

# Behavioural mechanisms that undermine species envelope models: the causes of patchiness in the distribution of great bustards *Otis tarda* in Spain

Patrick E. Osborne, Susana Suárez-Seoane and Juan Carlos Alonso

P. E. Osborne (p.e.osborne@soton.ac.uk), Centre for Environmental Sciences, School of Civil Engineering and the Environment, Univ. of Southampton, Highfield, Southampton SO17 1BJ, U.K. – S. Suárez-Seoane, Área de Ecología, Departamento de Biodiversidad y Gestión Ambiental, Facultad de Ciencias Biológicas y Ambientales, Univ. de León, Campus de Vegazana, s/n. ES-24071 León, Spain. – J. C. Alonso, Museo Nacional de Ciencias Naturales, CSIC, José Gutiérrez Abascal 2, ES-28006, Madrid, Spain

Despite the general success of species envelope models, capturing the fine-scale detail of patchiness in the distributions of some species is problematic. For great bustards in Spain, apparently suitable habitat patches remain unoccupied and cannot be distinguished from occupied patches in current distribution models. We consider philopatry and conspecific attraction as main behavioural mechanisms which could account for this patchiness, and then look for evidence of their influence on the distribution of great bustards across the whole of Spain. We compared the characteristics of habitat patches classed as suitable by a distribution model according to whether they were actually used or not. Occupied patches were larger than unoccupied patches and over-used in proportion to their size, suggesting aggregation and a metapopulation structure. Arguing that conspecific attraction may serve to transfer information about site history and environmental predictability (at least over a short time period), we compared the coefficients of variation in time-series of vegetation and climatic factors at occupied and unoccupied sites. Great bustards chose sites which were more environmentally stable at critical periods in the breeding cycle, “public information” that can only be gained from others rather than through sampling. There is thus evidence that both metapopulation dynamics and conspecific attraction influence the large scale distribution of great bustards in Spain. We discuss how alternative predictor variables and multi-stage analyses may help us to incorporate behavioural mechanisms into distribution models, but acknowledge that there are limits to the value of species envelope models for animal species making decisions.

Unprecedented developments in computing technology and earth observation have made it possible to study the distributions of species at larger spatial scales and finer resolutions than ever before. While a plethora of techniques exist for developing species distribution models (Elith et al. 2006), they all rely on identifying the environmental conditions at locations where a species is known to occur (the “envelope”), and then assuming that other locations with similar conditions will also have the species. This approach has been hugely successful in both applied and theoretical ecology (Guisan and Zimmermann 2000). There are, however, situations where even “good” distribution models fail to capture local patterns of occurrence,

particularly at finer spatial resolutions. There could be many technical reasons for this (e.g. selection of inappropriate explanatory variables, co-registration errors, poor sampling design) but even allowing for these, some species may not occur as distribution models predict. One such example is that of the great bustard *Otis tarda* in Spain.

The great bustard is globally-threatened (Heredia et al. 1996) with a total population estimated at 41 000–46 000 individuals restricted to the Old World. Recent estimates from its largest stronghold on the Iberian Peninsula put its population there as ca 25 000 birds (Alonso et al. 2003). It is considered vulnerable because a population reduction of >30% is predicted

during the coming decade (BirdLife International 2004), mainly due to habitat loss and nest destruction on agricultural land. The great bustard's distribution stretches from Morocco (in the west) to China (in the east) and is patchy at both global (Morales and Martín 2003) and local scales (Lane et al. 2001).

Patchiness in distributions may take many forms but a major division is into saturated fragmented distributions, where all suitable habitat patches are occupied, and unsaturated fragmented distributions, where some apparently suitable habitat patches remain unoccupied. The great bustard's distribution in Spain fits this latter category, as do the distributions of other steppe birds in Spain, such as the little bustard *Tetrax tetrax* (García et al. 2007). Osborne et al. (2001) and Suárez-Seoane et al. (2002) have shown that great bustards do not occupy all the habitat fragments identified as suitable in distribution models and Lane et al. (2001) have found that occupied and unoccupied sites cannot be distinguished in the field. This is despite the models being very successful at predicting known occupied locations. Understanding why apparently suitable habitat remains unoccupied and how to incorporate this into distribution models is vitally important if models predicting the impacts of land use or global climate change are to be useful as management tools.

There are several possible explanations, which are not mutually exclusive, for the great bustard's distribution pattern in Spain and the failure of our "static" models (i.e. based on the environmental conditions at a particular time) to discriminate occupied and non-occupied patches. Some of these are related to historical processes, for example, where local extinctions in the past have caused suitable patches to be unoccupied in the present (Alonso et al. 2003), while others correspond to behavioural mechanisms related to dispersal through philopatry and conspecific attraction.

Philopatry in great bustards includes natal philopatry (Alonso et al. 1998, Martín et al. 2002) of young females and adult philopatry (Alonso et al. 2000, Morales et al. 2000), i.e. absence of breeding dispersal. Theoretically, habitat patch occupancy could be an accident of history determined by the first settlers, with offspring simply settling nearby. Therefore, philopatry could result in an unsaturated, patchy distribution because individuals avoid the risks associated with seeking new areas by breeding close to their birthplaces. Alonso et al. (2000), Morales et al. (2000) and Martín et al. (2002) have shown that great bustards exhibit high site fidelity, returning to traditional sites to display and nest year after year. In this case, the explanation for an unsaturated distribution would be lack of ecological time to occupy all available habitat. If this is the dominant mechanism causing patchiness, we would predict no average difference in habitat quality in either

space or time, or in patch size, between occupied and unoccupied patches.

Most animal species have a dispersal phase that facilitates outbreeding and increases genetic diversity. In great bustards, young males disperse among genetically unrelated leks, whereas young females show the opposite tendency (Alonso et al. 1998, Martín et al. 2002). Animal (in contrast to plant) species are expected to show adaptive habitat selection because they have the ability to assess the environment and make choices that are at least approximately optimal (Rosenzweig 1991, Krebs and Kacelnik 1991). Since dispersing individuals (especially juveniles) lack personal experience of new habitat patches encountered, they may either disperse at random or adopt one of two habitat selection strategies (Doligez et al. 2003, Nocera et al. 2006, Parejo et al. 2006): 1) they may assess the habitat using environmental cues that correlate with or influence expected fitness (sampling); or 2) they may use the presence of others to indicate habitat quality, giving rise to either conspecific (Reed and Dobson 1993) or heterospecific (Mönkkönen et al. 1990, 1999, Forsman et al. 2002) attraction. Theoretical models of patch use such as the ideal free distribution (Fretwell and Lucas 1970) make the assumption that individuals have perfect ability to find and assess each patch through sampling and should choose accordingly. However, sampling incurs costs, such as increased travel time, loss of foraging opportunities; increased risk of predation (Coolen et al. 2003) and might also be impractical over large geographic areas. If an individual is unable to sample enough patches to track quality and respond to changes rapidly, then using the presence of others to indicate quality may be a better alternative. Indeed, while sampling may indicate the quality of a site at a specific time, it does not necessarily indicate its past performance or its future potential. This "site history" and its potential clues to future success, is locked in the presence of others, especially at traditional sites. We may thus regard site history as "public information" that individuals may access through the presence of others (Valone and Templeton 2002). Knowledge of a site's history may be an especially valuable commodity where an environment is unpredictable yet a key determinant of fitness (e.g. through high rainfall causing chick mortality). Lane et al. (2001) and Alonso et al. (2004) have proposed that great bustards aggregate at specific sites through conspecific attraction. While aggregation at traditional sites and avoidance of other patches could simply be due to the great bustard's dispersed lek breeding system (Morales and Martín 2003), traditional sites may also be those that are better more often, i.e. are more environmentally stable. If conspecific attraction for information transfer is the dominant reason for the great bustard's

patchy distribution, we would predict occupied patches to be the more environmentally stable over time.

In this paper we look for landscape-scale evidence for conspecific attraction and philopatry as explanations of the pattern of occupied habitat patches across Spain and why large scale models might fail to reveal subtle details of animal distributions. This quest poses severe data challenges at both the temporal and spatial scale. The great bustard is a wide-ranging species, tracked individuals in the largely sedentary Spanish population moving up to 250 km during the non-breeding season (Alonso et al. 2001, Alonso 2007). Any realistic patch-use model must therefore be built at the regional (country-wide) scale. Examination of environmental predictability requires data over long time periods and this is rarely available, especially over large spatial scales. A further difficulty is that empty but suitable habitat patches must be identified and this is extremely time-consuming in the field. Our focus is therefore on analysis of large scale distribution patterns and hypothesis testing that may be achieved through the GIS environment. As it is not possible to obtain accurate bustard survey data for each habitat patch at the national scale over a number of years, our analysis provides a broad picture that complements the more detailed local scale analyses of Alonso et al. (2004).

## Methods

### Great bustard analysis

The analysis builds on the predictive distribution model for the great bustard in Spain at 1 km<sup>2</sup> resolution from Suárez-Seoane et al. (2002). The model had a cross-validated AUC (area under the ROC curve) of 0.95 and correctly classified 89.2% of points at the optimum cut value (see Suárez-Seoane et al. 2002 for details), matching the latest survey data (Alonso et al. 2003) with minor discrepancies. This model was based on 1234 pixels where the species was present in the breeding season and an equal number of sites with verified absence, and has the advantage of mapping unoccupied but suitable habitat patches. As bustards are known to use the same sites year after year, the presence locations from surveys in the 1990s may reasonably be regarded as traditional sites. We used this model to characterise occupied and unoccupied patches, and to interrogate other GIS data layers (e.g. related to environmental predictability) following two different approaches: a patch-based analysis and a point-based analysis.

1) Patch-based analysis. Firstly, we re-classed the original predictive model into a binary image of suitability at the 0.7 probability threshold as we were interested in the higher probability areas (cf. Osborne

and Suárez-Seoane 2006). A patch recognition algorithm was then used to group contiguous pixels into patches of good habitat separated by at least 1 km (the resolution of the maps) from poorer quality habitat. The patch map was overlaid on the presence locations recorded from the field so that patches could be classed as used (one or more records) or vacant (no records). The resultant two-class patch image was used to extract environmental data at relevant periods and to calculate patch size metrics.

2) Point-based analysis. The disadvantage of the patch-based approach is that all contiguous pixels within an occupied patch are assumed to be suitable even though we had no actual knowledge of use. We accounted for this potential bias by undertaking a complementary point-based analysis. First, we re-classed the predictive model into nine integer classes of probability from 0.1–0.2 to 0.9–1.0, discarding lower probabilities as too small. We then used these classes to label the original field-derived presence and absence points that were used to build the models. This gave us a surface of 18 different classes of points that were used to extract environmental data. For example, the class “0.9–1.0 absent” would indicate a site predicted to be highly suitable but at which no bustards were recorded in the field. The resultant 18-class point image was used to extract environmental data.

### Environmental data

We used two sources of satellite data: the archive of Advanced Very High Resolution Radiometer (AVHRR) data from the NOAA satellites, held by the Natural Environmental Research Council at Dundee, Scotland; and the METEOSAT-derived European Energy and Water Balance Monitoring System (EWBMS) data products from EARS, The Netherlands (Rosema 1993, Rosema et al. 2001). In using both satellite data sources, the variables we were able to extract (e.g. for inter-annual variability) were constrained by the availability of processed imagery.

To analyse vegetation biomass, monthly Maximum Value Composites of Normalised Difference Vegetation Index (NDVI) data were extracted from the NOAA imagery for 1983, 1985, 1990, 1993, 1996 and 1999. In addition to the quality control checks used by Suárez-Seoane et al. (2002), care was taken to check for inter-annual variations in data characteristics that would render comparisons invalid. Although NDVI products can be calculated from uncalibrated data, we found anomalies (a gradual “brightening”) over this long time series of data that was entirely due to filter degradation. We therefore corrected the visible channel albedos (channels 1 and 2) for filter degradation using Rao and Chen’s (1995) approach together with updates

from the Dundee Satellite Receiving Station web site (<<http://www.sat.dundee.ac.uk/cal>>). For each year we then calculated the mean annual NDVI and the maximum NDVI during the hatching period (May and June). The six annual measures for each variable were then combined to produce data layers for the coefficient of variation in annual NDVI (NDVI annual) and NDVI during the hatching period (NDVI hatch). The logic in examining inter-annual variability in NDVI was to detect changes in the cereal-fallow mosaic which could impact on breeding performance and hence long-term site suitability.

The EWBMS data comprised a series of products based on METEOSAT imagery, including rainfall, net radiation, actual evapotranspiration and a soil moisture indicator (see Rosema 1993, Rosema et al. 2001 and Suárez-Seoane et al. 2004 for details of their derivation and use). Data were available for each 10-d period (dekad) from January 1996 to December 1999. Using data in Morales et al. (2002) we identified three critical periods during the bustard breeding cycle when weather impacts on survival: winter, when body reserves are built up (12 dekads from January to March and October to December); egg hatching (6 dekads from May to June); and chick rearing (9 dekads from July to September). As with the NDVI data, we created layers for each of the climate variables during each of the time periods and then used these to calculate the coefficient of variation over the four years. We checked for collinearity by calculating Pearson correlation coefficients between the climate variables and across the time periods using the 2468 points used for model building (Suárez-Seoane et al. 2002). Only evapotranspiration and soil moisture showed one correlation above 0.7 (0.89 during the rearing period) and thus all variables and time periods were examined for differences between occupied and unoccupied patches. The METEOSAT-derived data layers were originally at  $5 \times 5$  km resolution but were expanded to  $1 \times 1$  km to allow efficient analysis with the other data. As this artificially increased the sample size of pixels by a factor of 25, we applied a systematic 1-in-25 pixel filter to the patches to base the statistical analyses on the original sample size of METEOSAT pixels. Data availability limited our analysis of climate variability to a four year period and it is an untested assumption that this may be used as a surrogate for longer term variation.

Using these data we analysed the characteristics of occupied and unoccupied patches and pixels across the whole of Spain. For the point-based analyses where we are effectively testing a single hypothesis over a range of habitat suitability classes (e.g. evapotranspiration differs between occupied and unoccupied locations during the hatching period) we applied Bonferroni correction in interpreting the *p* values to reduce Type I errors (i.e. rejecting  $H_0$  when  $H_0$  is true). However, there is no

consensus among statisticians for when Bonferroni corrections should be applied (Perneger 1998) and the routine application that has crept into ecology can be counter-productive (Moran 2003, Nakagawa 2004, and see Neuhäuser 2004 and Verhoeven et al. 2005 for alternatives to Bonferroni procedures). We therefore report the uncorrected *p* values throughout to provide insight into the overall patterns obtained.

## Results

### Patch size

The patch recognition algorithm identified 508 patches (36 occupied and 472 vacant) containing apparently suitable habitat (Fig. 1). Occupied patches (i.e. those with one or more records) were significantly larger than unoccupied patches (medians 63.5 vs 5.0 km<sup>2</sup>,  $p < 0.001$ , Mann-Whitney U test). This analysis does not, however, take account of the probability of birds encountering patches of different sizes at random. Correcting for a null model where use is proportional to area, small patches were used more often than expected while the largest patches were underused ( $\chi^2 = 36.66$ , DF = 3,  $p < 0.001$ ). Also, the density of patch use (i.e. the no. of occupied 1 km squares divided by patch area) differed significantly among patches of different sizes (Kruskall Wallis test,  $\chi^2 = 110.39$ , DF = 3,  $p < 0.001$ ), density increasing with patch size.

### Environmental variability

#### Patch-based analysis

Eight out of 14 tests for differences in the temporal variability of the environment among occupied and vacant patches were significant at  $p < 0.05$ . There were highly significant differences (at  $p < 0.001$  without Bonferroni correction) in the inter-annual variation in all climatic measures, but only minor differences in NDVI between occupied and vacant patches (Table 1). In the hatching period, occupied patches had less variable evapotranspiration and soil moisture than vacant ones. The net radiation balance was more variable in occupied patches. During the chick rearing period, both rainfall and soil moisture were significantly less variable in occupied patches. Only rainfall differed (at  $p < 0.01$ ) between used and vacant patches during the winter period, occupied patches being more variable.

#### Point-based analysis

We found very minor differences in the inter-annual variation in NDVI between presence and absence points (Table 2) in line with the results from the patch-based analysis (Table 1), but significant differences in the

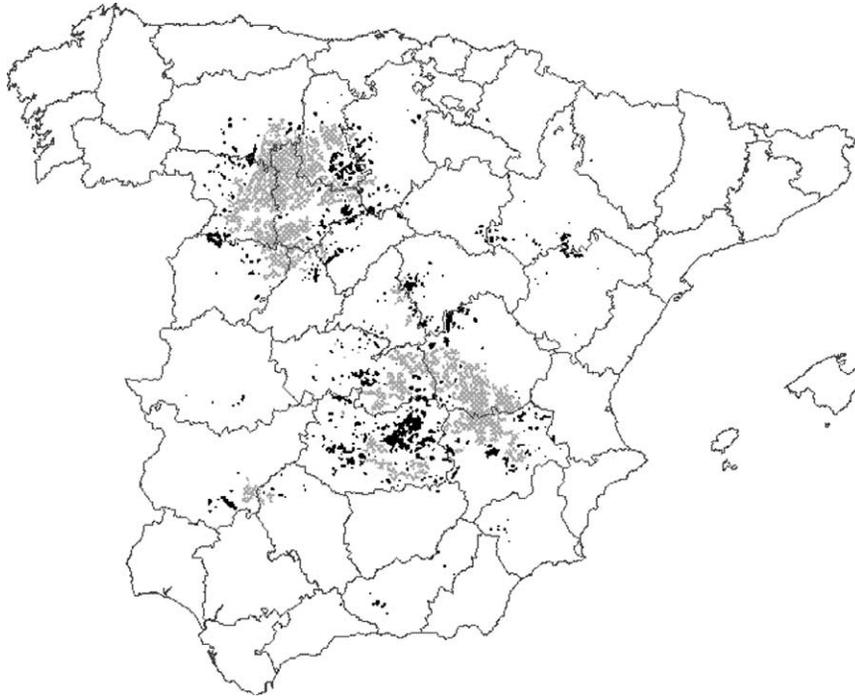


Fig. 1. Distribution of occupied (grey) and vacant (black) habitat patches defined as suitable for great bustards in Spain.

climatic variables (Table 3). Among the latter, 37 comparisons were significant at the 0.05 level compared with only 5 or 6 expected by chance alone. Occupied points with higher predicted suitability were significantly less variable in rainfall during the hatching and rearing periods than unoccupied points; in contrast, rainfall was more variable in the winter on the occupied breeding sites. Evapotranspiration was also significantly less variable at occupied than unoccupied sites with higher suitability during the hatching period (Fig. 2); a similar trend was apparent during the rearing and wintering periods too (Table 3). Radiation balance had a tendency

to be more variable at occupied points in the hatching period but became significantly less variable during the rearing (Fig. 2) and winter periods. The soil moisture indicator again showed a tendency to be less variable at occupied points with higher predicted suitabilities, although few differences achieved statistical significance.

## Discussion

Great bustards are absent from areas of Spain that appear suitable both on the ground and from snapshot

Table 1. Interannual variation (mean  $\pm$ SE) in climate and vegetation in occupied and vacant habitat patches based on the characteristics of the 1 km squares they contain. Sample sizes are 17135 occupied and 7185 vacant pixels for NDVI, and 699 occupied and 283 vacant pixels for the climatic variables.

Variable	Period	Occupied patches	Vacant patches	z test	p
NDVI	annual	2.85 $\pm$ 0.005	2.83 $\pm$ 0.008	2.31	*
	hatch	4.94 $\pm$ 0.013	4.94 $\pm$ 0.020	0.06	
Evapotranspiration	hatch	10.70 $\pm$ 0.190	12.65 $\pm$ 0.374	4.64	***
	rear	17.77 $\pm$ 0.225	18.05 $\pm$ 0.387	0.62	
	winter	6.88 $\pm$ 0.107	7.12 $\pm$ 0.191	1.10	
Net radiation balance	hatch	8.48 $\pm$ 0.088	7.52 $\pm$ 0.124	6.29	***
	rear	3.16 $\pm$ 0.051	3.44 $\pm$ 0.087	2.72	**
	winter	5.62 $\pm$ 0.062	5.80 $\pm$ 0.100	1.50	
Rainfall	hatch	41.17 $\pm$ 0.440	41.53 $\pm$ 0.795	0.39	
	rear	401.35 $\pm$ 3.083	437.26 $\pm$ 7.065	4.66	***
	winter	46.57 $\pm$ 0.375	44.65 $\pm$ 0.496	3.10	**
Soil moisture	hatch	13.13 $\pm$ 0.188	14.42 $\pm$ 0.336	3.35	***
	rear	14.35 $\pm$ 0.186	16.07 $\pm$ 0.335	4.49	***
	winter	5.65 $\pm$ 0.095	5.55 $\pm$ 0.148	0.58	

Table 2. Interannual variation in NDVI (mean  $\pm$ SE) over a full year (annual) and during the hatching period (hatching) for 1 km squares where great bustards were present or absent. \*\* = significant at  $p < 0.01$  (without Bonferroni correction).

HSI class	Sample sizes		Annual			Hatching		
	Present	Absent	Present	Absent	p	Present	Absent	p
0.1–0.2	19	74	3.16 $\pm$ 0.158	3.26 $\pm$ 0.109		4.93 $\pm$ 0.441	5.12 $\pm$ 0.265	
0.2–0.3	31	66	3.38 $\pm$ 0.124	3.01 $\pm$ 0.070	**	5.31 $\pm$ 0.270	4.97 $\pm$ 0.205	
0.3–0.4	36	36	3.15 $\pm$ 0.110	3.15 $\pm$ 0.108		5.20 $\pm$ 0.260	4.90 $\pm$ 0.272	
0.4–0.5	53	33	3.19 $\pm$ 0.100	3.14 $\pm$ 0.131		5.16 $\pm$ 0.245	5.26 $\pm$ 0.289	
0.5–0.6	81	32	2.99 $\pm$ 0.083	3.04 $\pm$ 0.128		4.95 $\pm$ 0.178	4.78 $\pm$ 0.321	
0.6–0.7	111	26	3.05 $\pm$ 0.068	2.88 $\pm$ 0.114		5.02 $\pm$ 0.145	4.77 $\pm$ 0.298	
0.7–0.8	152	24	3.01 $\pm$ 0.062	2.85 $\pm$ 0.133		5.25 $\pm$ 0.138	5.48 $\pm$ 0.325	
0.8–0.9	293	28	2.92 $\pm$ 0.044	2.86 $\pm$ 0.110		4.99 $\pm$ 0.103	4.98 $\pm$ 0.243	
0.9–1.0	492	18	2.79 $\pm$ 0.034	2.88 $\pm$ 0.130		5.11 $\pm$ 0.079	5.16 $\pm$ 0.418	

Table 3. Interannual variation in four climatic variables (mean  $\pm$ SE) during the hatching, rearing and wintering periods for 1 km squares where great bustards were present or absent. Uncorrected significance levels: \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ . For a conservative view (Bonferroni corrected), consider only \*\*\* as significant. Sample sizes are given in Table 2.

	HSI class	Hatching period			Rearing period			Winter		
		Present	Absent	p	Present	Absent	p	Present	Absent	p
Evapo-transpiration	0.1–0.2	11.2 $\pm$ 1.22	10.1 $\pm$ 0.72		21.8 $\pm$ 1.37	16.9 $\pm$ 0.85	**	6.7 $\pm$ 0.70	7.4 $\pm$ 0.37	
	0.2–0.3	11.7 $\pm$ 1.09	12.4 $\pm$ 0.81		17.1 $\pm$ 1.10	17.9 $\pm$ 0.91		7.8 $\pm$ 0.55	8.3 $\pm$ 0.35	
	0.3–0.4	11.2 $\pm$ 0.70	10.6 $\pm$ 0.90		21.5 $\pm$ 1.06	16.2 $\pm$ 1.05	***	6.9 $\pm$ 0.43	6.7 $\pm$ 0.45	
	0.4–0.5	10.0 $\pm$ 0.69	11.4 $\pm$ 1.06		18.1 $\pm$ 1.07	19.7 $\pm$ 1.22		6.9 $\pm$ 0.42	8.3 $\pm$ 0.54	*
	0.5–0.6	9.7 $\pm$ 0.46	10.7 $\pm$ 0.85		18.4 $\pm$ 0.75	16.6 $\pm$ 1.31		7.7 $\pm$ 0.36	7.3 $\pm$ 0.60	
	0.6–0.7	10.3 $\pm$ 0.43	11.3 $\pm$ 1.42		19.0 $\pm$ 0.61	19.1 $\pm$ 1.52		7.5 $\pm$ 0.31	8.5 $\pm$ 0.72	
	0.7–0.8	9.8 $\pm$ 0.39	13.2 $\pm$ 1.76	**	18.5 $\pm$ 0.55	19.7 $\pm$ 1.47		7.3 $\pm$ 0.25	9.0 $\pm$ 0.85	*
	0.8–0.9	9.0 $\pm$ 0.24	13.2 $\pm$ 1.20	***	16.9 $\pm$ 0.36	20.5 $\pm$ 1.54	**	6.8 $\pm$ 0.16	7.4 $\pm$ 0.66	
	0.9–1.0	9.6 $\pm$ 0.18	12.5 $\pm$ 2.16	**	17 $\pm$ 0.27	19 $\pm$ 1.60		6.7 $\pm$ 0.13	8.2 $\pm$ 0.69	*
Radiation	0.1–0.2	7.1 $\pm$ 0.49	7.6 $\pm$ 0.23		3.1 $\pm$ 0.34	3.2 $\pm$ 0.20		6.1 $\pm$ 0.36	5.3 $\pm$ 0.18	
	0.2–0.3	7.6 $\pm$ 0.37	6.7 $\pm$ 0.24	*	3.1 $\pm$ 0.17	3.6 $\pm$ 0.17		5.6 $\pm$ 0.28	5.6 $\pm$ 0.19	
	0.3–0.4	7.3 $\pm$ 0.32	7.2 $\pm$ 0.32		3.0 $\pm$ 0.19	3.1 $\pm$ 0.21		5.8 $\pm$ 0.36	5.4 $\pm$ 0.28	
	0.4–0.5	8.5 $\pm$ 0.27	6.6 $\pm$ 0.30	***	3.0 $\pm$ 0.20	3.8 $\pm$ 0.22	*	5.6 $\pm$ 0.18	5.8 $\pm$ 0.27	
	0.5–0.6	8.2 $\pm$ 0.21	8.6 $\pm$ 0.43		3.2 $\pm$ 0.14	3.7 $\pm$ 0.29		5.5 $\pm$ 0.21	5.8 $\pm$ 0.30	
	0.6–0.7	8.1 $\pm$ 0.22	8.3 $\pm$ 0.45		3.2 $\pm$ 0.11	3.8 $\pm$ 0.32	*	5.8 $\pm$ 0.18	6.3 $\pm$ 0.33	
	0.7–0.8	8.7 $\pm$ 0.18	7.7 $\pm$ 0.53		2.9 $\pm$ 0.09	4.2 $\pm$ 0.35	***	5.5 $\pm$ 0.13	6.4 $\pm$ 0.37	**
	0.8–0.9	9.3 $\pm$ 0.12	8.8 $\pm$ 0.49		2.8 $\pm$ 0.06	3.7 $\pm$ 0.28	***	5.4 $\pm$ 0.09	5.8 $\pm$ 0.33	
	0.9–1.0	9.7 $\pm$ 0.09	8.5 $\pm$ 0.56	**	2.7 $\pm$ 0.05	3.7 $\pm$ 0.32	***	5.3 $\pm$ 0.06	5.9 $\pm$ 0.34	*
Rainfall	0.1–0.2	44.5 $\pm$ 2.92	38.3 $\pm$ 1.52		412.5 $\pm$ 24.65	421.0 $\pm$ 13.67		43.7 $\pm$ 1.85	42.9 $\pm$ 1.15	
	0.2–0.3	45.4 $\pm$ 1.79	42.4 $\pm$ 1.25		422.7 $\pm$ 10.61	455.9 $\pm$ 13.51		42.8 $\pm$ 1.75	42.3 $\pm$ 1.45	
	0.3–0.4	46.7 $\pm$ 1.88	36.9 $\pm$ 1.76	***	426.8 $\pm$ 10.41	441.2 $\pm$ 14.59		42.1 $\pm$ 1.71	47.3 $\pm$ 1.54	*
	0.4–0.5	40.4 $\pm$ 1.41	42.7 $\pm$ 1.81		413.8 $\pm$ 9.23	448.4 $\pm$ 14.54	*	44.6 $\pm$ 1.05	42.5 $\pm$ 1.75	
	0.5–0.6	38.1 $\pm$ 1.46	37.0 $\pm$ 1.71		396.1 $\pm$ 8.00	415.5 $\pm$ 15.96		44.6 $\pm$ 1.00	43.4 $\pm$ 1.33	
	0.6–0.7	41.4 $\pm$ 1.19	41.2 $\pm$ 2.28		399.7 $\pm$ 6.75	423.1 $\pm$ 20.27		45.9 $\pm$ 0.92	44.3 $\pm$ 2.09	
	0.7–0.8	38.6 $\pm$ 1.02	44.4 $\pm$ 2.04	*	388.7 $\pm$ 6.3	427.5 $\pm$ 23.93	*	46.7 $\pm$ 0.71	46.3 $\pm$ 1.47	
	0.8–0.9	37.8 $\pm$ 0.59	45.1 $\pm$ 1.55	***	380.1 $\pm$ 3.93	437.1 $\pm$ 15.69	***	48.6 $\pm$ 0.49	43.9 $\pm$ 1.59	**
	0.9–1.0	35.9 $\pm$ 0.45	44.1 $\pm$ 3.15	***	366.0 $\pm$ 2.58	444.0 $\pm$ 22.72	***	50.0 $\pm$ 0.36	45.3 $\pm$ 1.89	*
Soil moisture	0.1–0.2	12.9 $\pm$ 1.27	12.5 $\pm$ 0.78		18.4 $\pm$ 1.33	14.4 $\pm$ 0.68	**	5.2 $\pm$ 0.53	5.2 $\pm$ 0.28	
	0.2–0.3	13.9 $\pm$ 1.09	14.3 $\pm$ 0.79		14.9 $\pm$ 1.12	14.7 $\pm$ 0.78		5.9 $\pm$ 0.53	5.8 $\pm$ 0.35	
	0.3–0.4	13.2 $\pm$ 0.71	13.0 $\pm$ 0.91		18.2 $\pm$ 1.09	15.2 $\pm$ 0.93	*	4.8 $\pm$ 0.40	5.9 $\pm$ 0.45	
	0.4–0.5	14.7 $\pm$ 0.54	13.6 $\pm$ 1.09		13.9 $\pm$ 0.91	16.7 $\pm$ 0.81	*	5.3 $\pm$ 0.27	5.7 $\pm$ 0.42	
	0.5–0.6	13.8 $\pm$ 0.54	11.6 $\pm$ 0.99	*	15.1 $\pm$ 0.62	13.1 $\pm$ 1.09		5.5 $\pm$ 0.33	4.8 $\pm$ 0.36	
	0.6–0.7	14.4 $\pm$ 0.46	13.9 $\pm$ 1.36		15.5 $\pm$ 0.47	15.6 $\pm$ 1.14		4.9 $\pm$ 0.24	5.7 $\pm$ 0.47	
	0.7–0.8	13.9 $\pm$ 0.40	17.0 $\pm$ 1.46	**	14.8 $\pm$ 0.46	15.4 $\pm$ 1.34		4.1 $\pm$ 0.19	6.2 $\pm$ 0.51	***
	0.8–0.9	13.2 $\pm$ 0.29	14.8 $\pm$ 1.26		13.4 $\pm$ 0.28	16.1 $\pm$ 1.25	**	5.0 $\pm$ 0.13	5.6 $\pm$ 0.39	
	0.9–1.0	13.1 $\pm$ 0.26	13.8 $\pm$ 1.63		13.3 $\pm$ 0.22	14.7 $\pm$ 1.12		5.1 $\pm$ 0.11	5.7 $\pm$ 0.51	

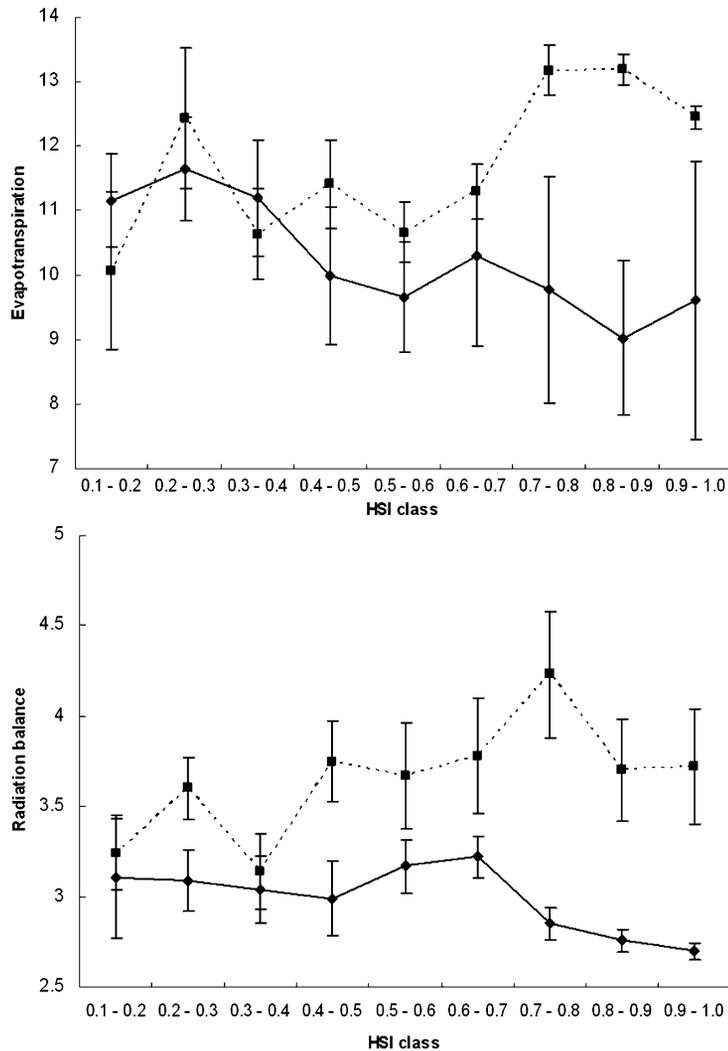


Fig. 2. Inter-annual variation in evapotranspiration during the hatching period (upper) and radiation balance during the rearing period (lower) for locations with (solid line) and without (dashed line) great bustards. The graphs show means  $\pm$  SE. The x-axis is the Habitat Suitability Index value (= probability of occurrence) from the model of Suárez-Seoane et al. (2002).

analysis of habitat requirements within a GIS environment (Lane et al. 2001, Osborne et al. 2001, Suárez-Seoane et al. 2002). Our analysis here, however, shows that occupied patches of suitable habitat are significantly larger than unoccupied patches and that they possess different climatic characteristics over time. How can we explain these findings?

Although great bustards have a tendency to return to their birthplaces (Alonso et al. 1998, Martín et al. 2002), philopatry alone does not explain the difference in size we found between occupied and unoccupied patches. The “lack of dispersal” hypothesis as an explanation for vacant but suitable patches would predict all close patches to be occupied irrespective of size (above a minimum threshold which is below the pixel size used in the analysis). When we took account

of random encounter rates by dispersing birds, large patches were used less often than expected by chance but, where they are occupied, a greater area of the patch was used than expected. These results suggest an aggregated distribution with a number of vacant but suitable habitat patches. This and the tendency for occupied patches to be larger is consistent with metapopulation theory because extinction rates are expected to be lower and recolonisation rates higher for larger than smaller patches (Hanski 1999). Indeed, Spanish great bustards are thought to exhibit a metapopulation type structure (Alonso et al. 2004).

The choice of the “right” habitat patch will strongly influence the survival and reproductive success of a population (Parejo et al. 2006). For some species, variability in the availability of resources at a given

location is predictable whereas for others it is not (Roshier 2003). If patches differ in how predictable the availability of resources or conditions determining fitness will be, selection would operate to favour the evolution of behavioural mechanisms which provide clues to site history. In the present study, we found that vacant and occupied habitat patches that were objectively defined as suitable could be distinguished by inter-annual variability (i.e. predictability) measured over a short time period, even though the sites appeared identical. For example, while the variability in evapotranspiration was significantly greater in vacant patches than occupied patches during the hatching period, average evapotranspiration itself did not differ between them ( $Z = 0.64$ ,  $p = 0.55$ , third dekad of May, data averaged over four years). The environmental differences between occupied and vacant patches also made sense in terms of maximising expected fitness. For example, choosing sites with more predictable soil moisture and evapotranspiration appears logical for great bustards nesting on the ground in dry conditions since it would reduce the energy expenditure of the incubating female. Similarly, rearing chicks in areas with more predictable rainfall presumably increases their chances of survival because cold, wet chicks may die of hypothermia. Moreover, by choosing sites with predictable climatic conditions the female may be ensuring a more regular supply of invertebrate food for the growing chicks. There is thus evidence that the sites where great bustards choose to aggregate have greater temporal stability in climatic factors and there is a logical link between this stability and expected breeding performance (Morales et al. 2002). Indeed, local differences in breeding productivity (Alonso et al. 2004) could be driven by climatic factors, directly influencing population persistence at the local (patch) scale. Interestingly, we found greater variability in winter rainfall at occupied than at vacant sites which might appear contrary to our argument about the benefits of climatic stability. However, breeding sites (which we modelled) are not necessarily used during the winter when bustards are more mobile, so winter rainfall may not directly impact the birds. More work is needed on seasonal habitat selection and how the presence or lack of critical features in one season affects occupancy during the other.

From a methodological standpoint, it is important to question whether our results could have an artefactual explanation. Spatial analyses are complicated by the non-independence of adjacent pixels and climatic variables will always display spatial autocorrelation at some spatial scale. The key issues here are whether spatial autocorrelation was higher in occupied than in vacant habitat patches due to the aggregation of pixels, and whether this impacted on the analysis through Type I errors. We doubt that this is the case. In formal

testing using Moran's I, we found significant autocorrelation in all the climatic variables analysed, but very small differences between occupied and unoccupied patches. The largest difference in spatial autocorrelation occurred for evapotranspiration in the winter, but there was little difference in the variability of this measure between occupied and unoccupied patches (e.g. Table 1). Logically, high spatial autocorrelation would lead to consistent variation between years and almost certainly lower variability than that observed among pooled isolated pixels. Yet spring net radiation balance and winter rainfall were more variable between years where pixel aggregation was greatest. We therefore conclude that although spatial autocorrelation and other spatial issues cannot be discounted entirely, they are not a significant biasing factor in this study.

It should also be highlighted that the unoccupied patches identified in this study were small ( $5 \text{ km}^2$  on average), perhaps too small for a lek. Furthermore, they could have been used as breeding sites by females, even though they were not used during the display season when our data were collected. Indeed, great bustards occupy much less surface area when lekking than during other seasons, and further work is needed on distributions outside the display period if a full picture of habitat use is to be built up (Suárez-Seoane et al. unpubl.). In this sense, existing distribution models for breeding bustards may not be incorrect, even though they predict use beyond the lek sites used to build them.

If there is evolutionary advantage in knowing a site's history, there would be strong selective pressure for learning this information from others (i.e. site history is public information (Valone and Templeton 2002)) because it cannot be sampled directly. We envisage a gradient among species where the balance between use of public information and personal sampling for patch selection differs, great bustards being at one extreme by aggregating at traditional sites. Understanding how species achieve this balance needs theoretical development (Templeton and Giraldeau 1996, Valone and Templeton 2002). When habitat patches differ in quality but between-patch quality is correlated over time, individuals gain higher lifetime fitness by using public information over personal experience (Boulinier and Danchin 1997). Mönkkönen et al. (1999) have analysed the ecological conditions that may favour heterospecific attraction over sampling. They found that using the presence of others is an efficient way to choose the best patch not only when interspecific competition is intense, but also when the benefits from social aggregation exceed the effects of competition. The high cost of sampling empty habitat patches also increases the fitness of employing heterospecific or conspecific attraction over sampling.

Gaining information on site history through conspecific attraction is only likely to be a successful habitat

selection mechanism if the rate of environmental change is slow because it introduces inertia into species responses to change. The “Ghosts of Habitats Past” (Knick and Rotenberry 2000) may keep a species on an increasingly unsuitable site for many years. The models of Lane and Alonso (2001) and Osborne (2005) show that 5% of an original great bustard population could theoretically persist 34 yr after a site is too poor for breeding (although longevity is likely to be shorter) and Lane et al. (2001) warned that great bustards are very slow to leave traditional sites and colonise new areas. Great bustards are considered vulnerable mainly due to habitat changes (BirdLife International 2004) but global warming is also likely to make central and southern Spain too dry for them (Huntley et al. 2006, in press) prompting Osborne (2005) to urge research into translocation techniques. In these circumstances, using others as a cue to settlement is maladaptive and likely to lead to local extinctions.

Our study has messages for conservation and distribution modelling which apply not only to great bustards but also to other animal species. First, envelope models should consider incorporating predictors which capture temporal variation as well as averages, for example, in the variability of rainfall as well as the mean. This mirrors the call from Heikkinen et al. (2006) for more ecologically appropriate climate variables in models. Second, patch size (an ecological property) influences occupancy and analyses which treat pixels independently and as if they are spatially independent do not capture this. While a pixel might have the characteristics of good habitat, it will not be used if the contiguous block of suitable pixels it occupies is too small. Thus measures of the extent of suitable habitat which sum the number of suitable pixels before and after change are likely to be misleading, especially at fine spatial resolutions. Unfortunately, incorporating the effects of patch size into envelope models is not straightforward and dynamic behavioural based modelling approaches may be needed. Indeed, patch size can only be determined after habitat suitability has been calculated and this suggests that a two-stage or multi-scale analysis is necessary. At its simplest, patches of contiguous pixels that meet some size criterion could be identified by running a patch size filter over an image after a predictive model has been built, assuming the minimum viable patch size is known. Another approach which “cleans” images of isolated pixels is spatial autoregressive modelling, although it falls short of eliminating all patches below an ecological minimum viable area. The autologistic modelling approach of Augustin et al. (1996), for example, uses an iterative approach to repeatedly weight the probability assigned to a pixel by the values of its neighbours. This process converges to a “cleaner” image where isolated pixels are removed or joined to

neighbouring areas (see Osborne et al. 2001 for an example on great bustards). Without these refinements, we have to be content that envelope models for animal species which are able to choose may show potential rather than actual distributions, particularly at finer spatial resolutions.

*Acknowledgements* – We thank Lluís Brotons for drawing to our attention the literature on heterospecific attraction; Tim Smyth at the Plymouth lab for carrying out the Rao and Chen calibration of the NDVI data; NERC for supplying the AVHRR satellite imagery; the staff at EWBMS for supplying the METEOSAT data; and Kate Howie for statistical advice. Comments by Miguel Araujo, Risto Heikkinen and an anonymous referee greatly helped to sharpen the text. This study was partly supported by EU programme “Environment and Climate” (ENV4-CT98-5130).

## References

- Alonso, J. C. (ed.) 2007. La Avutarda Común en Andalucía. – Consejería de Medio Ambiente, Junta de Andalucía, Sevilla.
- Alonso, J. C. et al. 1998. Proximate and ultimate causes of natal dispersal in the great bustard *Otis tarda*. – Behav. Ecol. 9: 243–252.
- Alonso, J. C. et al. 2000. Partial migration, and lek and nesting area fidelity in female great bustards. – Condor 102: 127–136.
- Alonso, J. A. et al. 2001. Long distance seasonal movements of male great bustards in central Spain. – J. Field Ornithol. 72: 504–508.
- Alonso, J. C. et al. 2003. Status and recent trends of the great bustard (*Otis tarda*) population in the Iberian Peninsula. – Biol. Conserv. 110: 185–195.
- Alonso, J. C. et al. 2004. Distribution dynamics of a great bustard metapopulation throughout a decade: influence of conspecific attraction and recruitment. – Biodiv. Conserv. 13: 1659–1674.
- Augustin, N. H. et al. 1996. An autologistic model for the spatial distribution of wildlife. – J. Appl. Ecol. 33: 339–347.
- BirdLife International 2004. Threatened birds of the World 2004. – CD ROM, BirdLife International, Cambridge.
- Boulinier, T. and Danchin, E. 1997. The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. – Evol. Ecol. 11: 505–517.
- Coolen, I. et al. 2003. Species difference in adaptive use of public information in sticklebacks. – Proc. R. Soc. B 270: 2413–2419.
- Doligez, B. et al. 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. – Anim. Behav. 66: 973–988.
- Elith, J. et al. 2006. Novel methods improve prediction of species’ distributions from occurrence data. – Ecography 29: 129–151.

- Forsman, J. T. et al. 2002. Positive fitness consequences of interspecific interaction with a potential competitor. – *Proc. R. Soc. B* 269: 1619–1623.
- Fretwell, S. D. and Lucas, J. H. J. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. – *Acta Biotheor.* 19: 16–36.
- García, J. et al. 2007. Spatial analysis of habitat quality in a fragmented population of little bustard: implications for conservation. – *Biol. Conserv.* 137: 45–56.
- Guisan, A. and Zimmermann, N. E. 2000. Predictive habitat distribution models in ecology. – *Ecol. Modell.* 135: 147–186.
- Hanski, I. 1999. *Metapopulation ecology*. – Oxford Univ. Press.
- Heikkinen, R. K. et al. 2006. Does seasonal fine-tuning of climatic variables improve the performance of bioclimatic envelope models for migratory birds? – *Divers. Distrib.* 12: 502–510.
- Heredia, B. et al. 1996. *Globally threatened birds in Europe*. – Council of Europe Publ., Strasbourg.
- Huntley, B. et al. 2006. Potential impacts of climate change upon geographical distributions of birds. – *Ibis* 148: 8–28.
- Huntley, B. et al. in press. *A climate atlas of European breeding birds*. – Lynx Editions, Barcelona.
- Knick, S. T. and Rotenberry, J. T. 2000. Ghosts of habitats past: contribution of landscape change to current habitats used by shrubland birds. – *Ecology* 81: 220–227.
- Krebs, J. R. and Kacelnik, A. 1991. Decision making. – In: Krebs, J. R. and Davies, N. B. (eds), *Behavioural ecology. An evolutionary approach*, 3rd ed. Blackwell, pp. 105–136.
- Lane, S. J. and Alonso, J. C. 2001. Status and extinction probabilities of great bustard (*Otis tarda*) leks in Andalusia, southern Spain. – *Biodiv. Conserv.* 10: 893–910.
- Lane, S. J. et al. 2001. Habitat preferences of great bustard *Otis tarda* flocks in the arable steppes of central Spain: are potentially suitable areas unoccupied? – *J. Appl. Ecol.* 38: 193–203.
- Martín, C. A. et al. 2002. Great bustard population structure in central Spain: concordant results from genetic analysis and dispersal study. – *Proc. R. Soc. B* 1487: 119–125.
- Mönkkönen, M. et al. 1990. Numerical and behavioural responses of migrant passerines to experimental manipulation of resident tits (*Parus* spp.): heterospecific attraction in northern breeding bird communities? – *Oecologia* 85: 218–225.
- Mönkkönen, M. et al. 1999. Evolution of heterospecific attraction: using other species as cues in habitat selection. – *Evol. Ecol.* 13: 91–104.
- Morales, M. B. and Martin, C. A. 2003. *Otis tarda* great bustard. – *BWP Update* 4: 217–232.
- Morales, M. B. et al. 2000. Migration patterns in male great bustards (*Otis tarda*). – *Auk* 117: 493–498.
- Morales, M. B. et al. 2002. Annual productivity and individual female reproductive success in a great bustard *Otis tarda* population. – *Ibis* 144: 293–300.
- Moran, M. D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. – *Oikos* 100: 403–405.
- Nakagawa, S. 2004. A farewell to Bonferroni: the problems of low statistical power and publication bias. – *Behav. Ecol.* 15: 1044–1045.
- Neuhäuser, M. 2004. Testing whether any of the significant tests within a table are indeed significant. – *Oikos* 106: 409–410.
- Nocera, J. J. et al. 2006. Inadvertent social information in breeding site selection of natal dispersing birds. – *Proc. R. Soc. B* 273: 349–355.
- Osborne, P. E. 2005. Key issues in assessing the feasibility of reintroducing the great bustard *Otis tarda* L. to Britain. – *Oryx* 39: 22–29.
- Osborne, P. E. and Suárez-Seoane, S. 2006. Identifying core areas in a species' range using temporal suitability analysis: an example using little bustards *Tetrax tetrax* L. in Spain. – *Biodiv. Conserv.*, DOI 10.1007/s10531-006-9058-1.
- Osborne, P. E. et al. 2001. Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. – *J. Appl. Ecol.* 38: 458–471.
- Parejo, D. et al. 2006. Testing habitat copying in breeding habitat selection in a species adapted to variable environments. – *Ibis* 148: 146–154.
- Perneger, T. V. 1998. What's wrong with Bonferroni adjustments. – *Brit. Med. J.* 316: 1236–1238.
- Rao, C. R. N. and Chen, J. 1995. Intersatellite calibration linkages for the visible and near-infrared channels of the Advanced Very High-Resolution Radiometer on the NOAA-7, NOAA-9, and NOAA-11 spacecraft. – *Int. J. Rem. Sens.* 16: 1931–1942.
- Reed, J. M. and Dobson, A. P. 1993. Behavioral constraints and conservation biology: conspecific attraction and recruitment. – *Trends Ecol. Evol.* 8: 253–256.
- Rosema, A. 1993. Using Meteosat for operational evapotranspiration and biomass monitoring in the Sahel region. – *Rem. Sens. Environ.* 45: 1–25.
- Rosema, A. et al. 2001. European energy and water balance monitoring system. – EU 4th Framework Program, Contract ENV4-CT97-0478, Final report.
- Rosenzweig, M. L. 1991. Habitat selection and population interactions – the search for mechanism. – *Am. Nat.* 137: S5–S28.
- Roshier, D. A. 2003. On animal distributions in dynamic landscapes. – *Ecography* 26: 539–544.
- Suárez-Seoane, S. et al. 2002. Large-scale habitat selection by agricultural steppe birds in Spain: identifying species-habitat responses using generalized additive models. – *J. Appl. Ecol.* 39: 755–771.
- Suárez-Seoane, S. et al. 2004. Can climate data from METEOSAT improve wildlife distribution models? – *Ecography* 27: 629–636.
- Templeton, J. J. and Giraldeau, L. A. 1996. Vicarious sampling: the use of personal and public information by starlings foraging in a simple patchy environment. – *Behav. Ecol. Sociobiol.* 38: 105–114.
- Valone, T. J. and Templeton, J. J. 2002. Public information for the assessment of quality: a widespread social phenomenon. – *Phil. Trans. R. Soc. B* 357: 1549–1557.
- Verhoeven, K. J. F. et al. 2005. Implementing false discovery rate control: increasing your power. – *Oikos* 108: 643–647.