001; Redpath et al., 2002).

Montagu’s harrier presence was mainly associated at a wide scale with land use and location, secondarily to topographic or weather variables. This species occurred more frequently in flat areas of continental Spain with large proportions of arable land (Table 2). This species is traditionally characteristic of grassland areas, and more recently has taken to occupy agricultural areas, nesting mainly within cereal crops (Arroyo et al., 2004), which concurs with our results. On the other hand, spatial variation in Montagu’s harrier breeding density at a wide scale was affected by location (being also higher in the West), but also by climatic instability and soil permeability (density being higher in areas with high pluviometric irregularity and impermeable soils). These latter variables may be related to nesting habitat suitability. However, and against what could be expected, breeding density is not affected at this scale by land use variables.

Hen harrier favourability areas were concentrated in the Northern half of Spain, and both presence and density were higher in relatively high altitude areas and with low insolation (Table 3). García and Arroyo (2001) have shown that high temperatures are unfavourable for this species’ breeding, so their absence from hotter Southern Spain and their association with higher altitudes and latitudes is not surprising. Additionally, this species nests more frequently in scrub and bushy areas (Arroyo and García, 2008), which are more common in mountainous areas; shrublands, in fact, was the only land use variable which formed part of both models (although availability of arable land, another nesting habitat, also increased breeding density).

4.2 Distribution and favourability models as indicators of abundance
Regarding the coincidence between occurrence models and predicted abundance, we obtained significant positive correlations between predictions of both models, but results differed for the semi-colonial and the not colonial species, as the correlation was much lower for the Montagu’s harrier than for the hen harrier. In other words, in the hen harrier, spatial predictions from the favourability model and the breeding density model were largely concordant. Concurrently, 11 variables coincide in describing both models (Table 3). On the other hand, there were large discrepancies between the favourability model and the breeding density model in the Montagu’s harrier, both in terms of variables included in the models, or their spatial results.

The relationship between occurrence and abundance is directly influenced by mean abundance (Royle et al., 2005), as abundance itself influences the probability of detecting organisms. In general, stronger correlations between abundance and occurrence are expected when abundance is lower. Therefore, the different relationship between hen harrier and Montagu’s harrier P/A and abundance predictions may simply arise if mean abundance was lower in the former than the latter species. Mean observed abundance (within their distribution range) was indeed higher in the Montagu’s than the hen harrier (2.5 vs 0.9 pairs/km² respectively), although differences were not large enough to justify the strong difference in correlation values between both species (0.2 vs 0.8). Additionally, in our opinion, differences in abundance alone cannot explain the considerable spatial discrepancies between models for only one of the species.

On the other hand, imperfect detection may also influence results (Kéry et al., 2010). We could not estimate or integrate detection errors in our models. However, both species are likely to have the same biases relating to presence data (the same protocols are used, both species show very visible flights during pre-laying, used to identify potential breeding areas, etc.), and errors associated to detection for the estimation of
abundance data have already been (at least partially) taken into account (Arroyo and Garcia, 2008, see methods). Therefore, we do not believe that differences in detection probability alone can explain discrepancies observed.

Our results, in our opinion, are better explained by differences in territorial and spatial behaviour between both species. In more territorial species, nest site occupancy is likely to be strongly dependent on environmental quality. Concurrently, spatial predictions from the favourability model and the breeding density model are likely to be largely concordant, as found for the hen harrier. This means that areas identified as optimal with P/A models are also likely to contain the highest densities. This has implications for population monitoring and for conservation purposes: here, variations in presence/absence (which are sometimes the only information available) are highly likely to indicate population trends, and P/A models are adequate for identifying important areas for the species.

In contrast, there was a large discrepancy between the favourability model and the breeding density model in the semi-colonial Montagu’s harrier. There were large apparently favourable areas where predicted breeding density was low, and in contrast zones with high density that fell outside most favourable areas (Fig. 1). This suggests that other factors beyond those considered here strongly affect variation in abundance in this species. Conspecific attraction in semi-colonial or lekking species can lead individuals to leave unoccupied apparently suitable habitats (Heinänen et al., 2008; Osborne et al., 2007). In our case, it is known that local abundance of Montagu’s harrier is influenced by both social attraction and spatial heterogeneity in environmental quality (Cornulier, 2005), and is significantly related to the previous presence and productivity of the species (Arroyo et al., 2002). Thus, the reduced strength of coincidence between
occurrence models and abundance models may be related to the past demographic
history of the species in different areas.

This means that using results from P/A models for estimating variations in abundance
may render spurious results. In contrast, comparisons between both estimates may be
particularly relevant to identify population processes. In particular, it may be insightful
to evaluate what happens in areas with highest intersection values (highly favourable,
with high densities) in comparison with others with high favourability but low densities,
as these differences may be indicative of a problem (e.g. lack of prey in an area, or
unusually low reproductive values). For example, there are no conservation programs
for protecting Montagu’s harrier nests at harvest time in Castilla y León (with high
favourability but low breeding density), so it is possible that productivity is frequently
very low and this reduces the attractiveness of the area (Arroyo et al., 2002).
Additionally, it may be relevant to maintain monitoring programs and identify processes
in areas with high density but relatively low favourability, such as those in the
Mediterranean coast.

Several authors have suggested that relating P/A models to abundance could be a way
of validating the former (Lobo et al., 2008). But normally a positive and significant
association is considered enough to establish this relationship (Jiménez-Valverde et al.,
2009; Real et al., 2009). In the present study we have obtained positive and significant
associations for both species but we consider that it is important to take into account not
only the significance but also the rho values of the correlation. This is a restrictive
approach and in our case it is more realistic because it would not be consistent to
consider the occurrence/abundance relationship similar for both species when there is a
difference higher than 0.5 between the rho values for the two harrier species analyzed.
Overall, our results indicate that breeding system is likely to shape the relationship between presence/absence vs density models. In species that are relatively evenly-spaced, even if spatial variations in density occur, using the results of P/A models is likely to be adequate for population monitoring. In contrast, in other species where the social component is important in habitat selection, population monitoring needs to specifically take local abundance into account. These results have general implications because there are a considerable number of birds which are semi-colonial or aggregated species, and it would be necessary to combine information from both favourability models and abundance models to identify areas of conservation importance or concern for them.

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Table 1 Variables, and their associated factors, used to model harriers distribution in Spain.

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<th>Factor</th>
<th>Variable</th>
<th>Code</th>
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<td>Topography</td>
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<td>Slope (º) (calculated from Alti)</td>
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<td>Southward exposition degree (b)</td>
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<td>Westward exposition degree (b)</td>
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<td>Mean relative air humidity in January at 07:00 (%) (c)</td>
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<td>Water availability</td>
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<td>Mean annual runoff (mm) (d)</td>
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<td>Humidity index (c)</td>
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<td>Mean annual precipitation (mm) (c)</td>
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<td>Energy availability</td>
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<td>Mean annual solar radiation ((kWh/m²/day)*100) (c)</td>
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<td>Mean temperature in July (ºC) (c)</td>
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<td>Mean annual number of frost days (minimum temperature ≤ 0ºC) (c)</td>
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<td>Mean annual actual evapotranspiration (mm) (= min [Prec, PET])</td>
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<td>Annual temperature range (ºC) (= TJul - TJan)</td>
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<tr>
<td></td>
<td>Mean annual number of days with precipitation ≥ 0.1 mm (c)</td>
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<td>Continental index (c)</td>
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<td></td>
<td>Pluviometric irregularity (e)</td>
<td>P Irr</td>
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<tr>
<td>Disturbances</td>
<td>Maximum precipitation in 24 h (mm)</td>
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<tr>
<td></td>
<td>Relative maximum precipitation (= MP24/Prec)</td>
<td>RMS</td>
</tr>
<tr>
<td>Spatial location</td>
<td>Latitude (ºN) (f)</td>
<td>Lati</td>
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<tr>
<td></td>
<td>Longitude (ºE) (f)</td>
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<tr>
<td>Human presence</td>
<td>Distance to the nearest highway (km) (f)</td>
<td>DHI</td>
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<tr>
<td></td>
<td>Distance to the nearest urban center with more than 100 000 inhabitants (km) (f)</td>
<td>U100</td>
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<tr>
<td></td>
<td>Distance to the nearest urban center with more than 500 000 inhabitants (km) (f)</td>
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<tr>
<td></td>
<td>Human population density in 2000 (number of inhabitants/km²) (g)</td>
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<tr>
<td>Lithology</td>
<td>Soil permeability (d)</td>
<td>Perm</td>
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<tr>
<td>Land use</td>
<td>Arable land (b)</td>
<td>Arab</td>
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<td>Grasslands (i)</td>
<td>Gras</td>
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<tr>
<td></td>
<td>Shrublands (i)</td>
<td>Shru</td>
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**Table 2** Montagu’s harrier models. Variables: variables included in the models; Rank: order of entrance of the variables in the models; β: coefficients; SE: standard errors; P: significance: ***<0.001, **<0.01, *<0.05. Variables codes as in Table 1. In bold coincident variables for both models.

<table>
<thead>
<tr>
<th>Favourability model (presence/absence)</th>
<th>Breeding density model</th>
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<tbody>
<tr>
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Table 3 Hen harrier models. Variables: variables included in the models; Rank: order of entrance of the variables in the models; β: coefficients; SE: standard errors; P: significance: ***<0.001, **<0.01, *<0.05. Variables codes as in Table 1. In bold coincident variables for both models.

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In bold coincident variables for both models.
Figure legends

Figure 1 Predicted maps for Montagu’s harrier in Spain at 10 km x 10 km resolution. (a) Predicted favourability, (b) estimated abundance, (c) intersection, and (d) subtraction (favourability – scaled abundance).

Figure 2 Predicted maps for hen harrier in Spain at 10 km x 10 km resolution. (a) Predicted favourability, (b) estimated abundance, (c) intersection, and (d) subtraction (favourability – scaled abundance).
Figure 1