Running head: Ecological Distribution modelling and climate

Can climate data from METEOSAT improve wildlife distribution models?

Susana Suárez-Seoane^{12*}, Patrick E. Osborne² and Andries Rosema³

Jechnical coments

1

^{1*} Area de Ecología. Facultad de Ciencias Biológicas y Ambientales. Universidad de León. Campus de Vegazana, s/n. 24071 León, Spain. Fax: +34-987-291501. degsss@unileon.es

² School of Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA, Scotland, UK.

³ Environmental Analysis and Remote Sensing (EARS). Kanaalweg 1.2526 EB DELFT. The Netherlands

^{*} Address for correspondence

Abstract

Global climate change generated by human activities is likely to affect agroecosystems in several ways: reinforcing intensification in northern and western Europe, and extensification in the Mediterranean countries. If we are to predict the consequences of global warming for wildlife, distribution models have to include climate data. The METEOSAT temporal series from EWBMS offers an attractive alternative to using climatic surfaces derived from ground stations. The aim of this paper is to test whether this climatic satellite data can improve the distribution models obtained previously by Suárez-Seoane et al (2002) using habitat variables for three agro-steppe bird species: great bustard, little bustard and calandra lark in Spain. Rainfall, radiation balance, evapotranspiration and soil moisture images were incorporated together with the other variables used as predictors in the published stepwise GAM models. Changes in the predicted distributions from the habitat only and climatehabitats models were assessed by reference to the CORINE land cover categories. Inclusion of climatic variables from METEOSAT led to statistically superior models for all three species. There were large differences in the climatic variables selected and the original variables dropped among the species. Evapotranspiration variables were the most frequently selected. Maps of the differences between the habitat and climate-habitat models showed very different patterns for the three species. Inclusion of climate variables led to a wider range of land cover types being deemed suitable. Despite the statistical superiority of models, care is needed in deciding whether to use climatic variables because they may emphasize the fundamental rather than the realized niche. Used together, however, habitat and climate models can provide new insights into factors limiting species distributions and how they may respond to climate change.

Key words: Bustard, GAM, climate change, targe scale, METEOSAT, NOAA AVHRR, NDVI, steppe birds.

Introduction

Global climate change generated by the increased emissions of greenhouse gases is occurring and is unique and new (Gall et al. 1992). It is expected to affect agroecosystems in several ways (Peters 1990, Fuhrer 2003) in different parts of the world (Parry et al. 1999). Intensive agriculture may have the potential to adapt to changing conditions; in contrast, extensive agricultural systems or low-input systems may be affected more seriously (Fuhrer 2003). In Europe, climate change is likely to reinforce the current trends of intensification in northern and western Europe and extensification in the southeastern countries (Olesen and Brindi 2002). In the Mediterranean countries, characterised by a drier and warmer climate, disadvantages will predominate. The possible decreases in availability of the water resource may cause lower harvestable yields, higher yield variability and a reduction in suitable areas for traditional crops. The synergy between climate change and habitat destruction will probably threaten many more species than either factor alone (Peters 1990), thus causing great concerns for the future of biodiversity on agroecosystems.

International commitment to monitoring and measuring biodiversity has spawned much recent work on appropriate techniques to model species distributions over large geographic areas (Guisan and Zimmermann 2000, Corsi et al. 2000). Such models require consistent environmental data on a scale that cannot easily be gathered in the field, leading to the use of satellite imagery as a source of predictor variables (Palmeirim 1988, Rogers and Williams 1994, Mat_ji_ek 2003). The favoured product to date has often been Advanced Very High Resolution Radiometer (AVHRR) imagery, usually processed using the Normalised Difference Vegetation Index (NDVI) (Birky 2001, Osborne et al. 2001). For example, Suárez-Seoane et al. (2002) used a 12-month time-series of NDVI images as one set of predictors in models of steppe-bird distributions in Spain. NDVI is attractive for wildlife modelling because it acts as a proxy for vegetation cover and, in some cases, climate.

3

Although these models have been highly successful, we wondered whether they could be improved through the use of other, readily available remote sensing products, especially in relation to climate. The explosion of interest in global climate change makes the latter point important: if we are to predict the consequences of global warming for wildlife, distribution models are needed that make use of climatic data (Dyer 1994, Bridgewater and Woodin 1990). The traditional approach to incorporating climate in wildlife models has been to calculate climate surfaces from meteorological stations, using sophisticated trend surface models such as ANUSPLIM (Hutchinson 2000, Price et al. 2000). The alternative that has not been tried to our knowledge is to use satellite-derived climatic measures. The European Energy and Water Balance Monitoring System EWBMS (Rosema et al. 2001) has made available a series of 10-daily products based on METEOSAT data. Images accessible consist of rainfall, net radiation, actual evapotranspiration and a soil moisture indicator (SMI).

The main aim of this paper is therefore to test whether METEOSAT data can improve the previous models of Suárez-Seoane et al. (2002) for three bird species: great bustard *Otis tarda* little bustard *Tetrax tetrax* and calandra lark *Melanocorhypha calandra* living in the extensive agricultural steppes of Spain, an agrosystem which is expected to be negatively affected by climate change. Looking for an *improvement* in the models is a rigorous but realistic test: given the success of models built using NDVI, it is unlikely that ecologists will abandon the use of AVHRR data. The relevant question is therefore whether the EWBMS products can improve the best models based on NDVI. We aslo explore how models based on habitat alone and those based on climate and habitat differed, and how those differences should be interpreted.

Methods

A detailed explanation of the data sets and statistical methods is given by Suárez-Seoane et al

(2002) and only brief details will be given here except for the EWBMS products (Rosema 1993, Rosema et al. 2001). The supplied EWBMS data comprise measures of rainfall, radiation balance, evapotranspiration and soil moisture for each 10-day period (dekad) from 1996 to 1999. These products are derived from the METEOSAT satellite on the basis of hourly observations of the visible channel, which provides information on the earth's reflectivity or albedo, and the thermal infrared channel, which provides information on temperature. Rainfall mapping was based on determining the frequency of clouds at several levels, using the cloud top temperature. In addition, the WMO Global Telecommunications System was used to retrieve actual precipitation point data in near real time. The relationship between the observed rain gauge data and the cloud frequencies was determined by regression. Regression coefficients and residuals for each station were then interpolated in order to compute rainfall for each pixel. Radiation and actual evapotranspiration maps were based on both visible and thermal infrared observations of cloud free pixels that, by calibration and atmospheric corrections, were converted to surface temperature (T₀) and surface albedo (A). Using regression between noon and midnight surface temperatures, we also obtained the air temperature at the top of the atmospheric boundary layer (T_a). From observed albedo, temperatures and cloudiness, and according the time of the year and the position, we calculated global radiation and net radiation (I_n). Sensible heat flux (H) from the surface to the atmosphere was calculated from surface-air temperature difference. Finally, the subtraction of the sensible heat flux from the net radiation provided the actual evapotranspiration (LE = I_n - H). The Soil Moisture Indicator (SMI) is the ratio of actual over potential evapotranspiration.

In handling the climatic data, we had to consider both its quality and volume. The data for rainfall in particular were patchy. As we were interested only in an average picture over time, we dropped any images showing defects and averaged the remainder for each

dekad to produce an annual time-series of 36 images. This time series was further summarised using standardised principal components analysis (Eastman and Fulk 1993) and only the first three components for the four climatic variables were used subsequently. This is an efficient way to capture most of the information (72-82%; Table 1) in the time series without overburdening the statistical analysis with variables.

Models were built using stepwise Generalised Additive Modelling (Hastie and Tibshirani 1990) in S-plus (see Venables and Ripley 1999) and the GRASP interface (Lehmann et al. 2001). We used the variables from the models in Suárez-Seoane et al. (2002) (see Table 2) together with the 12 climatic variables described above as predictors, fitting each as cubic splines with four degrees of freedom. Models were generated by backward selection with p<0.01 for the variable to remain in the equation. After initial model generation, all splined variables that were not significantly curvilinear were replaced by linear terms to prevent over-fitting. Terms were dropped one by one from the final equation to assess their contribution to the model through a likelihood ratio test (Venables and Ripley 1999). Predictive performance was assessed through 10-fold cross-validation (Verbyla and Litvaitis 1989) and both fit and predictive performance were measured through Receiver Operating Characteristics (ROC) plots (Beck and Schultz 1986, Osborne et al. 2001). The original habitat models of Suárez-Seoane et al. (2002) were compared with the climate-habitat models produced here using the likelihood ratio test.

To make a visual comparison between the habitat and climate-habitat models (both of which produced maps of suitability ranging from 0 to 1), we generated a change surface by subtracting one from the other. The change surface theoretically ranged from -1 to 1 but as we were primarily interested in the largest changes, we discarded the middle third of the data, leaving two categories of change (-0.33 to -1, and 0.33 to 1). To aid in their interpretation, we overlaid these two change categories on the CORINE land cover map for Spain to extract

the underlying land-use categories.

Results

The climate-habitat models were significantly better (at p<0.001) than the original published habitat models for all three species studied based on the likelihood ratio test (Table 3). Of the 12 climatic variables tested, only Soil-3 was not included in any model and the evapotranspiration variables were the most frequently selected. There were large differences, however, in the climatic variables selected and the original variables dropped between species. For the great bustard, Evap-1 and Evap-2 became the most significant variables in the model and two NDVI variables were dropped. Rad-3 and Evap-2 were the most significant variables for the little bustard and three NDVI variables were dropped. Despite occupying similar habitat, the most significant variables for the calandra lark were NDVI-3 and altitude while the evapotranspiration variables were the best of the climatic predictors used. The AUC values of the climate-habitat models were all greater than 0.92 and after cross-validation, these values reduced very little, suggesting a good predictive power (Table 3).

The analysis of changes between the climate-habitat and habitat models illustrated very different patterns for the three species (Figure 1). The black areas, where the climate-habitat model probabilities were greater than those of the habitat model by 0.33 or more, indicate locations where the climate is presently suitable but habitat is lacking. Conversely, grey areas are those where habitats appear suitable but where climatic conditions are outside those predicted as suitable by the model (habitat model probability - climate-habitat model probability ≥ 0.33). The great bustard's distribution shows evidence of fragmentation due to loss of habitat in climatically suitable areas whereas the little bustard shows a east-west bias in climatically-suitable areas with available habitat. A change in climate to favourable

conditions could potentially open-up the non-irrigated arable lands in the western half of Spain to the species. Especially noteworthy is the potential expansion area predicted for northern Spain, i.e. Asturias and Cantabria, where little bustards are not currently found. The original habitat model for the calandra lark predicted widespread occurrence whereas the climate-habitat model has trimmed areas particularly from the south-east of Spain. Possible areas for expansion on the basis of presently suitable habitat are among the irrigated lands of the Ebro Valley and some non-irrigated arable lands along the coast.

Comparison of the CORINE land cover classes lost or gained by using the climate-habitat model as opposed to the habitat model showed some predictable and more subtle trends (Table 4). For all species, the climate-habitat models predicted occupancy of a wider range of habitats than the habitat models alone, e.g. all increased the representation of "other categories" i.e. non agricultural areas (Table 4). For the little bustard, increased use of areas with mixed cultivation patterns and patches of natural vegetation was predicted whereas calandra larks were predicted to make far lower use of irrigated land under the climate-habitat model than the habitat model showed.

Discussion

Our analysis has shown that climatic variables derived from METEOSAT data can produce statistically superior distribution models to those built on habitat data alone. This is an important finding and suggests that more use could be made of satellite-derived climatic data for large-scale ecological models, especially in areas where meteorological stations are sparse. As more sophisticated satellite platforms are launched, there is a temptation to regard the use of fine resolution imagery as the Holy Grail. In fact, the use of the appropriate scale is crucial when analysing landscape ecological data (e.g. O'Neill et al. 1988, Wiens and Milne 1989) and for large-scale distribution models this is often 1 km or greater. Models predicting

the effects of global climatic change are limited by the resolution of the models themselves and often use a continental scale (Hulme and Carter 2000). Viewed in this context, the EWBMS data at 6 km resolution offer an attractive alternative to ground station data. For finer resolution studies, the AVHRR data at 1 km resolution may themselves be used to derive climatic variables but these have not yet been incorporated into wildlife distribution models to our knowledge.

The three test species occupy dry, agricultural steppe habitats in Spain and it is not surprising that climatic variables should predict their occurrence, especially measures of evapotranspiration. Our previous models used NDVI variables from AVHRR data as a direct measure of habitat, but the fact that these were not uniformly dropped when climatic variables entered the models suggests that climate may act in more ways than simply determining habitat. The little bustard offers the simplest case where the main vegetation variable NDVI-1 was dropped in favour of climatic measures. Thus the bird's distribution is better explained by weather than climatic effects on broad vegetation types (which is, in effect, what NDVI-1 measures). By contrast, the model for the calandra lark retained the main NDVI variables even when climate was considered.

By using climatic variables derived from standardised principal components, we have captured much of the variation in climate but have not optimised the variables for the species. For example, Morales et al. (2002) have shown that breeding productivity of Spanish great bustard is positively correlated with winter precipitation and negatively correlated with the number of rain days during hatching. It would be possible to extract from the EWBMS data variables specifically to test whether these conditions influence overall distribution.

In answering the question posed in our title, it is important to clarify what is meant by "improve". Our climate-habitat models were superior in a statistical sense to those derived from habitat variables alone. In other words, they predicted more closely the original data and

cross-validation tests suggest they would perform better on new data than habitat-only models. Climatic envelope models are, however, blind to other limiting factors, a criticism that is valid against current large scale projects attempting to model the consequences of climate change on species (e.g. Pearson et al. 2002). Pure climate models indicate the potential distribution (or fundamental niche) but not where species actually occur (the realised niche), their absence being due to unmodelled factors such as vegetation type, disturbance, hunting pressure, competitive interaction, lack of dispersal ability etc. (e.g. Huntley 1991; Davis et al 1998; Hill et al. 1999). We believe that the original habitat based models of Suárez-Seoane et al. (2002) provide a closer approximation to the current distributions than models incorporating climate. The decision to include climate data in distribution models or not must depend on the purpose of the study. When viewed together, the two models identified climatically-suitable areas where habitat has been lost (and so presumably could be re-created) and areas with apparently suitable habitat but an unfavourable climatic regime. These latter areas could be of great significance in modelling climate change because they already offer suitable habitat and might be expected to be colonised first as species' distributions shift.

In the Mediterranean regions, the pattern of agriculture is diverse. A market-oriented type of agriculture with crop cultivation predominates but considerable areas of traditional small-scale agriculture still occur (Kostrowicki 1991). According to recent studies on climate change in Europe (Hulme and Carter 2000), Spain will see increasing temperatures and dryness, mainly in the south and east of the country, and an associated displacement of cereals northwards (Olesen and Brindi 2002). These changes will become critical for the future of steppe birds, all three species studied being at risk of extinction in the driest areas of south-eastern Spain, e.g. Almería. Tools to help model, predict and manage species distribution changes in relation to climate and habitat are essential to underpin conservation

efforts to save steppe birds.

Acknowledgements

We sincerely wish to thank all the people who provided us with Spanish bird distribution data, especially volunteers involved in the SACRE Program (co-ordinated by Ramón Martín and Juan Carlos del Moral from SEO/BirdLife); Javier Bustamante and Javier Seoane (Estación Biológica de Doñana, Spain); Eduardo de Juana (Universidad Complutense) and Carmen Martínez (Museo de Ciencias Naturales); Joan Estrada, Anna Folch, Santiago Mañosa, Jaume Bonfil and Ferrán González (GCA, Museu de Zoología de Barcelona); Xabier Vázquez Pumariño, Gustavo Martínez and Jorge Rubio; Carlos Astraín and Amaia Etxeberría; Benedicto Campos and Manuel López; and other people as Jesús Serradilla. Juan Carlos Alonso and his team provided additional data on great bustards that contributed to the original habitat models. Estanislao de Luis Calabuig helped with his comments to improve the manuscript. The AVHRR data were provided by NERC's Satellite Receiving Station at Dundee and were processed by the RSDAS, Plymouth. We especially wish to thank Neil Lonie and Luke Tudor for their help. Thanks to Pilar García for her help in building the DTM in INDUROT (Universidad de Oviedo). Kate Howie of the Mathematics Department, University of Stirling, is thanked for statistical discussions. Susana Suárez-Seoane was funded through a Marie Curie postdoctoral fellowship, by the European Commission's programme "Environment and Climate" (ENV4-CT98-5130).

References

- Beck, J. B. and Shultz, E. K. 1986. The use of relative operating characteristic (ROC) curves in test performance evaluation. Archives of Pathology and Laboratory Medicine 110: 13-20.
- Birky, A. K. 2001. NDVI and a simple model of deciduous forest seasonal dynamics. Ecological Modelling 15: 43-58.
- Bridgewater, P. and Woodin, S. J. 1990. Global warming and nature conservation. Land use policy 7: 165-168.
- Corsi, F., De Leeuw, J. and Skidmore, A. 2000. Modelling species distribution with GIS. In:

 Boitani, L. and Fuller, T.K. (eds.), Research Techniques in animal ecology. Columbia

 University Press, New York, pp OTO OTO.
- Davis, A. J., Jenkinson, L. S., Lawton, J. L., Sharrocks, B. and Wood, B. 1998. Making mistakes when predicting shifts in species range in response to global warming. -Nature 391: 783-786.
- Dyer, J. M. 1994. Land use pattern, forest migration and global warming. Landscape and Urban Planning 29: 77-83.
- Eastman, J. R. and Fulk, M. 1993. Long sequence time series evaluation using standardised principal components. Photogrammetric Engineering and Remote Sensing 59 (6): 991-996.
- Fuhrer, J. 2003. Agroecosystem responses to combinations of elevated CO₂, ozone and global climate change. Agriculture, Ecosystems and Environment 97: 1-20.
- Gall, G. A. E., Kreith, M., Staton, M. (1992). Global climate change. Agriculture, Ecosystems and Environment 42: 93-100.
- Guisan, A. and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135: 147-186.

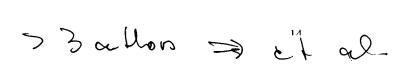
- Hastie, T. J. and Tibsharinani, R. 1990. Generalised Additive Models. Chapman and Hall, London.
- Hill, J. K., Thomas, C. D. and Huntley, B. 1999. Climate and habitat availability determine 20th century changes in a butterfly's range margin. Proceedings of the Royal Society of London Series-B Biological Sciences 266: 1197-1206.
- Hulme, M. and Carter, T. R. 2000. The changing climate of Europe. In: Parry, M. L. (ed.),

 Assessment of potential effects and adaptations for climate change in Europe: the

 Europe ACACIA project. The Jackson Environment Institute, University of East

 Anglia, Norwich, U.K, pp. 320.
- Huntley, B. 1991. How plants respond to climate change: migration rates, individualism and the consequences for plant communities. Annals of Botany 76: 15-22.
- Hutchinson, M. F. 2000. ANUSPLIN Version 4.1 User Guide. Centre for Resource and Environmental Studies, ANU, Canberra, pp. 51.
- Kostrowicki, J. 1991. Trends in the transformation of European agriculture. In: Brower, F. M., Thomas, A.J. and Chadwick, M. J. (eds.), Land use changes in Europe. Kluwer Academic Publisher, Dordrecht, pp. 21-47.
- Lehmann, A., Leathwick, J. R. and Overton, J. McC. 2001. GRASP v.2.0 User's Manual. Landcare Research, Hamilton, New Zealand.
- Mat____ek, L., Bene__ová, L. and Tonika, J. 2003. Ecological modelling of nitrate pollution in small river basins by spreadsheets and GIS. Ecological Modelling 170 (2-3): 245-263.
- Morales, M. B., Alonso, J. C. and Alonso, J. 2002. Annual productivity and individual female reproductive success in a Great Bustard *Otis tarda* population. Ibis 144: 293-300.
- O'Neill, R. V., Milne, B. T., Turner, M. G. and Gardner, R. H. 1988. Resource utilization scales and landscape pattern. Landscape Ecology 2: 63-69.

- Olesen, J. E., and Brindi, M. 2002. Consequences of climate change for European agricultural productivity, land use and policy. European Journal of Agronomy 16: 239-262.
- Osborne, P. E., Alonso, J. C. and Bryant, R. G. 2001. Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. Journal of Applied Ecology 38: 458-471.
- Palmeirim, J. M. 1988. Automatic mapping of avian species habitat using satellite imagery: Oikos 52: 59-68.
- Parry, M. L., Rosenzweig, C., Iglesias, A., Fisher, G. and Livermore, M. 1999. Climate change and world food security: a new assessment. Global Environmental Change 9: 51-67.
- Pearson, R. G., Dawson, T. P., Berry, P. M. and Harrison, P. A. 2002. SPECIES: A spatial evaluation of climate impact on the envelope of species. Ecological Modelling 154: 289-300.
- Peters, R. L. 1990. Effects of global warming on forests. Forest Ecology and Management 35: 13-33.
- Price, D. T., Mckenney, D. W., Nalder, I. A., Hutchinson, M. F. and Kesteven, J. L. 2000. A comparison of two statistical methods for spatial interpolation of Canadian monthly mean climate data. Agricultural and Forest Meteorology 101: 81-94.
- Rogers, D. J. and Williams, B.G. 1994. Tsetse distribution in Africa: seeing the wood and the trees. In P. J. Edwards, R. M. May and N. R. Webb (eds), Large-scale ecology and conservation biology, Blackwell Scientific Publications, Oxford, pp. 247-272.
- Rosema, A. 1993. Using Meteosat for Operational Evapotranspiration and Biomass Monitoring in the Sahel region. Remote Sensing and Environment 45:1-25.
- Rosema, A., L. Verhees, E. van Putten, H. Gielen, T. Lack, J. Wood, A. Lane, J. Fannon, T. Estrela, M.Dimas, H. de Bruin, A. Moene and W. Meijninger, 2001. European Energy



- and Water Balance Monitoring System, EU 4th Framework Program, Contract ENV4-CT97-0478, Final report.
- Suárez-Seoane, S., Osborne, P. E. and Alonso, J. C. 2002. Large-scale habitat selection by agricultural steppe birds in Spain: identifying species-habitat responses using Generalised Additive Models. Journal of Applied Ecology 39 (5): 755-771.
- Venables, W. N. and Ripley, B. D. 1999. Modern Applied Statistics with S-Plus. Springer, New York.
- Verbyla, D. and Litvaitis, J. A. 1989. Resampling methods for evaluating classification accuracy of wildlife habitat models. Environmental Management 13 (6): 783-787.
- Wiens, J. A. and Milne, B. T. 1989. Scaling of landscape in landscape ecology, or landscape ecology from a beetle's perspective. Landscape Ecology 3: 87-96.

	Component 1	Component 2	Component 3	Total in model
Rainfall	41.0	23.3	7.6	71.9
Radiation balance	71.1	6.1	5.0	82.2
Soil moisture	64.5	10.9	3.6	79.0
Evapotranspiration	52.5	17.2	4.7.	74.4

Table 1. Percentage variance retained by the first three principal components for each climatic measure used.

Variable	Definition
PC components 1 to 12	Standardised principal components obtained from the Normalised Difference Vegetation Index for each month based on a Maximum Value Composite of AVHRR imagery at 1 km ² resolution.
Altitude (ALT)	Mean altitude within a 5x5 array of 200m pixels.
Topographic variability 5 (TOPOV5)	Variation in altitude in a 5x5 pixel array of 200 m pixels, where altitude is measured to 5 m vertical resolution. Calculated as $TOPOVx = (n-1)/(p-1)$ where n = no. of different altitude classes in the array, p = no. of pixels in the array (i.e. 25), and x is the vertical resolution.
Topographic variability 10 (TOPOV10)	As for TOPOV5 but with 10 m vertical resolution.
Road density (ROADDEN)	Proportion of 200 m pixels in a 5x5 array containing roads.
Road distance (ROADDIST)	Distance in km to the nearest 200 m pixel containing roads. Calculated at 200 m resolution and averaged to 1 km
Town density (TOWNDEN)	Proportion of 200 m pixels in 5x5 array containing buildings or large built structures such as airfields.
Town distance (TOWNDIST)	Distance in km to the nearest 200 m pixel containing buildings or large built structures such as airfields. Calculated at 200 m resolution and averaged to 1 km
River density (RIVDEN)	Proportion of 200 m pixels in a 5x5 array containing rivers.
River distance (RIVDIST)	Distance in km to the nearest 200 m pixel containing rivers. Calculated at 200 m resolution and averaged to 1 km

Table 2. Predictor variables used for modelling the occurrence of agricultural steppe birds in Spain in Suárez-Seoane et al. (2002).

Predictor variables	Great bustard	Little bustard	Calandra lark
NDVI-1	22.3 L	Dropped	44.3 L
NDVI-2	Dropped	23.9 S	32.5 S
NDVI-3	37.0 S	34.7 S	92.4 L
NDVI-4	26.4 S	-	-
NDVI-5	18.9 S	-	21.1 S
NDVI-6	Dropped	-	Dropped
NDVI-7	-	-	Dropped
NDVI-9	-	Dropped	-
NDVI-10	21.0 S	Dropped	14.3 L
NDVI-12	19.0 S	•	-
Rivden	13.2 S	-	14.9 L
Rivdist	Dropped	17.5 S	-
Roadden	-	-	30.8 L
Roaddist	57.0 S	Dropped	Dropped
Townden	-	-	Dropped
Towndist	23.7 S	31.1 S	41.4 S
Altitude	41.1 S	33.8 S	64.8 S
Topov5	Dropped	Not tested	Not tested
Topov10	Not tested	26.6 S	18.4 L
Rain-1	-	21.4 S	27.5 S
Rain-2	•	•	25.3 L
Rain-3	46.0 S	29.5 S	15.4 S
Rad-1	-	_	15.4 S
Rad-2	29.3 S	-	13.3 S
Rad-3	21.1 S	71.2 S	_
Soil-1	51.3 S	28.2 S	26.4 S
Soil-2	21.8 L	-	-
Soil-3		-	-
Evap-1	92.9 S	24.8 S	39.0 S
Evap-2	60.9 S	49.9 S	48.7 S
Evap-3	•	22.6 S	-
Published GAM AUC	Marine Caracteria Cara	14 and 15	
cv AUC	0.96	0.90	0.90
	0.95	0.88	0.89
Climate GAM AUC			
cv AUC	0.97	0.93	0.92
	0.96	0.91	0.91
Significance of difference	F=21.69, DF=1 and	F=8.38, DF=1 and	F=16.04, DF=
between models	15.0, P<0.001	20.9, P<0.001	and 20.5, P<0.0

Table 3. The main body of the table shows the value of Chi-squared for change in the model deviance when the predictor is dropped and is an index of its importance. S indicates the variable was fitted as a spline, L as a linear term. Variables that appeared in the original model but were not selected in the climate model are indicated by "dropped". Variables that were not selected for the species in either model are marked -. Topov5 and topov10 were alternative measures of terrain variability and only one was included in each model.

CORINE LANDCOVER	Great bustard	ustard	Little bustard	ustard	Caland	Calandra lark
	Lost	Gained	Lost	Gained	Lost	Gained
12: non-irrigated arable land	48.69	40.42	36.68	36.16	22.46	23.00
13: permanently irrigated land	5.52	2.62	4.91	2.83	31.22	5.09
15: vineyards	4.38	1.64	3.35	3.46	1.03	2.22
17: olive groves	2.42	1.62	5.96	1.67	1.68	2.57
18: pastures	0.52	0.05	1.69	60.0	0.51	0.27
19: annual crops assoc. with permanent crops	0.03	0.02	0	0.05	0.14	80.0
20: complex cultivation patterns	7.22	5.69	6.41	11.28	8.59	8.45
21: agriculture, w/ signif. areas of nat. vegetation	2.9	8.3	6.27	10.29	5.79	7.45
22: agro-forestry areas	4.76	6.43	6.30	4.46	0.65	7.55
26: natural grassland	5.04	4.72	5.41	3.53	2.53	5.97
Other categories	18.52	28.49	23.02	26.18	25.40	37.35

Table 4. Percentage composition of CORINE land cover categories lost or gained by replacing the original habitat models with those based on climate and habitat.

List of Figures

Figure 1. Pictures resulting from overlapping both the published and the climatic models. Black colour shows areas of extreme habitat but suitable climate: a direct habitat change could produce either the disappearing or the increasing of the species. Grey means areas of climate tension, where habitat is suitable and climate is extreme: climate change will affect directly species distribution (probably increasing in northwestern Spain and diminishing is southeastern).

Figure 1

