



## RESEARCH PAPER

# Are Centrally Displaying Males Always the Centre of Female Attention? Acoustic Display Position and Female Choice in a Lek Mating Subterranean Insect

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**Abstract**

Several conceptual models seek to explain patterns of male display and factors that influence female mate choice in lek mating systems. The central advantage model predicts that males displaying at or near the lek centre should be more attractive to females than are males positioned along the lek periphery. Females may exhibit biases toward these centrally displaying males based on either spatial or display-related cues. We tested the prediction of the central advantage model in investigating the importance of male display position in the subterranean and lek mating prairie mole cricket (*Gryllotalpa major*). *Gryllotalpa major* males form mating aggregations in the early spring and produce an acoustic advertisement signal from a constructed calling chamber at the soil surface. Pair formation occurs in the calling chamber, and males typically maintain these structures for the duration of the reproductive season. To assess whether *G. major* females exhibit a preference for males calling from centrally located acoustic burrows, we documented the spatial position and number of female attractions for all advertising males across the focal lek. Six spatial attributes related to display position were reduced using principal component analysis and examined for an association with male attractiveness. We found that in general, female attractions were distributed randomly across the lek; male attractiveness was not related to proximity to the lek centre nor to any factor associated with display position. The most highly attractive males, however, were located further from the lek centre and from nearest calling neighbours than other attractive males. Advertising males that segregate themselves within the aggregation and locate nearer the lek margin may gain a geometric advantage resulting in the increased probability of attracting a searching female.

**Introduction**

The proximal mechanisms and evolutionary patterns of lek mating systems have received considerable attention from investigators. While a precise definition of what comprises lekking behaviour is still debated, most accept the general parameters proposed by Bradbury (1985). Lek mating systems typi-

cally exhibit an exaggerated mating skew, with a small proportion of the display participants (generally males) monopolising the majority of the matings (Widemo & Owens 1995). Females that visit these display aggregations often exhibit a strong preference for particular male phenotypes, preferences that may be related to intrinsic elements of the display, to the display position itself, or to both (Kirkpatrick & Ryan

1991; Niyazi et al. 2008). Addressing the interplay of these two factors has been an especially challenging problem for investigators (Bradbury 1981; Saether et al. 2005), especially in lek systems in which males exhibit mobility during display. The position of male display can influence the intensity of a signal received by an attending female (Robert 2005), and less robust males can exploit the physical constraints of signal transmission by optimising display position in relationship to other more dominant males (Thornhill 2000; Shuster & Wade 2003). In most studies focused on aggregated mating assemblies, males are minimally constrained from relocating the spatial position of sexual display during sessions (Gjerde & Wegge 1989; Höglund & Robertson 1990; Gibson 1996; Field et al. 2002; Hingrat et al. 2008; Castellano et al. 2009; Cordoba-Aguilar et al. 2009). In those lek mating systems in which male position is relatively fixed during display, males often relocate spatially between bouts (Partecke et al. 2002; Dijkstra et al. 2008; Duraes et al. 2009; Young et al. 2009). This spatial plasticity can have implications for resolving female preference and male attractiveness (Bro-Jorgensen 2008).

Explanations for the observed patterns of male display and female mate choice in lek mating systems have been offered in the form of several conceptual models (see Höglund & Alatalo 1995 for a review). These models may consider the effect of factors such as intrinsic display parameters, female display preferences and visitation dynamics, lek size and attendance, male display position and inter-male spacing on the lek, inter-lek spacing and/or ecological variables when measuring male mating success. Most lead to specific predictions regarding male attractiveness and its relationship with signal quality and male display position within the lek and in regard to other advertising males.

One particularly ubiquitous pattern that emerges in lek mating systems is that of central male dominance. Field studies have shown that in many lek mating systems, centrally displaying males attract more visiting females; this can occur irrespective of female preference for intrinsic elements of male display (Höglund & Lundberg 1987; Fiske et al. 1998; Kokko et al. 1998; Bro-Jorgensen 2008). Thus, in the central advantage model, males occupying the central location of the lek are predicted to achieve greater mating success than males advertising along the lek periphery. This geographically biased mating skew can emerge because of (1) asymmetry in male display, with central males exhibiting a more conspicuous signal and visiting females exhibiting a

preference for display attributes, (2) female assessment of male quality based upon territory occupation alone, (3) lower mate search costs associated with higher male density and lower predation risk near the lek centre. Thus, if searching females are utilising male position as a proxy for dominance or merely optimising mate search costs by preferentially sampling near the lek centre, no strong preference for elements of the male display may necessarily be observed.

The prairie mole cricket (*Gryllotalpa major* Saussure) is a burrowing insect (Orthoptera: Gryllotalpidae) found only in a few isolated tallgrass prairie fragments located in the south-central United States (Fig. 1). Males aggregate in leks in the early spring to advertise for mates and construct an acoustic calling chamber at the surface terminus of a complex subsurface burrow system from which they broadcast an acoustic sexual advertisement call (Audio S1) for approximately 30 min each evening beginning at sunset (Walker & Figg 1990; Hill 1999, 2000; Hill et al. 2006). Males maintain these calling chambers throughout the reproductive season and typically do not relocate them unless the structure is physically disturbed (own data). Leks often occur on or near the same grassland sites across years (Hill pers. comm.), but it is not known whether males use these same areas outside of the reproductive season for foraging or refugia. Males are not observed to modulate the intensity of acoustic display in response to direct intrasexual encroachment, group size, or shifts in female availability, but temporal (chirp rate) and spectral (harmonic structure) elements of the male acoustic signal do correlate with nearest neighbour distance (Hill 1998). Two



**Fig. 1:** Male prairie mole cricket (*Gryllotalpa major* S.) and inset map of study site and current area of distribution of the species in Arkansas, Kansas, Missouri and Oklahoma USA (shaded).

elements of the male sexual display call are known to correlate with male size: dominant frequency and the number of syllables per chirp, with larger males producing calls of lower dominant frequency and greater numbers of syllables per chirp (Howard & Hill 2006).

Sexual behaviour in *G. major* females has not been well documented and is only mentioned in the literature anecdotally. Airborne females search for mates across the extent of the lek, flying 1.5–5.0 m above the ground, presumably assessing individual male spatial position and/or acoustic attractiveness amid the complex acoustic chorus (Howard & Hill 2006). While females can likely detect signalling males from about 76 m (Howard et al. 2008), they typically drop to the substrate within 3–5 m of a displaying male and then perform walking phonotaxis to the male's calling chamber for pair formation and mating. Females are not known to use the acoustic burrow as a resource for oviposition, however (Hill 1999). It is not known whether female mate choice in this system is passive and represents a scramble for available males, or whether females are actively discriminating between displaying males based upon elements of the acoustic display, or whether females are concentrating mate selection efforts in a preferred spatial location within the lek. While the mechanisms of female choice in lek mating animals have been the focus of intense study (Gibson & Bradbury 1985; Höglund & Lundberg 1987; Beehler & Foster 1988; Gibson 1992; Gibson & Bachman 1992; Kokko 1997; Saether et al. 2005; Duval & Kempnaers 2008; Castellano 2009; Young et al. 2009), no published study has yet examined female choice in a lek mating system in which displaying males remain entirely sessile during advertisement and exhibit such a high level of display site fidelity throughout the reproductive season.

Here, we test the predictions of the central advantage model in investigating the importance of male display position in determining female mate selection in *G. major*. As costs associated with predation risk are thought to be high for searching females, and as these costs are thought to be lower near the lek centre where male density is highest, we hypothesise that centrally displaying *G. major* males will exhibit a competitive advantage in attracting mates in general support of the central advantage model. Thus, we predict a non-random pattern of female responses to male display across the lek, with female attractions concentrated near the lek centre and spatially marginal males receiving fewer female visits.

## Methods

### Study Site

The study took place at The Nature Conservancy's Tallgrass Prairie Preserve in Osage County, Oklahoma, USA from 14 to 30 Apr. 2009 (Fig. 1). The 16 000 ha study site is known to support a large, self-sustaining population of *G. major*, which has been under study by the authors since 2005. The focal lek was located at 325–335 m above mean sea level on a west-facing slope above a spring-fed tributary stream of Sand Creek (36°51'26"N, 96°25'12"W). The botanical assemblage at the site is typified by C<sup>4</sup> grass species, but some woody growth, primarily post-oak (*Quercus stellata* W.) and blackjack oak (*Quercus marilandica* M.), encroaches along the hilltop to the east of the lek boundary.

### Field Procedures

Beginning on the evening of 14 Apr. 2009 and over the following 16 d that made up the 2009 reproductive season, the acoustic burrows of advertising males were located upon each male's entry into the focal lek. The acoustic burrow, only occupied by the male during the evening display period, was numbered and covered with a cone trap constructed of light-gauge aluminium screening to collect any females attracted to the males' sexual advertisement call (Video S1). The cone trap was set in the soil such that it did not come in contact with or alter the structure of the burrow opening, nor interfere with the transmission of the call. Only females attempting to enter a male's burrow were trapped, but the trap design prohibited contact between the responding female and the calling male; thus, males continued to display for the duration of the bout even when successful in attracting a respondent. All cone traps were checked for the presence of females once the calling session concluded each evening, with the number of females associated with each male's burrow documented. All females were removed from the traps, held in containers with moistened soil, provided food and water *ad libitum* and released at the site at the conclusion of the study. The location of the acoustic burrow of each male on the lek was documented using a Trimble Pro XRS GPS unit with a TSC1 asset recorder (Navigation Limited, Sunnyvale, CA, USA), accurate to submetre precision ensuring that the burrow coordinates utilised in calculating the spatial arrangements of the lek were resolved beyond the observed nearest neighbour distances.

## Spatial Analysis

Burrow coordinates collected in the field were exported into a geographic information system (ArcGIS 9.3; Environmental Systems Research Institute, Redlands, CA, USA) using Trimble Pathfinder Office software (Navigation Limited) to construct a map from which to calculate metrics describing the spatial arrangement of displaying males across the lek. The following spatial data were produced using the Spatial Analyst and Spatial Statistics tools in ArcGIS 9.3: distance from lek centre, near neighbour distance, far neighbour distance, mean neighbour distance, distance to lek edge and number of males advertising within 10 m. The lek centre was calculated as the mean  $X$  and  $Y$  values of all of the burrow locations across the lek, and the number of proximal males was calculated using a 10 m buffer polygon created around each acoustic burrow. For purposes of this study, the lek edge distance was defined as the Euclidian distance from the male's burrow to the nearest boundary line of a minimum convex polygon created from a composite of all of the burrow locations. Standard  $z$ -scores calculated from these raw spatial data were then used in all subsequent analyses.

## Statistics

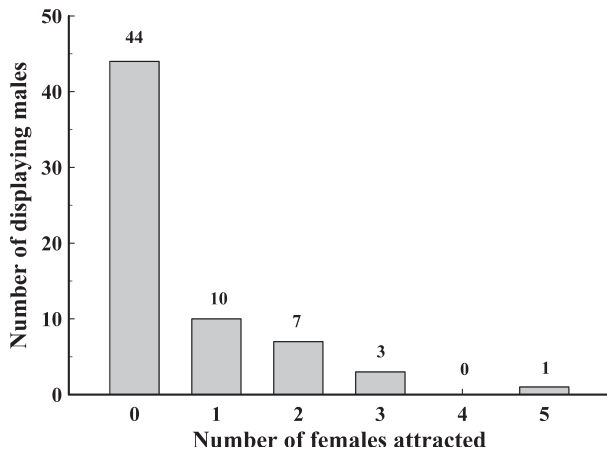
To characterise the spatial arrangement of displaying males across the lek, the Average Near Neighbour Ratio was calculated. This metric compares the mean near neighbour distance of all males across the lek to a hypothetical random distribution to assess the level of clustering or dispersal among displaying males. To test the primary prediction of the central advantage model, a combination of standard parametric and spatial statistics was used. To test for an association between male attraction status (females attracted: Y/N) and the distance the male displayed from the lek centre, these data were entered into a nominal logistic regression model with a chi-square test for significance. To test for an association between the number of females attracted and distance from the lek centre, ANOVA on a bivariate fit linear regression model was used. To detect a non-random spatial pattern of female responses to male calling song across lek, with a special interest in clustering at the lek centre, the Moran's  $I$  spatial autocorrelation test statistic was used (Mitchell 2005). Given a set of features (male acoustic burrow locations) and feature attributes (number of female attractions), this test evaluates

whether the attribute variable pattern displayed is clustered, dispersed or random. To identify the geographic location of any detected spatial clustering with respect to the feature attribute, the Getis-Ord  $G_i^*$  test statistic was used. This test identifies where across the landscape significantly high or low values of a feature attribute (number of female attractions) are clustered spatially. To identify differences in spatial attributes between attractive and unattractive males, an unequal variance  $T$ -test was used (Ruxton 2006).

To detect whether females were selecting mates because of spatial cues, we examined the relationship between male display position within the lek, and attractiveness to visiting females. Prior to testing spatial data for a relationship with female response, principal component analysis was used to collapse inter-correlated variables into rotated (Varimax) factors. Factors with an Eigenvalue greater than 1.0 were retained, tested for normality and log transformed where appropriate. To detect an association between a male's display position with attraction status (female attracted: Y/N), the reduced factors were entered into a nominal logistic regression model with a chi-square test for significance. To detect an association between a male's display position and the number of females attracted, ANOVA on a bivariate fit linear regression model was used. A *post hoc* multivariate effects likelihood analysis was then used to detect which variable(s) within the factor contributed most of the effect to the significant association. Any identified variables were then tested for significant spatial relationships using the Moran's  $I$  and Getis-Ord  $G_i^*$  spatial statistics, as described previously. All tests for significance were two-tailed. Statistical tests were conducted using SPSS for windows version 17.0 (SPSS, Inc. Chicago, Illinois, USA), JMP 7.0 (SAS Institute Inc., Cary, NC, USA) and the spatial statistics toolbox in ArcGIS 9.3.

## Results

Over the 17 d of the study, 65 males were observed acoustically displaying within the focal lek site. The area of the lek (as defined by minimum convex polygon method) was 15 764 m<sup>2</sup>, with a male density of one male per 242.52 m<sup>2</sup>, and a mean inter-male distance of  $58.41 \pm 21.35$  m. The 65 males were distributed in a clustered pattern (Average Near Neighbour Ratio = 0.754,  $Z = -3.790$ ,  $n = 65$ ,  $p = 0.0002$ ,  $n = 65$ ), with a mean near neighbour distance of  $6.39 \pm 8.24$  m. While only three males emerged to display on the first evening of activity,



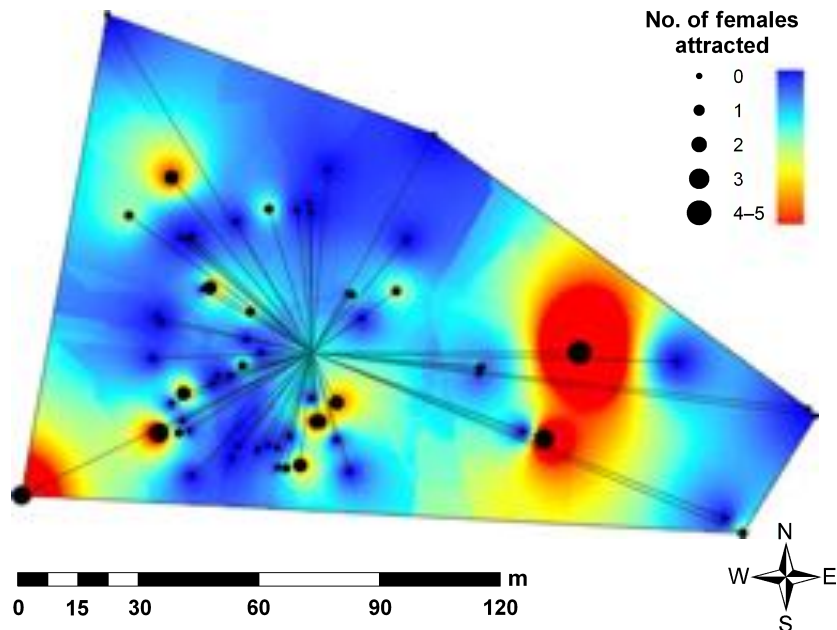
**Fig. 2:** *Gryllotalpa major* female response frequencies across the lek, exhibiting the skew commonly reported in lek mating systems. Sixty-five displaying males were visited by 38 females. Sixty-six per cent of the males attracted no females, while 11 of the males (17%) accounted for 74% of the female attractions.

88% of the males had entered the display aggregation by the eighth evening of the study. Female attendance on the lek was even more temporally concentrated than that of males. The first females arrived on the lek on the fifth day of male display, with 90% of the females visiting during three non-consecutive evenings. A total of 38 females responded to the sexual advertisement call of displaying males, exhibiting a response pattern con-

sistent with the classic mating skew documented in most lek mating systems (Fig. 2).

**Central Advantage Model Prediction**

Analysis of the pattern of female response with regard to male display position indicated no association between male proximity to the lek centre and either attraction status (chi-square test:  $\chi^2 = 0.069$ ,  $p = 0.792$ ,  $df = 1$ ) or number of attractions (ANOVA:  $F_{1,64} = 0.201$ ,  $p = 0.655$ ). Analysis of the spatial pattern of female response to male sexual display indicated no spatial autocorrelation between male calling position and attractiveness to females (Global Moran's I index = 0.44,  $Z = 1.09$ ,  $p = 0.28$ ,  $n = 65$ ), with female responses distributed randomly (Fig. 3). Principal component analysis collapsed the six spatial variables into two rotated factors representing 79.7% of the observed variation in the dataset (Table 1). Neither reduced spatial factor, however, exhibited an association with either attraction status or number of attractions (Table 2). However, the Getis-Ord  $G_i^*$  test identified four highly attractive males within the lek (Figure S1). While neither spatial factor distinguished these males from other males, separate analyses of individual spatial variables (Table 3) indicated that these highly attractive males displayed at greater mean distances from the lek centre (unequal variance  $T$ -test:  $t = 2.17_{5.05}$ ,  $p = 0.04$ ) and from their nearest neighbours (unequal variance  $T$ -test:  $t = 2.30_{5.85}$ ,  $p = 0.03$ ) than did other successful males (Fig. 4).



**Fig. 3:** Map of *Gryllotalpa major* female response to male display across the lek arena, with marker size and colour bar indicating the number of females attracted to the male calling from that position.

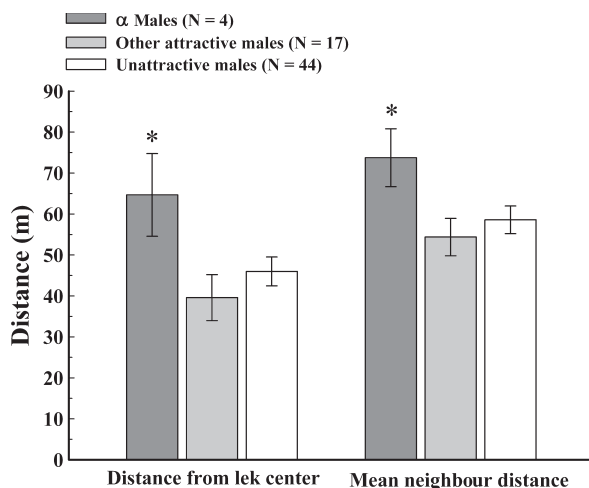
**Table 1:** Raw spatial data (n = 65) were reduced using PCA to produce two rotated factors (Sp1, 2) with Eigenvalues greater than 1.0 accounting for 79.7% of the dataset variation

Raw variable	$\bar{x}$	SD	Min.	Max.	Factor
Far neighbour	148.55	22.97	108.90	204.00	Sp1
Mean neighbour	58.41	21.35	41.07	131.00	Sp1
Centre distance	45.46	23.53	2.32	114.40	Sp1
Edge distance	23.67	13.03	0.00	52.30	Sp1
Near neighbour	6.39	8.24	0.72	43.67	Sp2
10 m neighbours	3.77	2.18	1.00	9.00	Sp2

**Table 2:** Chi-square test on logistic regression of attraction status (female: Y/N), lek centre distance and two reduced test variables, with  $\chi^2$ , p values and degrees of freedom from a whole model test provided

Test variable	Attraction status			No. of attractions		
	$\chi^2$ value	p	df	F ratio	p	df
Lek centre dst	0.069	0.792	1	0.201	0.655	1,65
Spatial factor 1	0.178	0.673	1	0.027	0.870	1,65
Spatial factor 2	0.477	0.490	1	1.953	0.167	1,65

Test variables were also examined with ANOVA against a bivariate fit linear regression to the number of females attracted, with F ratio, p values and degrees of freedom provided.



**Fig. 4:** Histogram of *Gryllotalpa major* male subgroup (highly attractive  $\alpha$  males, lesser attractive males, unattractive males) and mean acoustic display distance from the lek centre and from other nearest males. Significantly different subgroups are noted with asterisks.

## Discussion

Our results demonstrate that in prairie mole cricket mating aggregations, male mating success is not driven

by proximity to the lek centre as predicted by the central advantage model. Despite exhibiting a nearly obligate subterranean existence, adult prairie mole cricket males aggregated briefly at the surface for the sole purpose of pair formation, competing intensely for flying females. While our results show that the sex ratio across the lek strongly favoured males as in lekking fiddler crabs and Kakapos (Trewick 1997; Croll & McClintock 2000), with a mating skew in which only 32% of the males attracted females, sex ratio alone did not explain the skew. Males began establishing display sites at the lek several days prior to the presence of females as in lek mating gallinaceous birds, marine iguanas and Hawaiian *Drosophila* (Bradbury 1985; Shelly 1989; Shelly 1990; Gibson 1992; Dronney 1994; Wikelski et al. 1996; Partecke et al. 2002; Boyko et al. 2004), with most males in attendance on the evening of first female arrival. Advertising males exhibited near complete site fidelity to the display position, as do male Cichlids (Dijkstra et al. 2008; Genner et al. 2008). A few late-arriving males, most of which were unsuccessful in attracting a female, constructed acoustic burrows in proximity to established attractive callers. Most females arrived at the lek in the first 20 min of acoustic activity, which coincided with the dusk transition when the risk of predation is likely lowest (Rintamaki et al. 1995; Hamilton et al. 2006). Unlike lek mating systems in which centrally displaying males achieve a disproportionate number of matings, however (Gibson & Bradbury 1985; Saether et al. 2005; Castellano 2009), prairie mole cricket males advertising near the lek centre did not differentially attract searching females.

In lek mating species, females are known to discriminate between males such that steep mating skews for particular display phenotypes are often observed (Bradbury & Gibson 1983; Saether et al. 2005). While our study detected this form of skewed mating pattern, suggesting the presence of female preference in the system, this bias was not strongly associated with male calling position within the focal lek. We interpret these results with some caution, however, as both male display behaviour and female mate selection criteria could differ between leks that exhibit dissimilar biotic or abiotic structure. While not under examination in this study, *G. major* females may be selecting mates based upon characteristics of the male sexual advertisement call. Elements of the male calling song are known to correlate with signaller size, and female discrimination for these or other calling song characteristics

**Table 3:** Between group comparison of highly attractive ( $\alpha$ ) males with two other subgroups of males on the lek

Variable	$\alpha$ males (n = 4)		Unattractive males (n = 44)		Test statistic	p	Other attractive males (n = 17)		Test statistic	p
	$\bar{x}$	SD	$\bar{x}$	SD			$\bar{x}$	SD		
Sp1	0.604	0.791	0.036	0.993	$t = 1.345_{3,92}$	0.25	-0.234	1.038	$t = 1.789_{5,75}$	0.06
Sp2	-0.988	1.310	0.058	0.965	$t = -1.565_{3,31}$	0.21	0.080	0.958	$t = -1.542_{3,79}$	0.10
NN dist. (m)	73.75	14.13	58.58	22.44	$t = 1.936_{4,52}$	0.06	54.37	18.87	$t = 2.303_{5,85}$	0.03
Lek ctr dist. (m)	64.68	20.22	45.99	23.39	$t = 1.745_{3,77}$	0.08	39.58	23.19	$t = 2.169_{5,05}$	0.04

$\bar{x}$  and standard deviations are provided, along with the results of an unequal variance T-test between the  $\alpha$  males and both other male subgroups.

could produce the observed mating skew. Field recordings and playback experiments could provide insights into the underlying mechanisms driving differential attractiveness in *G. major* males within the lek.

While the results of our study point to other mechanisms as possible explanations for the variation in male mating success in the system, our results do show that a few highly attractive males displayed further from the lek centre and from their nearest calling neighbours than other attractive males, defying our original prediction of a central male advantage and the pattern documented in other lek mating systems. One explanation could be that dominant males may attempt to limit spillover matings by lesser males by distancing themselves from their nearest competitors and the highly populated central region of the lek. A more parsimonious explanation might be that airborne females may simply find it less costly to localise those slightly segregated males within a highly clustered and noisy display environment. In much, the same fashion that clustering reduces predation on interior occupants and raises in contact with predators in marginal herd members (Hamilton 1971), peripheral males may have a geometric advantage over males advertising in the lek interior in terms of the probability of encountering a searching female. This male spacing strategy could be driven by the physics of sound transmission and the constraints to sound production imposed by the size range of the signaller (Bennet-Clark 1998), along with the intrinsic auditory sensitivity range of the species (Römer & Bailey 1986; Forrest & Green 1991; Mason et al. 1998; Howard et al. 2008). The acoustic signal of males displaying from the lek periphery may effectively mask the signal of interior males (Bailey & Morris 1986; Römer 1993; Gerhardt & Huber 2002), or may generate a precedence effect (Wyttenbach & Hoy 1993; Litovsky et al. 1999; Lee et al. 2009) among phonotactically responding females. Thus, female mate choice and male display in this system may

have evolved as a simple solution for minimising predation among searching females while simultaneously maximising the fitness-related benefits received by males able to exploit the presumably costly display territory associated with the lek margin.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** 3D map of Ordis Gi\* scores across the lek.

**Audio S1.** Thirteen second clip of the *G. major* male sexual advertisement signal.

**Video S1.** *G. major* female response to male acoustic display and cone trap structure.

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