

# Manipulating Lek Size and Composition Using Decoys: An Experimental Investigation of Lek Evolution Models

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**ABSTRACT:** Four theoretical models have been proposed to account for the origin and maintenance of leks: hotspot, female preference, hotshot, and black hole models. Each has been validated in particular cases, and most are not mutually exclusive; therefore, it has been difficult to contrast and separate them, empirically and experimentally. By using decoys to mimic natural leks in the little bustard, artificial leks attracted wild birds. Then, by manipulating artificial lek size and structure (sex ratio, male phenotype), the study of responses of wild males and females allowed us to test specific predictions derived from the four classical models of lek evolution. The hotspot model was not supported because female decoys did not attract wild males. Conversely, hotshot males do exist in this species (attracting both wild females and males), as does a female preference for a particular lek size (four males). Finally, males aggressive toward decoys attracted fewer females, consistent with one of the mechanisms by which the black hole model may work. Therefore, three models of lek evolution were partly or fully supported by our experimental results: hotshot, female preference, and black hole models. We suggest that these models actually fit within each other, ensuring the evolution, functioning, and long-term maintenance of leks.

**Keywords:** black hole, exploded lek, female preference, hotshot, hotspot, little bustard.

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The lek is a rare mating system (Höglund and Alatalo 1995; see also Jiguet et al. 2000 for an updated review in birds) and remains perhaps one of the most controversial evolutionary puzzles. A lek consists of clustered male territories that females visit strictly for the purpose of mating (there is no male parental care in lekking species; review in Höglund and Alatalo 1995). Male territories therefore do not hold resources attractive to females other than the males themselves. Leks are characterized by (i) male clustering; (ii) extreme bias in female choice, resulting in skewed male mating success; and, in many cases, (iii) stability of lek location over time (Höglund and Alatalo 1995). In comparison with other territorial mating systems, the extreme clustering of lekking male territories raises the ultimate question of the benefits of this aggregative behavior in contrast to its associated costs such as competition (Bradbury and Gibson 1983; Wiley 1991; Isvaran and St. Mary 2003). Local clustering of males may facilitate the apparent unanimity of female choice for particular males (Bradbury et al. 1985; Wiley 1991), which may be explained either by independent female choice or by copying as a strategy to reduce the costs of mate assessment (Bradbury and Gibson 1983; Höglund et al. 1990, 1995; Uehara et al. 2005 for a modeling approach). Stability of lek location might result from the different sex roles (Emlen and Oring 1977); that is, leks may settle through male initiation at locations with a high probability of encountering females (Bradbury 1981; Bradbury et al. 1986) or as a response to predation risk (Aspbury and Gibson 2004; Boyko et al. 2004). Much interest has also centered on the possibility that leks may be driven by female choice (Bradbury 1981; Gibson 1992). Finally, in black grouse and manakins, males are related to each other in a lek, so those who do not mate still gain inclusive fitness by increasing lek size and the mating success of the dominant male (Shorey 2002).

Four main models have been proposed to account for the origin and maintenance of leks (reviewed in Sutherland 1996; see also Isvaran and St. Mary 2003), although they may not be mutually exclusive. The hotspot model is the only one that assumes that males are the driving force of

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lekking behavior (Bradbury and Gibson 1983; Bradbury et al. 1986). Hotspots are sites where female densities are highest and where males cluster in order to maximize their chances of encountering females. The locations of leks are determined by the overlapping female home ranges, independent of resource distribution (Bradbury et al. 1986), or by nondefendable resources to which females are attracted (Höglund and Alatalo 1995). In this case, male clustering is determined by female concentration. Alternatively, two other models stipulate that female choice is the driving force: the female preference and hotshot models. The former focuses on female preference for clumped males (Bradbury 1981; Gibson et al. 1990), with an increased per capita male mating success in larger leks (Alatalo et al. 1991; but see Kokko et al. 1998). Females may prefer clustered males for different reasons, for example, reduced costs of mate sampling, higher absolute quality of the best male in larger groups, or deflection of predators from nest sites (Beehler and Foster 1988). The latter model assumes that females prefer to mate with hotshot males, not with clustered males per se (Arak 1982). Leks occur because less preferred males join the preferred ones and parasitize their attractiveness, therefore increasing their probability of obtaining mates (Beehler and Foster 1988). Thus, hotshots are attractive to both females and males. Finally, the black hole model (Clutton-Brock et al. 1992; Stillman et al. 1993) assumes that females are highly mobile, moving within the habitat and mating with the male in whose territory they finally happen to be present. There is no female preference for a particular kind of male or lek size. In such a scenario, simulations have shown the optimal male nearest-neighbor distances to be at their shortest (Stillman et al. 1993, 1996), like females being sucked into black holes. Though the first description of this model envisaged female mobility as a consequence of sexual harassment, there are potentially other mechanisms that could lead to the same result, for example, mate choice processes (Stillman et al. 1996).

Comparative tests of these four models have not yet been performed. Empirical studies, such as detailed analyses of spatial distribution of individuals (e.g., Sæther et al. 2005), have provided some insights into the evolutionary processes involved in lek origin and maintenance (Höglund and Alatalo 1995). By comparing spatial distributions of males on the lek and of the nests (or female home ranges; Bradbury 1981; Bradbury et al. 1986), empirical studies helped to disentangle the relative roles of male versus female sex on lek evolution. An alternative is to study behavioral activity on leks and address directly the processes involved in lek formation (Gibson et al. 1990; Kokko 1997; Gjerde et al. 2000; Partecke et al. 2002). Simulation models and theoretical studies have rarely been performed (e.g., Gibson et al. 1990; Stillman et al. 1993,

1996; Johnstone and Earn 1999; Isvaran and St. Mary 2003) and seldom compared all four models of lek evolution simultaneously. Finally, the most powerful means, though not necessarily the easiest, is to conduct experimental investigations (Höglund and Robertson 1990; Höglund and Alatalo 1995). However, there have so far been remarkably few experimental studies investigating ecological and/or behavioral processes involved in lek formation or maintenance (but for invertebrates, see Dronev 1994, on a Hawaiian fruit fly *Drosophila grimshawi*; Jones and Quinnell 2002, on the sandfly *Lutzomyia longipalpis*; for vertebrates, see Lank and Smith 1992, on the ruff *Philomachus pugnax*) and even fewer using decoys (Höglund et al. 1995, on the black grouse *Tetrao tetrix*). In this study, we report on such an experiment, in which we explored the behavioral processes by which males aggregate in leks, using artificial leks made of male and female decoys.

Our study model, the little bustard *Tetrax tetrax*, is a bird that exhibits an exploded lek mating system. By varying the size and the population structure (sex ratio, male phenotypic quality) of artificial leks and then recording the responses of wild males and females, we tested specific predictions derived from the four classical models of lek evolution (see table A1 in the online edition of the *American Naturalist*). On the basis of the principal mechanisms inherent in these models, we made non-mutually exclusive predictions with regard to wild male and female responses according to (i) lek size, (ii) lek composition (sex ratio), (iii) relative phenotypic quality of male decoys, and (iv) wild male aggressiveness toward decoys. A key feature of the hotspot model is that females attract males, and therefore we expect that the presence and number of female decoys will affect wild male response rate (frequency of visits) to the artificial leks. Conversely, the key assumption of the female preference model for lek evolution is that wild female response rate will increase with the number of male decoys on the artificial lek. Under a hotshot model of lek evolution, we would predict that male decoys with different phenotypes will differentially attract females and males and, specifically, that higher-quality males (indicated by their phenotype) will attract more females. Last, we investigated the principal mechanism by which the black hole model may operate, female harassment (see also Isvaran and St. Mary 2003), which predicts that aggressive males should be less attractive to females. We experimentally measured male aggressiveness toward male decoys and then compared this measure with their attractiveness to wild females.

## Methods

### Study Areas

The main study area was located in the Département des Deux-Sèvres, central-western France (46°15'N, 0°30'W).

It covers 340 km<sup>2</sup> of farmland habitat, mainly an intensive cereal cropping system. Land use was a mixture of winter cereal crops (approximately 35% of the surface); other winter crops such as rapeseed and peas (approximately 15%); spring-sown crops (sunflower and corn, approximately 25%); fallow, pastures, and other permanent or semipermanent crops reserved for livestock rearing (approximately 15%); and about 10% of nonagricultural cover (forests and villages). A second study area was also used for the experiments, located in the Département du Maine-et-Loire, in central-western France (47°07'N, 0°11'W). It covers approximately 10 km<sup>2</sup> of farmland habitat, 50% of which was pastures and fallow.

### *Study Species*

The little bustard is a medium-sized steppe bird that shows an exploded lekking system (Jiguet et al. 2000, 2002), shared with several other members of the Otididae family (Morales et al. 2001; Hingrat et al. 2004). Breeding females' home ranges cover approximately 470 ha (range = 30–3,400 ha; Jiguet 2001; Morales et al. 2001). Males actively defend display territories of approximately 40 ha, though they also show significant aggregative distribution (Jiguet et al. 2000). Our main study area held a low density of displaying males (0.1 male/km<sup>2</sup>), though locally density could reach up to 2 males/km<sup>2</sup>. The second study area had a more stable population with higher male density (approximately 2 males/km<sup>2</sup>). In both areas, sex ratio was slightly biased toward males (Jiguet et al. 2000). The species is migratory in southwestern France, with males and females wintering in central Spain (V. Bretagnolle, F. Jiguet, and M. Morales, unpublished data). Males arrive first on the breeding grounds, from the end of March onward, and attend lekking sites from April to July. Numbers of displaying males usually peak in May, while most egg laying starts at the beginning of June (Jiguet and Bretagnolle 2001). Females breed mainly in grasslands or alfalfa fields (Jiguet et al. 2002).

Displaying males were carefully monitored in each study site and year (1998–2000). Study areas were searched for males at least once per week during the breeding season to detect displaying males. Each location where a male was sighted at least once was subsequently monitored twice per week throughout the study period. All males could be identified unambiguously using their individual head marking patterns (Jiguet and Ollivier 2002). All observations of identified males were recorded daily, and occurrences of female(s) accompanying a displaying male were noted. The total number of males in the study area was calculated for each week of the survey for each site. It varied over the breeding season because of new arrivals or the redistribution of males in leks. Male attractiveness

was calculated as the proportion of observations with female(s) for each male from its arrival to the end of June (this variable was arcsine transformed for statistical analyses), as in previous studies on exploded lekking bustards (Morales et al. 2003).

### *General Experimental Design*

Experiments consisted of artificially mimicked leks using male and female decoys. We made decoys (40 females and 60 males; overall shape differed between sexes) of expanded polystyrene foam molded in a preshaped plaster matrix and painted with matte paint to match little bustard plumages. Three types of male decoys with different phenotypes were made (hereafter noted M1, M2, and M3), according to phenotypic traits within the range of observed variation in the wild for that species (see Jiguet and Ollivier 2002; see also figs. A2, A3). The M1 male decoys were painted with yellow eyes, a symmetric V-neck collar, and black and white breast bands of equal widths. The M2 decoys differed from M1 decoys only in their eye color, which was red instead of yellow, because a dark eye color might indicate an older age in that species (Jiguet and Ollivier 2002). Observations collected during 1997–2001 further suggested that female little bustards were more attracted to symmetric males than asymmetric males (Jiguet 2001). The M3 decoys differed from M1 decoys by having asymmetric patterns in both the V-neck collar and breast bands (the white band being about three times wider than the black one). We made 36 M1, 12 M2, and 12 M3 decoys; using different decoys allowed for slight variations within the groups (within M1, M2, and M3).

Tests were conducted in spring 1998–2000, from the beginning of April to the end of May (hence before females started to breed). Artificial leks were set up in agricultural habitats similar to those used by little bustards to lek, and male decoys were dispatched within a square of 30 ha (the same area for all leks and the size of the smallest recorded female home range), with a minimum distance of 100 m between decoys. All decoys were placed in natural posture in agricultural fields with bare ground or low vegetation height so that they were easily detectable by wild birds. No more than five different artificial leks were used simultaneously over the 340-km<sup>2</sup> main study area, all being at least 2 km apart from each other. Each artificial lek was left for 3 days and visited once every day in the evening (a time when bustards are highly active) to search for visiting wild birds. The number and sex of visiting bustards were noted. In case of successful attraction of wild birds, the artificial lek was immediately removed. The same site was never used twice during a 3-week period, even in the case of no response. Before using a new site or reusing a previous experimental site, we confirmed that no wild bird

(male or female) was already attending the site. A distance of at least 1 km separated each artificial lek from the closest known displaying site of wild males. Artificial leks were characterized by (i) number of male decoys (i.e., lek size); (ii) number of female decoys; (iii) sex ratio (number of male decoys divided by total number of decoys); (iv) date of experimental setup (recorded as the day number from the beginning of April onward; April 1 = 1); (v) number of wild males present over the whole study area during the corresponding week; and (vi) surface area of grassland and alfalfa (preferred nesting habitat for females) within the 30 ha where the artificial lek was set up, ranging from 0 to 22 ha (i.e., from agricultural habitat highly unsuitable to suitable for breeding females).

#### Control Experiments

In order to confirm that bustard decoys were actually recognized by wild birds as conspecifics, we presented six different decoy types to 10 different displaying males. These decoys were a female decoy, an M1 male decoy, a male decoy shape (uniformly painted matte gray), a female decoy shape (similarly colored with matte gray paint), a male decoy shape painted with the plumage characteristics of an adult shelduck *Tadorna tadorna* (this duck, like little bustard males, is three colored—brown, black, and white—and shows similar obvious plumage contrasts), and a decoy of Eurasian curlew *Numenius arquata*. Before setting up a decoy in the same field where the male was displaying, we performed an ad lib. focal sampling of behavior during 10 min. After setting the decoy in the field, we performed another ad lib. focal sampling of behavior during 10 additional minutes. Snort-call rate (mean/min) and time dedicated to agonistic and vigilance behavior (s) were compared before and during the exposure to the decoy.

#### Experiment 1: Manipulating Lek Size and Lek Sex Ratio

In the first set of experiments, we set up artificial leks of varying size and sex ratio, using sites with variable habitat composition. In each artificial lek, only M1 decoys were used and dispatched within a 30-ha area, with a minimum distance of 100 m between them. When female decoys were used, they were either placed in groups of four females if no male decoy was used or grouped with the same number of female(s) accompanying each male decoy. The different lek sizes tested were zero (only female decoys used,  $n = 21$ ), one ( $n = 14$ ), two ( $n = 11$ ), four ( $n = 35$ ), six ( $n = 8$ ), eight ( $n = 41$ ), and 16 ( $n = 10$ ), for a total of 140 different tests performed.

#### Experiment 2: Manipulating Male Phenotypic Traits in Artificial Leks

In a second set of experiments, we varied the phenotypic composition of the artificial leks with respect to males, in order to test whether the homogeneity of the lek composition could influence the response of wild birds. Lek size was constant, set at four (median natural lek size), and we contrasted artificial leks made of decoys of homogeneous phenotypes versus leks consisting of decoys of heterogeneous phenotypes. We used the following lek compositions: (1) four M1, (2) four M2, (3) four M3, (4) one M1 and three M3, (5) one M2 and three M3, and (6) one M2 and three M1. Five replicates of each treatment were tested (hence  $n = 30$ ).

#### Experiment 3: Testing Female Preference for Particular Male Phenotypic Traits

In a third set of experiments, we used male decoys in pairs, disposed in either M1-M3 or M2-M3 pairs. The M1 and M2 decoys both differed from M3 decoys in showing symmetric black and white neck and breast patterns. The decoys were placed in fields regularly visited by wild males or females (however, we avoided fields with regular display sites to avoid bias due to female attraction by wild males). The two decoys were 50 m apart. Experimental fields were visited at least once a day to record the visit of wild birds. Each time a wild male or female was recorded close to the decoys, we noted its distance to each of the decoys. After each visit by wild birds, decoys were randomly moved to reinitialize the experiment. Forty different fields were used to conduct the experiments. We conducted 57 tests with M1-M3 decoys and 72 tests with M2-M3 decoys that successfully attracted wild birds, either males or females.

#### Experiment 4: Male Aggressiveness and Attractiveness

In the last set of experiments we first measured wild male aggressiveness toward a male decoy and then compared a male's measure of aggressiveness with the male's attractiveness toward wild females. These tests were carried out in spring 2000 in the main study site, using an M1 male decoy presentation. The decoy was placed about 100 m from the tested male. Ad lib. focal sampling of behavior (snort-call rate/min, proportion of time spent in agonistic posture) was noted for 10 min after the decoy was placed. We conducted two tests on 13 different males ( $n = 26$ ).

#### Statistical Analyses

Response latency was the number of days between the experimental setup of the artificial lek and the first wild

bird visit (0 if response occurred within the same day). For experiment 1, both generalized linear models (GLMs) and nonlinear generalized additive models (GAMs) were used. Response rate (1 = success, 0 = failure) was analyzed using logistic regressions and GAMs with a binomial distribution and a logit link for the 140 tests of experiment 1. To analyze the absolute number of visiting males or females on artificial leks, we used log-linear models and GAMs with a Poisson error distribution (log-link function). For experiments that used at least one male decoy (i.e., 119 of the 140 tests), the relative (per male decoy capita) number of visiting males or females was analyzed using GLMs and GAMs with normal error distribution (and identity link function). For each GAM, lek size and lek sex ratio were modeled using spline functions (Hastie and Tibshirani 1990). All models were first adjusted to date, weekly wild male numbers in the study area, and proportion of grass cover within the 30-ha lek area. Effects of lek size and lek sex ratio were adjusted to each other. Finally, two additional tests were performed with the effects of all six variables adjusted to each other to look for the potential effect of grass cover area on the male response rate (logistic regression) and numbers of visiting males (log-linear model), in order to test whether males prefer to visit leks situated in habitats preferred by females for nesting.

Experiment 2 was analyzed using Fisher's exact test to compare the response rate of wild males and females to homogeneous versus heterogeneous artificial leks. Experiment 3 was analyzed using exact binomial tests to determine deviation of the response pattern from randomness, and paired *t*-tests were used to compare the distances of wild males or females from each of the decoys for successful trials. Paired *t*-tests were also used for control tests and experiment 4 (i.e., all comparisons involving the same individual wild male). Correlation between male aggressiveness (i.e., snort-call rate and time devoted to agonistic behavior) and attractiveness was tested with Pearson's correlation coefficient. All statistical analyses were performed with S-Plus 2000 (MathSoft 1999).

## Results

### *Controls and Overall Success Rate of Experiments*

Male little bustard behavior was compared before and during presentation of one of the six different control decoys. Male and female bustard decoys induced significant alteration of wild male behavior: males significantly decreased their snort-call rate when facing a female decoy (paired *t*-test,  $n = 10$ ,  $t = -2.26$ ,  $P = .05$ ) and spent more time in agonistic and vigilant behavior when facing a male decoy ( $t = 2.96$ ,  $P = .016$ ). Neither of these two

behavioral parameters was altered significantly when males were facing a male shape, a female shape, or a shellduck-colored or a curlew decoy (all  $P > .1$ ).

Among all type 1 and 2 experiments ( $n = 170$ ), 57 (34%) were successful in attracting at least one wild bustard. In the case of a positive response, response latency was  $1.25 \pm 0.79$  days ( $n = 57$ ), validating a posteriori our 3-day artificial lek exposure.

### *Experiment 1: Varying Lek Size and Lek Sex Ratio*

Using GLMs, we found no significant effect of artificial lek size on the three measures of lek attractiveness to wild bustards (occurrence of a visit, number of visiting individuals, and same number per male decoy), either for males or for females (table 1). Only artificial lek sex ratio affected (positively) the number of visiting females, with an increase of  $0.13 \pm 0.06$  females/0.1 unit in sex ratio ( $\chi^2 = 124.4$ ,  $P = .043$ ). However, nonlinear models performed better than linear ones (table 1): artificial lek size had a significant quadratic effect on wild female response rate ( $\chi^2 = 15.2$ ,  $df = 3$ ,  $P = .001$ ; fig. 1, *top left*) as well as on that of males ( $\chi^2 = 18.9$ ,  $df = 3$ ,  $P < .001$ ; fig. 1, *bottom*), with response rate being maximal at intermediate lek sizes (four for females, six for males) and at intermediate sex ratio for females (no effect of sex ratio for males; see table 1). Additionally, artificial leks with only male decoys attracted significantly more wild birds (response rate = 9/54) than did those with only female decoys (response rate = 2/21; Fisher's exact test,  $P = .043$ ). Similarly, artificial lek size significantly affected absolute numbers of visiting females ( $\chi^2 = 7.83$ ,  $df = 2.8$ ,  $P = .042$ ) and males ( $\chi^2 = 10.03$ ,  $df = 2.8$ ,  $P = .016$ ) in nonlinear models, as it did for relative (i.e., per male decoy capita) numbers of visiting females ( $\chi^2 = 3.0$ ,  $df = 3$ ,  $P = .034$ ; fig. 1, *top right*) but not males ( $\chi^2 = 1.94$ ,  $df = 3$ ,  $P = .13$ ). There was no effect of sex ratio on either absolute or relative (per male decoy capita) numbers of visiting males or females (table 1).

Male response rate was unaffected by grassland area around the lek (logistic regression with all variables as dependant factors, adjusted to each other:  $\chi^2 = 0.13$ ,  $P = .72$ ). A similar result was found when using the number of wild males attracted to the lek (log-linear model,  $\chi^2 = 0.86$ ,  $P = .35$ ).

### *Experiment 2: Homogeneous versus Heterogeneous Phenotypes in Leks*

Two situations were compared in leks with four males: tests with all males of the same phenotype and tests with one male of a better phenotype compared with the three others (one symmetric vs. three asymmetric or one red-

**Table 1:** Results of linear (GLM) and nonlinear (GAM) models investigating the occurrence (presence/absence) of a visit either by wild males or by females ( $n = 140$  experiments), as well as absolute and relative (per male decoy capita) numbers of visiting males and females ( $n = 119$  experiments with at least one male decoy used), according to artificial lek size (number of male decoys) and sex ratio

	Linear		Nonlinear	
	Sex ratio	Lek size	Sex ratio	Lek size
Occurrence of a male visit	.59	.32	.34	< .001
Number of visiting males	.97	.65	.58	.016
Per capita number of visiting males	.39	.19	.42	.13
Occurrence of a female visit	.61	.63	.06	.001
Number of visiting females	.043	.80	.85	.042
Per capita number of visiting females	.26	.45	.73	.034

Note: GLM = generalized linear model; GAM = generalized additive model. Spline functions were used for GAMs (see text for more details). All models were first adjusted to date, weekly wild male numbers, and grassland area around artificial leks. Binomial family and logit link for response occurrence ( $\chi^2$  test), Poisson family, and log link for absolute numbers of visiting birds ( $\chi^2$  test), Gaussian family for relative numbers ( $F$ -test) were used. Only  $P$  values of tests are provided, in bold when significant.

eyed vs. three yellow-eyed). Response rates of wild males and number of visiting males did not differ between these two types of tests (Fisher’s exact test,  $P = 1$ ). Similarly, the response rate of females did not statistically differ (Fisher’s test,  $P = .169$ ), but for successful trials, merely more females attended artificial leks with heterogeneous male phenotypes than leks with all four males identical, though the difference was not significant ( $1.0 \pm 1.0$  vs.  $0.2 \pm 0.4$ ; ANOVA,  $F = 3.61$ ,  $df = 1, 28$ ,  $P = .068$ ).

*Experiment 3: Female Preference for Male Phenotypic Traits*

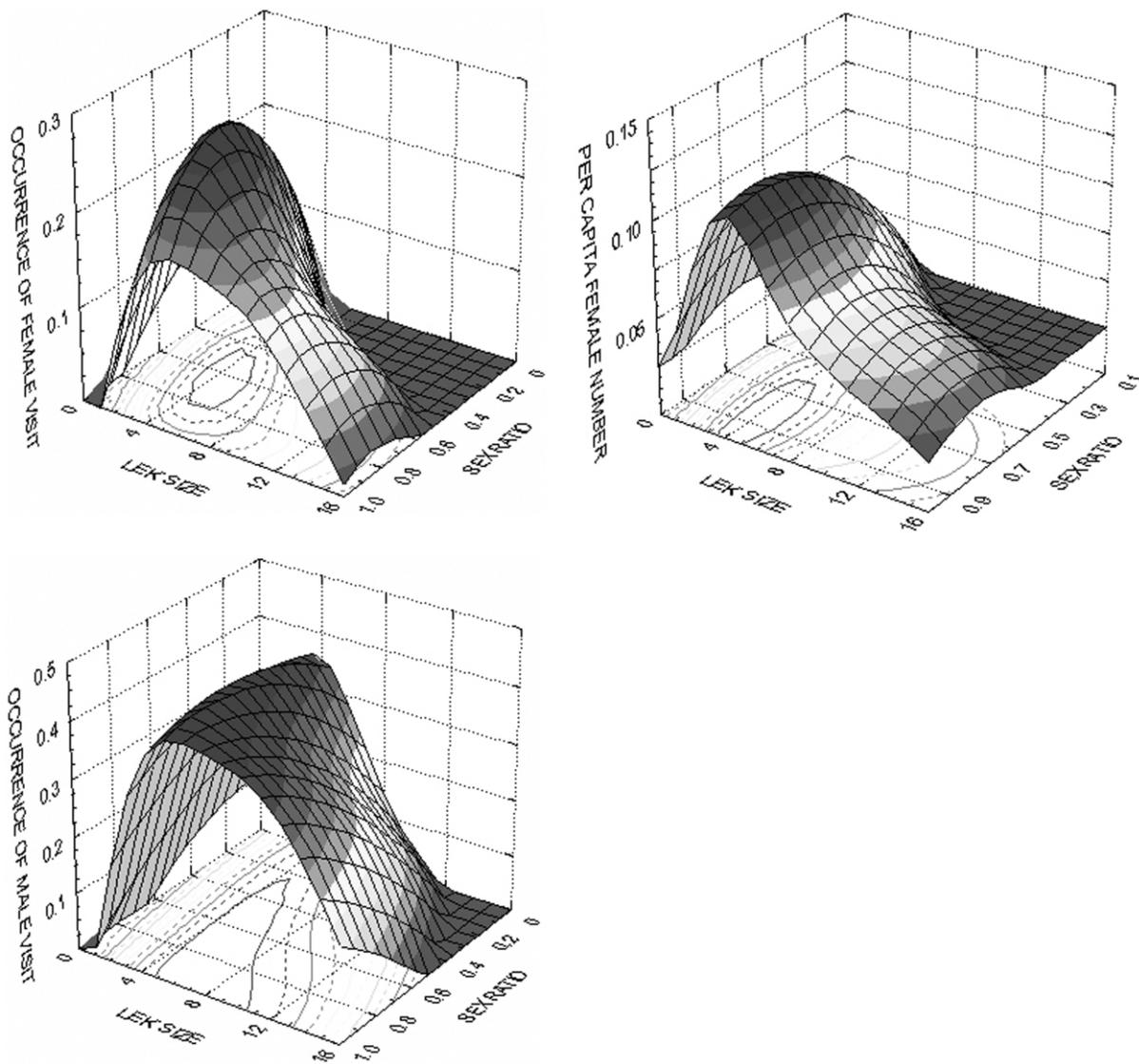
When visiting an M1-M3 pair of decoys ( $n = 57$  tests performed), females favored the M1 decoy (in 21 of 26 successful trials, exact binomial test;  $P = .002$ ) and stayed closer to the M1 than to the M3 decoy (paired  $t$ -test for comparing distances,  $t = -2.31$ ,  $df = 25$ ,  $P = .029$ ; fig. 2). Males also came closer to the M1 decoy (23 of 31 successful trials;  $P = .011$ ; distance:  $t = -2.10$ ,  $df = 30$ ,  $P = .045$ ; fig. 2). When visiting an M2-M3 pair of decoys ( $n = 72$  tests performed), females also came significantly closer to the M2 decoy (37 of 48 successful trials;  $P < .001$ ; distance:  $t = -4.21$ ,  $df = 47$ ,  $P < .001$ ), but males did not (16 of 24 successful trials;  $P = .15$ ; distance:  $t = -1.98$ ,  $df = 23$ ,  $P = .06$ ). There were no significant differences between M1-M3 and M2-M3 tests, with regard to the intensity of response in females ( $\chi^2 = 0.005$ ,  $df = 1$ ,  $P = .94$ ) or in males ( $\chi^2 = 0.096$ ,  $df = 1$ ,  $P = .76$ ).

*Experiment 4: Male Attractiveness and Harassment*

We found a significant negative correlation ( $r = -0.527$ ,  $n = 13$ ,  $P < .05$ ; fig. A1) between a male’s attractiveness to wild females and its aggressiveness toward a male decoy, as measured by its time spent in vigilance or aggressive posture. There was no such relation when using snort-call rate response to the decoy ( $r = -0.081$ ,  $n = 13$ ,  $P > .5$ ), though the snort call has a territorial as well as a female attraction function.

**Discussion**

Our experimental manipulation was aimed at testing whether males aggregated at locations with high female density (hotspots). We also evaluated the consistency of female preferences for particular lek size or particular male attributes, determining moreover whether males were attracted to hotspots. Last, we compared experimentally measured male aggressiveness and empirically estimated male attractiveness toward females. Very few experimental studies have been carried out on behavioral processes involved in lek formation or maintenance, at least in birds: one experimental manipulation on the ruff (Lank and Smith 1992) and one, using decoys, on black grouse (Höglund et al. 1995). A few experiments have been conducted on female choice on leks (e.g., Höglund and Robertson 1990) as well as on the proximate and ultimate mechanisms that cause male aggregations (e.g., Dronev 1994; Jones and Quinnell 2002), but so far most studies of how leks may form and how they have evolved are based on long-term empirical data (Gjerde et al. 2000; Partecke et al. 2002; Sæther et al. 2005). This is paradoxical because experimental tests manipulating lek size and/or structure



**Figure 1:** Smoothed spline functions of (*top left*) occurrence of visiting wild females on artificial leks, (*top right*) relative number of visiting wild females per male decoy capita, and (*bottom*) occurrence of visiting wild males to artificial leks, according to the lek size and lek sex ratio (number of male decoys divided by total number of decoys; see “Methods”).

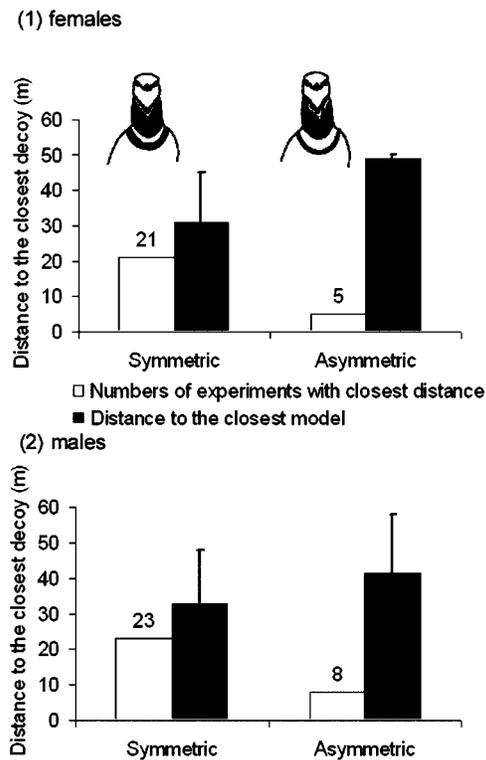
were considered to be very powerful and promising tools (Höglund and Alatalo 1995).

We showed that the little bustard was a suitable study model for an experimental investigation, as wild individuals responded positively (and rather rapidly) to artificially designed leks. Decoys were apparently identified as conspecifics because males significantly modified their behavior to bustard decoys of any sex but not to any other decoy types. Furthermore, the overall success rate of artificial leks in attracting either wild males or females within just 3 days allowed us to gather reasonable sample sizes even

though experiments were conducted in the wild. Although the biological model we used was an exploded lekking bird (Jiguet et al. 2000), general principles identified here could apply to other species with classic or other lek mating systems.

#### *Mechanisms of Lek Formation in the Little Bustard*

Leks may form at hotspots (high-female-density locations) in some species (Lill 1976; Emlen and Oring 1977; Payne and Payne 1977; Bradbury et al. 1986), but our experi-



**Figure 2:** Results of experiments using symmetric and asymmetric decoys (M1-M3 pairs; see “Methods”): visits of (1) females and (2) males to a pair of male decoys differing in showing symmetric and asymmetric neck and breast patterns. Open bars show numbers of experiments when wild birds get closer to the corresponding decoy; filled bars show the mean  $\pm$  SD distance to the closest decoy.

mental results did not support this mechanism in the case of the little bustard. Female decoys did not attract displaying males, despite being recognized as conspecifics. Moreover, any addition of female decoys to artificial leks of males did not improve attractiveness to wild males. Therefore, the presence of females per se is not responsible for the lek formation. Indeed, because male little bustards settle on leks before the arrival of females, they cannot make a direct assessment of female densities. However, males may settle on a predicted distribution of females, assessed either from female distribution in the previous year (Lank and Smith 1987) or from distribution of female-preferred habitat (see, e.g., Höglund et al. 1998). On the basis of our experimental design, we cannot therefore fully exclude the possibility that males use long-term tracking of female environmental distributions, though male visitation rate was not higher in areas of greater grassland and alfalfa (habitats preferred by females to lay their eggs; Jiguet et al. 2002). In our case, one reason that bustard males did not respond to the presence of females

may be that in low-density male-biased populations, access to the female resource might be less costly by aggregating at traditional sites or close to established males than by directly or indirectly assessing the female density. Moreover, crop rotation in agricultural landscapes might lower the efficiency of assessing the distributions of females or female-preferred habitat from one year to the other, and large male territories in exploded lekking species (Morales et al. 2001) might preclude close aggregation on female density hotspots.

Last, while sex ratio on the artificial lek affected female attraction, the linear relationship was negative: increasing the number of female decoys resulted in decreasing the number of wild females attending the artificial lek. Because the addition of female decoys to artificial male leks did not increase female visits, we suggest that female copying on little bustard leks is unlikely. The further nearly significant nonlinear effect of sex ratio on female visit occurrence might indicate an optimum for low costs in limited female copying.

Our results supported female preference for a particular lek size in the little bustard because female attraction was a quadratic function of lek size. The optimal lek size was about four males. Empirical evidence also showed that average male phenotypic quality (measured by symmetry of plumage ornaments; Jiguet 2001) is highest in leks with four males (Jiguet 2001). Therefore, it is possible that females developed a preference for leks of that size as an indirect mate choice on leks (Sæther et al. 2005) and that female benefits decrease above a choice among four males. This lek size also corresponds to the maximum number of visiting females per male capita, as well as median lek size in natural conditions, at least in southwest France (F. Jiguet and V. Bretagnolle, unpublished data). However, these results were obtained in a low-density population and might not hold true for other little bustard populations, especially if the mean natural lek size is higher. In our study, optimal lek size appeared to be much smaller than that observed for other lekking birds (Bradbury et al. 1989; Alatalo et al. 1992; Höglund and Alatalo 1995), though variation in lek size among species is a function of the relative ability of dominant and subordinate males to secure matings, and small lek sizes are predicted for species with an exploded lek mating system because male territories are larger and few males can aggregate on close display sites (Morales et al. 2001). Female response was also quadratic rather than linear: indeed, the per-male female visitation rate cannot increase indefinitely with lek size, at least because of mathematical limits, because when all local females visit a lek, adding more males must decrease the rate per male. Moreover, the female preference model predicts an optimal lek size linked to its stability (Beehler and Foster 1988; Hernandez et al. 1999; Widemo

and Owens 1999). Finally, the attraction of wild males to artificial leks varied with lek size, although optimal lek size was slightly larger (six; see fig. 1, *bottom*), and there was no evidence for an increase in per capita male attraction for males, which might be a consequence of the sex ratio being biased toward males in the studied populations (Jiguet et al. 2000). Greater numbers of male visits on larger leks is not expected theoretically because skew in male success changes with lek size as well as relative male quality, and male decisions in joining a lek are presumably only partly related to lek size (Widemo and Owens 1995, 1999; Kokko and Lindström 1997; Kokko et al. 1998).

We also found experimental support for male and female attraction to particular male traits. To our knowledge, this is the first validation of one assumption of the hotshot model in a lekking bird (Arak 1983; but see Sæther et al. 2005). However, a next step should consider why lower-quality males would benefit more by joining a lek than they would from other options. A possibility is that the sex ratio biased toward males in the studied populations is responsible for enhancing sneaking behavior of unsuccessful males. In contrast to our experimental results, the hotshot model does not predict female preference for a particular lek size (i.e., as long as the hotshot is present on the lek, females attend the lek; Beehler and Foster 1988). Anecdotal evidence obtained in the field also contradicts the hotshot model for lek formation: after males were captured and marked, they took several days to establish and defend their previous lekking position again. In four cases, we caught hotshots (i.e., symmetric males attended by most females), but the lek never disintegrated as a result of hotshot disappearance (as predicted from the hotshot model). Conversely, in each case, we observed a territorial switch by a neighboring male. Therefore, hotshots seem to exist in the little bustard, but the hotshot model of lek evolution was only partially supported by empirical data. We also found that females preferred leks with heterogeneous male qualities, suggesting that relative rather than absolute mate assessment mechanisms operate in the little bustard, which supports the idea that the presence of a relative hotshot increases the lek attractiveness.

Finally, the black hole model suggests that sexual harassment and male aggressiveness induce high female mobility (Trail 1985; Clutton-Brock et al. 1992; Stillman et al. 1993; Alatalo et al. 1997) that results in clumped male territories. This model has never been tested experimentally in the wild, and it is extremely difficult to test in higher vertebrates. We therefore tried to validate the black hole model for the little bustard through one of its main mechanisms, the depressed male attractiveness toward females for aggressive males. Indeed, we observed a negative relationship between male aggressiveness (measured experimentally) and attractiveness (measured empirically).

However, for practical reasons male aggressiveness was measured in our trials toward other males, not females. In addition, female little bustards (as well as great bustards *Otis tarda*) have a specially designed visual display (raised tail) when they refuse copulation and escape male harassment (Schulz 1985; V. Bretagnolle and F. Jiguet, personal observation), which could be a response to strong sexual harassment in this species, while females might evaluate male aggressiveness through their behavioral response to this visual display. Therefore, empirical and experimental data also provided at least weak support for the black hole model of lek evolution in the little bustard.

*Toward an Integrative Approach: A Russian Dolls  
Model of Lek Evolution*

Mechanisms potentially leading to lek formation have been much disputed. In grouse species, for instance, hotspot, female preference, and hotshot models have all been supported (Bradbury et al. 1989; Gibson et al. 1991; Alatalo et al. 1992; Höglund et al. 1992; Gibson 1996). For the less well-studied exploded lekking species, female mate choice, male territoriality, and male attraction to locations with high densities of females are involved in the dynamic of lek formation in the capercaillie *Tetrao urogallus* (Gjerde et al. 2000). The black hole model has been supported only in ungulates (Clutton-Brock et al. 1992, 1993). Sexual harassment to force copulation on leks is rare in more mobile birds (Foster 1983; Alatalo et al. 1997) but common in mammals (Clutton-Brock et al. 1993; Höglund and Alatalo 1995; Nefdt 1995; Nefdt and Thirgood 1997). Predictions from all four models of lek evolution have been addressed in the ruff: the hotspot (Lank and Smith 1987; Höglund et al. 1998), female preference (Lank and Smith 1992; Höglund et al. 1998), and hotshot (Widemo and Owens 1995; Widemo 1998) models are supported, while males more aggressive to other males got more matings (Widemo 1997), in contrast to our results. This suggests that aggressiveness toward males should be interpreted with caution because it is aggressiveness toward females that is the mechanism by which the black hole model operates.

Our experimental results on the little bustard supported mechanisms of three of the four competing models of lek evolution: we found female preferences for four-male aggregates but also female apparent direct choice for males of certain phenotypes, while these males were also attractive to other (presumably lower-quality) males. Similarly, predictions of alternative evolutionary models have been supported by different studies, with female preferences occurring in most cases (Höglund and Robertson 1990; Höglund and Alatalo 1995). This is not surprising because predictions deriving from those models are not mutually

exclusive (Clutton-Brock et al. 1993), and some of them are even shared by different competing models (Isvaran and St. Mary 2003). Rather than simply recognizing that theoretical models of lek evolution are not mutually exclusive, we actually speculate that their corresponding mechanisms can operate concurrently or even work sequentially in the little bustard, either temporally or spatially, and that the models may fit together like Russian dolls. At a large spatial scale and an initial stage, following the black hole model, female mobility and sexual harassment may induce male clustering. Then at a smaller spatial scale, female preferences for particular male traits as well as particular lek size may have been favored in initial clusters (Clutton-Brock et al. 1992). Kleptoparasitic (sneaking) behavior of unsuccessful males around the hotshots may ensure the long-term maintenance of leks, while the female preference and the hotshot mechanisms may explain where leks form and how they are structured (Sutherland 1996).

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