

Courtship behaviour in a lekking species: individual variations and settlement tactics in male little bustard

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Abstract

We analysed the display behaviour of male little bustard *Tetrax tetrax* to identify displays that are used in the context of male–male competition and those that are used for attracting females. Courtship was the main activity of males during the breeding season. Calling activity occurred throughout the day, and leks were attended for more than 4 months. Male sexual displays included snort call, wing-flash, and jump display. Snort call was performed throughout the day and mainly involved male–male interactions. In contrast, the wing-flash display was given only at twilight, and was performed most commonly when a female was present, supporting an inter-sexual function for this display. The jump display was performed only in the presence of female at anytime of the day. Analysis of individual variations in display behaviour revealed that intra-individual variation was low compared to inter-individual variation, especially for the jump display. It is, therefore, possible that display rates provide information on male quality. Four male settlement patterns could be defined, singles, paired, lekking and satellite lekking, but only wing-flash display and stamped snort call differed among those categories. We suggest that satellite males are attempting to benefit from proximity to higher status males, in accordance with the hotshot hypothesis of lek evolution. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Courtship behaviour; Sexual displays; Lek; Individual variations; Little bustard; *Tetrax tetrax*

1. Introduction

Mating systems are remarkably variable in birds (Verner and Willson, 1966; Emlen and Oring, 1977; Oring, 1982; Davies, 1991), with one of

the most extreme forms being lek systems (Andersson, 1994; Höglund and Alatalo, 1995). Mating systems were formerly considered as being species-specific with little intra-specific variation, but recent studies have reported that several species show flexible mating patterns (review in Lott, 1991). Alternative male mating tactics sometimes co-occur within species (Lott, 1991; Davies, 1992; Gross, 1996), including lekking species (e.g. van Rhijn, 1973; Lank and Smith, 1987; Lanctot and Weatherhead, 1997). Moreover, as a consequence

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of extreme skews in male mating success (Bradbury et al., 1985; Wiley, 1991), lekking may have promoted the evolution of alternative and parasitic male strategies (van Rhijn, 1973; Lott, 1991; Widemo, 1998), and some males may adopt a mixture of tactics (Cartar and Lyon, 1988). Flexible strategies are generally documented by using differences in display behaviour (Hogan-Warburg, 1966; Avery, 1984; Lanctot et al., 1998), and by comparing variability between and within individuals. Indeed, variance in male mating success is often related to phenotypic differences between males, e.g. behavioural variability in vigour of display and/or its duration (e.g. Sutherland, 1996).

The role of behaviour in mate attraction has been largely studied in lek mating systems (Beehler and Foster, 1988; Trail, 1990; Westcott, 1992), including male dominance and rank on leks (Trail, 1985; Kokko et al., 1998; Hernandez et al., 1999). Some studies suggest that leks may vary between two extremes, at one extreme, males share a common area and compete for individual dominance status, which regulates mate access (Gibson and Bradbury, 1987). At the other extreme, males hold exclusive territories within the lekking area, and interference in mating is limited to interactions between neighbours (Wiley, 1973; Lill, 1974). The latter situation typically applies for exploded leks (Emlen and Oring, 1977), in which male mating skew may result from female choice (Wiley, 1973). Overall, therefore, intra- and inter-individual variability is likely to be a good indicator of male quality, possibly used by females for mating decisions (Westcott, 1992; Gibson, 1996).

Most species of bustards (family Otidae) show elaborate courtship displays and a variety of mating systems. They range from solitary monogamous displaying males, to communal displaying by polygamous males, either over dispersed territories (exploded lek), or on true leks (Carranza et al., 1989; del Hoyo et al., 1996; Morales et al., 2001). In this paper, we describe the courtship behaviour of male little bustards *Tetrax tetrax*, in order to identify those displays that are used during male–male competition, and those that may be used for female attraction (although these

functions are not mutually exclusive). We focus on temporal, as well as individual variations in behavioural activity by comparing between and within male variability of displays. Our assumption is that a display component, which is highly variable between individuals, but fairly invariant within individuals, may provide a reliable indicator of male quality for prospecting females and thus play a role in male attractiveness. We also evaluate the potential effects of environmental factors on displaying. Based on consistent between-individual differences among males, we finally suggest that different behaviourally mediated settlement tactics co-occur in males of this lekking species.

2. Methods

2.1. Study areas and species

The study took place from 1997 to 1999. The main study area was located in the south of Département des Deux Sèvres, central western France (46°11'N, 0°28'W, c. 340 km², see Jiguet et al., 2000 for general description). Additional populations were surveyed in four other study sites in western France in 1997 (in the Départements of Charente, north of Deux-Sèvres, Maine-et-Loire and Indre). All four study sites are rather similar to the main study site with regard to crop cover, but are much smaller in size (ca. 20 km²).

The little bustard is a medium-sized bird species (average body weight 865 g, authors unpubl. data). Following the definitions of Emlen and Oring (1977), the mating system of the little bustard is an exploded lek (Schulz, 1985; Jiguet et al., 2000). Males display in aggregated sites that females attend primarily for the purpose of fertilisation, the defended display territories are a few hectares in size (Jiguet et al., 2000). Males arrive first on the breeding grounds, between March and April, whereas females arrive from April onwards.

Males were identified individually according to plumage characteristics (Arroyo and Bretagnolle, 1999). Male territories were modelled using the Ranges V package (Kenward and Hodder, 1996), using the core-weighting kernel model as an esti-

mator as this model best fits the biological characteristics of the species (Jiguet et al., 2000). Number of neighbours was defined as the number of displaying birds found within a 1 km radius around a given male. Distance between neighbouring males was calculated as the distance between the two territory centres. For a given male, lek size was measured as the number of neighbouring males plus one, so being one for singles, two for paired, and varying from three to five for leks in our study sites. Lek attendance was measured by (1) the date of arrival; and (2) the duration of stay in weeks.

Based on prior knowledge of this species (Jiguet et al., 2000), we defined satellite lekking males, as opposed to resident lekking males, as displaying males that showed an erratic behaviour, attending leks for short time and switching between different leks during the breeding season. Thus, we a priori categorised our males into four categories, according to lek size and attendance. For instance in 1998, 25 males monitored in the main study site belonged to singles ($n = 7$), paired (7, in one of the pairs only one male was monitored), lekking (7) and satellites (4).

2.2. General behaviour and sexual displays

Behavioural activities were categorised as vigilance, moving (walking, running and flying), comfort activities (resting, preening), feeding, and displaying. The displays of the little bustard were split into three categories (for terminology, see Cramp and Simmons, 1980; Schulz, 1985), (1) snort call is the basic display, consisting of a brief vocalisation uttered with a sharp toss of the head. The snort call is sometimes preceded by 1–4 stereotyped foot steps (stamped snort call). (2) Wing-flash, the bird stamps its feet on the ground, utters snort call and then beats its wings with feet still touching ground, producing a characteristic whistle from the 7th primary, the wing-flash is always preceded by foot stamping, of variable duration. (3) Jump consists of foot stamping, snort calling and finally a jump with the wings beating to enhance both the whistle and the visual signal of the white wings. The height of the jump varies from 20 to > 100 cm.

2.3. Sampling of behavioural activities

We used focal sampling of behaviour to record bird activities (Altmann, 1974). Behavioural data were collected during two breeding seasons (April–July 1997 and 1998), except for the jump display for which data obtained in 1999 were also used to increase sample size. Weeks of sampling were numbered from the first week of April onwards (e.g. week 1, 30 March–5 April; week 16, 13–19 July; in 1998). Hour of sampling was considered as the hour when observations started (UT + 2).

Two time scales were used for focal sampling. In 1997, focal sampling of behaviour was based on a min time-scale: all behavioural activities were recorded as being present/absent during a given min, with sexual displays being further analysed by their frequency of occurrence per min. In 1998, the time scale used in focal sampling was the second i.e. each second of survey was attributed to a particular behaviour, as we noted the time when the birds switched from one activity to another.

Data from the main study site ($N = 153$ focal samplings, 31 males) and other sites ($N = 176$ focal samplings, 35 males) in 1997 were obtained from a random sample of individually identified males. Focal duration was between 10 and 30 min per male at each sampling. In 1998, particular attention was given to focal observations made at twilight (i.e. just after dawn or before dusk) in order to record sexual displays that occur only at that time (Schulz, 1985, see below). For this purpose, a set of 25 males were monitored in the main study site during half an hour a week ($N = 198$ focal samplings), but data were available for 20 males only for all weeks 4–13 ($N = 182$ focal samplings). Focal sampling of the jump display was performed each time a male was seen jumping, as this behaviour was recorded rarely.

2.4. Data analysis

All males studied performed the snort call display, which was analysed using its rate (i.e. snort call rate = total number of snort calls/total duration of the given focal, in minutes). The wing flash

display was less commonly used, and in particular was given only during part of the focal. It was, therefore, analysed using two descriptors, wing flash rate (i.e. total number of wing flash displays/duration of focal sampling dedicated to the wing flash display, i.e. from the first to the last wing flash display, in min), and wing flash occurrence (i.e. total number of wing flash displays/total duration of focal sampling, in min). The jump display was even more rarely recorded, and, therefore, was analysed using the proportion of males that jumped in, the population in a given year, and calculating its rate (jump rate, total number of jumps/duration of focal sampling dedicated to the jump display, i.e. from the first to the last jump display, in min). Foot stamping before the snort call was categorised as present or absent for each snort-call, and analysed as the percentage of snort-call preceded by stamps during the entire sampling period.

The seasonal pattern of behavioural activities was analysed at a one week-lag, using data from the main site in 1997 only ($N = 153$ focal samplings, 31 males). A finer analysis was developed for displays (snort call, wing flash and jump), for which data from all sites and both years were used ($N = 527$ focal samplings, 127 males). To test for the possible existence of significant variation in display rates according to season or time of day, we performed analyses of variance (ANOVA). In order to avoid pseudo-replication, ANOVAs were performed using the mean value per male and per week (season analysis), or per male, per hour and per week (daily analysis). As week showed a significant effect, we tested for the existence of a seasonal trend with Spearman non-parametric test, using mean value per week. We also investigated the potential variation of snort call rate according to study sites (three sites with sufficient data) or year (1997 vs. 1998), for weeks 4–13. Using this data subset ($N = 383$ focal samplings, 88 males), we performed a two-way ANOVA on snort-call rate using year and site effects as well as their interaction as dependant factors. We also studied the time lag between beginning of civil twilight to end of wing-flashing (in the morning), or from begin-

ning of wing-flashing to end of civil twilight (in the evening). The civil twilight is defined as the time when the centre of the Sun is geometrically 6° below the horizon (Martin, 1990). This is the limit at which twilight illumination is sufficient for terrestrial objects to be clearly distinguished by human eyes. As numbers of focal samplings involved in these analyses vary, we give for each analysis the number of focal samplings we used and the corresponding number of individual males. Overall, 1–17 (mean 4.2) focal samplings were available per male.

Other factors potentially affecting display rates included environmental factors (such as meteorological conditions) and male identity. These factors were investigated using focals obtained during twilight hour within weeks 4–13, because there was no seasonal effect on display rates during this period (see Section 3). We extracted 10 consecutive min per focal sampling (6–15 min of the focal samplings). We used nested ANOVAs to compare inter- and intra-individual variations in snort call and wing-flash rates. We considered the number of displays per minute of the extracted sample. The latter analysis was conducted for eight males during 8 weeks. Relationships between displays and lek parameters were also examined in order to investigate whether the four a priori defined lekking categories corresponded to behavioural strategies.

Number of focal samplings per male was variable (1–17), thus in order to avoid potential pseudo-replication, an index of individual male display rate was obtained by averaging sexual displays min^{-1} over the whole study period for each male. We also used the coefficient of variation, for males with at least three focal samplings, as an index of stereotypy of display behaviour for each male. Data were thus available for 17 males with regard to mean values, and 14 males for coefficients of variation (for wing-flash rate only, as we had three or more focal samplings of wing flash display only for this subset of 14 males).

Data are presented as mean \pm S.D. (range). All analyses were performed using the SAS 6.11 package (SAS Institute, 1994). Statistical level of significance is 0.05.

3. Results

3.1. Time budgets and seasonal patterns

The main activity of the males during the breeding season was displaying, which were recorded in $72 \pm 21\%$ of the min over the study period. These displays reached $82 \pm 9\%$ from weeks 5 to 14 (i.e. May and June). Other activities, such as moving ($43 \pm 10\%$), feeding ($32 \pm 8\%$), vigilance ($30 \pm 9\%$) and comfort activities ($21 \pm 15\%$) were less important. Displays always included calling, sometimes associated with wing-flash (32% of all calls when only twilight observation periods are considered), or jump (< 1%, $N = 14\ 135$ calls).

Snort call rate showed significant variations over the breeding season, i.e. from weeks 1 to 16 ($F = 7.31$, $df = 15$, $N = 527$ focal samplings averaged per week for 127 males, $P < 0.001$; Fig. 1). However, this resulted mainly from variation in snort call rate at the beginning and end of the breeding season (Fig. 1). No significant trend was found when considering weeks 4–13 ($r_s = 0.105$, $N = 10$, $P > 0.5$), and season was, therefore, not further considered in subsequent analyses over weeks 4–13. Average snort call rate per min was 3.8 ± 1.7 (range 0–8.1, $N = 453$ focal samplings) for weeks 4–13. During this period, neither year, study site, nor their interactions significantly af-

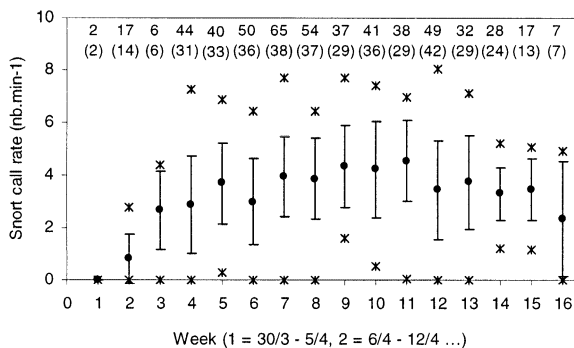


Fig. 1. Variation of the snort call rate over the breeding season (plain dots; means \pm S.D.; stars, extreme values). The two sample sizes indicated at top refer to total number of focal sampling observations per week, and total number of males each week (within brackets).

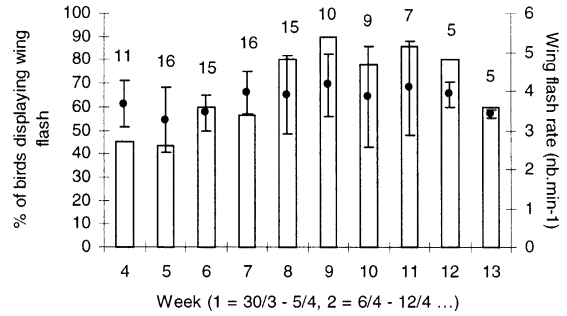


Fig. 2. Variation of the wing-flash display occurrence and wing-flash rate over the breeding season. Black dots, wing-flash rates. White bars, proportions of males using wing-flash display among the breeding male population monitored in 1998, sample size (number of males) given above each column.

ected snort call rate ($F_{\text{year}} = 1.40$, $df = 1$, $P = 0.24$; $F_{\text{site}} = 1.49$, $df = 2$, $P = 0.23$; $F_{\text{year} \times \text{site}} = 1.06$, $df = 2$, $P = 0.35$, respectively; $N = 383$ focal samplings, 88 males), even when including week of sampling in the model.

Wing-flash rate showed no significant seasonal variation in 1998 ($F = 1.75$, $df = 9$, $N = 71$ focal samplings for 20 males, $P = 0.099$; weeks 4–13; Fig. 2), with a mean value for weeks 4–13 of 3.8 ± 0.9 (range 1.7–6.0). A significant trend was found with the proportion of birds using wing-flash ($r_s = 0.622$, $N = 10$, $P < 0.05$; Fig. 2). The jump display was rarely used in the population we studied, for instance, only 7 males used jumps at least once during the entire breeding season in 1998 ($N = 54$ males). During jump displays, number of jumps per minute was 3.7 ± 0.8 (range 2.4–5.1, $N = 22$ focal samplings).

3.2. Daily patterns in courtship displays rates

Using data from years 1997–1998 combined, we found a significant daily variation in snort call rate ($F = 3.52$, $df = 17$, $P < 0.0001$, $N = 527$ focal samplings, 127 males; Fig. 3). There was in particular a marked decline in calling rate from 10:00 to 19:00 h. Wing-flash occurred only at twilight (Fig. 3) or even at night when moon was present and weather mild (pers. obs.). However, the lag between the time it ended (morning) or started (evening) and civil twilight was variable. We in-

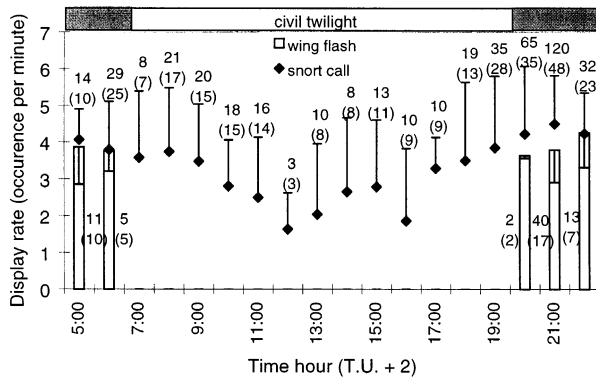


Fig. 3. Variation of the wing-flash (white bars, mean \pm S.D.) and snort call (black dots, means \pm S.D.) rates depending on the time h (UT + 2). Numbers of focals given for each dot/bar, as well as number of individuals monitored (in brackets). Horizontal grey bars indicate temporal variations in end/beginning of civil twilight along the study period.

investigated whether the presence of a female could affect this time lag, and found it was greater when males were accompanied by a female ($F = 4.47$, $df = 1$, $P = 0.038$; $N = 68$ focal samplings, 18 males). For a subset of eight males, both situations occurred (i.e. a female was sometimes present). Again, time lag was significantly higher in presence of female than in its absence (17.4 ± 8.2 vs. 6.7 ± 9.2 min, respectively; $P = 0.018$).

When wing-flash occurred, we found no signifi-

cant variation in its rate according to hour ($F = 0.21$, $df = 4$, $P = 0.93$, $N = 71$ focal samplings for 20 males; Fig. 3). For 19 males that performed wing-flash display, wing-flash rate was significantly lower than snort call rate (3.8 ± 0.8 vs. 6.3 ± 1.4 , Wilcoxon signed ranks test: $z = -3.82$, $P < 0.0001$). However, snort call rate of these 19 males was identical to snort call rate of six males that never performed wing-flash display (6.0 ± 1.7 for the latter, Mann–Whitney's test, $U = 56.0$, $P = 0.95$). The jump display was performed whatever the h during the daylight, although not at dawn or dusk. It was, however, only performed in the presence of a female, this being also supported by the fact that jumping behaviour started in males when a hidden female became visible to them (pers. obs., $N = 4$).

3.3. Factors affecting display rates

Between male variation was statistically greater than within male variation for snort call, wing-flash and jump rates (Table 1), though both levels of variation were significant for the two former displays. Male identity, but not the presence of a neighbouring calling male (that could be heard from the display site) nor the presence of a visiting female affected significantly display rates (model 2 in Table 2). The effects of environmental

Table 1
Effects of intra- versus inter-individual variability in snort call, wing-flash and jump rates

Source	Df	Mean-square	F	P
<i>Snort call</i>				
Model	39	14.36	9.82	0.0001
Male identity	7	21.77	14.89	0.0001
Focal sampling \times male identity	32	12.04	8.24	0.0001
<i>Wing-flash</i>				
Model	24	4.36	4.55	0.0001
Male identity	6	6.19	6.47	0.0001
Focal sampling \times male identity	18	3.53	3.69	0.0001
<i>Jump</i>				
Model	19	6.55	6.61	0.0001
Male identity	13	9.14	9.23	0.0001
Focal sampling \times male identity	6	1.28	1.29	0.2637

Data are analysed using nested ANOVA. Nested notation is indicated with asterisks (i.e. 'focal sampling*male identity', equivalent of 'focal sampling (male identity)' under SAS notation).

Table 2
Factors affecting snort call and wing-flash rates

Effect variables	Snort call			Wing-flash		
	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>
Model 1	R^2 model = 0.189			R^2 model = 0.125		
Weather	1.14	1	0.288	0.03	1	0.853
Morning/Evening	2.94	1	0.090	0.14	1	0.706
Crop type	1.25	10	0.270	0.32	8	0.547
Vegetation height	0.85	1	0.360	0.32	1	0.572
Model 2	R^2 model = 0.444			R^2 model = 0.504		
Other male	2.91	1	0.092	0.38	1	0.538
Presence of female	0.46	1	0.497	0.28	1	0.596
Male identity	2.40	20	0.003	2.83	16	0.003

Two kinds of models are produced, whether only environmental factors are considered, or when biological factors (i.e. congeners) are investigated. Test were performed using general linear models.

as well as individual factors on snort call and wing-flash rates were also investigated for 21 males. Weather, hour of sampling (classified as morning twilight or evening twilight), crop type and vegetation height, had no significant effects on snort call and wing-flash rates (model 1 in Table 2). Factors affecting the use of the wing-flash display during a sampling period (wing-flash occurrence) were investigated using logistic models and maximum likelihood approach, week of sampling, vegetation height and presence of female were found to predict wing-flash display (Table 3). The wing-flash display was most likely to occur late in the season, on display sites with low cover, and in presence of female.

3.4. Courtship displays and lek parameters

Potential correlation between male displaying behaviour and their lek attendance, lek size they attended and territory size, were tested using explanatory statistics. Significant correlation were found between the number of neighbouring males, and wing-flash occurrence ($r = 0.604$, $N = 17$, $P = 0.006$) or trample duration ($r = -0.625$, $P = 0.004$), but not with snort call rate (and its CV),% of stamped snort call, wing flash rate (and its CV) and time lag to twilight ($N = 17$ for all but wing flash CV for which $N = 14$; see Section 2). Snort call rate% of stamped snort call, and wing-flash

rate did not differ between single, paired, satellite and lekking males (Table 4; $P = 0.67$, $P = 0.46$ and $P = 0.32$, respectively), but wing-flash occurrence differed significantly between lekking males and other categories ($P = 0.016$). Time lag between wing-flash and twilight was also higher in lekking males, but the difference was only marginally significant ($P = 0.061$). Finally, the four a priori male settlement categories differed in the trample duration before wing-flash, with the longest trample duration being found in single and paired males, and the lowest in satellite and lekking males ($P = 0.049$). Therefore, single and paired males showed low wing flash occurrence, long trample duration before wing-flash and mod-

Table 3
Factors affecting wing-flash display occurrence during a focal sampling

Source	df	χ^2	<i>P</i>
Week	1	18.13	0.000
Vegetation height	1	8.24	0.004
Presence of female	1	9.46	0.002
Likelihood ratio	49	59.64	0.141

Factors tested include both environmental and biological factors (week of sampling, h of sampling, vegetation height, presence of female, presence of another male). Data were tested using logistic models and maximum-likelihood analysis. Only the most parsimonious model is presented (i.e. with lowest deviance).

Table 4
Variations in male courtship behaviour according to their settlement category (see text for definitions of the four a priori categories)

Male settlement category	Snort call rate	Stamped snort call	Wing-flash rate	Wing-flash occurrence	Trample duration before wing-flash	Time lag to twilight
Singles ($N = 7$)	5.7 ± 1.3	$39 \pm 22\%$	4.1 ± 0.5	0.7 ± 0.7 (a)	3.7 ± 1.2 s (a)	9.1 ± 3.5 min
Pairs ($N = 7$)	6.0 ± 2.1	$33 \pm 25\%$	3.4 ± 1.1	0.6 ± 0.7 (a)	3.8 ± 0.5 s (a)	5.0 ± 2.9 min
Satellites ($N = 4$)	6.7 ± 1.6	$44 \pm 32\%$	3.2 ± 0.5	0.7 ± 0.8 (a)	3.0 ± 1.6 s (b)	8.6 ± 9.0 min
Leks ($N = 7$)	6.4 ± 1.1	$56 \pm 27\%$	4.1 ± 0.6	2.2 ± 1.1 (b)	2.8 ± 0.5 s (b)	15.1 ± 5.5 min
Kruskal–Wallis (H)	1.56	2.57	3.50	10.43	7.87	7.40
Tests ^a (P)	0.668	0.464	0.321	0.016	0.049	0.061

^a Kruskal–Wallis tests are given with H and P values; (a) significantly differs from (b).

erately long time lag between wing-flashing and twilight. Conversely, lekking males showed high wing-flash occurrence, short trample duration before wing-flash, and long time lag to twilight, while satellite males differed from lekking males in showing low wing-flash occurrence (see Table 4 for summary statistics).

4. Discussion

4.1. Territorial versus sexual functions of the courtship displays

Snort call rate did not differ whether a female was close to the display site or not. Playback tests using the snort call conducted on territorial males always induced response with snort call, and in some cases, visits to the loudspeaker (unpublished data). Finally, males performed snort call display almost all day long, thus suggesting that the snort call is mainly involved in male–male interactions, being a territorial signal allowing males to keep contact within the exploded lek and maintain their territories (see Westcott, 1992). There is no proven inter-sexual function for the snort call.

Wing-flash playback tests led Schulz (1985) to conclude that this display had a territorial (thus intra-sexual) function. In our study, the probability that a given male used wing-flash display increased with group size (see also Petretti, 1993), thus supporting a territorial function for this display, depending on local population density (i.e. lek size). The wing-flash display was most likely performed when a female visited the display site. The longer time dedicated to the wing-flash display in the presence of female further supports an inter-sexual function for this display, although it is not known whether female presence is the cause or a consequence of this behaviour. Vegetation height was also found to affect the occurrence of wing-flash display, and it is likely that in habitats that preclude the propagation of visual cues (e.g. high vegetation) males will not invest in such displays. Some males did not use wing-flash display at all, possibly because this display is costly. First, it reduces snort-call rate when wing-flash is used. Second, it is likely to be more costly en-

ergetically than snort call (as male uses its wings). Thus, because of cost, males probably saved energy by using the display only when females were present (see Vehrencamp et al., 1989).

Lastly, the jump display has an obvious inter-sexual function, as it is only performed in the presence of female at anytime of the day, although more often in the morning or in the evening (Schulz, 1985; Petretti, 1993 pers. obs.). Jump display was also given in direct response to the arrival of a female on the display site, although not all males did so. Jump display is moreover the only display which showed no intra-individual variation; more generally, most of the variance in display rates originated from between individual variation. It is, therefore, possible that courtship display rates are behavioural traits that provide information on male quality to congeners, males or females (Bradbury and Gibson, 1983). However, there was also significant within individual variation for two of the three measured display rates. Similarly, Lill (1974, 1976) found that inter-male variability in song rate was obscured by very high variations within each male in two species of manakins. We thus suggest that the jump display, being the most extravagant display, highly variable between but not within individuals, is the best candidate of all behaviour traits to be involved in active female attraction. Male mating success is, however, impossible to assess in the little bustard, as copulations are only exceptionally seen (Schulz 1985; pers. obs.).

4.2. Temporal pattern of the display activities

Courtship was the main activity recorded in male little bustard during the breeding season. Almost every single min was dedicated to self-advertisement to congeners, although calling rate varied throughout the season, with a gradual increase at the start of the breeding season (see also Baines, 1996). Display activity peaked around sunrise and sunset, as in other lekking birds (Baines, 1996) and other bustard species (Rahmani, 1984; Ridley et al., 1985; Anegay, 1994). However, unlike other bustards (see del Hoyo et al., 1996), or the little bustard in southern Italy (Petretti, 1993), calling activity took place all day

long. Such relatively constant display activity pattern is also known in the Ruff *Philomachus pugnax* and is considered unusual among lekking birds (van Rhijn, 1991). As male little bustards defend territories of a few hectares in size (Jiguet et al., 2000), food resources are available within their territories, and thus they can maintain high levels of display activity while feeding at the same time.

Usually, males of larger lekking species attend leks only briefly, and all copulations occur within a few days (e.g. Avery, 1984; Gibson, 1996). Conversely, tropical lekking bird species attend leks and display throughout the year (e.g. Lill, 1974, 1976; Trail, 1985). Some non-tropical species, such as the black grouse, also attend leks throughout the year (Rintamäki et al., 1999), although display activity peaks in March–May (Baines, 1996). Yearly lek attendance is excluded for a migrating species, but the little bustard is further atypical in that lek attendance and display occur during 4 months, an unusually long period for a migrating species. This probably reflects the long copulation and egg-laying periods in this species an hypothesis confirmed by the chronology of the nest discoveries in the study areas (unpublished data).

4.3. *Between male variation in behaviour and settlement tactics*

Variation in male mating behaviour according to differences in male age, size, social status, or genetic polymorphism has been documented in many animal taxa, leading to different mating tactics (Alcock, 1979; Davies, 1982; Lank et al., 1995). We found significant differences in display rates among four a priori categories of males based on their lek parameters (number of neighbours and attendance), although subtle. Wing-flash and stamped snort call were most likely to occur in true lekking males. Isolated versus group display behaviour has been reported in other lekking taxa (Höglund and Stöhr, 1996; Lanctot and Weatherhead, 1997; Westcott and Smith, 1997), as well as satellite behaviour (Gosling and Petrie, 1990; Westcott and Smith, 1994), e.g. in Ruff (Hogan-Warburg, 1966) in which it is genet-

ically based and stable (Lank et al., 1995). Satellite Ruffs have no defined territory and gain access to territories defended by resident males by acting submissively (van Rhijn, 1973). In the little bustard, we never recorded any submissive behaviour. The display behaviour of satellite males was, however, less vigorous than that of lekking males, with reduced occurrence of wing-flash. We suggest that satellite males are trying to benefit from the proximity of higher status males, in accordance with the hotshot hypothesis of lek evolution (Beehler and Foster, 1988). Thus, settlement tactics may be alternatively used by males to gain access to the female resource (Bradbury and Gibson, 1983), as males are able to decide whether they join clumps or not (Apollonio et al., 1992; Pruett-Jones, 1988). For example, a resident male displaying in a lek of size 3 in 1997 switched to satellite behaviour the following year, attending two different leks during the breeding season. We thus suggest that males may use conditional tactics rather than different strategies (Dawkins, 1980; Lank and Smith, 1987; Gross, 1996).

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