Competing effects of topographic, lithological, vegetation structure and human impact in the habitat preferences of the Cream-coloured Courser

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Received 20 November 2006; received in revised form 28 June 2007; accepted 17 July 2007

Abstract

The Cream-coloured Courser *Cursorius cursor* is a poorly known species inhabiting arid environments of the Western Palaearctic. The easternmost main islands of the Canary archipelago (Fuerteventura and Lanzarote, North Atlantic Ocean, Spain) harbour a stable population. The species showed an intense habitat selection pattern in these islands. Its probability of occurrence was highest in locations of relatively flat terrain (maximum slope steepness $<11\%$), below 197 m a.s.l., with scarce shrub cover less than 16%, and a rock cover less than 23%. Roads were the only human disturbance among those considered in the study (i.e., dirt tracks, urban developments, agriculture), having a clear negative effect on the occurrence of the Cream-coloured Courser. This paper highlights the importance of an issue deserving greater attention in future studies: fine-grained habitat features, which are not directly related to vegetation structure, but are relative to topographic and lithological traits, largely determine habitat selection of birds inhabiting arid environments.
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Keywords: Arid environments; Canary islands; Cream-coloured courser; Ecological thresholds; Habitat selection; Human disturbance

1. Introduction

Habitat preferences in birds are determined by morphological traits related to locomotion, behavioural functions, the ability to obtain food and shelter for breeding and safely against predators. The proximate stimuli for habitat choice might be structural features of the environment, nesting and foraging opportunities and the presence of potential competitors or predators (Cody, 1985). Among birds, vegetation structure has been identified as the main feature determining the habitat 'gestalt'. The influence of vegetation traits has been

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demonstrated in a wide variety of studies carried out in temperate areas with birds living in pasturelands, shrublands and woodlands, or in a mosaic of a broad array of these environments (see Jones, 2001; Wiens, 1989 for a review).

Arid environments have simple vegetation structure characterized by sparse cover of xeromorphic dwarf shrubland and perennial and/or annual herbs. In such scarcely vegetated environments, it is probable that other factors play a major role. Thus, lithological traits may have an important influence on locomotion, constraining or impeding mobility over rough surfaces. On the other hand, topographic characteristics related to altitude or steepness of the terrain may affect habitat selection through climatic effects on temperature/humidity and indirectly through vegetation (Vander Haegen et al., 2000), or added costs to locomotion when walking up- or downhill in foraging routines (Daley and Biewener, 2003; Gabaldón et al., 2004). These traits are usually related to important gradients in arid environments, being better correlated with richness, abundance and composition of the avifauna than any other variable, including vegetation (Kaboli et al., 2006). Therefore, although structure, physiognomy, and taxonomic composition of the vegetation are often thought to have a great predictive potential for bird distribution in temperate areas, the role of vegetation traits may vanish in other structurally simple environments (Kaboli et al., 2006; Naranjo and Raitt, 1993). On the other hand, anthropogenic impact on bird communities of arid ecosystems related to urban developments, agricultural activities, grazing or transport infrastructures may exert a prominent role in these structurally simple environments through disturbances of foraging routines, roosting and nesting (Desmond, 2004; Germaine et al., 1998; Gonnet, 2001; Green and Baker, 2003; Ingelfinger and Anderson, 2004; Isacch et al., 2005; Khoury and Al-Shamlih, 2006; Le Cuziat et al., 2005).

The Cream-coloured Courser (*Cursorius cursor* Latham, 1787) inhabits arid environments and is mainly distributed along the Sahelian stretch and the Middle East, but it also occurs patchily in the Western Palearctic (Del Hoyo et al., 1996; Urban et al., 1986). The Canary Islands harbour a stable population (Martín and Lorenzo, 2001), although nearly all breeding birds in the Canary archipelago are located in the islands of Lanzarote and Fuerteventura. Information on Cream-coloured Courser is remarkably scarce and anecdotical in almost any aspect of its biology (Del Hoyo et al., 1996; Perrins, 1998; Urban et al., 1986), and this lack of accurate knowledge prevents appropriate conservation measures from being taken. Besides, the Cream-coloured Courser is a genuine representative of avifaunas of arid environments, and the obtained conclusions may constitute a rather good reference for future studies on these habitats. Therefore, this paper focuses on the general patterns of habitat selection of this scarce species, testing the different influence of topographic, lithological, vegetation structure and human impact factors in structurally simple arid environments.

2. Methods

2.1. Study area

Lanzarote (29°N, 13°37′W; 815 km^2) and Fuerteventura (28°27′N, 14°00′W; 1730 km^2) are the easternmost main islands of the Canary archipelago, lying only 100 and 120 km from the North-African coast, respectively. Both islands show a smooth relief in accordance with their ancient geological history and erosion (20–22 million years for Fuerteventura, 16–19 million years for Lanzarote). The combined effects of direct Saharan influence on climate and a flat topography result in a dominance of scarcely vegetated arid steppe landscapes, which have been extensively grazed and cultivated.

The impoverished plant communities mostly consist of a few species of xerophytic shrubs (*Launaea arborescens*, *Lycium intricatum*, *Salsola vermiculata*, *Suaeda* spp. and *Euphorbia* spp.), therophytic forbs and several perennial grass species. However, the degree of development of vegetated patches is relatively diverse due to local conditions, such as humidity, slope of terrain, goat grazing and human uses. With regard to soil lithology and compactness, the study areas also comprise a broad range of conditions, from stony lava fields to loose sand dunes. The cities and small villages are widely spread throughout both islands, though they become particularly dense and large near the coast due to tourist activities.

2.2. Bird sampling and habitat data

Bird surveys were carried out in 2005, during the second fortnight of February and the first one of March. The survey method was the line transect, frequently used in extensive assessments of abundance, general distribution patterns and habitat preferences of birds (Bibby et al., 2000). A total number of 1374 line transects of 0.5 km (measured by means of portable GPSs) were made, focused on the main steppe-like and desert areas of the two islands (Supplementary figure). To a lesser extent, other habitats (e.g., traditional cultivations established on steppe landscapes, hilly slopes) were also considered, increasing the environmental variability surveyed for the species. The sampling locations and the approximate number of transects to gather on them, were roughly determined in proportion to the surface in the islands of main landscape types. Apart from the mere availability of a safe place to park, the starting point of each sampling line was randomly determined. Next, the observers walked through the target area trying (a) to perform 0.5 km transects as homogeneous as possible and (b) to attain an extensive cover of the sampling location. The transect lines were not biased by an *a priori* potential of the habitat to harbor Cream-coloured Coursers, because this field work was not exclusively focused in sampling this species, and because most locations were so intensively sampled that there is little room for any geographical bias.

The transects were carried out on windless and rainless days, walking cross-country or by little used dirt tracks at a low speed (1–3 km/h approximately), during the 4 h after dawn and the 2.5 h before dusk.

The variables used to characterize the 0.5 km transects were the averages of three visual estimations (at 125, 250 and 375 m within the line transect) on 25-m radius circular plots: coverages of (1) grass, (2) annual forbs and (3) shrubs (in percentages); (4) mean height of the shrub layer (in cm); (5) rock cover (in percentage); (6) mean size of the stones on the ground, if any (in cm); (7) soil typology (according to the following classes: (0) lava fields, (1) stone/gravel soils, (2) compact sandy soils, (3) sandy soils and (4) loose sand dunes); (8) altitude above sea level (measured with GPS receptors) and (9) the amount of any agricultural land-use (estimated in 250-m width bands along the transects and expressed in percentage). Afterwards, the distances from the center of each transect to the nearest (10) road (in m) and (11) city (in m), (12) the maximum slope of terrain (in m) and the length of (13) paved roads (in m) and (14) dirt tracks (in m) within circles of radius 250 m were measured on 1:25,000 maps. Supplementary table summarizes the mean values and ranges for these variables in the 1374 transects sampled.

2.3. Habitat preferences

Two analytical approaches were used to study the habitat preferences of the species according to two different proccesses. The first one compares the use of habitat patches with their availability in the study region, defining the habitat selection of the courser within environmental gradients. The second one models the occurrence of the species, trying to establish the main environmental variables (and their threshold values) responsible for its distribution in the islands.

A principal components analysis (PCA) was carried out with habitat variables describing the 1374 line transects, to obtain a reduced number of factors that summarize habitat structure. The correlation matrix between original variables was used, and a 'varimax' rotation increased interpretability of the resulting factors.

To analyse habitat selection, we have employed a use–availability sampling design (Keating and Cherry, 2004). We used the factor scores obtained from the PCA (i.e., the position of each line transect along each environmental factor) to assess the general habitat preferences of the Cream-coloured Courser. For each axis, we tested whether the mean position of the line transects where the species was present (i.e., representing the average preferred habitat) differed from the mean of the whole sample of 1374 transects, which equals zero (representing the mean habitat features sampled overall). Significant deviations from zero indicate the preference of the Cream-coloured Courser towards one or the other side of the PCA gradients. The differences between the set of observed mean scores and the expected value were tested first with a multivariate Hotelling's T-test, and then with individual 'protected' *a posteriori* t-tests for each PCA axis. Therefore, the sample sizes in these analyses were defined by the number of transects where the species was present ($N = 46$), comparing an observed mean (i.e., that of the courser) with an expected average (zero in each principal component representing the mean of the factor scores of all transects sampled).

Similarly, we compared the standard deviation of factor scores in transects occupied by the species (SD, representing its degree of ecological tolerance around the mean preferred habitat) versus the standard deviation of the whole sample of 1374 transects, which equals one (representing the total environmental variability sampled). Standard deviations significantly lower than one ($SD<1$) mean that the species has narrow habitat preferences, whereas $SD>1$ imply eurytopic preferences. Differences in standard deviation were tested using the *t*-test comparing an observed SD (that of the Cream-coloured Courser) with an expected one ($SD = 1$ for the whole sample of all transects).

To assess whether the species preferred the same habitats in Lanzarote and Fuerteventura, a MANOVA test was carried out with the dependent variables being the seven PCA axes and the islands considered as a factor.

Finally, species occurrence (absence = 0, presence = 1) in census samplings was modeled with the 14 original descriptors as explanatory variables, and analysed using classification trees. This is a statistical tool where the response variable undergoes successive univariate splits, according to threshold values of the explanatory variables that maximize the differences between the two resulting groups of samples. Classification trees deal with non-linear relationships between response and explanatory variables, and with interactions among the latter, and thus are suitable for modelling complex ecological scenarios (De'Ath and Fabricius, 2000; Venables and Ripley, 1999). The predictive power of the obtained classification tree was evaluated by means of a cross-validation procedure using 25 random sampling iterations. In each iteration, the whole sample was randomly divided into three groups, and two of them were used to predict the third one according to the classification tree obtained.

All statistical analyses were carried out using Statistica 6.0 (StatSoft, 2001).

3. Results

3.1. Used versus available areas

Table 1 shows the seven main axes of covariation among habitat variables, which accounted for 71.6% of the original variance among sampling transects. These multivariate factors of the PCA can be worded in the following way: PC1, a lithological gradient ranging from lava fields to loose sand dunes, so that locations with the most compact soil had bigger and more abundant rocks; PC2, a topographic gradient relating steeper slopes with higher altitudes, where grass cover is also higher; PC3, an axis showing an increase of cover and

Table 1
Principal component analysis with varimax rotation summarizing the 14 environmental variables (names as in Supplementary table)

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Dist. Urban	−0.024	−0.065	0.015	**−0.844**	−0.011	−0.141	0.030
Dist. Road	0.072	0.008	−0.077	**−0.484**	**−0.686**	−0.002	0.040
L-TRACKS	0.105	0.009	−0.041	−0.066	−0.031	0.078	**0.923**
L-ROADS	0.003	−0.013	0.009	−0.131	**0.902**	0.098	−0.016
SLOPE	0.037	**0.838**	0.106	−0.178	−0.064	0.001	−0.028
ALTITUDE	0.190	**0.672**	0.046	0.298	−0.089	0.301	0.115
HERB. COVER	−0.036	**0.579**	-0.051	0.384	0.176	−0.129	0.078
THEROPH. COVER	−0.189	0.226	0.282	0.377	−0.023	−0.000	**0.434**
SHRUB COVER	−0.112	−0.048	**0.830**	−0.079	−0.023	−0.179	0.009
SHRUB HEIGHT	0.044	0.141	**0.819**	0.102	0.085	0.174	0.011
SOIL INDEX	**−0.789**	−0.199	0.097	−0.043	−0.064	−0.097	−0.163
ROCK COVER	**0.787**	−0.078	−0.145	−0.032	−0.109	−0.286	−0.092
ROCK SIZE	**0.717**	0.016	0.095	−0.033	−0.018	0.127	−0.010
AGRIC. COVER	0.011	0.046	−0.021	0.110	0.096	**0.926**	0.071
Eigenvalues	1.86	1.61	1.50	1.41	1.36	1.17	1.10
% var.	13.3	11.5	10.7	10.1	9.7	8.4	7.9

Significant correlations ($p<0.001$) between variables and principal components are in bold. %var—percentage of original variance explained.

height of shrubs; PC4, a gradient inversely related to distance to the nearest city and paved road; PC5, a gradient focusing on increasing road influence; PC6, an agricultural gradient, ordering the transects with regard to percentage of cultivations and PC7, an axis on density of dirt tracks per transect; additionally, locations with more unpaved trails also had higher cover of therophytic forbs (Table 2).

The average position of the Cream-coloured Courser in these seven principal components significantly differed from zero (Hotelling's T test, $T = 2.54$, d.f. $= 7.39$, $p < 0.0001$). That is to say, the species showed an intense habitat selection pattern, preferring positions on the environmental gradients that were different from the average habitat characteristics in Lanzarote and Fuerteventura.

The 46 transects where the species was detected had factor scores significantly less than zero (i.e., the null hypothesis of average environmental conditions) on PC1 ($t = 4.4$, $p < 0.0001$), PC2 ($t = 3.4$, $p < 0.01$) and PC3 ($t = 2.9$, $p < 0.01$, d.f. $= 45$ in the three tests). Standard deviations were significantly less than one (i.e., the null

Table 2
Mean and standard deviation of the position of the transects where the Cream-coloured Courser was detected ($N = 46$) in the seven environmental gradients given by the PCA in Table 1

	Mean	SD
PC1, lithological gradient	−0.397	0.787
PC2, topographic gradient	−0.313	0.478
PC3, shrub development	−0.282	0.651
PC4, proximity to the nearest city	−0.043	1.093
PC5, road influence	−0.133	0.949
PC6, agricultural gradient	−0.044	0.383
PC7, density of dirt tracks	−0.157	0.874

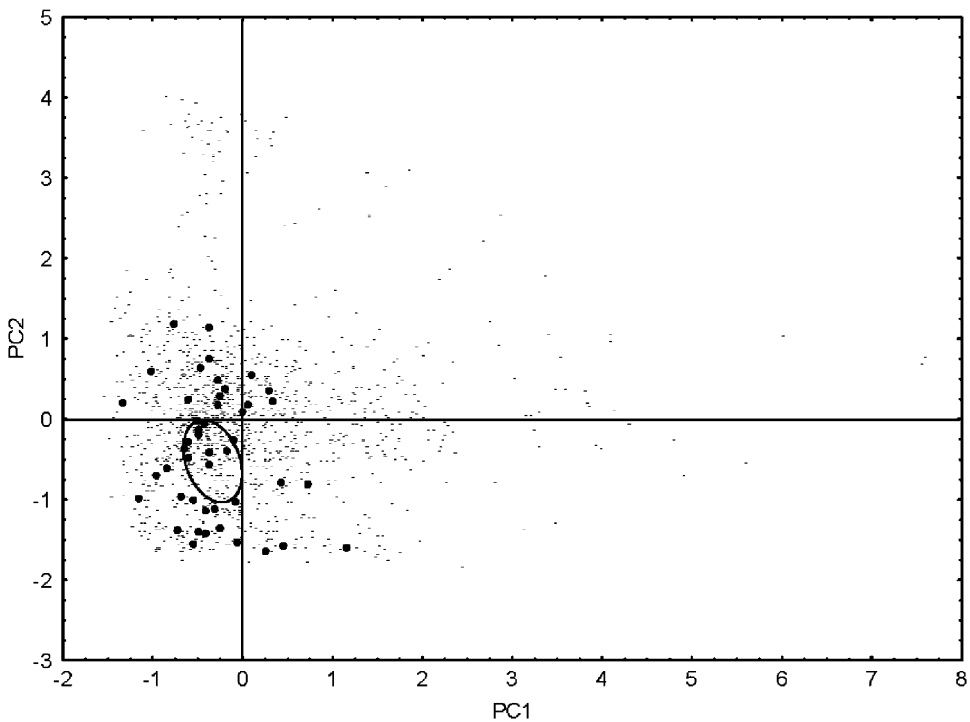

Fig. 1. Comparison between the abiotic habitat characteristics (see Table 1) of locations occupied by the Cream-coloured Courser (larger dots) and the whole environmental diversity sampled. The gradient PC1 represents a lithological gradient ranging from lava fields to loose sand dunes, while PC2 defines a topographic gradient relating steeper slopes with higher altitudes, where grass cover is also higher. The ellipse represents the 95% confidence interval around the mean of the courser.

hypothesis of environmental variability) on the same axes (PC1: $t = 10.5$, $p<0.0001$; PC2: $t = 2.6$, $p<0.01$ and PC3: $t = 5.2$, $p<0.0001$; d.f. = 45 in the three tests). No significant differences were found for the means and standard deviations of the factor scores of the species in the remaining components. To summarize, the Cream-coloured Courser preferentially occupied locations with sandy soils with a low cover of small stones (PC1), at lower altitudes, with mild slopes and with very scarce herbaceous cover (PC2; Fig. 1), and with a low development of the shrub layer (PC3).

The MANOVA analysis testing for environmental differences between both islands in transects occupied by the species was significant (Wilks' lambda = 0.67, $F_{7,38} = 2.73$, $p = 0.02$). Post hoc univariate ANOVAS identified that the locations where the Cream-coloured Courser was present had a less developed shrub layer in Lanzarote than in Fuerteventura ($F_{1,44} = 5.47$, $p = 0.02$).

3.2. Modelling of habitat preferences

The classification tree was highly significant ($\chi^2 = 66.3$, d.f. = 7, $p<0.001$; Fig. 2), with a correct prediction of presence–absence of the species in 59.5% of all the transects, and 91.3% of transects where the species was present. The cross-validations performed to assess the accuracy of this model showed a similar overall correct classification (63.0%; SD = 4.4%, $n = 25$ cross-validations).

The most important variables in habitat preferences of the Cream-coloured Courser showed that the probability of occurrence increased significantly ($p<0.01$ in all splits) in locations below 197 m a.s.l., with a scarce shrub cover lower than 16%, and flat terrain less than 11% in maximum slope; otherwise, the species was virtually absent. The remaining splitting criteria determining the maximum probability of occurrence (10.2%) were the mere presence of therophytic forbs, roads farther than 135 m, rock cover less than 23%, and grass cover less than 5%.

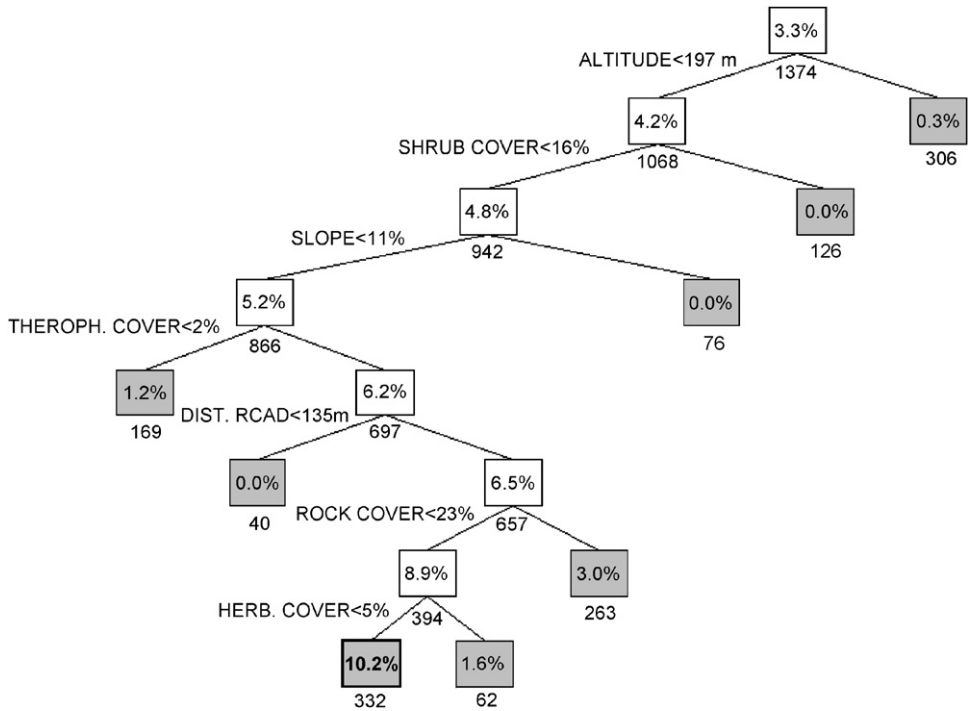

Fig. 2. Classification tree describing the pattern of habitat preferences of the Cream-coloured Courser in Lanzarote and Fuerteventura (Eastern Canary Islands). The probability of presence of the species is expressed inside each box as a percentage. Grey boxes indicate final environmental conditions (with bold type for the most favourable set of conditions). The number of transects meeting the previous set of conditions is shown below each box. The splitting variables and threshold values selected refer to left branches of the tree, so that right branches met opposite conditions. See Supplementary table for the acronyms of the variables.

4. Discussion and conclusions

Habitat selection can be envisaged as a hierarchical spatial process that may yield various patterns depending on the scales of investigation. It is widely assumed that animals usually select specific macrohabitats at a landscape scale and specific microhabitats within the preferred macrohabitats (Kotliar and Wiens, 1990). Failure to view habitat selection as a hierarchical process may result in a narrow and possibly misleading notion of the value of habitats to animals (McLoughlin et al., 2004). The application of classification trees has proved useful to discern this hierarchical process in the Cream-coloured Courser. This study also highlights the importance of fine-grained features in habitat preferences, because environments that otherwise can be judged to be 'apparently homogeneous' according to vegetation characteristics, are indeed largely heterogeneous, differing in fine-grained variables that maximize the occurrence of the species. Overall, the pattern of habitat selection of the Cream-coloured Courser stresses its preference for bare plains of sandy soils, showing that the responsiveness of species inhabiting rather simple habitats can be tightly determined by abiotic features. The influence of large-scale abiotic factors (e.g., seasonal precipitation, sun radiation) on distribution and abundance of birds in the southwestern Palearctic and in arid environments has often been reported, due mainly to their indirect effects through primary productivity (e.g., Carrascal and Palomino, 2006; De Juana and García, 2005; Newton and Newton, 1997; Van Heezik and Seddon, 1999). However, this work underlines the direct importance of local abiotic factors such as slope steepness, rock cover or pebble size, which have been rarely tested (see also Carrascal et al., 2006; Ferns and Hinsley, 1995; Illera, 2001; Knight and Beale, 2005; Seoane et al., 2006 for other bird species inhabiting arid environments).

The probability of occurrence of the Cream-coloured Courser is highest in areas with steepness of terrain lower than 11% and rock cover lower than 23% (Fig. 2). The Cream-coloured Courser probably avoids the steeper and rougher terrains because of the higher biomechanical and energetic constraints imposed on ground locomotion in these areas (Daley and Biewener, 2003; Gabaldón et al., 2004). Ground foraging species tend to have long tarsi (Fitzpatrick, 1985; Osterhaus, 1962), and an adaptive explanation for this association is based on cursorial efficiency (Fitzpatrick, 1985). The Cream-coloured Courser is a cursorial species with long tarsus–metatarsus (Perrins, 1998). Walking involves an alternate exchange between the kinetic energy and the potential energy of the center of mass within each stride. Therefore, the better the exchange between kinetic and potential energy, the cheaper the cost of locomotion. Alexander (1976) pointed out that most of the energy used during walking would go to replace the kinetic energy in the vertical direction lost during each step. It would be advantageous to keep this vertical component small (Cavagna et al., 1977). The selection of relatively flat terrains of denudated soils with a low rock cover lets the courser to walk avoiding any vertical component in the movement without going uphill or climbing over rocks.

The Cream-coloured Courser preferred almost unvegetated areas, in agreement with its diet and foraging strategy. The species has a highly specialized diet composed of small ground beetles which are preyed while exposed on the ground when moving. (Mian, 1999; and see also similar results on congeneric species in Kok and Kok, 2002). Also, a short vegetation cover increases ground-foraging efficiency and also decreases predation risks (Watts, 1990; Whittingham and Evans, 2004). Goat overgrazing is a conservation concern in the Eastern Canary Islands because it leads to permanent damage of soil under arid or semi-arid conditions (Rodríguez et al., 1993). The major structural changes caused by overgrazing by domestic animals to the lower strata of the vegetation reduce the availability of shelter and food for many organisms and are recognized as a severe conservation problem for a variety of birds (Tucker and Evans, 1997). Nevertheless, consumption by large goat herds of the majority of the primary production near ground level, which negatively affects the biomass and diversity of wildlife (Donlan et al., 2002; Gangoso et al., 2006; Rodríguez et al., 2000), is not expected to severely influence the Cream-coloured Courser, as it prefers soils with a very low vegetation cover. This is probably the only species of the arid and steppic areas of Fuerteventura and Lanzarote that is not negatively affected by goat overgrazing, while this is an important problem for the other bird species of these environments (Martín and Lorenzo, 2001).

It has been suggested that the perceived general decline of the species in the archipelago is mainly due to human threats, such as the extensive growth of the road network and urban developments (Emmerson and Lorenzo, 2004; González, 1999), though no systematic study has been carried out to confirm and quantify these effects. Urban impact (measured as the distance to the nearest city or small village) did not have a clear

negative effect on the occurrence of the Cream-coloured Courser. Nevertheless, urban development may pose an important conservation concern for the species in these islands, since the courser prefers areas at lower altitudes, where tourist urban sprawl entails increasing threats of habitat transformation (Palomino and Carrascal, 2005). On the other hand, our results show that nearby roads closer than 135 m had a negative influence on probability of occurrence of the species. Roads normally facilitate human access to otherwise undisturbed land, which is particularly problematic near leisure facilities and has already been identified as a major conservation concern for the species (Emmerson and Lorenzo, 2004). Contrary to this pattern, some works have reported that roads traversing open-lands can attract birds if road verges support better-developed vegetation (e.g., Arnold and Weeldenburg, 1990; Camp and Best, 1993; Meunier et al., 1999). However, in our study area road presence did not favour more developed vegetation (correlation between road length and forb and grass cover: $r = 0.003$, $p = 0.912$ and $r = 0.043$, $p = 0.105$, respectively; and see also Table 1), and the Cream-coloured Courser did not show preferences for well-vegetated areas (Fig. 2).

The Cream-coloured Courser was present, although in low numbers, in other Canary Islands (Tenerife and Gran Canaria) in the first half of the 20th century (Martín and Lorenzo, 2001 and references therein). There, the species was always linked to coastal steppe areas. Moreover, the only actual confirmed breeding record outside Fuerteventura and Lanzarote is in the flatlands of southern Tenerife (Emmerson and Lorenzo, 2004). Tenerife and Gran Canaria are very mountainous islands with a high cover of rocks and dense euphorbia shrublands (Anonymous, 1980). The irregular presence and the very low population size of the courser in these two central Canary islands can be parsimoniously explained considering its habitat preference patterns described in this paper. Thus, the available surface in Tenerife and Gran Canaria of lowland areas (<200 m a.s.l.), flat or with a steepness lower than 11%, with a very sparse vegetation cover (shrub cover less than 16%) and with denudated, non-rocky soils is very low, limiting the probability of existence of stable populations of the species. Therefore, it is not necessary to invoke human impacts as the main responsible for the decline of this species in Tenerife and Gran Canaria.

In summary, habitat preferences of the Cream-coloured Courser are mainly dictated by abiotic factors related to altitude, steepness of the terrain and rock cover. Human disturbances related to agriculture, overgrazing by goatherds and urban developments seem not to have an important influence on this species, although roads have a clear negative effect on its occurrence. Overall, this paper highlights the importance of fine-grained habitat features, not directly related to vegetation structure, and linked to topographic and lithological traits on habitat selection of birds inhabiting arid environments, which has been reported in areas as different and distant as the Canary Islands (this paper), southwestern USA (Naranjo and Raitt, 1993) and Iran (Kaboli et al., 2006).

Acknowledgements

We wish to thank the Consejería de Medio Ambiente y Ordenación Territorial del Gobierno de Canarias for giving us the opportunity to study this and other species in the Eastern Canary Islands (project CENTINELA, for the monitoring and management of Macaronesian endangered species, within the EU initiative Interreg III-B Açores-Canarias-Madeira 2000–2006). In particular, Maria Nieves Perez Zurita was always prompt and helpful with the paperwork. This paper is also a contribution to the project CGL2005-02642/BOS of the Spanish Ministry of Education and Science. Claire Jasinski kindly improved the English of the manuscript. An initial version of the manuscript benefited from the positive criticisms by two anonymous referees.

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jaridenv.2007.07.007.

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