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MATING SYSTEM OF THE HOUBARA BUSTARD *CHLAMYDOTIS UNDULATA UNDULATA* IN EASTERN MOROCCO

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SUMMARY.—*Mating system of the Houbara Bustard* Chlamydotis undulata undulata *in eastern Morocco.* **Aims:** Among polygynous mating systems, the lekking strategy is recognised when the four following criteria are met: (1) display males aggregate at specific sites; (2) there is no male parental care; (3) the only resource females find at the lek are males' gametes; (4) females can freely select their mate(s). In Morocco, the Houbara Bustard mating strategy partially fulfills this definition. Display males are greatly separated and form so-called 'exploded-leks' where females can forage or even nest, therefore failing to fulfil the third criteria of the lek definition. When leks contain critical resources for females, the strategy is a resource-based mating system. To verify the importance of resources in the Houbara mating system the breeding habitat use and selection of 7 females and 13 males was studied and compared to food resources availability (arthropod biomasses) and vegetation structure. The spatial relationship between female home-ranges, nests and leks was then studied.
Results and Conclusions: Both sexes were significantly selective in comparison to habitat availability, but breeding habitat use significantly differed between sexes. Habitat preference and avoidance were not related to arthropod biomasses that appeared homogeneously distributed across habitats. Females brood preferentially in the reg with tall perennials that was not preferred by males. The percentage of overlapping between female breeding ranges and leks was low (21%) and 78% of nests were outside leks. Critical resources for females were not situated within leks. The mating strategy of the Houbara population is a true 'exploded-lek'.

Key words: exploded-lek, food resources, habitat use, habitat selection, vegetation structure.

RESUMEN.—*El sistema de apareamiento de la Hubara* Chalmydotis undulata undulata *en el Este de Marruecos.*
Objetivos: Entre los sistemas de apareamiento poligínico, la estrategia de los leks o arenas es reconocido cuando se cumplen cuatro criterios: (1) los machos se exhiben en lugares específicos, (2) no existe cuidado parental por parte del macho, (3) el único recurso que obtiene la hembra en la arena son los gametos del macho, (4) las hembras pueden elegir libremente su pareja/as. En Marruecos, la estrategia de apareamiento de la Hubara parcialmente encaja en esta definición. Los machos en exibición están muy separados entre ellos y forman los llamados «exploded-leks», donde las hembras pueden buscar alimento o incluso nidificar, es decir, no cumplen el tercer criterio anteriormente expuesto. Cuando las arenas contienen recursos críticos para las hembras, la estrategia es un sistema de apareamiento basado en recursos. Para verificar la importancia de los recursos en el sistema de apareamiento de las Hubaras, el uso y selección del hábitat de 7 hembras y 13 machos fue estudiado. Además, se estudio la disponibilidad trófica (biomasa de artrópodos) y la estructura de la vegetación. La relación espacial entre el territorio de las hembras, los nidos y las arenas fue finalmente estudiada.
Resultados y Conclusiones: Ambos sexos fueron significativamente selectivos en comparación a la disponibilidad de hábitats, pero el uso del hábitat reproductiro difirió entre sexos. Las preferencias de hábitat no estaban relacionadas con la biomasa de artrópodos que aparecían homogéneamente distribuidos entre hábitats. Las hembras nidifican en regs con vegetación alta perene que fueron zonas no seleccionadas por los machos. El porcentaje de solapamiento entre los territorios de las hembras y las arenas de los machos fue bajo (21%), y el 78% de los nidos se encontraban fuera de las arenas o leks. Los recursos críticos para las hembras no se encontraban situados dentro de las areas. Por todo ello, el sistema de apareamiento de la población de Hubaras estudiadas es un verdadero «exploded-lek».

Palabras clave: «exploded-lek», recursos alimenticios, uso del hábitat, selección de hábitat, estructura de la vegetación.

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INTRODUCTION

Studying a species' mating system and assessing mechanisms of male and female habitat selection, as well as the role of resources, is obviously of value for conservation (Höglund, 1996; Morales *et al*., 2001). The African Houbara Bustard *Chlamydotis undulata undulata* has suffered a major decline in all parts of its range due to over-hunting and habitat degradation (Collar, 1980; Goriup, 1983; Goriup, 1997). Previous studies on the Houbara breeding biology reported the existence of a polygynous mating system, with the absence of any male parental care (Collins, 1984; Gaucher, 1995) and, because the 'lek' mating system seems predominant among bustard species (Johnsgard, 1994; Jiguet *et al*., 2000; Morales *et al*., 2001), the Houbara has traditionally been classified as a lekking bird. According to Bradbury (1981), lekking species should meet four criteria: (1) males aggregate at specific sites for displaying; (2) there is no male parental care, so that males contribute nothing to the next generation apart from gametes; (3) the only resource females find at the lek are the males themselves, that is, male genes; (4) females can freely select their mate(s), although the necessity of this latter condition has been highly debated (Höglund & Alatalo, 1995).

In Morocco, the knowledge of the polygynous strategy of the Houbara was recently improved. Data collected on the distribution of breeding birds showed strong differences in the use of space and aggregation of males on traditional display sites that females visited for the purpose of mating, without any male parental care (Hingrat *et al*., 2004). These behaviours apparently fulfilled the definition of the lek mating system (Bradbury, 1981; Höglund & Alatalo, 1995). However, males aggregated in a dispersed fashion, called 'exploded-leks', compared to true leks where display males are separated by only a few meters or less (Bradbury, 1981; Oring, 1982). One consequence of the lower level of aggregation found in 'exploded leks' is that males may hold large territories within which females can potentially forage and even nest, therefore failing to fulfil the third criteria of Bradbury's definition. Today, owing to a lack of knowledge on habitat characteristics, food resource availability and birds' requirements, the Houbara mating system remains undefined.

Species where male display sites include resources critical for females are said to form 'resource-based leks' (Alexander, 1975). In the extreme, when males indirectly control access to females by monopolizing critical resources, the mating system is called a 'resource-defence polygyny' (Emlen & Oring, 1977). Differences between 'exploded-leks', 'resource-based leks' and 'resource-defence polygyny' are thin and unclear (Höglund & Alatalo, 1995; Jiguet *et al*., 2000). To differentiate a true 'exploded-lek' from a 'resource-based lek' or a 'resource-defence polygyny' (hereafter referred as resource-based systems) one would study whether critical resources used by females to breed are situated within adult male territories or within display male aggregates.

The aim of this study was to assess whether the Houbara mating strategy is a true 'exploded-lek' or a 'resource-based system'. First, it is needed to evaluate critical resources or suitable habitat types for females to breed. Therefore, the relationship between food resources availability, vegetation structure and males and females habitat use during the breeding season was studied. Male and female habitat requirements were then compared to test whether both sexes used similar habitat types during the breeding season. However, birds may used similar habitat types or resources without any spatial interactions, i.e. in different areas. To assess whether habitat types used by females for foraging or nesting were situated within male aggregates, the spatial relationship between female home-ranges, nests distributions and display male aggregates was investigated.

MATERIAL AND METHODS

Study area

The study was carried out in Morocco, in an area of 663 km2 named Al Baten, situated in the Middle Atlas and centred at 33.23°N - 03.94°W, 130 km south-east of Fez. Al Baten is a piedmont characterised by slightly undulating gravel plains of semi-desert steppe habitat (Fig. 1). The climate is Mediterranean sub-desertic with cold winters and a mean annual rainfall of less than 200 mm. The Al Baten area harbours a breeding population of Houbara Bustards which has been protected from hunting since 1996 (Lacroix, 2003).

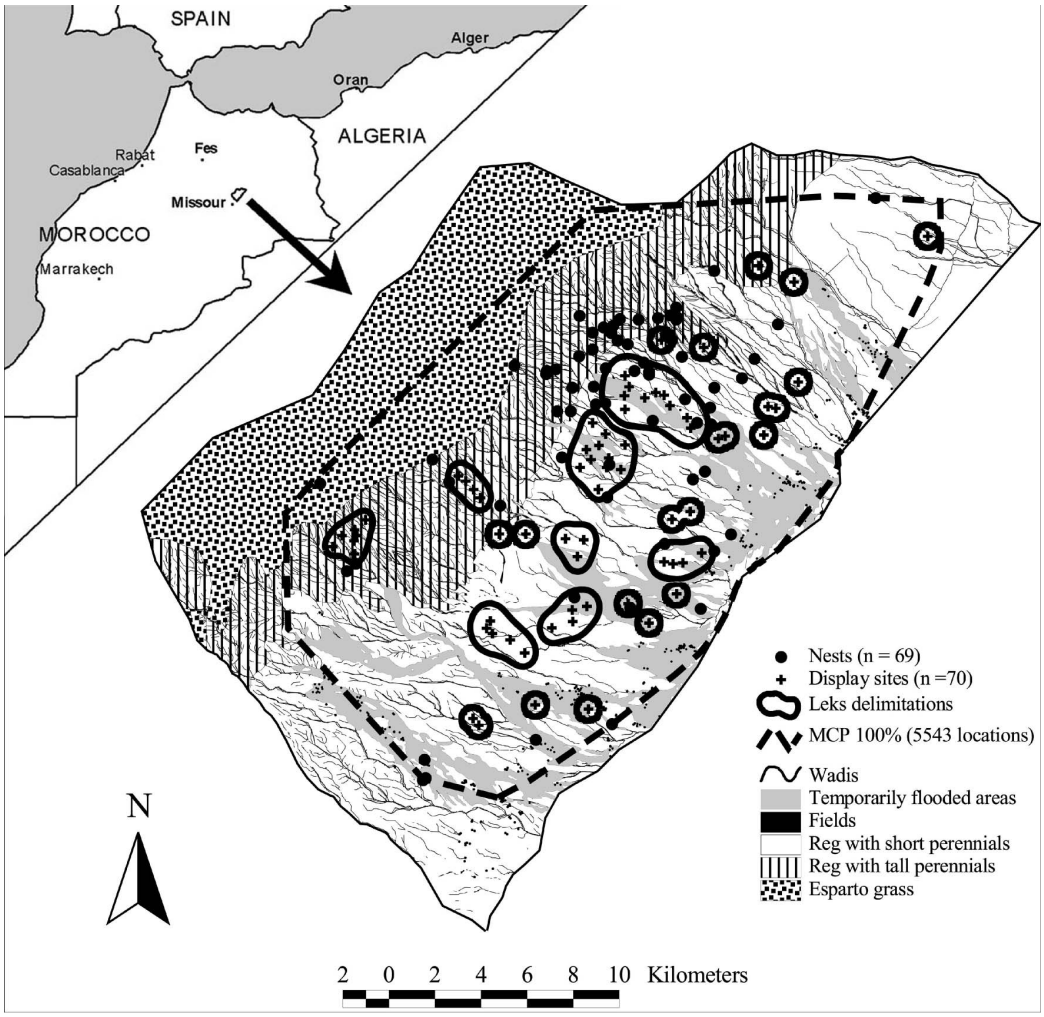

FIG. 1.—Location of the study area, Al Baten (663 km2). Delimitation of the 100% Minimum Convex Polygon based on all radio-locations of wild Houbara Bustards collected since 1996 (n = 5543). The six defined habitat types are mapped. The 69 nests and 70 display sites recorded between 2000 and 2002 are figured, and leks are delimited.
*[Localización del area de studio, Al Baten (663 km2). Los límites son el 100% del polígono mínimo convexo basado en todas las radio-localizacoines de Hubaras registradas desde 1996 (*n = *5543). Se representan los seis tipos de habitats, y los 69 nidos y 70 arenas registradas entre el año 2000 y el año 2002, así com los límites de las arenas o leks.]*

Habitat types, vegetation structure and food resources availability

To investigate relationships between habitat use, vegetation structure and food resources availability, results from a habitat classification made on Al Baten in 2002 (Hingrat, 2005) were used. During this previous work, 32 sampling sites were identified according to their differences in topography, hydrology and dominant perennial plants. In each sampling site, the vegetation structure was measured using

two 20-meter long transects. With a graduated rod the height of each perennial plant in contact with the line was recorded every 10 cm. The average vegetation height was then calculated for each transect. Vegetation cover was estimated from the ratio of points in contact with plants (100 x $\sum$ points in contact / 200). Arthropods were sampled during one complete year in each sampling sites using two pitfall traps collected twice a month. Six main habitat types have been defined according to the topography, the hydrology, the perennial vegetation structure and the arthropod assemblages and biomasses: (1) the esparto grass steppe (*Stipa tenacissima*, Graminea), in mountain slopes and hills upon 1000 m a.s.l.; (2) the reg with short perennials (RSP), covered by *Lycium intricatum* (Solanaceae) associated with Chenopodiaceous plants; (3) the reg with tall perennials (RTP), covered by association of *Lycium intricatum* with taller bushes as *Launea arborescens, Noaea mucronata* and *Stipa tenacissima*; (4) wadis characterised by associations of *Zizyphus lotus* (Ramnaceae), *Retama sphaerocarpa* (Leguminosae) and numerous species from adjacent reg; (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*; and (6) cultivated fields mainly situated in TFA. Indeed, TFAs are often ploughed to cultivate wheat and the production relies entirely on rainfall. All these habitats were mapped (Fig. 1) using a Geographic Information System (GIS, ArcView 3.2 Environmental Systems Research Institute, Inc. 1996). Wadis 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 - ANCFCC). Details on habitat vegetation structure are given in the Table 1.

The Houbara is an omnivorous bird, its diet consisting of plants, arthropods and small vertebrates (Slaytor, 1989; Johnsgard, 1991; Tigar, 1995; Khan, 1996; Tigar & Osborne, 2000). During the breeding season, animal items become more important in the animal diet and chicks feed mainly on invertebrates in their first weeks after hatching (Collar & Goriup, 1983; Tigar & Osborne, 2000), as it has

TABLE 1

Characteristics of the six habitat types defined on Al Baten (663 km^2). The mean perennial vegetation cover and height (± standard deviation) are indicated for the six habitat types.
[Características de los seis tipos de hábitat definidos en Al Baten (663 km^2). La cobertura de herbáceas perennes y la altura (± desviación típica) se indica para cada tipo de hábitat.]

Habitats types *[Tipo de hábitat]*	Area (km^2) *[Área (km^2)]*	Cover (%) *[Cobertura (%)]*	*SD [DT]*	Height (cm) *[Altura (cm)]*	*SD [DT]*
Esparto grass *[Espartales]*	61	35.0	17.7	42.7	6.6
Fields *[Campos]*	3.3	12.0	12.0	19.3	13.3
Temporarily flooded areas *[Áreas temporlmente inundadas]*	106.7	22.3	19.0	12.2	6.9
Reg with short perennials *[Reg con plantas perennes bajas]*	314.3	3.0	2.6	4.9	2.1
Reg with tall perennials *[Reg con plantas perennes altas]*	151.2	3.0	2.4	10.5	9.5
Wadis	26.5	10.4	7.8	24.4	35.5

been shown in other bustard species (Lane, 1999; Jiguet, 2002). Thus, food resource availability for the Houbara during the breeding season was estimated using arthropod availability measured from January to June 2002 in the six defined habitat types . The overall sample of arthropods was dominated by ants (82%) and beetles (8%) in terms of abundance, which is a characteristic of arthropod assemblages in semi-desertic and desertic areas (Tigar & Osborne, 1997; Seymour & Dean, 1999; Tigar & Osborne, 1999; Dangerfield *et al*., 2003). The dominance of these two groups was also observed in the diet of the Houbara (Collins, 1984; Tigar, 1995; Saint Jalme & Van Heezik, 1996; Tigar & Osborne, 2000). Thus, ants and beetles were used as indicators of food resource availability in the six habitat types.

To test for spatial variations in food resources availability between habitat types two indexes, of ant and beetle activity-biomasses, were computed from the biomass of individuals trapped per effective trap per trap day. The biomass was estimated by weighting the abundance of each individual by its body length (in millimetres).

Bird trapping and tracking

Adult Houbara Bustards were trapped in the Al Baten study area in three consecutive breeding seasons, from 2000 to 2002. Females were cached using nylon snares placed around the nest or surrounding a wild caught chick (Launay *et al*., 1999; Seddon *et al*., 1999). For males snares placed around a bait female on displaying sites (Hingrat *et al*., 2004). Two different types of battery-powered transmitters were used: solar backpacks (45 g, ATS) and necklaces (18 g, 36 months, HSL RI-2CSP, Holohil System Ltd., Ontario, Canada). Houbaras were monitored from the ground and by aerial telemetry. Ground radio-tracking was undertaken by direct observation with 4-wheel drive vehicles using a portable scanner-receiver and a 3-element yagi antenna (AF Antronics, Inc., Urbana, Illinois). Aerial locations were taken from a Maule-7 B-235 aircraft using one 2-element yagi antennas fixed to each wing strut. Aerial and ground radio-tracking were both generally carried out weekly.

Breeding home-range estimation

During the breeding season 2002, seven females and 13 males were radio-tracked on Al Baten with at mean 24.8 (± 6) radio-locations [18-38]. Breeding home-ranges were estimated using the fixed kernel method (95% probability density distribution) with the 'cross validated *h*' calculated from a least-square cross-validation (LSCV). This method is widely recognised as an efficient estimate of the probability density distribution of locations (Silverman, 1986; Worton, 1987; Seaman & Powell, 1996) and provides meaningful estimations of Houbara home-ranges and clearly identify their non-convex and multi-modal shapes (Hingrat *et al*., 2004). The mean home-range size was compared between sexes using the Mann-Whitney U-test.

Breeding habitat use and selection

In eastern Morocco the Houbara breeding season extends from January to June. Males display from January to May, and females nest from February to June, with a peak in May (Hingrat et al., 2004). This six month period corresponds to the winter (January – March) and spring (April – June). In a previous work, a significant increase in arthropod availability between these two successive seasons was observed (Hingrat 2005). To compare habitat use of males and females with arthropod availability, the analysis was conducted separately in winter and in spring.

In each season and for each sex, habitat use was estimated as the proportions of habitat types within buffer zones of 100 m radius around birds' radio-locations. Buffer zones were preferred to exact locations themselves because of the following biases in location recordings: (1) observer accuracy, (2) avoidance movements of birds during ground tracking, (3) the speed and altitude of the plane during aerial tracking, and (4) the intrinsic accuracy of the global positioning system (White & Garrot, 1990; Gantz & Stoddart, 1997; Hulbert & French, 2001).

Habitat selection was examined for males and females separately using the 'Neu's method'. This test is based on the chi-square goodness-of-fit analysis (Fleiss, 1981), coupled with the placement of Bonferroni confidence inter-

vals around proportional use to estimate which habitat types were selected disproportionately (preferred or avoided) to their availability (Neu *et al*., 1974). To circumvent problems linked to the definition of habitat availability due to the delineation of an arbitrary study area (Aebischer *et al*., 1993; Litvaitis *et al*., 1996), McClean's recommendation (1998) was applied by delimiting a minimum-sized study area using the outermost boundary of a 100% Minimum Convex Polygon (MCP) based on all Houbara locations recorded since 1996 (n = 5543) on Al Baten (Fig. 1).

The difference in habitat use between sexes was compared using one-way MANOVA based on log-ratios of habitat proportions within buffer zones (Aitchison, 1986). The log-ratio transformation overcomes the problem of lack of independence between the proportions of habitat types used that sum to 1 (unit-sum constraint) by converting the n – 1 log ratios, using one habitat proportion as the denominator (Aitchison, 1986; Aebischer *et al*., 1993).

The areas of each habitat type within the study area and the buffer zones (around radiolocations) were calculated using the ArcView 3.2 GIS. Chi-square goodness-of-fit analyses were performed using RSW (Resource Selection Analysis Software for Windows) (Leban, 1999). Multivariate analysis of variance were conducted using SYSTAT 7.0.

Nests and display sites 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 a total sample of 69 nest locations. The same year, Le Cuziat *et al*. (2005) conducted point count surveys in order to assess the overall population density in the area. From these data set, sightings of display males were used to improve this data and to assess display site occupancy over three consecutive breeding seasons. In subsequent analyses the sample was composed of 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 close sites (less than 500 meters), only those where owners have been seen displaying simultaneously were considered. Otherwise, the site with the most sightings was retained.

Leks delimitation

The «nearest neighbour test» (Clark & Evans, 1954) showed that the 70 traditional display sites had an aggregated distribution over the study area (R = 0.53, z = –7.39, P < 0.001). However, how to spatially delimit male aggregates? In lekking species, males of the same lek interact visually or by vocalizations (Höglund & Alatalo, 1995; Ligon, 1999). In the Houbara the display behaviour is highly conspicuous (Collins, 1984; Johnsgard, 1994) and display male can be seen at more than one kilometre by conspecifics (Hingrat, 2005). However, because of topography, males could be very close but not visible to each other. To test this hypothesis we estimated the conspicuousness of display males at the four cardinal directions using a dummy placed in the centre of each site. We measured conspicuousness, as the maximum distance at which the dummy was still visible, from 0 to 1000 metres. The conspicuousness was measured to the naked eye, respecting the female body size, i.e. that during observations the observer looked at the site at 30 cm above the ground.

The mean conspicuousness calculated for the 70 display sites at the four cardinal points were 0.902 ± 0.180 km at the north, 0.912 ± 0.187 km at the west, 0.908 ± 0.165 km at the south and 0.941 ± 0.133 km at the east. From these results, all males situated less than 1 km to each other were considered to belong to the same lek. To outline leks, around each of them, a Fixed Kernel with 80% probability density and a cross validated smoothing parameter (Worton, 1989) was performed. With this method, the smoothing parameter (or bandwidth) was a function of display males distribution. For solitary males or pairs on which the Kernel method cannot be apply (Worton, 1989), a buffer zone of 500 m radius was drawn, which corresponded to the mean bandwidth used in kernel calculations.

Spatial relationships between female home ranges, nests and leks

To evaluate whether females used habitat types situated within leks during the breeding season two parameters were used: the mean percentage of overlap between female breeding home-ranges and leks and the percentage of nests situated within leks.

RESULTS

Breeding Habitat use and selection

In both seasons (Fig. 2), males and females were observed mainly in the reg with short perennials (RSP), in temporarily flooded areas (TFA) and in the reg with tall perennials (RTP). Wadis and fields were less used and esparto grass totally unused by males.

In winter, the chi-square goodness-of-fit test showed that males were selective for habitat types because habitat proportions within buffer zones significantly differed from habitat availability ($\chi^2 = 615.4$, $P < 0.001$). According to Bonferroni confidence intervals TFA and RTP were significantly preferred by males, whereas RSP, wadis and esparto grass were significantly avoided. Females were also selective for habitats in comparison to their availability ($\chi^2 = 129.8$, $P < 0.01$). They preferred TFA and RSP, whereas they avoided RTP.

In spring males and females were selective for habitat types ($\chi^2 = 1095.0$, $P < 0.001$, and $\chi^2 = 40.1$, $P < 0.01$, respectively). Males preferred TFA and avoided RSP and Esparto grass. Females also avoided RSP, but they preferred RTP and used other habitat types in proportion of their availability.

The comparison of log-ratios of habitat proportions within buffer zones, showed that males and females differed in their habitat use in winter (one-way MANOVA, $F = 5.32$, $df = 5$, $P < 0.001$) and in spring ($F = 8.48$, $df = 5$, $P < 0.001$).

However, as esparto grass was totally unused by males, it may have skewed the analyses. Thus, the comparison was repeated with five habitat types only (by excluding the esparto grass) and a significant difference was found in habitat use between sexes in winter ($F = 6.46$, $df = 4$, $P < 0.001$) and spring ($F = 6.75$, $df = 4$, $P < 0.001$).

Food resources availability

In winter, means comparison showed significant variations in ant and beetle activity-biomasses between habitat types. These variations were mainly due to the mean of ant and beetle activity-biomasses in fields that were significantly higher than in all other habitat types (Fig. 2; Table 2).

In spring, ant and beetle activity-biomasses increased in all habitat types. Means of ant activity-biomass did not vary significantly between habitat types (Table 2; Fig. 2). For beetles, means comparison showed a significant variation of the activity-biomasses between habitat types. The mean of beetle activity-biomass in fields was significantly higher than in all other habitat types (Table 2; Fig. 2). Excluding fields, food resources appeared to be uniformly distributed throughout the study area in winter and spring.

Spatial relationships between female home ranges, nests and leks

The seven females radio tracked on Al Baten had significantly greater breeding home-ranges (14.1 ± 9.4 km2) than the 13 males (3.3 ± 2.1 km^2; $U = 79$, $P < 0.01$). At mean, only 21% (± 17) of female home-ranges overlapped leks. And, only 22% of the 69 nests were situated within leks. These results indicate that habitat types used by females for foraging and nesting were mainly situated outside leks.

DISCUSSION

This study provided three lines of evidence consistent with the existence of an exploded-lek mating system in the Houbara Bustard in Morocco. First, during the Houbara breeding season (winter and spring) food resources were uniformly distributed throughout the study area and were not monopolized by males. Second, habitat use significantly differed between sexes and the favoured habitat of breeding females was not preferentially used by males. Third, areas used by females for foraging and nesting were mainly situated outside display male aggregates.

The finding that food resources were uniformly distributed between habitat types in win-

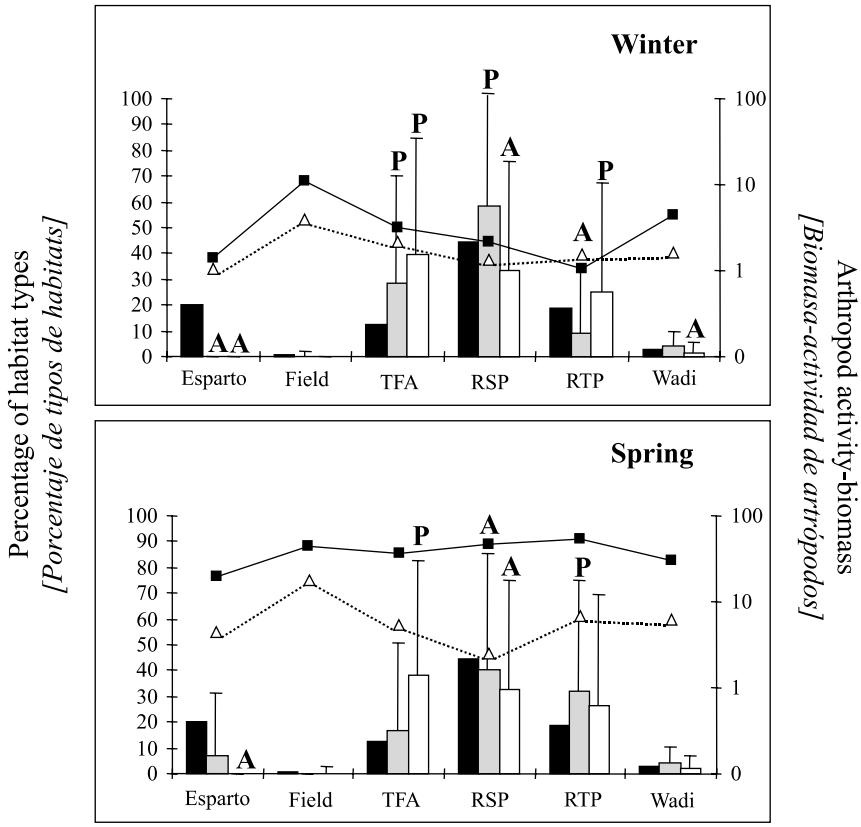

FIG. 2.—Habitat use by seven female (grey bars) and 13 male (white bars) Houbara Bustards compared to habitat availability (black bars) in the four seasons (seasons were defined as in Table 2). Habitat availability was delimited by a 100% Minimum Convex Polygon based on all radio locations of wild Houbara Bustards collected since 1996 (n = 5543). Bars represent mean proportions (± SD) of each habitat type within buffer zones (100 m radius) around seasonal radio-locations. Subscript letters indicate a significant difference between the use and the availability ($P < 0.05$), with P for habitats preferred and A for habitats avoided . In each season we indicated the mean ant (squares) and beetle (triangles) activity-biomass within the six defined habitats: esparto grass on hills (Esparto), fields, temporarily flooded areas (TFA), reg with short perennials (RSP), reg with tall perennials (RTP) and wadis.

*[Hábitat utilizado por 7 hembras (barras grises) y 13 machos de Hubaras (barras blancas) en comparación a la disponibilidad de habitat (barras negras) en las cuatro estaciones definidas como en la Tabla 2. La disponibilidad de habitat fue delimitada por el 100% del polígono mínimo convexo basado en todas las radiolocalizacoines de Hubaras registradas desde 1996 (*n = *5543). Las barras son los valores medios (*± DT*) de cada tipo de habitat. Las letras sobre las barras denotan diferencias significativas (*P < *0,05)entre el hábitat utilizado y el disponible, con P para el hábitat preferido u A para el hábitat evitado (Neu* et al.*, 1974). En cada estación se indica la biomasa-actividad de hormigas (cuadrados) y coleópteros (triángulos) en los 6 hábitats definidos (ver Tabla 1).]*

ter and spring indicated that there was little opportunity for resource monopolization by males (Emlen & Oring, 1977). Emlen & Oring (1977) argued that in such conditions territoriality is generally promoted and display males tend to be regularly distributed. In our study, display males were aggregated and birds were selective compared to habitat availability. These results indicated that habitat preference or avoidance of birds were not directly related to arthropod

TABLE 2

Means of ant and beetle activity-biomasses (± standard deviation) in the six defined habitat types (see Table 1) for each season. Seasons were defined as follow: Winter (January-March) and Spring (April-June). The variation of the mean ant and beetle activity-biomasses between habitat types was tested using a one-way ANOVA. In each season, pairwise comparisons between means were conducted using a Post-hoc Bonferonni adjustement. Means within lines that share similar superscript letters did not differ significantly ($P > 0.05$). N is the number of functional trap events per habitat and per season.
*[Media biomasa-actividad de hormigas y coleópteros (± desviación típica) en los seis tipos de hábitats (ver Tabla 1) para cada estación. Las estaciones se definieron como: Invierno (enero-marzo) y primavera (abril-junio). La variación entre habitats en estas variables se analizó usando un ANOVA de una vía. En cada estación, comparaciones apareadas entre medias se realizaron usando pruebas de Bonferroni ajustadas. Medias en la misma fila con letras iguales no difieren significativamente (*P > *0,05).]*

			Esparto	Fields	TFA	RSP	RTP	Wadis	*F*	*P*
WINTER *[Invierno]*	Ants *[Hormigas]*	*n*	*27*	*53*	*52*	*52*	*33*	*93*		
		Mean ± SD *[Media ± DT]*	1.4 ± 1.3 [a]	11.2 ± 11.4 [b]	3.1 ± 3.0 [a]	2.2 ± 4.1 [a]	1.1 ± 1.7 [a]	4.5 ± 7.4 [a]	15.75	< 0.001
	Beetles *[Coleópteros]*	*n*	*27*	*53*	*52*	*52*	*33*	*93*		
		Mean ± SD	1.0 ± 3.2 [a]	4.1 ± 4.7 [b]	2.2 ± 2.4 [a]	1.3 ± 2.3 [a]	1.5 ± 1.7 [a]	1.6 ± 2.0 [a]	7.42	< 0.001
SPRING *[Primavera]*	Ants *[Hormigas]*	*n*	*25*	*63*	*49*	*46*	*28*	*87*		
		Mean ± SD	19.9 ± 12.4	43.5 ± 5.8	36.3 ± 45.7	47.2 ± 143.6	52.7 ± 178.3	30.6 ± 39.3	0.66	0.65
	Beetles *[Coleópteros]*	*n*	*25*	*63*	*49*	*46*	*28*	*87*		
		Mean ± SD	4.5 ± 4.8 [a]	17.6 ± 29.9 [b]	5.3 ± 6.9 [a]	2.5 ± 2.4 [a]	6.8 ± 11.5 [a]	6.3 ± 8.4 [a]	7.02	< 0.001

availability, but were probably linked to additional factors. In terrestrial birds, the survival and their breeding success might not solely rely on food availability, but also on vegetation cover and height in particular habitat types (Cody, 1985). In the case of breeding females, a shift was observed in their habitat preference between winter and spring with an increase in the usage of the reg with tall perennials (RTP). This habitat types was used by the majority of females for nesting and especially by two of them that reared chicks until fledging. Houbara chicks are unable to fly until one month old, and during the first few weeks following hatching they are easy prey for foxes or raptors (Saint Jalme & Van Heezik, 1996; Combreau *et al*., 2002). At this stage the female entirely relies on the chicks' camouflage and ability to freeze motionless to avoid detection (Combreau *et al*., 2002). The RTP, probably offered both a high abundance in food resources and a suitable vegetation cover and height for brooding.

Although RTP appeared as a key habitat type for breeding females, it was not preferentially selected by males in spring. Moreover, habitat use differed significantly between sexes throughout the breeding seasons. In fact, males and females habitat requirement differed because males and females activities were different. During the breeding season, males are faithful to their display sites and their main activities are displaying and feeding. In contrast, females visit leks for mating and move from foraging to nesting and brooding areas (Hingrat *et al*., 2004). Consequently, female breeding home-ranges appeared to be significantly greater than those of males.

Despite the importance of RTP for brooding, females also used other habitat types that may be situated within male ranges and leks. However, the low percentage of overlap between female breeding home-ranges and leks (21%) and the low percentage of nests located within leks (22%) showed that habitat types situated within display males aggregates were not preferentially used by breeding females.

Despite their differences in habitat requirements, both sexes avoided cultivated fields and esparto grass. A recent study conducted in eastern Morocco showed a negative impact of human presence on Houbara distribution (Le Cuziat *et al*., 2005) and fields are probably avoided because of their proximity to farms and because other habitat types are still available in the area. Esparto grass is a particular steppe habitat, with a high vegetation cover and height. Houbaras are known to avoid too vegetated habitats were high bushes might hamper their visibility and predator detection.

In lekking species, mate choice of females is based on characters that are not related to immediate gains such as access to resources (Emlen & Oring, 1977). But these criteria appear to be unclear in exploded-lekking species, as male territories may contain critical resources for females (or their brood) (Bradbury, 1981; Oring, 1982). In such conditions it is difficult to differentiate 'resource-based mating systems' from 'exploded-leks' (Jiguet *et al*., 2002). In the case of the Houbara Bustard, critical resources or suitable habitat types for breeding females were not situated within adult male territories or within display male aggregates. Thus, the Houbara Bustard mating strategy in Morocco corresponded to a true 'exploded-lek'.

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