Environmental and social constraints on breeding site selection. Does the exploded-lek and hotspot model apply to the Houbara bustard *Chlamydotis undulata undulata*?

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Habitat selection is a hierarchical process where the distribution of individuals is constrained by environmental factors acting from the landscape scale to specific microhabitats such as breeding sites. However, interactions between conspecifics might greatly influence bird distribution and habitat use, especially in lekking birds. In the lekking Houbara bustard *Chlamydotis undulata undulata*, we investigated the respective role of environmental and social constraints on the distribution of nests and display sites. We measured environmental variables around 69 nests and 70 display sites at different spatial scales: the landscape, the breeding range, and the display and nest site scale. The variables were compared to those measured at 50 random plots to determine whether environmental features are actively selected. Social variables were included by studying spatial relationships between displaying male density, nests and female movements throughout the year. At the landscape scale, human presence acted as a limiting factor for the establishment of nest and display sites. At the breeding range scale, habitat requirements differed between sexes. Breeding females used a heterogeneous complex of habitats provided by the network of wadis (water courses) crossing the reg (gravel plain) covered by tall perennial plants. In contrast, display males looked for conspicuousness and courtship ability by selecting the reg with short perennials, and used temporarily flooded areas for feeding. Males aggregated on traditional display site where they experienced the greatest female density. This result supported the hotspot model in the evolution of leks in the Houbara bustard. It underlies an overriding effect of female attraction on male settlement in the individual habitat selection process.

Habitat selection has been described as a hierarchical process where the observed animal’s use of the available habitats should be considered the outcome of choices made at different levels (Johnson 1980, Aebischer et al. 1993). Firstly, individuals of a species live in a certain part of a region where habitats are available and accessible, i.e. the species or population range. Secondly, within this region, the area delimited by an animal’s movements during its life cycle constitutes its home-range. Thirdly, within its home-range, an animal will select for specific sub-areas and use them disproportionately, i.e. preferred habitats (Johnson 1980). But, the evolution of habitat preference in vertebrates is determined by, and determines, the species’ morphological structure and behavioural functions (Cody 1985). In birds, one behavioural aspect of habitat selection concerns the degree to which free choices of habitats are made as opposed to social interactions, and particularly the necessity of mating (Emlen and Oring, 1977). Thus decisions at the individual level may be constrained by the distribution of conspecifics (Cody 1985), especially in species exhibiting complex mating systems, such as lekking birds (Wolff et al. 2002).

A lek is defined as aggregated display males that females visit solely for the purpose of mating. After fertilization, the female nests and rears its chicks alone (Höglund and Alatalo 1995). Consequently, in lekking birds, habitat use usually differs between sexes (Höglund and Robertson 1990, Wolff et al. 2002). In the past decades there have been numerous attempts to explain why males of lek-breeding birds cluster their mating territories at specific non-resource-based sites, but only two kinds of models have received most theoretical and empirical supports: female initiated models or male initiated models (for reviews see Höglund and Alatalo 1995, Ligon 1999). Female initiated models explain leks’ origin and persistence throughout female preferences for: (i) larger groups of males, the ‘female preference model’ (Bradbury 1981), and (ii) for dominant males, namely ‘hotshot’ (Beehler and Foster 1988). In the ‘female preference model’, females mate on larger male aggregations, either to reduce the cost of mate searching (Alexander 1975), or because lek size acts as an arbitrarily Fisherian trait (Queller 1987). In the ‘hotshot model’, the dominance of certain males creates highly skewed mating between...
males and generates opportunities for less successful ones to acquire mates either through close proximity to a successful individual (Beehler and Foster 1988) or via inheritance of his territory or social status (Gibson et al. 1991).

In the male initiated model, display males might cluster because areas with high female densities generate 'hotspots' with locally high mate encounter rates (Bradbury and Gibson 1983, Bradbury et al. 1986). Obviously, all these models are not mutually exclusive (Emlen and Oring 1977, Lank and Smith 1992, Ligon 1999). But, whether or not female initiated models explain why males congregate, they do not account for broader-scale features of male dispersion, such as where leks are located or how males are distributed among them (Gibson, 1996). According to Gibson (1996), the 'hotspot' hypothesis provides a potential explanation for these features. However, the 'hotspot' has not gained wide acceptance because most studies have failed to find spatial relationships between breeding males and females, because they focused on the spatial occurrence of static locations (nests and display sites) or on movements of females in the breeding season only (Westcott and Smith 1994, Westcott 1997). Westcott (1997) not only studied static nest locations of the ochre-bellied flycatcher *Mionectes oleagineus*, but also female movements throughout and before the breeding season, and found that these, and not nest locations or best feeding sites, predicted lek occurrence. To clearly show whether female behaviour influences the distribution of display males, researchers should focus on pre-laying female behaviour (Gibson 1996, Westcott 1997).

Recent studies in Morocco on the North African Houbara bustard *Chlamydotis undulata undulata*, showed that the mating system matches the definition of a lek (Hingrat et al. 2004, Hingrat and Saint Jalme 2005). Furthermore, display males appeared less aggregated than in classical leks (e.g. sage grouse, ruff) and they displayed in so-called exploded-leks (Gilliard 1969, Höglund and Alatalo 1995), which might be the widespread mating strategy among bustards (Jiguet et al. 2000, Morales et al. 2001, Jiguet et al. 2002).

In parallel, habitat-use studies based on home-range composition of male and female Houbara bustards showed differences between sexes in habitat requirements during the breeding season (Hingrat et al. 2007b). These differences were probably related to sex specific requirements in the conduct of activities such as breeding and displaying, but also to the lekking strategy of the species.

Recent work on the Asian houbara *Chlamydotis macqueenii* in China (Yang et al. 2002, 2003) showed that breeding females usually favour densely vegetated habitats for concealment, while in contrast, display males look for high conspicuousness. In these studies, males and females were treated separately and the polygynous mating system of the Houbara, although reported earlier (Launay and Loughland 1995), was not considered. However, owing to the necessity of mating, the spatial distribution of display males and breeding females might not be independent and may override the influence of habitat features.

The objective of this paper was to understand the respective role of environmental and social constraints in the distribution of nests and display sites in an endangered population of Houbara bustards in eastern Morocco. Results were analysed and discussed in the light of various models explaining the evolution of leks with particular attention given to the hotspot model theory applied to the exploded-lek.

### Materials and Methods

#### Study area

The study was carried out in a core area of 663 km², named Al Baten (Fig. 1). This area harbours a breeding population of Houbara bustards, protected from hunting since 1996.
(Lacroix 2003). Al Baten is a piedmont characterised by slightly undulating gravel plains of semi-desert steppe habitat extending from the Middle Atlas to the Moulouya River. The climate is Mediterranean sub-desertic with cold winters and a mean annual rainfall of less than 200 mm. In this arid area, six main habitat types have been previously defined according to the topography, the hydrology, the vegetation structure and the arthropod assemblages and biomasses (Hingrat et al. 2007a): (1) the esparto grass steppe *Stipa tenacissima* (Gramineae), on mountain slopes and hills above 1000 m asl (mean vegetation cover = 35% and mean height = 42.7 cm), (2) the reg with short perennials (RSP), gravel plains covered by *Lycium intricatum* (Solanaeaceae) associated with Chenopodiacceous plants (3% and 4.9 cm), (3) the reg with tall perennials (RTP), covered by association of *Lycium intricatum* with taller bushes such as *Launea arborescens*, *Noaea mucronata* and *Stipa tenacissima* (3% and 10.5 cm), (4) wadis, water courses characterised by associations of *Zizyphus lotus* (Rhamnaceae), *Retama sphaerocarpa* (Leguminosae), and numerous species from the adjacent reg (10.4% and 24.5 cm), (5) temporarily flooded areas (TFA) created by merging wadis and where the accumulation of fine particles make deep and productive soils densely covered by *Salsola vermiculata* associated with *Atriplex halimus* (22.3% and 12.2 cm), and (6) cultivated fields (12% and 19.3 cm) mainly situated in TFA. Indeed, TFA are often ploughed to cultivate wheat and the production relies entirely on rainfalls.

All these habitats were mapped using a Geographic information system (GIS, ArcView 3.2 Environ. Syst. Inst., 1996). In addition, since 2000, the coordinates of the following habitat features were systematically recorded using a GPS locator: tracks, nomads' tents, wells, isolated buildings (farms and enclosures), villages and towns. Wadis, roads and towns were extracted on the GIS by digitizing a topographic map at a 1:100 000 scale (Agence Nationale de la Conservation Foncière, du Cadastre et de la Cartographie-ANCFFC).

**Nests and display males surveys**

Houbara bustard nests and display sites were systematically monitored between 2000 and 2001. Details on census techniques can be found in Hingrat et al. (2004). In 2002, an additional nest survey was conducted and 44 nests were located on Al Baten. Added to the 25 nests located in 2001, that gave us a total sample of 69 nest locations.

In parallel, Le Cuziat et al. (2005) conducted point count surveys in order to assess the overall population density in the area. From this dataset, we used sightings of display males to improve our data and assess display site occupancy over three consecutive breeding seasons. Thus, in subsequent analysis we used 70 traditional display sites where a male has been seen displaying several times over a season or at least two years between 2000 and 2002. In the case of groups of nearby sites (less than 500 m), we retained only those where birds had been seen displaying simultaneously. Otherwise, we retained the site with the most sightings.

**Habitat use and selection by display males and breeding females**

Habitat use was estimated from the proportion of each of the six defined habitat types within the birds’ range. It was delimited for each individual using a buffer centred on each nest and display site. The scale used was designed to keep the range size relevant to the bird’s ecology, with a buffer area similar to the mean size of an adult breeding core range. In males, the ‘display range’ was defined as the area where a male spent 50% of its time during the breeding season and conducted its main activities (displaying and feeding). It was calculated using radio tracking data recorded weekly on 15 males between 1997 and 2002, and the fixed kernel method with a 50% probability density and a cross validated smoothing parameter (Worton 1989). The mean breeding core range was 0.751 ± 0.816 km². The females ‘breeding range’ corresponded to the feeding area surrounding the nest. In Algeria, Gaucher (1991) reported the feeding behaviour of an incubating female and measured a maximum distance from the nest of 520 metres. Thus, we selected a radius of 500 m for both sexes, that gave us buffer zones of 0.785 km², and allowed comparisons between male ‘display ranges’ and female ‘breeding range’ composition.

To investigate habitat selection we used the chi-square goodness-of-fit test coupled with the placement of Bonferroni confidence intervals around the proportional use to estimate if habitats were selected disproportionately to their availability (Neu et al. 1974). Because the arbitrary delimitation of a study area may produce spurious results (Aebischer et al. 1993, McClean et al. 1998), we calculated a minimum-sized study area by determining the outermost boundary of a 100% Minimum Convex Polygon (MCP) based on all Houbara locations recorded since 1996 on Al Baten (n = 5543). Then we tested for difference in habitat use between sexes using a one-way MANOVA based on log-ratios of the habitat proportions within buffer zones (Aebischer et al. 1993).

The habitat proportions within the study area (MCP) and buffer zones were calculated using the GIS ArcView 3.2. Chi-square goodness-of-fit analyses were conducted using RSW (Resource Selection Analysis Software for Windows; Leban 1999).

**Display and nest site selection**

**Display site variables**

Display site selection was analysed at three spatial scales: (1) at the landscape scale in order to include environmental variables of the study area that may influence male distribution, (2) at the display range scale, to include the immediate surroundings of the site, and (3) at the display site scale, i.e. where the male performs its courtship behaviour (Table 1).

At the landscape scale we considered seven variables that represented human features that may influence male distribution (Table 1). Within display ranges we measured three variables related to habitat composition. Of these, the total edges length was an estimation of habitat heterogeneity (Table 1). At the display site scale we recorded 13 variables that may directly act on the achievement of the courtship behaviour within a plot of 100 m radius. The radius length was chosen according to observations of males performing...
Table 1. Environmental variables measured at 70 Houbara bustard display sites, 69 nest sites and 50 random sites in eastern Morocco.

<table>
<thead>
<tr>
<th>Variables/Scales</th>
<th>Origin and description of variables</th>
</tr>
</thead>
<tbody>
<tr>
<td>Landscape scale</td>
<td>Variables measured on map for nests and display sites</td>
</tr>
<tr>
<td>DROAD</td>
<td>Distance to the nearest asphalted road</td>
</tr>
<tr>
<td>DTRACK</td>
<td>Distance to the nearest track</td>
</tr>
<tr>
<td>DBUILD</td>
<td>Distance to the nearest permanent inhabited building</td>
</tr>
<tr>
<td>DTOWN</td>
<td>Distance to the nearest town</td>
</tr>
<tr>
<td>DTRACK</td>
<td>Distance to the nearest cultivated field</td>
</tr>
<tr>
<td>LEDGE</td>
<td>Total edge length within each buffer</td>
</tr>
<tr>
<td>DEDGE</td>
<td>Distance to the nearest habitat transition</td>
</tr>
<tr>
<td>DDRAIN</td>
<td>Distance to the nearest drainage system (temporarily flooded areas or wadi)</td>
</tr>
<tr>
<td>Display sites</td>
<td>Variables measured on map within buffer zones of 500 m radius around nests (breeding range) and display sites (display range)</td>
</tr>
<tr>
<td>VEGCOV</td>
<td>Percent cover of vegetation</td>
</tr>
<tr>
<td>%SILT</td>
<td>Percent cover of silt</td>
</tr>
<tr>
<td>%SAND</td>
<td>Percent cover of sand</td>
</tr>
<tr>
<td>%SGRAV</td>
<td>Percent cover of small gravel (2–5 mm)</td>
</tr>
<tr>
<td>%GRAV</td>
<td>Percent gavel (5–10 mm)</td>
</tr>
<tr>
<td>%STONE</td>
<td>Percent cover of stones (50–100 mm)</td>
</tr>
<tr>
<td>%LSTONE</td>
<td>Percent cover of large stones (100–200 mm)</td>
</tr>
<tr>
<td>%ROCK</td>
<td>Percent cover of rocks (&gt;200 mm)</td>
</tr>
<tr>
<td>%OUTCROP</td>
<td>Percent cover of rock outcrop</td>
</tr>
<tr>
<td>CONSP</td>
<td>Conspicuousness index</td>
</tr>
<tr>
<td>HABITAT TYPES</td>
<td>Habitat type where the display sites were located among the six categories: temporarily flooded areas (TFA), fields, wadis, reg with short perennials (RSP), reg with tall perennials (RSP) and esparto grass.</td>
</tr>
<tr>
<td>TOPO</td>
<td>Topography of the site (three categories: Convex/Flat/Concave)</td>
</tr>
<tr>
<td>SSHAPE</td>
<td>Soil shape (three modalities): Smooth/ Gently undulating/Undulating</td>
</tr>
<tr>
<td>Breeding sites</td>
<td>Variables collected within 100 m radius around the nest</td>
</tr>
<tr>
<td>HABITAT TYPES</td>
<td>Habitat type where nests were located among the six categories (see above)</td>
</tr>
<tr>
<td>TOPO</td>
<td>Topography of the site (three modalities: Convex/Flat/Concave)</td>
</tr>
<tr>
<td>VEGCOV</td>
<td>Percent cover of vegetation</td>
</tr>
</tbody>
</table>

their courtship. The vegetation cover was estimated visually. We also recorded visually the percentage cover of eight substratum classes (Table 1). Finally, we estimated the conspicuousness of display males using a dummy placed in the centre of each site. The dummy was an artificial display male materialised with a white plastic bag fixed upon a tripod at 30 cm above the ground. We measured conspicuousness in the four cardinal directions, as the maximum distance at which the dummy was still visible, from 0 to 1,000 metres. The conspicuousness was measured with the naked eye, respecting the female body size, i.e. that during observations the observer looked at the site from a height of 30 cm above the ground. A conspicuousness index (CONSP) was calculated as the mean of the four cardinal measurements.

All variables were measured for 70 display sites and for 50 random sites. Random sites were created using the random point generator from the ‘Animal Movement Extension’ (Hooge and Eichenlaub 1997) in ArcView 3.2. Display site variables and the conspicuousness were measured directly in the field, while landscape variables and display range variables were extracted from habitat maps using the GIS ArcView 3.2.

Nest site variables
We used the same variables as for males at the landscape scale and within the breeding range. At the nest site scale (100 m radius) we considered only the variables HABITAT, TOPO and VEGCOV (Table 1).

At a smaller scale, the nest stand, we measured the distance to the nearest bush and its height. We also estimated female visibility of its surroundings by measuring the distances from the nest to potential obstacles that may obstruct immediate visibility. Distances were recorded in the four cardinal directions with a ‘range finder’, which uses a laser ray to measure the distance to any object. We fixed it on a tripod at 20 cm from the ground to comply with the female’s position while incubating and peering around vigilantly (personal observation). We calculated the mean of the four distances as a visibility index.

Variables at the landscape scale, breeding range scale, nest site scale were measured for 69 nests and for 50 random sites created using the ‘animal movement extension’ (Hooge and Eichenlaub 1997). Because the Houbara nest consists simply of a small depression in the ground, it was not possible to identify the exact location of nests found in 2001. Thus, variables at the nest stand (visibility index, distance to the nearest bush and its height were recorded only on the 44 nests located in 2002 just after the female had left. In addition, because these three variables might be related to the vegetation patch characteristics chosen by the female within its breeding range for laying, we also measured them on a control points placed systematically at 50 metres to the north of each nest within the same vegetation patch.

Display and nest site selection analyses
Nest site and display site selection were quantified through both univariate tests and logistic regression. A t-test was used to analyse differences between sites and random plots for continuous variables and $\chi^2$ tests for categorical variables (Table 1). In order to reach normality distributions, distance variables were square root or fourth root transformed as appropriate, frequencies variables were arcsine transformed.

We then used logistic regressions from the generalized linear model (GLM) framework to identify minimal subsets of uncorrelated factors that best explain display males and breeding females presence-absence. In both cases we used a binomial linear model with a logit-link function. We applied stepwise logistic procedures which automatically add and remove terms from a given GLM using Akaike’s information criterion (AIC) (Burnham and Anderson 1998), with $\text{AIC} = \text{DEV} + 2 \, np$ (where $\text{DEV} = \text{model}$
deviance and \( n_p \) = number of estimated parameters). The model with the lowest AIC was selected as the most parsimonious model that fitted the data, i.e. the one that incorporated the most variation using the smallest number of estimated parameters. Among variables, only those for which significant univariate differences (t-test or \( \chi^2 \), \( P < 0.05 \)) were detected between used sites (display sites or nest sites) and random sites were included in multivariate analysis. Multicolinearity was limited by computing pairwise Pearson correlations (Burnham and Anderson 1998). Whenever a correlation was significant (\( P < 0.05 \)), the variable with the lower biological meaning was dropped. Untransformed variables were used for both GLM analyses, as normality is not required (Guisan and Zimmermann 2000). Final models retained only uncorrelated variables that were significant at the 5% level. The goodness of fit of the two GLM was checked by both the ratio of the model deviance to its degree of freedom (deviance/df < 1) and the ratio of the Pearson \( \chi^2 \) to its degree of freedom (Pearson \( \chi^2/\text{df} \)). Ratios near to 1.0 indicate that the model correctly fits the data with no substantial overdispersion (McCullagh and Nelder 1989).

In the case of nest stands, we used t-tests (with square root transformed data) to compare the means of the three variables visibility index, distance to the nearest bush and its height calculated for nests found in 2002 with means calculated for random nests (within the same vegetation patch), as with means of the 50 random sites. All statistical analyses were performed using Systat 7.0.

**Lek delimitation**

Bradbury (1981) defined a ‘male active space’ as the area over which signals it produce (vocal or visual) are detectable by other males or females. The Houbara bustard has a striking courtship behaviour which is an effective long-distance visual signal in open semi-desert habitats (Johnsgard 1994, Gaucher et al. 1996).

The ‘conspicuousness index’ calculated for the 70 display sites (see above) showed that display males can be seen at a mean distance of 916 m (±85). Thus, we assumed that all males situated less than 1 km to each other were in visual contact and belonged to the same lek. To outline leks, on each of them we performed a fixed kernel with 80% probability density and a cross-validated smoothing parameter (LSCV; Worton 1989). With this method, the smoothing parameter (or bandwidth) was a function of display male distribution. However, the Kernel method cannot be applied with less than three locations (Worton 1989). Between males displaying in duos and males within leks (excluding singles) the mean distance to the nearest neighbour was 550 m (±84). Hence, to delimit the active space of solitary males and pairs, we drew a buffer zones of 500 m radius around these display sites.

**Spatial relationships between nests and display sites**

The spatial distribution of nests and display sites was tested with the “nearest neighbour method” (Clark and Evans 1954). To test whether nests and display sites were spatially related, we counted the number of nests situated within leks. For each nest and 50 random sites we then measured the following variables related to male distribution: the distance to the nearest display site, the distance to the nearest lek centre, and the distance to the nearest lek perimeter. Distance variables were square-root transformed to reach normal distributions, and values calculated for nests and random sites were compared using t-tests. We also compared the mean size (number of display males) of the closest lek for nests and random sites, using the non-parametric Mann-Whitney U-test.

**Display site density and female movements**

Adult males that possess a traditional display site are sedentary with a home-range centred on their site (Hingrat et al. 2004). Here we tested whether males established their display site according to female movements, i.e. where the probability of encountering female is higher. We used radio-locations of seven adult females followed at least weekly during one complete year from winter 2001 to Autumn 2002. Females were monitored from the ground (visual sighting) and via aerial telemetry (for methodological details see Hingrat et al. 2004). We then divided the annual cycle of each female into three successive periods according to its behaviour: (1) the non-breeding period, (2) the pre-breeding period, set from the first of January (start of male displays) to the first nest of each female, and (3) the breeding period, which includes movements of the female around its nest and with its chicks after hatching.

The display site density was calculated using a Fixed Kernel (LSCV), performed on all confirmed display sites (n = 70), with probability densities ranging from 0 to 100%. It was then converted into a grid (200 × 200 metre cell size), giving cells of values ranging from 0% (no display site) to 100%. We assigned to each female location the cell size), giving cells of values ranging from 0% (no display site) to 100%. We assigned to each female location the value of the cell in which it was located. Data of the seven females were pooled and we compared means of display sites density calculated for the three periods using a one-way ANOVA and a Bonferroni adjustment.

**Results**

**Habitat use and selection by display males and breeding females**

The composition of display and breeding ranges indicated that both sexes used mainly regs with short and tall perennials (RSP, RTP), temporarily flooded areas (TFA) and wadis, while fields and the densely covered esparto grass were less used (Fig. 2). In comparison to habitat availability, display males and breeding females appeared to be significantly selective in their use of the different habitats types (\( \chi^2 = 1068.2, \text{df} = 5, P < 0.001 \) for males; and \( \chi^2 = 1266.6, \text{df} = 5, P < 0.001 \) for females). Habitat use differed significantly between sexes (MANOVA, \( F = 2.8, P < 0.02 \)). Display males significantly preferred RSP and TFA, and significantly avoided all other habitat types (Fig. 2). Breeding females significantly preferred RTP and wadis, and significantly avoided all other habitats (Fig. 2).
not closer to edges than random sites and even appeared to be significantly farther from drainage systems (Table 2).

At the display sites scale, analysis showed that the vegetation cover was significantly lower on display sites than on random sites (Table 2). The conspicuousness of males was significantly greater on display sites than on random sites. The display sites substratum had a significantly greater proportion of gravel and stones, and a significantly lesser amount of silt than random sites. We also found a significant lesser proportion of rocks on display sites, that preferentially occurred in steep areas such as on mountain slopes and wadi banks.

For the variable HABITAT types, to meet $\chi^2$ test assumptions, we pooled categories that were poorly represented in samples. Flooded areas, field and wadis were pooled in a group called ‘flooded systems’. In a same way, esparto grass and RTP were grouped together and referred hereafter as ‘Esparto-RTP’. The $\chi^2$ test showed that males used habitat types non-randomly for displaying ($\chi^2 = 26.65$, df = 2, $P < 0.001$), owing to a strong preference for RSP (76%) and avoidance of ‘flooded systems’ (6%, Fig. 3a). The topography of Houbara display sites was significantly different from random sites ($\chi^2 = 64.02$, df = 2, $P < 0.001$), and display sites were preferentially localized on elevated points, with 87% of sites that were ‘Convex’ (Fig. 3b). The soil texture type selected by males for displaying appeared also significantly different from random ($\chi^2 = 30.85$, df = 2, $P < 0.001$), with a striking preference for ‘smooth’ surfaces (93%, Fig. 3c).

Table 2. Comparisons between environmental variables recorded for 70 Houbara male display sites and 50 random sites in eastern Morocco (df = 118). Differences between means were examined by t-test.

<table>
<thead>
<tr>
<th>Variables /Scales</th>
<th>Display sites</th>
<th>Random sites</th>
<th>t-value</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Landscape scale</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>DROAD</td>
<td>6.441</td>
<td>4.475</td>
<td>2.52</td>
<td>&lt;0.05</td>
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<td>DTRACK</td>
<td>0.188</td>
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</tr>
<tr>
<td>DBUILD</td>
<td>4.496</td>
<td>3.601</td>
<td>1.24</td>
<td>0.218</td>
</tr>
<tr>
<td>DTOWN</td>
<td>8.928</td>
<td>8.534</td>
<td>4.46</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>DNOMAD</td>
<td>0.786</td>
<td>1.083</td>
<td>0.69</td>
<td>0.493</td>
</tr>
<tr>
<td>DWELL</td>
<td>5.205</td>
<td>5.358</td>
<td>-1.95</td>
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</tr>
<tr>
<td>DFIELD</td>
<td>2.645</td>
<td>2.045</td>
<td>5.28</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Display range scale</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>LEDGE</td>
<td>9.64</td>
<td>8.092</td>
<td>-2.84</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>DEDGE</td>
<td>0.104</td>
<td>0.123</td>
<td>-1.94</td>
<td>0.054</td>
</tr>
<tr>
<td>DDRAIN</td>
<td>0.12</td>
<td>0.073</td>
<td>2.62</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Display site scale</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>VEGCOV</td>
<td>4.1</td>
<td>9.1</td>
<td>-5.63</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>%SILT</td>
<td>8.9</td>
<td>30.5</td>
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<td>&lt;0.001</td>
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<td>%SAND</td>
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<td>2.1</td>
<td>-1.34</td>
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<tr>
<td>%SGRAV</td>
<td>23.7</td>
<td>19</td>
<td>1.66</td>
<td>0.100</td>
</tr>
<tr>
<td>%GRAV</td>
<td>41.1</td>
<td>25.7</td>
<td>5.81</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>%STONE</td>
<td>20.9</td>
<td>16.4</td>
<td>2.01</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>%LSTONE</td>
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<td>3.3</td>
<td>0.05</td>
<td>0.962</td>
</tr>
<tr>
<td>%ROCK</td>
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<td>1.4</td>
<td>-2.5</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>%OUTCROP</td>
<td>1.1</td>
<td>1.6</td>
<td>-0.69</td>
<td>0.494</td>
</tr>
<tr>
<td>CONSP</td>
<td>0.916</td>
<td>0.651</td>
<td>6.95</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

δ code and units of variables are described in Table 1.
For breeding, females selected areas (breeding range scale) with a significant greater extent of edges, and nests were significantly closer to these edges than random sites.

At the nest site scale, the $\chi^2$ test showed that females chose habitat types non-randomly for laying (variable HABITAT types: $\chi^2 = 14.88, df = 4, P < 0.01$). They laid mostly in RSP (42%), and RTP (36%) (Fig. 4a). The topography of nest sites did not differ from random sites (Fig. 4b).

Additional tests made at the nest sites scale showed that females laid their eggs closer (Mean $= 2.7 \pm 1.6$ cm) to a bush than random sites within the study area (Mean $= 5.9 \pm 5.5$ cm; $t = 3.60; P < 0.001$). This result was not an effect of vegetation patch characteristics as nests were also closer to a bush than control nests placed within the same patches (Mean $= 6.2 \pm 3.6$ cm; $t = 5.76; P < 0.001$). For the two variables, height of the closest bush and visibility index, we found no differences between nests and random nests, neither with control nests within the same vegetation patches.

Display and nest site selection analysis using the generalized linear model

We used logistic regressions from the generalized linear model (GLM) framework to identify minimal subsets of uncorrelated factors that best explained display males and breeding females presence-absence. Therefore, we first excluded factors that presented significant pair-wise correlations.

For males, at the landscape scale, we dropped DROAD and DTOWN that were positively correlated to DFIELD, and DTRACK that was negatively correlated to DROAD. At the display site scale we excluded TOPO, HABITAT type and VEGCOV that were positively correlated to CONSP; and SSHAPE,%SILT,%STONE and%ROCK that were positively correlated to%GRAVEL. Finally, the five variables incorporated in the model were:%GRAVEL, CONSP, LEDGE, DDRAIN and DFIELD. The most parsimonious model (df $= 3, AIC = 87.20$, L. Ratio $\chi^2 = 83.80, P < 0.001$) showed a significant effect of the three following variables:%GRAVEL, CONSP, DFIELD on the occurrence of display males (Table 4). The model fitted the data correctly with no evidence of a substantial overdispersion (deviance/df $= 0.67$; Pearson $\chi^2$/df $= 1.20$).

For females, the following variables that presented significant pairwise correlations were excluded: DROAD and DTOWN at the landscape scale that were positively correlated to DFIELD, as well as HABITAT and TOPO at the breeding range scale that were correlated to LEDGE. Finally, we used DFIELD, LEDGE, DEDGE for model building. The stepwise procedure retained LEDGE and DEDGE that produced the most parsimonious model (df $= 2, AIC = 139.77$, L. Ratio $\chi^2 = 28.14, P < 0.001$). But, only the variable LEDGE had a significant effect on the breeding female occurrence (Table 5). The model fitted the data correctly with no evidence of a substantial overdispersion (deviance/df $= 1.15$; Pearson $\chi^2$/df $= 1.03$).
The 70 traditional display sites had an aggregated distribution over the study area ($R = 0.53$, $z = -7.39$, $P < 0.001$). The display sites distribution consisted of 14 single males, four pairs, and eight leks ranging from three to 11 males (Fig. 1).

Nest sites distribution compared to leks

Nests were not randomly distributed and a tendency towards clumping existed ($R = 7.50 	imes 10^{-6}$, $z = -12.54$, $P < 0.001$). Fifteen nests (22%) were located within leks, and the remaining nests (78%) tended to aggregate in the periphery of leks (Fig. 1). Paradoxically, nest sites were not closer to display males (1.5 km ± 0.9), or to the lek centre (1.8 km ± 1.2) or perimeter (1.0 km ± 1.0) than random sites. However, the mean size of the nearest lek was significantly greater for nest sites (6.5 males ± 4.2) compared to random sites (3.5 males ± 3.4; $U = 1069$, $P < 0.001$).

Female movements compared to display site density

Between the three periods of the female annual cycle (non-breeding, pre-breeding and brooding), the display site density calculated at female locations varied significantly (ANOVA, $F = 4.31$, df = 2, $P < 0.05$). The mean display site density was significantly greater at locations used by females in the non-breeding period ($n = 121$, $D = 32.5\% \pm 19.6$) compared to the density observed at locations of females during the brooding period ($n = 95$, $D = 23.7\% \pm 22.7$; Bonferroni adjustment $P < 0.05$). In the pre-breeding period, the display site density at female locations ($n = 72$, $D = 29.9\% \pm 24.4$) did not differ from the two other periods.

Discussion

Our results showed that houbaras selected their breeding habitat according to environmental variables at different scales.
spatial scales from the landscape scale to the nest or display site. At the landscape scale, when selecting their display and nest sites, males and females strongly avoided all habitat characteristics related to human activity: fields, asphalted roads, towns, villages and farms. In our model all these environmental features representing the ‘human presence’ were summarized by one variable: ‘distance to fields’. Though fields are a source of food resources (alfalfa and invertebrates) and vegetation cover for Houbaras (Martin et al. 1996, Medina 1999), they are also a source of human interference (Lavee 1985). In previous studies, it has been shown that human activity drives Houbara population distribution and individual habitat use (Le Cuziat et al. 2005, Hingrat et al. 2007b). In term of breeding sites selection, human activity acts as a limiting factor for Houbaras and therefore participates with main geographic features such as deserts, mountains or permanent rivers, in the delimitation of accessible habitats.

Surprisingly, display sites were closer to tracks than random sites, and some males even displayed directly on them (pers. obs.). These tracks were too little used by vehicles to disturb Houbaras in comparison to asphalted roads and probably provided artificial open sites for displaying. In the black grouse Tetrao tetrix, males sometime use forest clearings for lekking (Alatalo et al. 1992).

At the breeding and displaying range scale, habitat use differed significantly between sexes. This result is a direct consequence of the Houbara social organisation. In lekking species, habitat requirements differ between males and females because each sex develops its own strategy to increase its fitness (Emlen and Oring 1977, Westcott 1997). While males try to gain multiple mates, females provide full parental care and their relationship with males is reduced to fertilisation (Bradbury 1981). The success of their offspring may rely partially on their mate choice (male quality; Bradbury and Gibson 1983, Andersson and Iwasa 1996) and on the habitat types selected for breeding and brooding (Jiguet et al. 2002). Here, analyses on female breeding range composition, clearly showed a preference for the reg with tall peripherals (RTP) and wadis. Previously,

Table 4. Generalized Linear Model for display site selection with binomial error distribution and logit-link function. The table shows the significance of Wald statistic for the three retained variables: percentage cover of gravel (% GRAV), conspicuous index (CONSP), and distance to the nearest field (DFIELD).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient</th>
<th>SE</th>
<th>Wald</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-14.2175</td>
<td>2.8797</td>
<td>24.3745</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>% GRAV</td>
<td>6.7998</td>
<td>2.1775</td>
<td>9.7531</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>CONSP</td>
<td>0.0128</td>
<td>0.0027</td>
<td>22.1796</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>DFIELD</td>
<td>0.0004</td>
<td>0.0001</td>
<td>4.0295</td>
<td>&lt;0.05</td>
</tr>
</tbody>
</table>

Hingrat et al. (2007b) showed a significant increase in the use of RTP by females which bred chicks until fledging. The network of wadis crossing the RTP provided a great amount of edges increasing habitat heterogeneity. Females favoured these heterogeneous habitats which may provide concealment against predators during their feeding trips, but also to its brood in the first days after hatching when their mobility is low. Moreover, females laid their eggs preferentially close to edges. When a breeding female is disturbed, it escapes discreetly, hiding behind bushes, and quickly reaches the nearest edge or depression. Despite this edge proximity, areas with tall vegetation such as wadis and temporarily flooded areas (TFA) were not selected directly for breeding, and 79% of nests were located in the regs (RSP and RTP). Two non-exclusive hypotheses may explain why females avoided laying in water courses: (1) rainfall and runoff might remove their clutch, and (2) water courses are favoured by foraging mammalian predators. Analyses at a finer scale revealed that on the reg females still looked for concealment by laying adjacent to a bush. Additionally, bush proximity probably helps in regulating incubation temperature and egg water loss, providing shade and protection against the wind.

In male display ranges, we observed a great amount of edges, and males preferentially used TFA and RSP. As pointed out by Yang et al. (2002), Houbaras are edge foragers and alternatively use well vegetated and open habitats. The use of these two different habitats possibly reflected the two main activities of breeding males, respectively feeding and displaying.

Houbara males display for several hours, early in the morning and in late afternoon, and spend the rest of the day feeding or roosting. In lekking males, the display behaviour is frequently energetically demanding (Vehrencamp et al. 1989). During one night of display, a male great snipe Gallinago media can lose as much as 6% of its body mass (Höglund et al. 1992). Hence, an easy access to food resources might be important in display site selection. Yang et al. (2002) showed that in China, Houbara display sites were close to bushy patches of wadis and depressions, that offered food and cover against predators. Similarly, in eastern Morocco, males favoured TFA for its cover (22.3%), height (12.2 cm), and food resources availability (Hingrat et al. 2007a).

For displaying, males selected RSP because of its low vegetation cover (3%) and height (<5 cm) and settled on elevated points. All these characteristics enhanced male conspicuousness, which appeared to be a significant prerequisite in male display site selection. Since males display to attract females, the greater their conspicuousness, the greater their probability of accessing mates. In lekking species, behavioural traits such as male display activity and lek attendance are positively correlated with male mating success (Alatalo 1995, Fiske et al. 1998). The Houbara male courtship behaviour is complex and characterized by a fast running course (Johnsgard 1994, Gaucher et al. 1996). On Al Baten, this run was performed on a small area with a smooth soil surface mainly covered by gravel. Percent gravel was a significant factor in the display site selection because it represented places with a convex topography situated on the regs. In depressions (wadis or TFA) the water flow creates an undulating soil surface with numerous channels that may
hamper the male trot. Males displayed on sites improving both their conspicuousness and courtship ability.

An important consequence of lekking is the associated disadvantage of competition (Emlen and Oring 1977) and courtship disruptions (Trail 1985, Trail and Koutnik 1986). In terms of costs and benefits, males will distribute themselves on leks to maximise their own fitness. Benefits in lekking have been shown in the ruff (Höglund et al. 1993), and in the Black grouse (Alatalo et al. 1992), where males on larger leks enjoy higher mating success than those on smaller leks. Conversely, lekking has a cost. The mean rate of fights and courtship disruptions per male is often positively correlated with the lek size (Trail 1985, Trail and Koutnik 1986, Trail and Adams 1989, Alatalo et al. 1992, Höglund et al. 1993). While the ‘cost and benefits’ mechanism can account for both the occurrence of leks and the variation of their size, it also accounts for the spacing of males within a lek and have been proposed as an explanation of exploded-lek behaviour (Foster 1983). In the Houbara, as it has been suggested for other lekking birds (Foster 1983, Högland and Alatalo 1995), the distance between males (550 m ± 84) might be a trade-off between the aggregating behaviour and male-male interaction rates.

Analyses of spatial relationships between display males and breeding females revealed that (i) nests had an aggregative distribution, (ii) nests were preferentially outside leks, and (iii) compared to random sites, nests were located in the periphery of larger leks.

The aggregative distribution of nests might be explained by the preference of females for particular nest sites (see above), their fidelity from year to year to nest areas (Hingrat et al. 2004), but also by a possible conspecific attraction or female copying behaviour (Danchin et al. 1998). Breeding females avoided leks probably because habitats between males were unsuitable for laying and brooding (see above). In addition, harassment by males might be costly for brooding females (Trail and Adams 1989).

These differences in habitat use between sexes did not explain why females tended to nest in the periphery of larger leks. In several lekking birds, females nest close to the lek where they mated (Pepper 1972, Bradbury et al. 1989). In this case, the observed distribution of Houbara nests could indicate that females preferentially mated on larger leks, in agreement with the ‘female preference model’ (Alexander 1975, Bradbury 1981, Bradbury and Gibson 1983, Queller 1987). However, if females moved to larger leks to mate and nest close to them, we would expect a highest display site density in areas used by females for breeding than in areas used in the non-breeding season. In contrast, we found that display site density was greater in areas visited by females in the non-breeding season.

Spatial relationship between nests and leks do not always support the ‘female preference model’. In the lekking sage grouse Centrocercus urophasianus, Bradbury et al. (1989) found that the number of nests was related to the nearest lek size. However, radio-tracking studies showed that breeding females moved from overlapping wintering areas to dispersed breeding ranges, and then visited a lek often close to the nest to mate. Females selected nest sites independently from male distribution (Bradbury et al. 1989). Later, Gibson (1996) showed that sage grouse leks form according to the ‘hotspot model’, and lekking males settle in areas through which females travel from wintering to nest areas in order to increase their probability of encountering females. The results of Gibson (1996) confirmed those of Westcott (1994, 1997) on the ochre-bellied flycatcher Mionectes oleagineus, who proposed a ‘female traffic’ version of the hotspot model. Indeed, Westcott (1997) showed that leks formed on female travel routes (influenced by topography) and not near the best feeding sites. He argued that because birds feed on fruiting plants whose occurrence is unpredictable in space and time, and because females breed asynchronously throughout a long reproductive season, receptive females are spread unpredictably and sparsely in space and time. Therefore, males have solved this problem by lekking on traditional display sites situated on female traffic routes, maintaining a maximum exposure to females, and being readily locatable by females over the entire length of the breeding season (Lill 1974, Westcott 1997).

The African Houbara bustard is a partial and differential migrant (Hingrat 2005). Males are sedentary with small annual home ranges (at mean 17 km²), while most of females are migratory with large home ranges (146 km²) and move from wintering to breeding areas (Hingrat et al. 2004). In the non-breeding season, food resources decrease (Hingrat et al. 2007a). Migratory females leave their breeding range while the remaining ones form mixed flocks of both sexes and juveniles. At the scale of Al Baten, whether female density decrease, it probably increase locally in some habitat types due to bird flocking and habitat sharing (Hingrat et al. 2007b).

In the breeding season, whether arrivals of migratory females probably increase their density on Al Baten, it might not be assessed by males because: (1) the Houbara breeding season is long (5–6 months), (2) females breed asynchronously and arrive successively, (3) females are dispersed and (4) they behave solitarily. Moreover, at this time of the year, food resources are abundant and uniformly distributed (Hingrat et al. 2007a), and thus not economically defendable by males (Emlen and Oring 1977).

Consequently, during the breeding season, male Houbara bustards probably meet a similar dilemma to that of male Sage grouse or male ochre-bellied flycatchers, that is: the unpredictability of mate availability. How can male Houbara bustards increase their probability of encountering females?

We propose two non exclusive hypotheses to explain how Houbara males could increase their probability of encountering mates: (1) males might experience highest female densities during the non-breeding period when they forage in mixed flocks. Males would settle their display site close or within habitats shared with females to maintain a maximum exposure. This hypothesis is strongly supported by one of the most puzzling Houbara breeding behavioural trait: most of males display on traditional display sites from January while earliest breeding females occur in March (Hingrat et al. 2004). Because male display on traditional display sites, before females started to breed and during the whole season, female can experience male presence and relocate them easily within (Rintamäki et al. 1999), or between seasons (Lill 1974). (2) because females exhibit breeding areas fidelity from year to year, and tend to aggregate in best breeding habitats, some males could experience the highest female density near nest sites and attempt to locate their display site as close as possible. This
strategy might be relevant, especially for males that rely on female that look for new mates to initiate a replacement clutch (after egg lost). Clutch replacement is common in the African Houbara bustard (Hingrat 2005).

Based on our results, it is too soon to exclude any hypothesis and more studies on Houbara breeding behaviour are needed. Data on male display site fidelity, male-male interaction, male mating success and paternity would help us to highlight which hotspot model better explain Houbara bustard lek formation. The main underlying assumption of the hotspot model is that the distribution of display males is strongly influenced by female distribution (Bradbury and Gibson 1983). In return, female use of space might be influenced by mechanisms such as fidelity to a particular breeding area, lek or mate (Lill 1974, Haas 1998, Rintamäki et al. 1999). The habitat selection process in both sexes will be influenced by their respective mating strategy. But, these mechanisms do not completely override environmental factors. In the sage grouse, lek locations depend on the occurrence of meadow habitats (Bradbury et al. 1989). In the ochre-bellied flycatcher, leks are located on female travel routes, but these routes are set by the topography of creeks (Westcott 1997).

In the case of the Houbara bustard we suggest the following sequential and hierarchical events in the habitat selection process of individuals. First, at the landscape scale, geographical features delimit available habitat types whose accessibility for the bird population is constrained by human activities. Second, the bird ecology and habitat characteristics can explain female distribution, and thus the initial aggregation of males at hotspots, creating leks. Secondary mechanisms resulting from female choice may strengthen the tendencies of males to aggregate (female preference and hotspot models) and may be responsible for male-male interactions which promote exploded-leks. At this level, display male location will also be driven by male hierarchical status and the availability of suitable display sites (conspicuousness and courtship facilities). Finally, once a male has established on a traditional display site, its annual habitat use patterns will depend on its degree of fidelity to the display site surroundings which possibly rely on its past mating success and its hierarchical position within the lek (Widemo 1997, Rintamäki et al. 1999).

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