

The effects of land use and climate on red kite distribution in the Iberian peninsula

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Received 27 April 2002; received in revised form 2 September 2002; accepted 10 September 2002

Abstract

The main breeding populations of the red kite (*Milvus milvus* L.), have been declining in the Iberian peninsula during the last decade. However, there is a lack of regional assessments of habitat suitability that identifies limiting ecological factors for the species and areas with conservation problems. In this work we present a regional model for the distribution and abundance of breeding red kites in the Iberian peninsula. The occurrence and estimated abundance in 100 km² UTM squares resulting from road censuses were modelled with broad-scale explanatory variables obtained from satellite imagery, thematic digital cartography, climatic data and spatial coordinates. The occurrence model incorporated mainly climatic variables and had a good discrimination ability, while the abundance model incorporated mainly land-use variables and had a lower explanatory power ($r^2=0.14$). The predictions somewhat overestimated the results of the censuses, and this agrees with the decline of population size and range observed for this species in the Iberian peninsula. These models are relevant in the conservation of the species: first, they suggest the limiting factors for red kite in the Iberian peninsula, and, second, they generate predictive maps pointing out both areas in which conservation problems may be acute (suitable locations that are unoccupied), and areas where no data is available but the red kite is likely to be present (thus guiding further survey and research).

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Keywords: Generalized additive models (GAM); *Milvus milvus*; Poisoning; Predictive habitat modelling; Road count

1. Introduction

The development of effective conservation programs for a given species requires clear understanding of its ecological requirements, and of the factors determining its distribution and abundance. However, regional-scale studies on the abundance and distribution of species are difficult to perform, and results from regional-scale census are rarely analysed in detail for conservation purposes. The wider availability of digital cartography and environmental data derived from satellites, plus recently developed methods based on the use of geographical information systems (GIS) and statistical modelling techniques such as generalized linear models (GLM) or generalized additive models (GAM), provide powerful tools that can be used to model the distribution and abundance of species (see a review in Guisan

and Zimmermann, 2000). Variables derived from climate, topography, habitat type or structure, or human pressure can be used as predictors in these models (Austin et al., 1996; Lavers and Haines-Young, 1996; Corsi et al., 1999; Osborne et al., 2001). The models may then be used to evaluate if the census has covered adequately all potential areas for the species and indicate where coverage should be improved. Models can also detect suitable areas for the species but currently unoccupied, and consequently, may give insight into conservation problems at regional or local scales, indicating areas where conservation actions should be given priority (Lawton and Woodroffe, 1991; Donazar et al., 1993; Osborne et al., 2001).

The red kite (*Milvus milvus* L.) is a raptor species that may be considered almost exclusively European (Cramp and Simmons, 1980). With the exception of some small relict populations of uncertain status in Mediterranean Northern Africa (Viñuela, 1996), the Iberian peninsula is the southern edge of its distribution. Red kite populations

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disappeared or were strongly reduced over all its range during the nineteenth and first half of twentieth centuries, mainly due to human persecution, and thus it was considered a globally endangered species up to the 1980s (Collar and Andrew, 1988). After the implementation of legal protection for raptors during the 1960s–1970s, populations of red kites in central Europe quickly recovered. However, the species still had a poor conservation status in the southern edge of its range (Viñuela, 1996), and during the last 10 years alarming population declines have been detected in the three main strongholds of the species, Germany, Spain, and France (Viñuela et al., 1999; Mammen, 2000; Thiollay, 2001). Spain held the second most important European breeding population of the species in 1994, estimated to be 3300–4100 breeding pairs (Viñuela et al., 1999), but by that time most populations for which data were available were declining, apparently due to illegal predator control by hunting and poisoning (Villafuerte et al., 1998).

The red kite is considered a generalist species, with no important habitat requirements, and able to breed in a wide range of climates (Cramp and Simmons, 1980; Carter, 2001). The only requirement often cited for this species is a mixture of forest patches to breed and open areas to search for food. It has been suggested that human landscapes created in some agricultural areas, with a mixture of forest patches and open croplands, probably favoured the expansion of the species in the past (Carter, 2001). However, only partial and local data about the factors determining distribution and abundance of the species have been published (reviewed in Viñuela et al., 1999; Carter, 2001), and it has been suggested that habitat alterations induced by land-use changes may strongly affect its breeding success, abundance, and distribution (Hille, 1995; Mammen, 2000).

In this paper we present regional-scale predictive models of distribution and abundance of breeding red kites for the Iberian peninsula ($\sim 600,000$ km²). The models consider climatic, topographic, and habitat factors, to improve our understanding of those which are the main natural factors determining the occurrence and abundance of the species. The Iberian peninsula may be particularly suitable for this study, because limiting factors affecting its distribution may be more easily identified here than at the core of its range. Furthermore, we develop predictive models of the occurrence and abundance of red kites in Spain, aiming to identify suitable areas for red kites that are currently unoccupied. The results may help to locate areas with particular conservation problems. The red kite may be considered an excellent subject for habitat modelling because it is not very common (in this case it would frequently occupy suboptimal areas), nor very rare (in this case much of the suitable areas could be unoccupied).

2. Methods

2.1. Red kite data and variables considered

Data for our study comes from the national red kite census performed in 1994 for most of Spain (Viñuela et al., 1999), and a census of Andalusia performed in 1996 (Bustamante et al., 1997). In both censuses an average of 40 km of road transects were driven at a low speed in each of a number of 10×10 km UTM squares during the breeding season. In a sample of 61 UTM squares covering different types of landscapes in several geographic areas, red kite populations were surveyed simultaneously by road transects and nest searching/detection of territorial pairs by standardized observation. Within this sample we calculated an index of relative density (IRD, no. of kites in 100 km of road transect), and for each square sampled the IRD were used to predict the number of breeding pairs in the square by means of a linear regression on estimated populations through nest detection. The regression explained $>85\%$ of the variance in IRDs, and thus road transects proved to be an adequate method to estimate the number of breeding pairs (Viñuela, 1997). Some areas of Spain were not exhaustively sampled, but enough previous information existed to assume that no kites bred there; these squares were included in the analysis as squares where the species was absent (Fig. 1). Thus, we had information on the occurrence of the species in 2990 UTM squares (386 with presence of red kites and 2604 with absence) and an estimate of breeding pairs for each sampled square. We decided to extend our predictions to Portugal, in spite of not having a contemporary survey there, because Spain and Portugal share similar environmental features and there are no natural barriers for red kites between the two countries.

To build models to predict the distribution and abundance of the species, we tested as predictors 11 broad-scale variables: six land-use/land-cover variables derived from CORINE digital map (CEC, 1991), two topographic variables (altitude and slope) derived from a digital elevation model (DEM), two climatic variables (rainfall and temperature), and an index of plant productivity derived from satellite imagery (PPI, Table 1). This index comes initially from a monthly maximum value composite of NDVI images (a radiometric vegetation index, Díaz-Delgado and Pons, 2001) from the sensor AVHRR of the NOAA satellites (1 km² spatial resolution). We performed a principal component analysis on 166 NDVI images dated between 1984 and 2000, and selected the first component (our index PPI), which explained 95.8% of variation in data (see for details Lillesand and Kiefer, 1994; Osborne et al., 2001). Predictors were in origin at different resolutions (from DEM at 100 m to CORINE at 250 m and NOAA imagery resampled

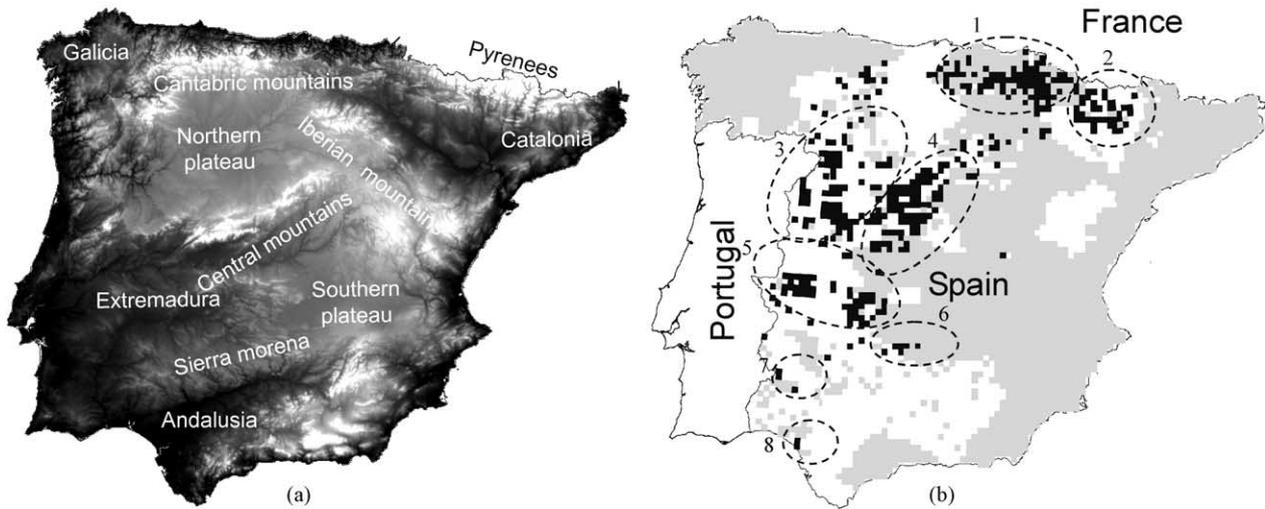


Fig. 1. (a) Study area. Topography of the Iberian peninsula with geographical names as used in the text. Darker shades correspond to lower altitudes. (b) Location of 10×10 UTM squares with red kite presence (black squares), absence (grey squares) or no data available (but presumably absence in most cases, white squares). Main breeding areas: 1. Southwestern Pyrenees, 2. Central Pyrenees, 3. Northern Plateau (nucleus of Salamanca-Zamora), 4. Central Mountains, 5. Extremadura, 6. Eastern Sierra Morena, 7. Western Sierra Morena, 8. Doñana marshland.

Table 1

Predictive variables tested in the models for occurrence and abundance of breeding red kite in the Iberian peninsula. A single mean value was obtained for each 10×10 km UTM square in the analysis

| Predictor | Description | Source |
|-----------|--|--------------------------------------|
| FOR | Percentage of forest | Modified from CORINE ^a |
| DEH | Percentage of <i>dehesas</i> (sparsely forested areas, mainly of <i>Quercus ilex</i> subsp. <i>ballota</i> and <i>Q. suber</i>) | Modified from CORINE ^a |
| PAS | Percentage of pastureland | Modified from CORINE ^a |
| TRE | Percentage of tree cultures (mainly olive groves, fruit trees, but also vineyards) | Modified from CORINE ^a |
| IRR | Percentage of irrigated cultures | Modified from CORINE ^a |
| NIC | Percentage of non-irrigated cultures | Modified from CORINE ^a |
| ALT | Mean altitude (m) | Digital elevation model ^b |
| SLO | Mean slope (degrees) | Digital elevation model ^b |
| TEMP | Mean annual temperature (10 ⁻¹ °C) | Meteorological stations ^c |
| RAIN | Mean annual precipitation (mm) | Meteorological stations ^c |
| PPI | Plant productivity index | Satellite imagery ^d |

^a Variables obtained by pooling the original 44 categories of the CORINE land cover cartography as follows: FOR is Forests category; DEH, Agro-forestry areas (annual crops or grazing lands under the wooded cover of forestry species); PAS, Pastures and Natural grassland; TRE, Permanent crops (i.e., those not under a rotation system); IRR, Permanently irrigated land and Rice fields; and NIC, Heterogeneous agricultural and non-irrigated cultures (except Agro-forestry areas). Map resolution is 250 m (see <http://reports.eea.eu.int/COR0-landcover/en> for details of the CORINE programme).

^b Variables obtained from a Digital Elevation Model of the Iberian peninsula at 100 m horizontal resolution.

^c Raw data provided by the Spanish Instituto Nacional de Meteorología and spatially modelled at resolution 1 km² (own data, unpublished).

^d Raw data provided by the LATUV (Laboratorio de Teledetección de la Universidad de Valladolid) is a monthly maximum value composite of a radiometric vegetation index (NDVI) from the sensor AVHRR of the NOAA satellite resampled at 10×10 km² (see text for details).

at 10×10 km) and data were averaged within the 10×10 km UTM squares (Table 1).

2.2. Statistical analyses

We built GAMs (Hastie and Tibshirani, 1990) of occurrence and abundance of breeding red kites in 10×10 km UTM squares. For studying patterns of occurrence, the response variable was the presence/absence of red kite in each square and we used a binomial error and a logistic link. To model the breeding abundance (i.e. density pattern) the response variable

was the estimated number of breeding pairs per square (including only the 386 squares with one or more kites) and we used a Poisson error with a log link. Both models started by including all the predictors as smooth terms (a smoothing spline with 3 degrees of freedom) and we made a backwards stepwise search of a best subset model. In every step, we tested the significance of variables by a likelihood ratio test of the current full model versus the reduced model without each particular variable. Non-significant variables ($P > 0.05$) were tested with a simpler form (that is, with fewer degrees of freedom) and, if the effect was non-significant, they were

excluded from the model. We aimed to obtain a parametric model to facilitate the transfer of results to a GIS to generate maps, and because parametric models may be more interpretable than complex non-parametric curves (Guisan and Zimmermann, 2000). Therefore, we transformed all the smoothed variables to suitable parametric terms guided by visual inspection of partial residual plots. For example, we transformed curvilinear forms that showed a maximum either to quadratic polynomials (see ALT in Fig. 2b) or to piecewise linear functions with a threshold beyond which the response is constant (see PAS in Fig. 2d). These models are called hereafter *environmental models*.

We converted the environmental models into a modified version of *autologistic models* (Augustin et al., 1996) to take into account the possible spatial autocorrelation of the squares, that is, the fact that neighbouring squares are likely to have similar environmental characteristics or that high red kite density in a given square may influence the density in neighbouring, less favourable squares. To this aim, we estimated the probabilities of the models for every UTM square in the Iberian peninsula, then we took the average of probability in each group of nine adjacent squares and included this new variable—an autocovariable—within the environmental models. Finally, we modelled the amount of unexplained variation in the autologistic models with the cartesian coordinates in UTM projection (latitude, longitude and their interaction) to account for regional trends in the pattern of distribution (Legendre, 1993). We entered coordinates as non linear terms (natural cubic splines with 3 knots in the 0.1, 0.5 and 0.9 quantiles, Harrell, 2001).

There is not an unanimously accepted measure of performance for logistic models such as the coefficient of determination R^2 in linear regression. Therefore, we assessed the discrimination ability (Pearce and Ferrier, 2000) of the occurrence models with three different measures. First, the commonly used correct classification rate. Second, Cohen's Kappa statistic, which estimates the correct classification rate adjusted by chance (Titus et al., 1984). In this case we chose the threshold to be the mid-point between the mean estimate for presence and the mean estimate for absence (Fielding and Haworth, 1995). And third, the area under the curve (AUC) of a receiver operating characteristic (ROC) plot (Swets, 1988). From all possible pairs of squares, one with presence and the other with absence of breeding kites, the AUC measures the proportion of such pairs in which the occupied square has a higher probability of presence than the unoccupied square. Finally, we used Spearman correlation (r_s) to analyse the agreement of predicted and actual abundance, but Pearson correlation (r) to measure the amount of explained variation in both the occurrence and abundance models (Mittlböck and Schemper, 1996).

To evaluate the models we followed a data-splitting strategy, developing the models with a random selection

of 75% of the squares (the *training* set) and holding the rest of data to evaluate the models (the *test* set). The correct estimates of discrimination ability of the models in new scenarios are those for the test set, which are reported here. Final estimates of model coefficients were obtained with the complete dataset, and predictions were produced for all squares in the Iberian peninsula, including Portugal and the non-sampled Spanish UTM squares.

Models were developed with S-PLUS 2000 (Math-Soft, 1999) and AUC calculated non-parametrically with AccuROC 2.5 (Vida, 1993).

3. Results

3.1. Occurrence model

The environmental model was highly significant ($P < 0.0001$) and included eight of the original set of 11 variables (Table 2). The variable PPI (plant productivity) generated the major change in deviance (about 30% of the total accounted for), and was included in the model as a quadratic polynomial (Fig. 2a). Red kite occurrence showed a maximum at a value of 1896 units of our index (range 0–2500). The topographic variables accounted for a further 25% of the model change in deviance (Table 2). Red kite probability of occurrence had a quadratic relationship with mean altitude (ALT) and a piecewise linear relationship with slope (SLO), with maximum probability of occurrence for altitudes around 850 m, and decreasing probability of occurrence with topographic ruggedness (Figs. 2b, d). The most important land-use/land-cover variable related to red kite occurrence was % pasture (PAS) (15% of explained deviance), so that an increasing coverage of pasturelands was associated with increasing probability of red kite occurrence (Fig. 2c). Other land cover and climatic variables had less importance, in terms of change in deviance (Table 2). The model showed a linear decrease in probability of occurrence with increasing % tree cultures (TRE), a slight linear increase with increasing % non-irrigated crops (NIC), a small maximum for intermediate values of % forest (FOR) (65% of explained deviance) and, finally, a stairway-like decrease with annual temperature (TEMP) (Fig. 2f–h).

The autocovariable was also significant (change in deviance = 128.8, change in $df = -1$, $P < 0.0001$) and improved the discrimination ability of the model (Table 3). Final models with the addition of the spatial coordinates had a correct classification rate of some eight to nine in each 10 squares, which is 48% more than what was expected by chance (as estimated by Kappa). According to the AUC, nine out of 10 pairs of squares (one square occupied and the other one unoccupied) are correctly rated. Overall, the occurrence model could explain about 40% ($r = 0.63$, $t = 44.6$,

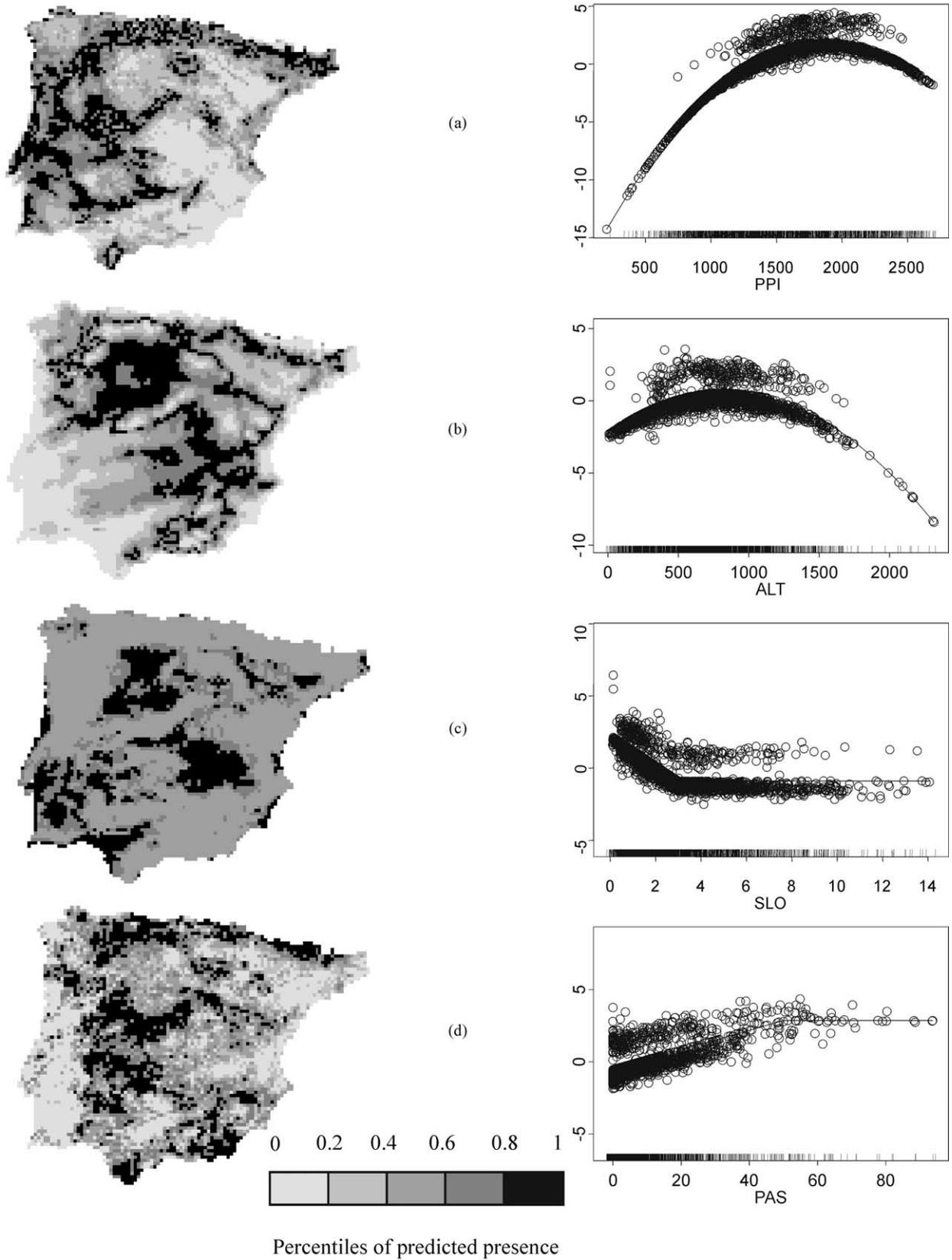


Fig. 2. Probability of red kite presence in the Iberian peninsula predicted by individual variables in the model, with corresponding maps (darker squares indicate a higher predicted probability of presence). Final predicted presence for each square is the (transformed) sum of predictions of individual variables. (a) plant productivity index; (b) mean altitude (m); (c) mean slope (degrees); (d) % pastureland; (e) % tree cultures; (f) % non-irrigated cultures; (g) % forest; and (h) annual temperature ($10^{-1} \text{ }^\circ\text{C}$).

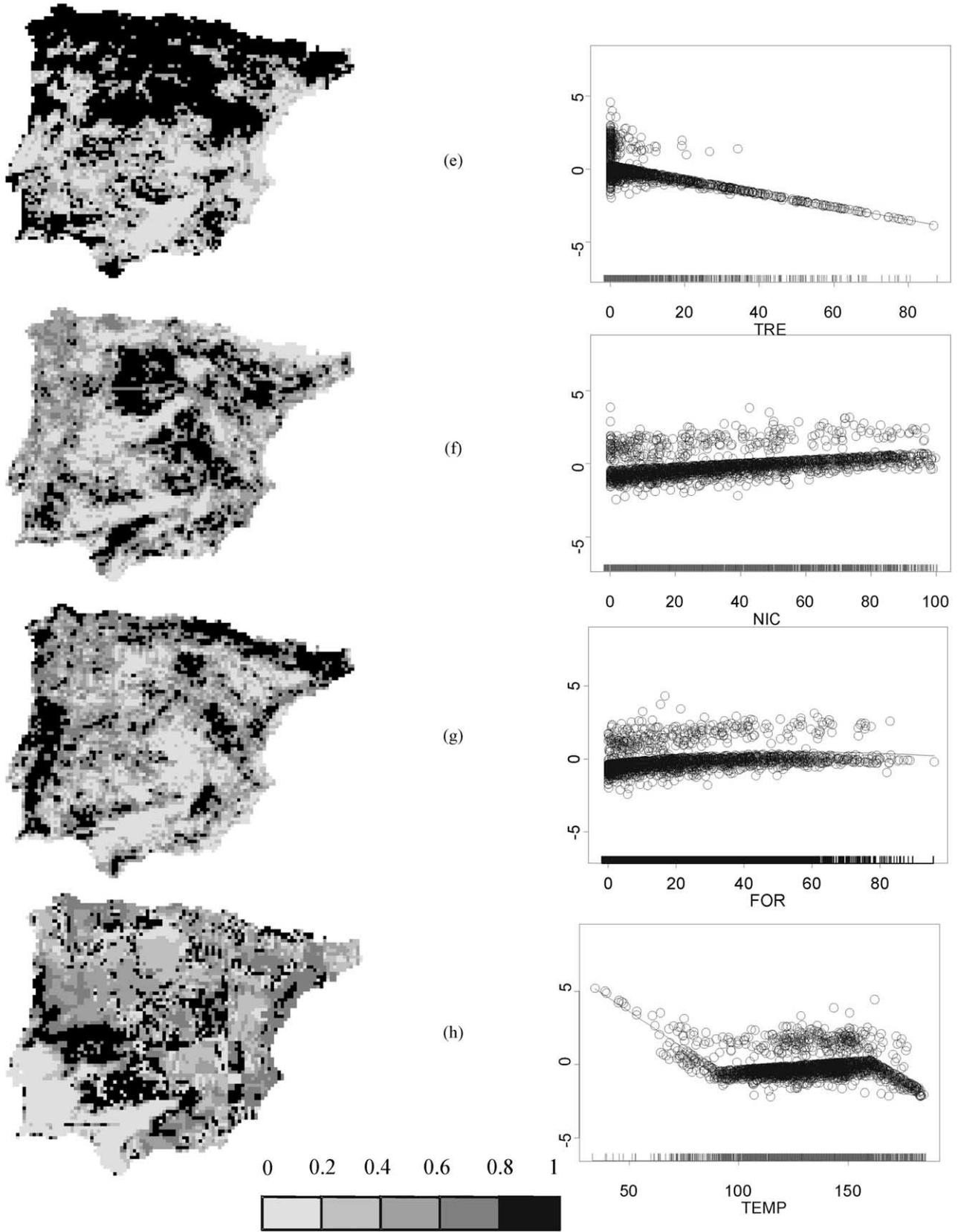


Fig. 2. (continued)

Table 2
Deviance table of the environmental model for occurrence of red kite in UTM squares

| Term | Coefficient | SE | Residual df | Change in df | Residual deviance | Change in deviance | <i>P</i> |
|--------------------------------|-----------------------|-----------------------|-------------|--------------|-------------------|--------------------|----------|
| Null | | | 2416 | | 1882 | | |
| Saturated | | | 2403 | 13 | 1289 | 593 | |
| Intercept | −17.406 | 2.346 | | | | | |
| PPI | 0.022 | 0.002 | | | | | |
| PPI ² | −5.8*10 ^{−6} | −5.9*10 ^{−7} | | −2 | | −168 | <0.0001 |
| SLO ^a | −0.851 | 0.117 | | −1 | | −89 | <0.0001 |
| PAS ^a | 0.068 | 0.008 | | −1 | | −87 | <0.0001 |
| ALT | 0.007 | 0.001 | | | | | |
| ALT ² | −4.1*10 ^{−6} | 6.2*10 ^{−7} | | −2 | | −58 | <0.0001 |
| TEMP ₁ ^a | −5.634 | 1.133 | | | | | |
| TEMP ₂ | −4.868 | 1.031 | | −3 | | −44 | <0.0001 |
| TEMP ₃ | −7.032 | 1.252 | | | | | |
| TRE | −0.061 | 0.019 | | −1 | | −8 | 0.005 |
| NIC | 0.047 | 0.004 | | −1 | | −8 | 0.005 |
| FOR | 0.026 | 0.012 | | | | | |
| FOR ² | −2.0*10 ^{−4} | 1.6*10 ^{−4} | | −2 | | −7 | 0.029 |

Change in degrees of freedom and change in deviance associated with each variable is estimated by comparison of the reduced model without each particular variable against the saturated model. Names of variables as in Table 1

Table 3
Estimates of discrimination ability for the red kite occurrence models in UTM squares

| Model type | Correct classification rate | Kappa | AUC |
|----------------------------------|-----------------------------|-------------|-------------|
| Environmental | 0.84 | 0.35 (0.07) | 0.84 (0.02) |
| Autologistic | 0.86 | 0.42 (0.07) | 0.88 (0.02) |
| Final (plus spatial coordinates) | 0.87 | 0.48 (0.07) | 0.92 (0.01) |

The *environmental* model is described in Table 2, the *autologistic* model is the same but entering an autocovariate (the mean of predicted probabilities in nine adjacent UTM squares) simultaneously with the rest of predictors, and the *final* model included the spatial coordinates to fit the unexplained variation in the autologistic model. Standard errors are given in parentheses [approximate SE for Kappa following Titus et al. (1984) and asymptotic SE for the area under the curve (AUC) according to Vida (1993)].

$P < 0.0001$) of the variability of the data according to the Pearson correlation between prediction and actual outcomes, which is a fair amount considering the low values of explained variance (or deviance) obtained typically in logistic regressions. Accordingly, a calibration plot shows a high agreement between observations and predictions, except for the upper end of the predicted range (Fig. 3a). It is interesting to note that predicted probabilities of occurrence correlated also significantly with estimated abundance ($r_s = 0.51$, $z = 27.9$, $P < 0.0001$).

The final model predicted a high probability of occurrence in the four main breeding areas of the species in the Iberian peninsula (Fig. 4a): southern slopes of the Pyrenees, western side of the Northern Plateau (between Salamanca and Zamora provinces), both sides

of the Central Mountains, and Extremadura (see also areas 2, 3, 4, 5 and 6 in Fig. 1). However, the model predicted the occurrence of red kites in an area larger than the current range of the species, where red kites are absent or present only sparsely (Cantabric and Iberian mountains, and Catalonia). On the other hand, the model predicts a low probability of occurrence in the Doñana marshlands (population 8, Fig. 1), where a small dense population occurs in an atypical area (in Doñana red kites breed in the narrow edge of marshland with pine forest, at sea level).

3.2. Abundance model

The environmental model was highly significant ($P < 0.0001$) and included five of the original set of 11 variables (Table 4), among which topographic variables accounted for most of the change in deviance (about 54%). SLO again suggests a lower predicted abundance for more rugged areas (Fig. 5 a), while ALT, which entered as a quadratic polynomial (Fig. 5b), suggests a higher abundance for intermediate altitudes (maximum at 900–1000 m). The rest of the variables in the model belong to the land-use/land-cover type: % irrigated crops (IRR) and TRE with a negative sign, and PAS with a positive sign (Fig. 5c–e).

The autocovariate was also significant (change in deviance = 0.48, change in df = 1, $F = 10.48$, $P = 0.001$), and improved the predictive ability of the model from $r_s = 0.21$ ($z = 2.2$, $P = 0.003$) to $r_s = 0.29$ ($z = 2.9$, $P = 0.003$). The inclusion of the geographical coordinates further enhanced the accuracy of the model ($r_s = 0.41$, $z = 4.3$, $P < 0.0001$). Overall, the abundance model could explain only a small amount of the variability of the data

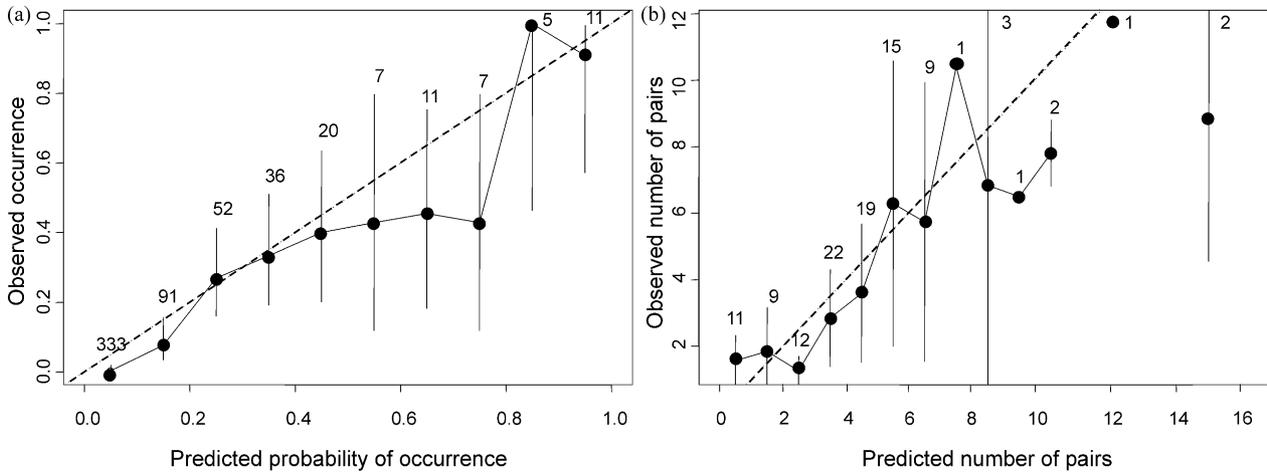


Fig. 3. (a) Comparison of observed and predicted occurrence of red kites in 10×10 km squares (following Pearce and Ferrier, 2000). (b) Comparison of observed and predicted number of breeding pairs. Dashed lines show perfect relationships. Vertical lines show 95% confidence intervals with the number of evaluated squares in each class. In (b) the model did not predict any square having 11, 13 or 14 pairs.

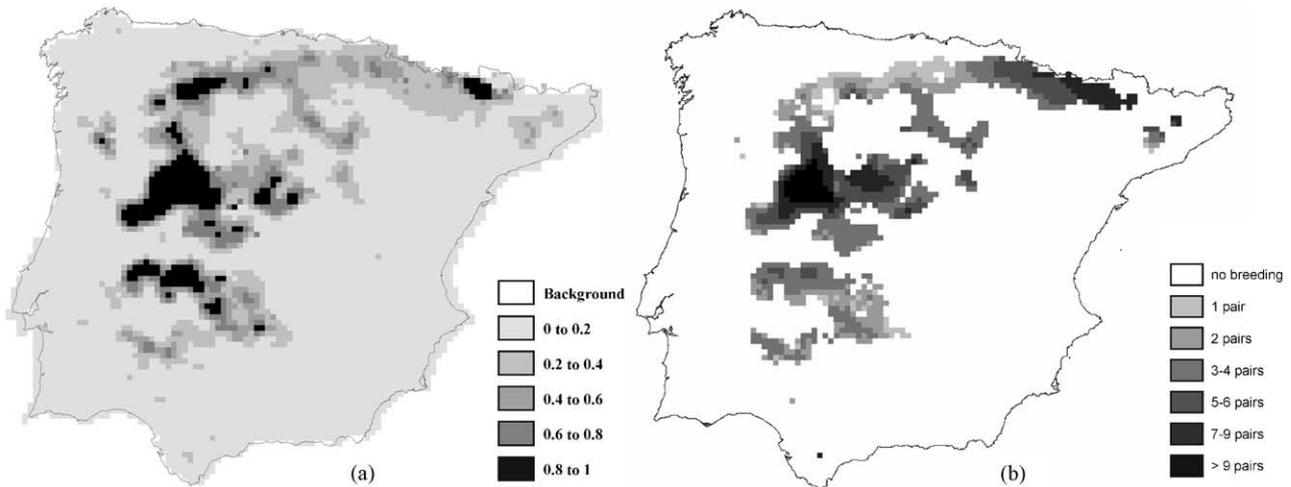


Fig. 4. (a) Final predictions of red kite occurrence (probability of presence) in 10×10 km UTM squares in the Iberian peninsula. (b) Final predictions of red kite abundance (in pairs/100 km²) in the Iberian peninsula. We represent only the squares for which presence of breeding red kite was previously predicted using a threshold of probability $P > 0.30$, which is the average between the predicted probabilities for squares with recorded presence of red kite and the probabilities for squares with absences (see Fielding and Haworth, 1995; Guisan et al., 1998).

Table 4
Deviance table of the environmental model for abundance

| Term | Coefficient | SE | Residual df | Change in df | Residual deviance | Change in deviance | F | P |
|------------------|-----------------------|----------------------|-------------|--------------|-------------------|--------------------|-------|---------|
| Null | | | 278 | | 12.07 | | | |
| Saturated | | | 272 | -6 | 9.54 | -2.53 | 9.01 | <0.0001 |
| Intercept | -4.366 | 2.108 | | | | | | |
| SLO ^a | -0.302 | 0.319 | | -1 | | -0.90 | 19.33 | <0.0001 |
| ALT | 0.003 | 0.005 | | -2 | | -0.46 | 4.91 | 0.008 |
| ALT ² | -1.5*10 ⁻⁶ | 3.1*10 ⁻⁶ | | | | | | |
| PAS ^a | 0.017 | 0.027 | | -1 | | -0.39 | 8.32 | 0.004 |
| IRR | -0.034 | 0.075 | | -1 | | -0.28 | 6.03 | 0.015 |
| TRE | -0.053 | 0.125 | | -1 | | -0.24 | 5.20 | 0.023 |

Change in degrees of freedom and in deviance associated with each variable is estimated by comparison of the reduced model without a particular variable against the saturated model. *P*-values corrected for underdispersion. Names of variables as in Table 1.

^a SLO and PAS modelled as piecewise linear functions (see Fig. 5a, c).

($R^2=0.14$, $P=0.0001$). The average model predictions agreed closely with observations in squares with low abundance, but overestimated the number of breeding pairs for squares with predicted numbers above nine pairs per 100 km² (but means are estimated here with low sample sizes, see Fig. 3b).

Final predicted abundances were highest for the western side of the Northern Plateau, Southern Pyrenees,

Central mountains and some areas in Extremadura, where the maximum densities of red kite actually occur. Predicted abundance was low in areas of the Cantabric Mountains and the Southern Plateau where low abundances have been observed. However, predicted abundance was high in other areas where no high density of red kites actually occur, such as some parts of the Iberian Mountains and Catalonia (Fig. 4b).

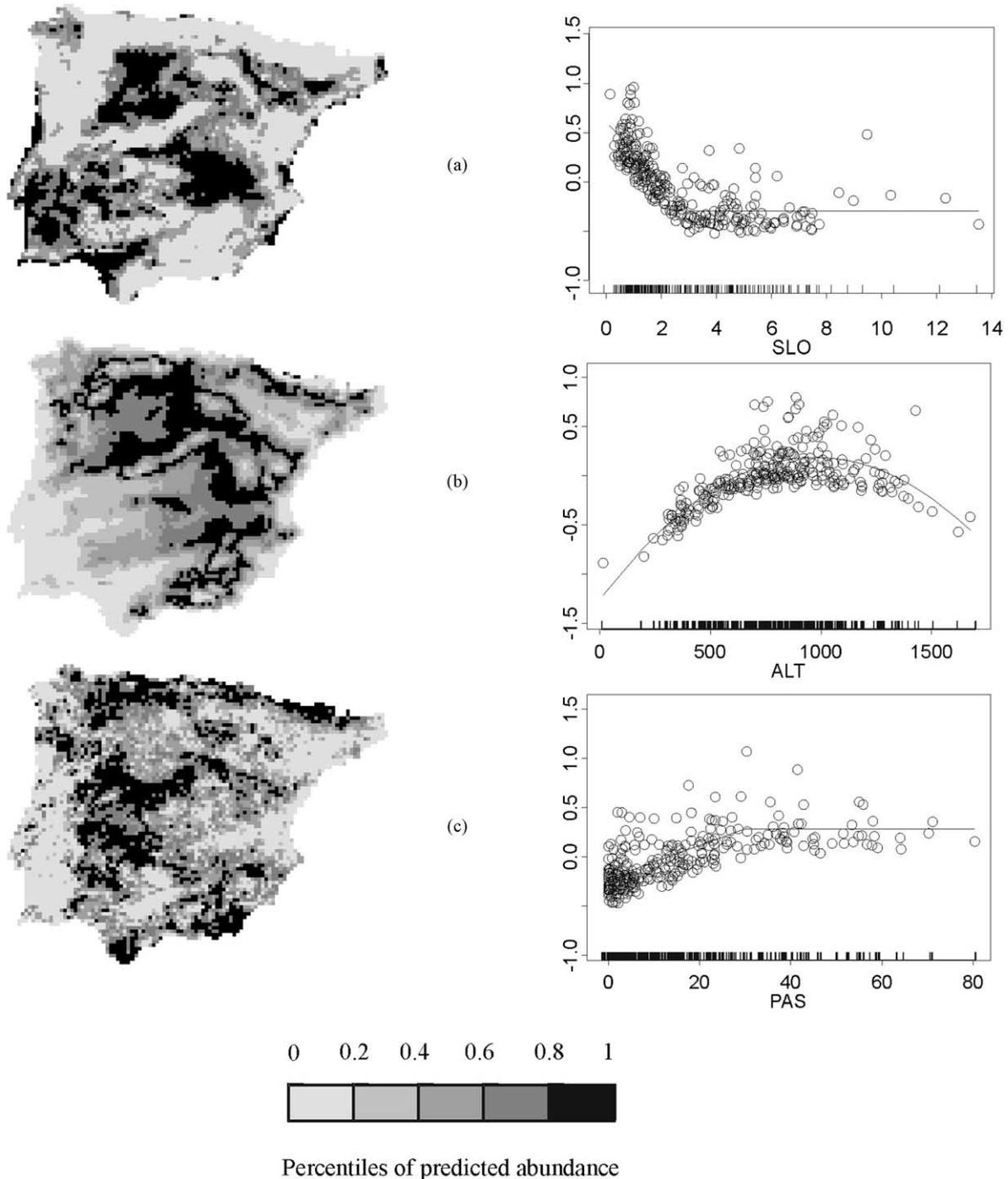


Fig. 5. Number of pairs of red kite in the Iberian peninsula predicted by individual variables in the model, with corresponding maps (darker squares indicate a higher predicted probability of presence). Final predicted presence for each square is the (transformed) sum of predictions of individual variables. (a) mean slope (degrees); (b) mean altitude (m); (c) % pastureland; (d) % non-irrigated cultures, and (e) % tree cultures.

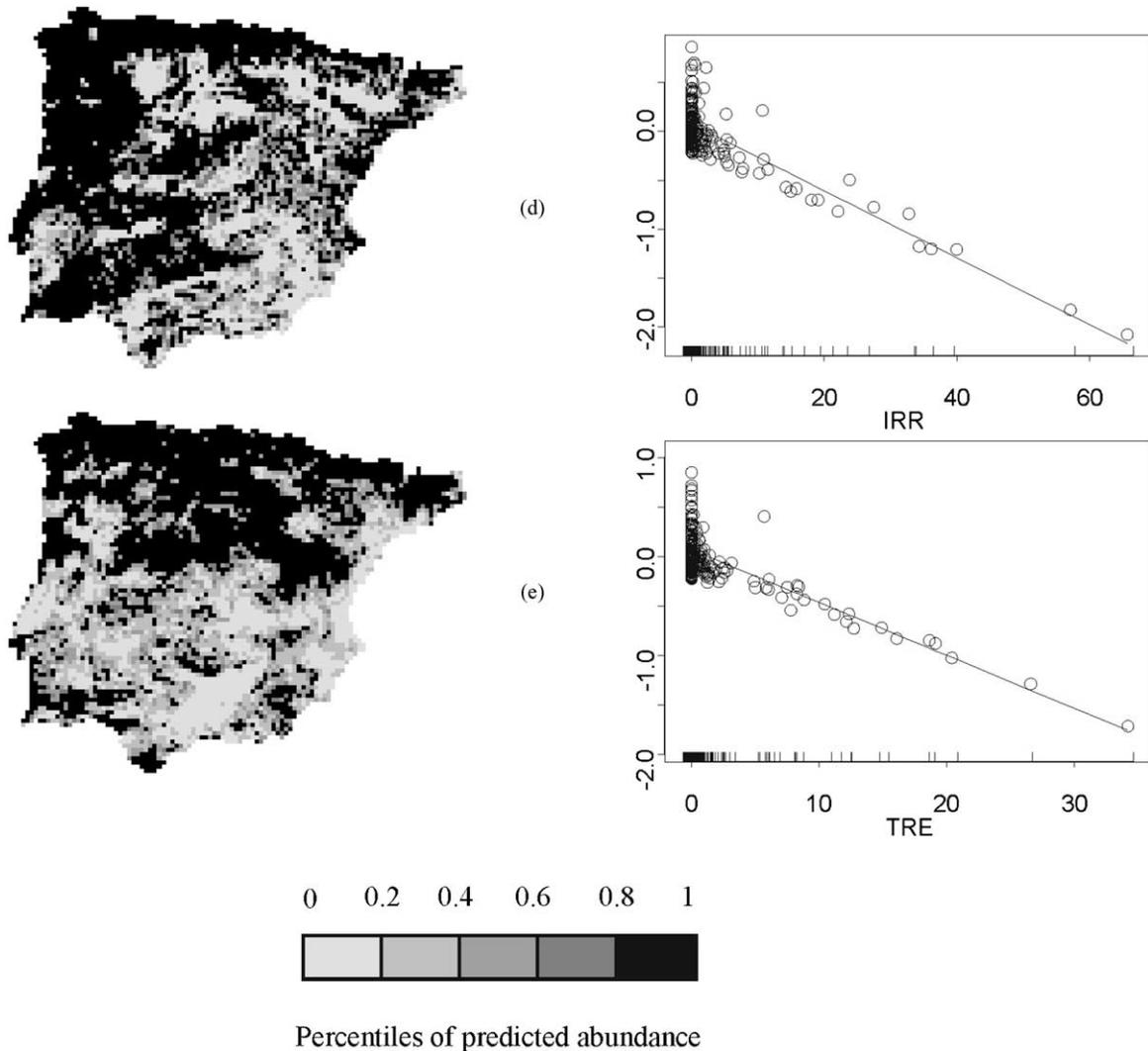


Fig. 5. (continued)

4. Discussion

4.1. Factors explaining red kite distribution

Our models show that the red kite distribution can be predicted from climate, topography and vegetation cover. The irregular and fragmented distribution currently observed in Spain can be explained largely by these factors although it may also have been influenced by the intensity of present or past human persecution upon the species (Viñuela et al., 1999). The variables PPI, ALT and TEMP represent 45% of the deviance explained by our environmental model. We consider these three variables represent the response of red kite to topo-climatic factors.

PPI is an index of plant productivity derived from NOAA AVHRR imagery that, at this spatial scale, represents the response of vegetation growth to rainfall and temperature. The bell-shape response of red kite occurrence to altitude probably also reflects a selection

of particular climatic conditions in the Iberian peninsula. The shape of the declining response to mean annual temperature shows an avoidance of the more Mediterranean and semiarid locations. We do not know the ultimate cause of the response of red kites to PPI. The highest values of the index are obtained in rainy areas of Atlantic climate in the north of the Iberian peninsula and the lowest values in the semi-arid Mediterranean southeast. Optimum PPI values for the red kite occur in areas surrounding the mountain ranges and increase in magnitude in a southeast to northwest direction (Fig. 2a). The predictive ability of PPI could be due to an avoidance by red kites of rainy climates and at the same time a preference for areas of relatively high biological productivity. For the black kite (*Milvus migrans*), it has been observed that rain in spring has a direct negative effect on hatching success (Viñuela and Sunyer, 1992), and on nestling growth rate (Hiraldo et al., 1990). The remnant red kite population in Wales (UK), living in a rainy climate, has one of the lowest

breeding rates known for the species, due to low hatching success and high nestling mortality, apparently associated with poor feeding rates (Lovegrove, 1990; Newton et al., 1994). In contrast, the reintroduced populations in southern and central England are in much drier parts of the country and have a much higher breeding success (Carter, 2001, personal communication).

The PPI index probably also reflects average biological productivity of the area so that areas with low PPI values must be areas with relatively low average biological productivity, where small prey or carrion sought by red kites may be more scarce. This could be especially relevant during the typical hot summer drought of Mediterranean latitudes that covers the critical period of transition to independence of fledglings (Bustamante, 1993). The preference of relatively high ground (optimum around 850 m), where summer drought is shorter and less intense, and the negative relationship between red kite occurrence and mean annual temperature, gives additional support to the idea that hot summers may be a limiting factor for the distribution of the species. Likewise, competition with black kites, which do better in hot areas, may help to explain the preference of cooler areas by red kites (as can be deduced by their world distribution Cramp and Simmons, 1980; and see Viñuela et al., 1999).

We tested the idea that biological productivity may be setting a lower limit to the distribution of the red kite and that rainfall has a negative effect once productivity is controlled for. An alternative environmental model of occurrence was built in which annual rainfall was added as a linear term. This alternative model indicated that there was a significant negative relationship between red kite occurrence and rainfall once the effect of PPI was controlled for. This model had a predictive ability similar to the environmental model [$Kappa = 0.45 (SE = 0.08)$, $AUC = 0.83 (0.03)$] (compare with Table 3), but being less parsimonious it was not selected by our statistical analysis procedure.

Topography was the next most important factor affecting red kite distribution. Slope was responsible for a 15% reduction in deviance accounted for in the environmental model. Red kites seem to show a preference for less rugged areas (at the 10×10 km resolution scale), as suggested also by Meyburg (1973) and Elósegui (1985). This may be through direct selection of more extensive open areas for hunting or an avoidance of mountainous areas with larger raptors such as imperial eagles (*Aquila adalberti*), golden eagles (*Aquila chrysaetos*) or eagle owls (*Bubo bubo*), which can prey on red kites (Cramp and Simmons, 1980; Ferrer, 1993; Serrano, 1998).

Interestingly, this pattern of distribution affected by climate and topography probably applies to the red kite population in France, where they are absent from the major part of the Atlantic west of the country, are very

scarce in Mediterranean areas in the southeast, and reach highest densities in mid-mountain areas and mountain valleys of the Pyrenees, Massif Central, the Vosges and Alsace (Voisin, 1994).

The variables that describe land-use/land-cover constitute the third group of predictors of red kite distribution, and account for 20% of the deviance explained by the model. Among these, the most important is the area of pasturelands, which explains 15% of the deviance. Pasturelands are also considered important for populations locally in Germany (Stubbe et al., 1995), where they may constitute optimal foraging habitat for prey such as voles and invertebrates (Hille, 1995).

Surprisingly, the area covered by *dehesas* (extensive pasturelands devoted to cattle, sheep or pig raising, with scattered oaks *Quercus* spp. or ashes *Fraxinus* spp.) (variable DEH) did not enter the distribution or abundance models. It has been argued that they constitute the most important breeding habitat for red kites in Spain (Viñuela et al., 1999), having the optimal landscape structure with extensive open lands for hunting and large scattered trees for breeding. However, there are extensive areas of *dehesas* in Extremadura and Andalusia without breeding red kites, and those where the species breeds are already identified by the combination of climatic and topographic variables. Also, the Agro-forestry areas in the CORINE land-use/land-cover map, which we used to assess the extent of *dehesas*, may be quite heterogeneous in regard to tree and shrub cover, since that class includes areas with closed tree or shrub canopies as well as those with very sparse or small trees unsuitable for breeding of large raptors.

4.2. Factors explaining red kite abundance

Red kite abundance was more difficult to model than distribution. Only altitude indicated a greater red kite abundance in mid-mountain areas and was responsible for 18% of the deviance accounted for by the model. Topography (mean slope) was responsible for another 35% and land-use/land-cover variables for another 36%. The abundance model indicated in general a pattern that agrees with the distribution model: greater abundance in mid-mountain areas with relatively flat relief and >30% pasture lands, and a rejection of the more intensively managed agricultural landscapes (irrigated cultures and tree crops). Contrary to the occurrence model, the abundance model gave more weight to land-use factors than topography and climate.

The calibration plot of the abundance model (Fig. 3b) indicated a very good adjustment of the model to test data for low densities but a clear overestimate for predicted values of more than nine breeding pairs per 100 km². This result might be congruent with an upper density limit in most habitats caused by red kite territoriality; but it could also be the result of a reduction in density due

to illegal predator control. This second explanation seems more realistic if we consider that few areas exist with very high red kite breeding densities (20 pairs per 100 km²) above those predicted by our model, and the fact that the calibration plot for the distribution model (Fig. 3a) also indicates a slight overestimate (eight out of 10 values are below the equal probability line).

4.3. Observed versus predicted distribution and abundance

Overall, the occurrence model explained a fair amount of variance and its predictive power was high, according to the standards suggested by several authors (e.g. Pearce and Ferrier, 2000) and comparing our results with those reported in previous habitat models (e.g. Austin et al., 1996; Tobalske and Tobalske, 1999; Osborne et al., 2001; Rico Alcázar et al., 2001). Moreover, the correlation between predicted probabilities and estimated abundance (higher probabilities of presence for squares with more kites) gives further confidence in the model. However, the abundance model had a relatively low predictive power.

Both models predicted occurrence of red kites in areas where the species is very scarce or does not currently breed. The most striking example is the southern slopes of the Cantabric mountains, where the habitat seems to be good for the species, but where only isolated pairs or small populations in restricted areas of the mountains have been found. The high probability of presence predicted in this area (Fig. 4a) contrasts with the low values predicted by the abundance model (Fig. 4b). Perhaps this discrepancy could be explained by factors related to human activities not considered in the models, such as the intensive use of rodenticides (to which red kites are particularly vulnerable Carter, 2001), and the recent increase of irrigated cultures in that zone (see Fig. 5d). The fact that land-use variables have more weight in the abundance model compared with climatic variables in the distribution model supports this view.

Our models also predict the presence of red kites in some areas of southern Spain in the western border of the Southern Plateau where only small relict populations remain. The reasons behind this discrepancy most likely relate to human factors, mainly illegal predator control (Villafuerte et al., 1998). Small game hunting has a high economic importance in this part of Spain, and illegal activities to control predators, such as poisoning, are still culturally rooted in the rural societies of these areas, and is causing conservation problems for other species as well (Viñuela and Villafuerte, in press). In Extremadura, where the problem of illegal predator control seems to be lower (Viñuela et al., 1999; Mañosa, 2002), there is still a healthy population of red kites.

A remarkable case is the population in Doñana National Park (population 8 in Fig. 1b) situated in an

area where our model predicts a low probability of occurrence. This dense population is located in an atypical breeding habitat where red kites may exist because of the exceptional productivity of the marshes (which was apparently not well reflected by our variable PPI).

The red kite had a much larger range in the past than that observed during 1994, and the species has almost disappeared from most of southern and eastern Spain, probably mainly due to incidental poisoning and shooting (Villafuerte et al., 1998; Viñuela et al., 1999). According to our models, most of this part of Spain probably had a sub-optimal habitat for the species, where high densities should be rare, and predator persecution is probably also more marked (Viñuela and Villafuerte, in press). Thus, perhaps those populations were more easily wiped out, while currently red kites populations in optimal areas of northern Spain are suffering a marked culling (estimated reduction of 50% in Castilla-León between 1994 and 2001: Viñuela and Contreras, 2001), but breeding populations still remain. Furthermore, this part of the Iberian peninsula is the edge of the range of the species, where declining populations disappeared first.

5. Conclusions

This study suggests that we can predict the present and potential occurrence of red kites in the Iberian peninsula with reasonable confidence. The general pattern of occurrence is mainly determined by natural factors such as climate, topography and vegetation cover, while their current population abundance is modulated by human-related factors (González et al., 1990; Donázar et al., 1993). We have not included anthropogenic factors, as these are very difficult to quantify, and this could explain the relatively low predictive power of the abundance model. The models indicate that some areas of optimum habitat were not thoroughly covered by the 1994–1996 census. We suggest that these areas should be prospected more thoroughly in the future if they lack recent information, since the red kite may breed there but have remained unnoticed. Our models also shows that the population in Doñana National park occupies a very atypical habitat. This has formed the focus of most ecological studies on the species in the past (e.g. Blanco et al., 1990; Viñuela and Bustamante, 1992; Bustamante, 1993; Van Kleef and Bustamante, 1999) but should receive less emphasis in future since the results may not be representative of other populations.

Acknowledgements

The national census of Red kites was funded by the Royal Society for the Protection of Birds, and coordinated

by SEO/Birdlife. More than 500 people, a too long list to be included here, participated in the census, and they are given credit in Viñuela et al. (1999). Red kite census in Andalusia was funded by the Consejería de Medio Ambiente (Junta de Andalucía) and coordinated by F. Hiraldo. LATUV (Laboratorio de Teledetección de la Universidad de Valladolid) and the Instituto Nacional de Meteorología respectively kindly provided raw data for our index of plant productivity and climatic information. We thank Ian Carter, Brian N.K. Davis and an anonymous referee for suggestions and comments on an earlier draft of this paper. Part of the data analysis and writing of this paper was funded by project no. 1DF-97-0648 from the Ministerio de Ciencia y Tecnología with FEDER funds from the European Union. JS acknowledges a predoctoral fellowship (Ministerio de Educación y Ciencia) during the writing of the manuscript.

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