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## The significance of hotspots to lekking topi antelopes (*Damaliscus lunatus*)

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**Abstract** Controversy has surrounded the question of why lek-breeding has evolved in certain ungulate species. Can the behavior be explained simply by males mapping onto a female distribution that is determined by factors unrelated to mating? Or are leks created because estrous females distinguish between males and favor males who cluster? Here I address these questions by looking at spatial distribution in lekking topi antelopes (*Damaliscus lunatus*). Contrary to the predictions of a model assuming male clustering in the zone of maximum female range overlap, territories were highly clustered also within this zone, and lek size correlated positively with population density. In support of models derived from the ideal free distribution of males onto female dispersion, leks were in areas with high female density during the rut. However, models not taking into account both individual variation in male quality and female mate preferences failed to explain the extreme male clumping also within high density areas, which was revealed by a strongly male-biased sex-ratio on leks. Additional support for the female preference-based model came from the finding that estrous females concentrated onto leks. Female preference for clustered males may develop if males initially follow an ideal free distribution of unequal competitors with high quality males slightly clustered at density hotspots; positive feedback between female benefits of preference for clustered males and male benefits of clustering could lead to contraction of the territorial network and lek behavior. Thus only the female preference-based model correctly predicted a

negative correlation between male mating rate and resource density.

**Keywords** Ideal free distribution · Unequal competitors · Female mate preference · Lek evolution · Ungulates.

### Introduction

While recent research has led to significant advances in our understanding of the evolutionary basis for most ungulate mating systems (e.g., Jarman 1974; Gosling 1986; Clutton-Brock 1989; Thirgood et al. 1999; Brashares et al. 2000), the question of why lekking develops in certain species has remained controversial (Gosling 1986; Clutton-Brock et al. 1993, 1996; Höglund and Alatalo 1995; Carbone and Taborsky 1996). The hotspot theme has had a pivotal role in inspiring spatial models of lek evolution, and of primary importance amongst these are the female home range overlap model (FHO) (Bradbury et al. 1986), the simple ideal free distribution (IFD) (Fretwell and Lucas 1970), the ideal free distribution of unequal competitors (IFDUC) (Sutherland and Parker 1985) and the ideal free distribution of unequal competitors with feedback from female mate preference (FP) (Sutherland 1996). The basic idea behind these models is that males position themselves strategically on hotspots where female encounter rate is highest, while female dispersion, at least originally, is unaffected by mating behavior. However, there are crucial differences between the models in what aspect of female distribution they treat as critical and whether any importance is placed on individual differences between males and female mating preferences.

Without invoking any underlying cause for female dispersion, the FHO model proposes that leks may develop in populations where there is moderate overlap of female home ranges (Bradbury et al. 1986). In replicated computer simulations of the model, promiscuous males settled optimally onto a population of mobile females,

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**Table 1** Predictions of four spatial models of lek evolution

	Area covered by lek territories	Sex-ratio on lek	Ratio of females in estrus on lek	Correlation male mating rate/resource density	Correlation lek size/population density
Female Home Range Overlap model (FHO)	Zone of max. female range overlap	Male-biased	Un-biased	(No prediction)	Negative
Ideal Free Distribution model (IFD)	Max. density zone	Un-biased	Un-biased	None	Positive
IFD model with Unequal Competitors (IFDUC)	Max. density zone	Female-biased	Un-biased	Positive	Positive
Female preference-based IFDUC model (FP)	Part of max. density zone	Male-biased	Higher	Negative	Positive

who may mate at any point within their home range. The value of a female to a male is reduced in proportion to the number of other males that she meets in total, which is directly related to the number of other males settled within her home range. The simulations showed that, following these rules, males cluster in zones of maximum overlap between female home ranges. Because a female is 'devalued' throughout her entire range when males settle anywhere within it, the advantage of settling in the zone of high female range overlap persists in spite of the presence of other males within this zone, thus the sex-ratio on leks becomes male-biased. As females are assumed to mate with equal probability anywhere within their range, the ratio of females in estrus is predicted to be similar on and off leks. Increasing density in the simulations lead to reduced male clustering because females became more evenly dispersed as measured by the dispersion index (variance / mean). Thus, lek size (i.e. the number of males in each tight cluster) correlates negatively with density. In summary, the range overlap model predicts that leks cover the area of highest female range overlap, that the sex-ratio on leks is male-biased, that the proportion of females in estrus is similar on and off leks, and that there is a negative correlation between lek size and density (Table 1).

Alternatively, leks could develop because males cluster in the areas of extreme female density, rather than at sites of maximum female range overlap (Alexander 1975; Kruijt et al. 1972; see also McNaughton 1988). In this case, both the IFD (Fretwell and Lucas 1970; Fretwell 1972) and the IFDUC (Sutherland and Parker 1985; Sutherland et al. 1988) models could explain lek systems in the same way they account for other territorial systems, i.e. by male dispersion being determined by female dispersion, which in turn is determined chiefly by resource dispersion (evidence speaks against major anti-predator benefits of lekking in ungulates, Balmford and Turyaho 1992; Bro-Jørgensen 2002). The critical feature of lek systems should then be an extraordinarily high female density in certain areas, where leks develop. As both models in common with the FHO model assume that female dispersion is determined by factors unrelated

to mating activity, they also predict a similar proportion of females to be in estrus on and off lek. However, in contrast to the FHO model they predict a positive correlation between population density and lek size because increasing female numbers in areas of high resource density will cause more males to settle on leks.

The IFD and IFDUC models are distinguished from each other by male settlement rules. In the IFD model, individual males set up territories in an ideal free manner, i.e. no competitive difference between individuals is assumed and males settle in direct proportion to the mean input of females (Fretwell and Lucas 1970; Parker and Sutherland 1986). Therefore, according to this model the sex-ratio on and off lek is predicted to be similar. Furthermore, because all males are equal competitors, no systematic variation in male mating rate is expected, and no correlation between male mating rate and resource density is predicted.

In contrast, the IFDUC model takes into account that males may vary in competitive ability and therefore settle in a despotic manner, where superior competitors exclude others (Fretwell 1969). The superior competitors are predicted to cluster in the most attractive areas where the concentration of resources, and hence females, is highest (Sutherland and Parker 1992). Because the superior competitors are able to defend a disproportionate number of females (Parker and Sutherland 1986), the sex-ratio on lek is predicted to be female-biased. Furthermore, because superior competitors achieve higher mating rates by defending lek territories where resources attract females, a positive correlation between male mating rate and resource density is predicted.

Based on the ideal free distribution of unequal competitors, a model of lekking has been developed which in addition assumes positive feedback between female preference for clustered males and the degree of male clustering (Sutherland 1996). If males initially settle in a despotic manner as described in the IFDUC model above, estrous females might benefit from a preference for mating with clustered males since high quality males (i.e. superior competitors) cluster in areas with high density of food resources and females. Given heritability of

male quality and the female preference for clustered males, these traits are predicted to covary and the female preference will spread in the population (for evidence of covariance between female preference and the preferred male trait, see Bakker and Pomiankowski 1995). With rising numbers of females mating in the area of maximum territorial clustering, benefits to males of setting up territories here will increase; as a result, escalating intramale competition will cause the territorial network to contract (see also Pelabon et al. 1999). The correlation between male quality and the degree of territorial clustering will strengthen which in turn will provide increasing benefits to females of preference for mating in clusters. The result is a runaway process leading to lek formation. Thus, according to the FP model, leks will form in areas of high density, but because females predominantly visit leks for mating purposes, the sex-ratio is predicted to be male-biased on lek and the proportion of females in estrus is predicted to be higher here. The model predicts a positive relationship between population density and lek size since at high densities increasing numbers of estrous females on lek will enhance the attractiveness of lek territories to males. Finally, the runaway process causes male clustering per se to replace food resources as the basis for attracting estrous females, and with the most successful males being defenders of overutilized territories in the lek center, a negative correlation between male mating rate and resource density is predicted.

Topi antelopes (*Damaliscus lunatus*) are among the half dozen ungulate species known to lek (Höglund and Alatalo 1995). They are medium-sized, homeomorphic antelopes in which both sexes wear lyrate-shaped horns. Being grazers, they favor open to lightly wooded grasslands (Estes 1991). Females are typically found in groups, the size of which depends on population density. Males defend territories, which are of key importance to secure matings. Using data on lekking topi antelopes, I here test the key predictions of the four spatial models of lek formation referred to above (Table 1).

Firstly, I investigate if leks cover the zone of maximum female range overlap (FHO) and whether they are found in areas of high female density (IFD, IFDUC, FP). Secondly, I test if the sex-ratio on the lek is male-biased (FHO, FP), female-biased (IFDUC) or unbiased (IFD). Thirdly, I test if the ratio of females in estrus on lek is higher than elsewhere (FP) or similar (IFD, IFDUC, FP). Fourthly, I test if food density and mating success of the territory holder is positively correlated (IFDUC), negatively correlated (FP) or uncorrelated (IFD). Finally, I test if lek size and population density is negatively (FHO) or positively correlated (IFD, IFDUC, FP).

## Methods

### Study area

The fieldwork took place between March and July 1998 in the Serengeti National Park (SNP), Tanzania (1°30'–3°20'S,

34°00'–35°15'E) and between November 1998 and June 2000 in the adjoining Masai Mara National Reserve (MMNR), Kenya (1°15'–1°43'S, 34°47'–35°24'E). The study sites were covered by open, rolling grassland, characterized by red oat grass (*Themeda triandra*), with woody vegetation along drainage lines. The numerous ungulate species included blue wildebeest (*Connochaetes taurinus*), Burchell's zebra (*Equus burchelli*), Thomson's gazelle (*Gazella thomsoni*) and impala (*Aepyceros melampus*), and predators included spotted hyena (*Crocuta crocuta*) and lion (*Panthera leo*). From the Focal Study Area (FSA; 153 km<sup>2</sup>) in MMNR, which included two leks (leks A and B), data was gathered on population density, spatial distribution, sex-ratios, female reproductive states, male mating rates, food density and lek sizes (see later). Additional data were collected from the Olorukoti plain (48 km<sup>2</sup>) in MMNR (population density, male mating rates, food density, lek size), and from the Dutwa plain (155 km<sup>2</sup>) in SNP (population density, lek sizes). One lek (lek C) was located on the Olorukoti plain, and two leks on the Dutwa plain. The topi rut in MMNR typically takes place during the long rains between mid-March and mid-May (Bro-Jørgensen 2001).

### Data collection

#### Total counts

Total counts were conducted by driving strategically defined routes mainly along the 'shoulder' of the sloping plains. As the study sites were open plains, visibility was typically several kilometers. In addition to frequent scans with binoculars (SUNAGOR 13–50×27), a telescope (FOCUS 20–50×70) was used for thorough scans at certain vantage points. To avoid counting individuals more than once, all surveys were completed within a day and herds were recognized by the presence of well-known individuals. The locations of herds and individuals were recorded using a GPS receiver (GARMIN GPS 40). Topi attain adult morphology at approx. 1.5 years (Mertens 1984), and adult males, adult females, and younger animals were counted separately.

In order to determine distributional patterns as well as overall population densities, 11 total counts were carried out within FSA (17 February, 14 April, 29 May, 6 June and 30 December 1999; 28 January, 27 February, 29 March, 30 April, 23 May and 23 June 2000). The variation in total rainfall over the 30 days before each total count (75±20 mm, mean±SE) closely reflected the annual variation in monthly rainfall measured between July 1998 and June 2000 (71±14 mm; Mann-Whitney:  $U=132$ ,  $n_1=11$ ,  $n_2=24$ ,  $P=1.00$ ). In order to determine population densities only, four total counts were carried out on both the Olorukoti and the Dutwa plains.

#### Individual identification surveys

During 3- to 4-h long surveys carried out through the duration of the study, locations of all known individuals in FSA were recorded using a GPS receiver. Care was taken to sample all parts of the study area regularly although the surveys were stratified in favor of areas known from the most recent total count to have high topi densities. Also, areas adjoining FSA were occasionally surveyed to assess whether individuals left the area. Individuals were recognized from natural variation, primarily in horn morphology, coloration, and scarring (Gosling and Petrie, 1990). The reliability of individual identification was confirmed by accordance of size measurements from separate sightings (repeatability: 0.91,  $F_{85,118}=26.64$ ,  $P<0.0001$ , see Bro-Jørgensen and Durant 2003).

#### Sex-ratio and female reproductive state on and off lek

For both the rut and non-rut period, the adult sex-ratio (females:males) was determined on leks and at random transects throughout the rest of the study area. While sex-ratio on lek was

calculated from all the adult topi present, the sex-ratio in the rest of the study area was determined by counting all the adult topi present within 500 m of either side of a 7-km random road transect. Counts were evenly distributed over the day.

During the rut, the proportion of females who were in estrus was measured on and off lek. In order to take diurnal variation into account, five different times of the day were sampled: dawn (0630 hours), mid-morning (0930 hours), noon (1230 hours), afternoon (1530 hours) and dusk (1830 hours). Each time of day was sampled on 15 separate days. I judged whether females were in estrus based on whether they caused excitement (i.e., intense displaying, tripping at a distance, 'freezing', or spontaneous ejaculation) in males following ano-genital sniffing.

#### *Male mating rates and food density*

During the rut, daytime scans for all matings were carried out on predetermined subsets of territories around three leks: at lek A 19 territories were surveyed for 10 days in 1999 and 20 territories were surveyed for 6 days in 2000, at lek B 21 territories were surveyed for 12 days in 2000, and at lek C 25 territories were surveyed for 4 days in 2000.

Forage quality on the territories was measured by a green leaf index using a method similar to that described in Balmford et al. (1992), which is based on the finding that topi select for green leaf in their diet rather than particular grass species (Duncan 1975). On 25 random sites within each territory, a 21×21-cm polystyrene tile weighing 25 g was left to rest on the grass and the following three measures were taken: greenness (the proportion of the four leaves closest to the corners of the quadrat which was scored as green rather than withered), grass cover (cover under the translucent tile estimated to the nearest 5%), and sward height (the distance from the ground to the centre of the tile). By multiplying the three measures and taking the mean of the 25 products, an index of food availability, the green leaf index, was calculated. Territories were sampled during the rut in May 1999 and May 2000.

#### *Lek size in relation to population density*

In order to determine the relationship between lek size (i.e. the number of territory-holding males per lek) and population density, I used data from both the present and previous studies on lekking topi. Data from the present study relates to the Dutwa plain, SNP in 1998, and the Burrungat and Olorukoti plains, MMNR in 2000. Data from previous studies relate to the Nyaruhuru and Central plains, Akagera National Park (ANP) in 1973 (Monfort-Braham 1974, 1975), the Dutwa plain in 1973 (Duncan 1975; density calculated from aerial census data provided by P. Duncan), and the Olorukoti plain in 1984 (Gosling and Petrie 1990; density estimate based on Ottichilo et al. 2000 and aerial survey maps from the Department of Resource Surveys and Remote Sensing, Ministry of Planning and National Development, Kenya). From the Dutwa and Olorukoti plains, data points were entered from both the present and the earlier studies. The justification for treating observations from the same plains as replicates in these cases is that major changes of lek organization had taken place between the studies, and in the case of Olorukoti, density had changed markedly as well. Thus no lek was included in the analysis more than once.

#### Data analysis

##### *Analysis of total counts*

Topi density was calculated for 153 1-km<sup>2</sup> grid cells covering the focal study area in order to test whether lek locations were characterized by high population density on a large scale. For this purpose, I defined lek vicinity cells as the 1-km<sup>2</sup> grid cells situated at least partly within a 1-km radius of one of the two leks (16 cells). Densities were then compared between the lek vicinity and else-

where by non-parametric statistics. Also, I calculated the dispersion indices for adults of the two sexes as the variance between grid cells divided by their mean (following Krebs 1989).

#### *Lek areas in relation to female range overlap*

Based on resightings during the individual identification surveys in FSA, I determined the ranges of females, who were resighted at least 20 times, and up to 54 times, between November 1998 and June 2000. Using the Animal Movement extension (version 2.0 Beta) (Hooge et al. 1999) to ArcView (version 3.2), ranges were mapped as the minimum convex polygons (MCPs) encompassing all relocation points of individual females. No significant correlation was found between the number of resightings and MCP size, supporting that 20 relocations was a reasonable cutoff point for inclusion in the analysis (Spearman rank correlation:  $r_s=0.30$ ,  $n=16$  females,  $P=0.26$ ).

The zone of highest overlap between female ranges was delineated based on the number of individuals whose MCPs covered the area. The extent of this zone was compared to the extent of lek areas and I investigated if male dispersion within it was even, random or clumped. Moreover, for each female, I estimated home range size as the asymptote of the curve describing the relationship between the number of relocations and the area of the MCP (Jennrich and Turner 1969). The curve was drawn by jack-knifing using the above mentioned software: based on 50 replications for each interval, the mean and standard error of MCPs were calculated for each of around ten increments in the number of relocations. On average, the MCPs encompassing all resightings were 17% smaller than the estimated home range sizes; this limited difference suggests that the pattern in MCP overlap might be indicative of true home range overlap.

#### *Analysis of female reproductive status*

The proportion of females in estrus followed a gamma distribution and was modeled as such in a generalized linear model using S-Plus 2000. The independent variables included in the analysis were location (on/off lek), the time of day and the interaction term between the two; these were tested by backward elimination.

## Results

### Lek areas in relation to population density and female range overlap

During the rut the vicinity of leks had a significantly higher concentration of topi, and of both males and females taken separately, as compared to elsewhere in FSA (Mann-Whitney,  $n_1=16$  1-km<sup>2</sup> cells,  $n_2=137$  1-km<sup>2</sup> cells, all topi:  $U=534.5$ ,  $P<0.001$ ; males:  $U=467.5$ ,  $P<0.001$ ; females:  $U=657.5$ ,  $P=0.003$ ). In contrast, no significant differences could be demonstrated for the period outside the rut (Mann-Whitney,  $n_1=16$  1-km<sup>2</sup> cells,  $n_2=137$  1-km<sup>2</sup> cells, all topi:  $U=786.5$ ,  $P=0.063$ ; males:  $U=858.5$ ,  $P=0.15$ ; females:  $U=1033.0$ ,  $P=0.71$ ). Males were generally more uniformly dispersed than females, and during the rut both sexes had a more even distribution (Table 2).

The mean home range size recorded for 16 females in the FSA was 49 km<sup>2</sup> (SE=4.7, range 19.1–80.6 km<sup>2</sup>). Because females typically moved in large herds, the zone of maximum female range overlap was continuous and extensive, covering 28 km<sup>2</sup> of the 153 km<sup>2</sup> study area. Rather than covering this entire zone, the two leks within

**Table 2** Dispersion indices (variance/mean) for the two sexes in relation to rutting activity in year 2000

	Dispersion index			
	January (pre-rut)	March (rut)	April (rut)	June (post-rut)
Females	66.8	16.1	29.8	60.7
Males	23.5	6.11	5.19	15.7

**Table 3** Results of a generalized linear model fitting the variation in the proportion of females in estrus as a gamma distribution with the dispersion parameter estimated at 1.00. The final model included only significant terms

Parameter	df	Coefficient	Deviance	F	P
Location (on/off lek)	1,147	42.48	197.66	197.14	<0.0001
Time of day × location	1,147	–	9.63	4.80	0.001

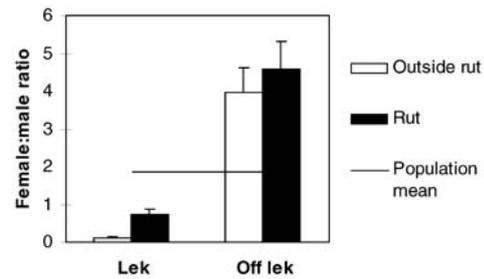
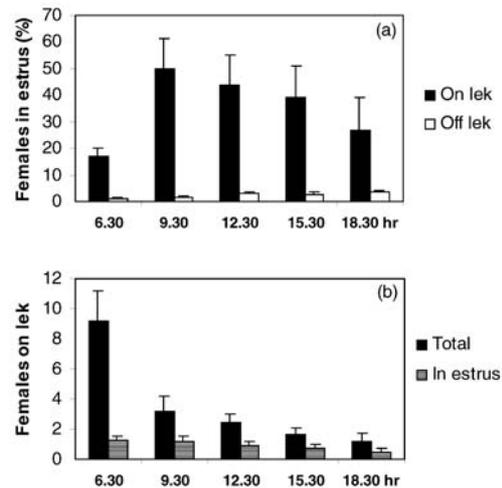
FSA were restricted to less than 1% of maximum overlap zone, being separated by 6.8 km. Thus also within the maximum overlap zone, males were highly clustered in the lek vicinity during the rut (Mann-Whitney:  $U=25.5$ ,  $n_1=10$  1-km<sup>2</sup> cells,  $n_2=18$  1-km<sup>2</sup> cells,  $P=0.001$ ). The ranges recorded for 11 of the 16 females encompassed both lek sites, six individuals were actually sighted at both leks, and all 16 female ranges encompassed at least one lek.

#### Sex-ratio on and off lek

The adult sex-ratio was found to be significantly more male-biased on lek than off lek both outside and during the rut (non-rut: on lek  $0.12 \pm 0.03$ , off lek  $3.98 \pm 0.64$ , Mann-Whitney:  $U=44$ ,  $n_1=88$  counts,  $n_2=30$  counts,  $P<0.001$ ; rut, on lek  $0.71 \pm 0.16$ , off lek  $4.59 \pm 0.70$ , Mann-Whitney:  $U=67$ ,  $n_1=29$  counts,  $n_2=30$  counts,  $P<0.001$ ; Fig. 1). Although the sex-ratio on the lek remained male-biased throughout compared to the population mean of 1.86, it was significantly less male-biased during the rut than outside the rut (Mann-Whitney:  $U=611.5$ ,  $n_1=88$  counts,  $n_2=29$  counts,  $P<0.001$ ). Off lek the sex-ratio was female-biased when compared to the population mean with no significant difference between the rut and the period outside the rut ( $U=399$ ,  $n_1=n_2=30$  counts,  $P=0.44$ ).

#### Female reproductive state on and off lek

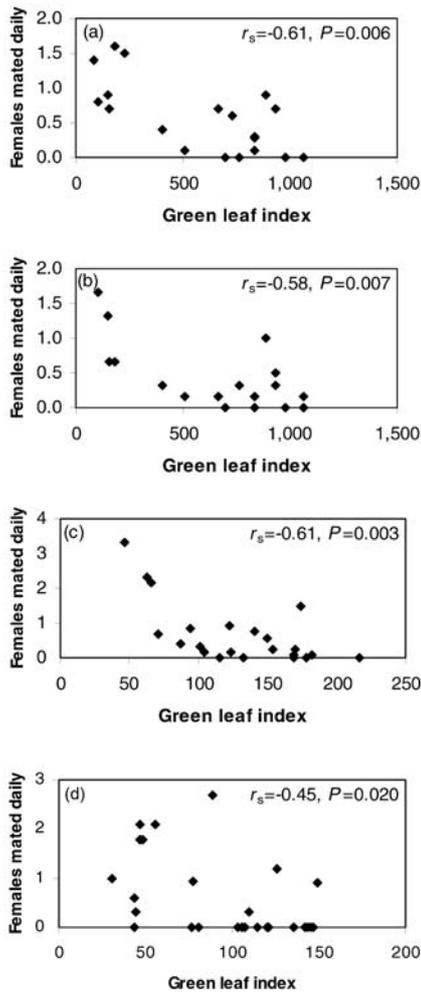
Modelling the proportion of females who were in estrus as a gamma distributed dependent variable showed that (1) a significantly higher proportion of females on the lek were in estrus compared to females off lek, and (2) the time of day showed a significant interaction with lo-

**Fig. 1** Adult sex-ratios (females:males) of topi antelopes (*Damaliscus lunatus*) on and off lek. On lek 88 and 29 counts were conducted outside and during the rut respectively, off lek 30 counts were conducted during both periods. Error bars indicate SE**Fig. 2. a** The mean proportion of females in estrus on and off lek through the day. **b** The mean total number of females on lek and the mean number of females in estrus on lek through the day. Each time interval was sampled 15 times. Error bars show SE

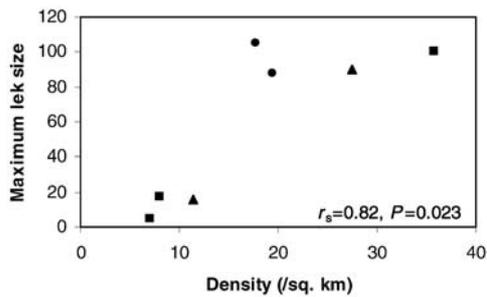
cation (on/off lek) in predicting the proportion of females in estrus (Table 3, Fig. 2a). The second result can be explained by the female visitation pattern on leks: while no significant diurnal variation in the number of estrous females on the lek was detected, the total number of females was highest around dawn (Kruskal-Wallis, diurnal variation on the lek in (1) the number of estrous females:  $\chi^2=7.92$ ,  $df=4$ ,  $n=75$  surveys,  $P=0.095$ , and (2) the total number of females:  $\chi^2=19.71$ ,  $df=4$ ,  $n=75$  surveys,  $P=0.001$ ; Fig. 2b).

#### Mating rates and food density

For each of three leks, one of which was sampled in two consecutive years, I found a negative correlation between the number of females mated daily on territories and food density as measured by the green leaf index (Spearman rank correlation, lek A 1999:  $r_s=-0.61$ ,  $n=19$ ,  $P=0.006$ ; lek A 2000:  $r_s=-0.58$ ,  $n=20$ ,  $P=0.007$ ; lek B 2000:  $r_s=-0.61$ ,  $n=22$ ,  $P=0.003$ ; lek C 2000:  $r_s=-0.45$ ,  $n=26$ ,  $P=0.020$ ; Fig. 3).



**Fig. 3a–d** The number of females mated daily on territories in relation to the territorial green leaf index during the rut in the wet season: **a** lek A 1999, **b** lek A 2000, **c** lek B 2000, **d** lek C 2000



**Fig. 4** Lek size in relation to density, showing the size of the largest lek within a plain in relation to its topi density. Data from: ■ Nyaruhuru and Central plains, ANP, Burrungat plains, MMNR, ● Olorukoti plains, MMNR, and ▲ Dutwa plains, SNP (references in Methods)

#### Lek size in relation to population density

Including data from previous studies on lekking topi, the size of the largest lek in a plain system was found to increase with increasing population density (Spearman rank correlation:  $r_s=0.82$ ,  $n=7$ ,  $P=0.023$ ; Fig. 4).

## Discussion

Only the FP model has none of its predictions contradicted by the results of this study (cf. Table 1). None of the other three models can explain why estrous females concentrate on leks or why there is a negative relationship between resource density and male mating rate. The fact that, on a large scale, leks are found in areas of high female density during the rut is also consistent with IFD and IFDUC models; however, in contrast to the FP model, these two models cannot explain the extreme degree of male clustering on a finer scale, which is revealed by the heavily male-biased sex-ratio on leks. Like the FP model, the FHO model correctly predicts a male-biased sex-ratio on leks, however, the positive correlation between lek size and population density speaks against this model as does the high degree of male clustering also within the zone of maximum female range overlap. The shortcoming of the three male-focused models suggests that accepting the existence of female mating preferences is crucial for understanding the nature of the lek system.

The FP model rests on the assumption that males who are superior competitors cluster on leks. Evidence supporting the idea that males in the study population are indeed unequal competitors is the fact that males holding central lek territories are significantly larger than others (Bro-Jørgensen 2002), which might be related to more intense fighting for such territories (Bro-Jørgensen and Durant 2003). Estimating lifetime reproductive success, the lek males indeed appear to do better than others (Bro-Jørgensen and Durant 2003). In fallow deer (*Dama dama*), another facultative lekking ungulate, inequality between males have recently been demonstrated by a positive correlation between the two essential fitness components, survival and reproduction (McElligott et al. 2002). Also here a positive correlation was found between reproductive success and phenotype, i.e. body size (McElligott et al. 2001).

Kin selection has been suggested as an explanation for male clustering onto leks (Kokko and Lindström 1996). If females are attracted to clustered males, it could pay for low quality males to cluster with their more attractive relatives as long as any reduction in their own mating success is more than compensated for by increased mating success of their relatives. The relevance of the kin selection model to ungulate lekking is not known, but when collecting data on kinship, it should be kept in mind that the FP model on its own may account for a higher degree of relatedness between lek males: if females preferentially mate with central lek males because their heritable high quality is revealed by their proximity to the lek center (Gosling and Petrie 1990; Bro-Jørgensen 2002), their sons would be more likely to obtain central lek positions than other males. For other explanations of relatedness between lek males, see Saether (2002).

In the present study, leks covered less than 1% of the zone of highest overlap between female ranges, because

females typically aggregated in herds which ranged over a large area (cf. Bradbury et al. 1989). Under such circumstances where the zone of maximum female range overlap is extensive, the FHO model does not predict the high degree of territorial clustering characteristic of lekking because the model does not contain any mechanism, which leads to clumping *within* the zone of highest overlap (Bradbury et al. 1986). Another property of the home range overlap model, which has not been dealt with here yet, is that it can explain leks spaced less than one female home range diameter apart; this feature is claimed to set it apart from female preference-based models (Bradbury et al. 1986). In topi, female home range diameter may exceed inter-lek distance (Montfort-Braham 1975; Bro-Jørgensen 2001), but does this really prove the FHO model right and female preference-based models wrong? Predicting that females according to the latter models only have one large lek within their home range is based on the logic that it enables comparison of the largest number of males. This inference fails to consider the costs of mate choice (Daly 1978; Pomiankowski 1987), but according to the female preference models, mate choice might still be only one of several components influencing female ranging patterns. For example, travel costs and heightened predation risk might work against too extreme clustering of males within female home ranges, especially if areas around larger leks become resource depleted or act as foci for predators. In sage grouse (*Centrocercus urophasianus*), costs such as increased predation risk were associated with travelling to leks (Gibson and Bachman 1992).

The concentration of estrous females on leks shows that female distribution is affected by sexual activity, which is not assumed by either of the FHO, IFD or IFDUC models. However, rather than reflecting active female mate choice as suggested by the FP model, it could be that intense harassment from non-territorial or resource-defending males causes estrous females to cluster on leks (Clutton-Brock et al. 1992). Speaking against this idea, no clear evidence of lower harassment levels on leks than on resource-based territories has been found (Carbone and Taborsky 1996); in fact, in topi harassment levels are higher on leks than elsewhere (Bro-Jørgensen 2003).

In conclusion, the present results points to the FP model as a plausible explanation for lek behavior in topi. Also in other lekking ungulates, male clustering onto leks cannot be explained simply by extreme female densities (lechwe *Kobus leche*, Nefdt 1992; kob *Kobus kob*, Deutsch 1994; fallow deer, Balmford et al. 1993; blackbuck *Antelope cervicapra*, Ranjitsinh 1989), and it is also here essential that the proportion of females who are in estrus is higher on lek (lechwe ~50%, Nefdt 1992; kob 36.4%, Balmford 1990; fallow deer 'the majority', Clutton-Brock et al. 1989). In topi, female mate competition on the central leks supports that active mate choice is the reason why estrous females move to leks (Bro-Jørgensen 2002). Thus, at least when it comes to lek behavior, male-focused models of ungulate mating systems

appear oversimplified, since they miss out on what seems to be a crucial force leading to the extreme degree of clustering, namely female mate preferences.

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## References

- Alexander RD (1975) Natural selection and specialized chorusing behaviour in acoustical insects. In Pimental D (ed) *Insects, science and society*. Academic Press, New York, pp 35–77
- Bakker TCM, and Pomiankowski A (1995) The genetic basis of female mate preferences. *J Evol Biol* 8:129–171
- Balmford A (1990) Lekking in Uganda kob. PhD thesis, University of Cambridge
- Balmford A, Turyaho M (1992) Predation risk and lek-breeding in Uganda kob. *Anim Behav* 44:117–127
- Balmford A, Rosser AM, Albon SD (1992) Correlates of female choice in a resource-defending antelope. *Behav Ecol Sociobiol* 31:107–114
- Balmford A, Deutsch JC, Nefdt RJC, Clutton-Brock T (1993) Testing hotspot models of lek evolution: data from three species of ungulates. *Behav Ecol Sociobiol* 33:57–65
- Bradbury JW, Gibson RM, Tsai IM (1986) Hotspots and the dispersion of leks. *Anim Behav* 34:1694–1709
- Bradbury JW, Gibson RM, McCarthy CE, Vehrencamp SL (1989) Dispersion of displaying male sage grouse. 2. The role of female dispersion. *Behav Ecol Sociobiol* 24:15–24
- Brashares JS, Garland Jr T, Arcese P (2000) Phylogenetic analysis of coadaptation in behavior, diet, and body size in the African antelope. *Behav Ecol* 11:452–463
- Bro-Jørgensen J (2001) Lek-breeding in topi antelopes (*Damaliscus lunatus*). PhD thesis, University of London
- Bro-Jørgensen J (2002) Overt female mate competition and preference for central males in a lekking antelope. *Proc Natl Acad Sci USA* 99:9290–9293
- Bro-Jørgensen J (2003) No peace for estrous topi cows on lek. *Behav Ecol* (in press)
- Bro-Jørgensen J, Durant SM (2003) Mating strategies of topi bulls: getting in the centre of attention. *Anim Behav* (in press)
- Carbone C, Taborsky M (1996) Mate choice or harassment avoidance? A question of female control at the lek. *Behav Ecol* 7:370–373
- Clutton-Brock TH (1989) Mammalian mating systems. *Proc R Soc Lond B* 236:339–372
- Clutton-Brock TH, Hiraiwa-Hasegawa M, Robertson A (1989) Mate choice on fallow deer leks. *Nature* 340:463–465
- Clutton-Brock TH, Price OF, MacColl ADC (1992) Mate retention, harassment, and the evolution of ungulate leks. *Behav Ecol* 3:234–242
- Clutton-Brock TH, Deutsch JC, Nefdt RJC (1993) The evolution of ungulate leks. *Anim Behav* 46:1121–1138

- Clutton-Brock TH, McComb KE, Deutsch JC (1996) Multiple factors affect the distribution of females in lek-breeding ungulates: a rejoinder. *Behav Ecol* 7:373–378
- Daly M (1978) The cost of mating. *Am Nat* 112:771–773
- Deutsch JC (1994) Lekking by default: female habitat preferences and male strategies in Uganda kob. *J Anim Ecol* 63:101–115
- Duncan P (1975) Topi and their food supply. PhD thesis, University of Nairobi
- Estes RD (1991) The behavior guide to African mammals. University of California Press, Berkeley, Calif.
- Fretwell SD (1969) Dominance behavior and winter habitat distribution in juncos (*Juncos hyemalis*). *Bird-Banding* 34:293–306
- Fretwell SD (1972) Populations in a seasonal environment. Princeton University Press, Princeton, N.J.
- Fretwell SD, Lucas HL (1970) On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheor* 19:16–36
- Gibson RM, Bachman GC (1992) The costs of female choice in a lekking bird. *Behav Ecol* 3:300–309
- Gosling LM (1986) The evolution of mating strategies in male antelopes. In Rubenstein DI, Wrangham RW (eds) *Ecological aspects of social evolution*. Princeton University Press, Princeton, N.J., pp 244–281
- Gosling LM, Petrie M (1990) Lekking in topi: a consequence of satellite behavior by small males at hotspots. *Anim Behav* 40:272–287
- Hooge PN, Eichenlaub W, Solomon E (1999) The animal movement program: USGS, Alaska Biological Science Center, Anchorage
- Höglund J, Alatalo RV (1995) *Leks*. Princeton University Press, Princeton, N.J.
- Jarman P (1974) The social organisation of antelope in relation to their ecology. *Behaviour* 48:215–267
- Jennrich RI, Turner FB (1969) Measurement of non-circular home range. *J Theor Biol* 22:227–237
- Kokko H, Lindström J (1996) Kin selection and the evolution of leks: whose success do young males maximize? *Proc R Soc Lond B* 263:919–923
- Krebs CJ (1989) *Ecological methodology*. Harper Collins, New York
- Kruijt JP, de Vos JG, Bossema I (1972) The arena system of black grouse, *Lyrurus tetrix tetrix* (L.). *Proc Int Ornithol Congr* 15:399–423
- McElligott AG, Gammell MP, Harty HC, Paini DR, Murphy DT, Walsh JT, Hayden TJ (2001) Sexual size dimorphism in fallow deer (*Dama dama*): do larger, heavier males gain greater mating success? *Behav Ecol Sociobiol* 49:266–272
- McElligott AG, Altwegg R, Hayden TJ (2002) Age-specific survival and reproductive probabilities: evidence of senescence in male fallow deer (*Dama dama*). *Proc R Soc Lond B* 269:1129–1137
- McNaughton SJ (1988) Mineral nutrition and spatial concentrations of African ungulates. *Nature* 334:343–345
- Mertens H (1984) Age-determination in the topi (*Damaliscus korrigum* Ogilby) in the Virunga National-Park (Zaire). *Mammalia* 48:425–435
- Montfort-Braham N (1974) Contribution à l'étude des structures sociales et du comportement des ongulés du Parc National de l'Akagera. Iere partie: le topi (*Damaliscus korrigum* -Ogilby). FULREAC, Université de Liège, Liège
- Monfort-Braham N (1975) Variations dans la structure sociale du topi, *Damaliscus korrigum* Ogilby, au Parc National de l'Akagera, Rwanda. *Z Tierpsychol* 39:332–364
- Nefdt RJC (1992) Lek-breeding in Kafue lechwe. PhD thesis, University of Cambridge
- Ottichilo WK, De Leeuw J, Skidmore AK, Prins HHT, Said MY (2000) Population trends of large non-migratory wild herbivores and livestock in the Masai Mara ecosystem, Kenya, between 1977 and 1997. *Afr J Ecol* 38:202–216
- Parker GA, Sutherland WJ (1986) Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Anim Behav* 34:1222–1242
- Pelabon C, Komers PE, and Höglund J (1999) Do leks limit the frequency of aggressive encounters in fallow deer? Linking local male density and lek occurrence. *Can J Zool* 77:667–670
- Pomiankowski A (1987) The costs of choice in sexual selection. *J Theor Biol* 128:195–218
- Ranjitsinh MK (1989) *The Indian blackbuck*. Natraj, Dehra Dun, India
- Saether SA (2002) Kin selection, female preferences and the evolution of leks: direct benefits may explain kin structuring. *Anim Behav* 63:1017–1020
- Sutherland WJ (1996) *From individual behaviour to population ecology*. Oxford University Press, Oxford
- Sutherland WJ, Parker GA (1985) Distribution of unequal competitors. In: Sibly RM, Smith RH (eds) *Behavioural ecology: ecological consequences of adaptive behaviour*. Blackwell, Oxford, pp 255–273
- Sutherland WJ, Parker GA (1992) The relationship between continuous input and interference models of ideal free distributions of unequal competitors. *Anim Behav* 44:345–356
- Sutherland WJ, Townsend CR, Patmore JM (1988) A test of the ideal free distribution with unequal competitors. *Behav Ecol Sociobiol* 23:51–53
- Thirgood S, Langbein J, Putman RJ (1999) Intraspecific variation in ungulate mating strategies: the case of the flexible fallow deer. *Adv Study Behav* 28:333–361