

# VARIATION IN LEKKING COSTS IN BLACKBUCK (*ANTILOPE CERVICAPRA*): RELATIONSHIP TO LEK-TERRITORY LOCATION AND FEMALE MATING PATTERNS

by

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## Summary

We studied variation in lekking costs in an Indian antelope, the blackbuck *Antelope cervicapra*, in relation to female mating patterns. We tested the hypothesis that central males had a higher mating success and faced higher costs than peripheral males. We used continuous focal animal sampling to estimate time-activity budgets of individually identified central and peripheral lekking males and bachelor males. Scan sampling was used to estimate the time spent on the lek by central and peripheral males and to monitor female visits to the lek. We mapped lek-territories and monitored territory additions, territory turnover, and the location of matings. We found that central males faced higher costs than peripheral males. Central males foraged less, spent more time on the lek and tended to have higher fighting rates than peripheral males. Corresponding to this difference in costs, mating benefits were also greater for central males. Our results suggest that lek-territory location may be an important cue in female choice. Male mating success was skewed and 90% of matings observed occurred in the lek-centre. Furthermore, three of the five most successful males previously held territories in the lek-periphery where they were not observed to mate. Territory turnover was higher in the centre than in the periphery and males tended to move towards the centre while shifting territories. Based on these findings, we suggest that central and peripheral males follow two different strategies in response to a female preference for central territories: while central males may try to maximise encounters with oestrous females by investing heavily in lekking,

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peripheral males seem to attempt to maximise their chances of gaining central territories by not compromising on foraging time and investing less in lekking. Since we did not directly measure male phenotype, its role in explaining the patterns we found remains to be studied.

## Introduction

Lekking is an unusual mating system in which males aggregate in an open area, defend clustered territories, and are sought out by females for the sole purpose of mating. Apart from the males, these territories are typically devoid of resources attractive to females (Bradbury, 1981). In ungulates, lekking often occurs along with other male mating strategies, most commonly resource defence polygyny (Clutton-Brock *et al.*, 1988; Balmford, 1990; Gosling, 1991), in the same population. In such cases, comparisons between alternative strategies have shown that lekking is a relatively 'high cost-high benefit' strategy (Gosling *et al.*, 1987; Gosling & Petrie, 1990; Apollonio *et al.*, 1992). Male mating success is highest on leks, but lekking males typically face higher costs than other males (Gosling *et al.*, 1987). For example, in fallow deer *Dama dama*, lekking males feed less than males on resource territories or not at all (Clutton-Brock *et al.*, 1988; Apollonio *et al.*, 1989). While a number of studies have focussed on variation in male mating strategies among and within populations, far fewer studies have investigated different behavioural strategies followed by males within a lek. Those that have concentrated mostly on displays and social interactions (*e.g.* Vehrencamp *et al.*, 1989). In topi *Damaliscus korrigum*, for example, males on central territories fight more frequently than males on the lek periphery (Gosling & Petrie, 1990). However, one might also expect variation among males in other components of lekking such as time-investment strategies. For instance, if some factor generates variation among males in their potential gains from lekking, males may also differ in the costs they are willing to incur. We studied variation in lekking costs among lekking males in an Indian antelope, the blackbuck (*Antilope cervicapra*).

One possible factor that could generate such variation is female mating patterns on the lek. We investigated whether female mating patterns could explain differences among males in lekking costs. Lekking presents an interesting case for the study of female choice since males are neither associated with resources useful to females nor do they contribute towards parental care. Male mating success on leks is usually highly skewed (Gibson

& Bradbury, 1985; Clutton-Brock *et al.*, 1988; Apollonio *et al.*, 1989). Since females seem to move fairly freely on leks (Clutton-Brock *et al.*, 1988; Apollonio *et al.*, 1989; Gosling & Petrie, 1990), female choice is thought to be partially responsible for this skew (Bradbury *et al.*, 1985; Alatalo *et al.*, 1991), although male-male competition may also modify mating patterns (Höglund & Alatalo, 1995). There is considerable debate over the cues that females use to exercise this choice. Mate choice cues appear to vary between species and even among populations of a species (Clutton-Brock *et al.*, 1988; Apollonio *et al.*, 1989). Gibson & Bradbury (1985) have broadly classified these cues into direct phenotypic cues such as body size and display rates, and indirect cues such as the location of a male's territory on the lek. While some studies have shown that female choice is related to characteristics of territories, such as their distance from the lek centre or from predator cover (Apollonio *et al.*, 1990; Deutsch & Weeks, 1991), others have found correlations between male mating success and male phenotype (Clutton-Brock *et al.*, 1988; Andersson, 1989; Höglund *et al.*, 1990; Gibson *et al.*, 1991; Balmford *et al.*, 1992). Several studies report that a combination of mate choice cues may be used within a lek (Apollonio *et al.*, 1989; Deutsch & Nefdt, 1992). The relative importance of direct and indirect cues in lekking populations is still controversial.

During a previous study, casual observations made at the traditional lek in our study area suggested that mating activity was higher on territories well within the lek (Y.V. Jhala pers. obs.). In the present study, we investigated the distribution of copulations among lekking males and among lek-territories to determine whether a male's mating success is related to the position of his territory. We tested the hypothesis that central males are more successful than peripheral males. A female preference for particular mating sites could influence male investment in lekking. If central lek-territories are indeed preferred by females, we would expect central males to invest more in lekking than peripheral males. To test this, we first compared the behaviour of lekking males with that of bachelor (non-reproductive) males to identify some costs of lekking and then looked for variation in these costs among lekking males. We collected data on time-activity budgets, display and fighting rates and daily time spent on the lek. Using these findings and additional data on territory succession, we describe two different behavioural strategies that lekking males adopt, apparently related to a female bias for central territories.

## Study animal

The blackbuck is native to the Indian subcontinent. Essentially a species of open plains, it is found in a wide range of habitats from arid grasslands and scrublands to marshy coastal plains and open woodlands (Ranjitsinh, 1989). This species exhibits a high degree of sexual dimorphism; the male is larger than the female, is strikingly coloured in black and white, and sports a magnificent pair of spiralling horns. The black of the male is replaced by an inconspicuous brown in the female. To date, most accounts of the social and reproductive behaviour of blackbuck have been descriptive and the dynamics of its social and mating systems are largely unknown. Blackbuck are primarily grazers (Mungall, 1978; Jhala, 1997) and herds are characteristically loose and unstable associations that can range from less than ten individuals to several hundred. The main social units in blackbuck are (1) solitary (usually territorial) males, (2) all-male or bachelor groups, composed of two or more juvenile, sub-adult or adult males, (3) female groups, composed of females of all age-classes, fawns, and juvenile and sub-adult males, and (4) mixed groups, in which the whole range of age classes of both sexes may be represented (Mungall, 1978). The mating system of blackbuck appears to be flexible. The basic pattern is territorial defence by males (Mungall, 1978; Schaller, 1967; Prasad, 1989), and in most places this resembles the resource defence territories described in many African antelopes (*e.g.* topi: Gosling, 1986). Blackbuck are reported to lek in a few areas (Ranjitsinh, 1989), but this has not been investigated in detail and recent reviews of lek-breeding ungulates (*e.g.* Clutton-Brock *et al.*, 1993) do not include this species. Based on year-round censuses of fawns and male territorial activity blackbuck are thought to breed through the year (Schaller, 1967; Ranjitsinh, 1989). However, two peaks in rutting have been observed, one from August to October and the other in March and April. The latter peak is the greater in our study area (Ranjitsinh, 1982).

## Study area

Velavadar National Park, 3400 ha in area, is a mosaic of semi-arid grasslands, shrublands, saline mudflats and tidal areas. The major woody species is mesquite (*Prosopis juliflora*) an exotic that was introduced into the area around 80 years ago. The climate is characterised by temperature extremes, and periodic floods and droughts. Velavadar harbours one of the highest concentrations of blackbuck in India (Ranjitsinh, 1989). The population in this park has fluctuated around 1,850 individuals since 1973 (Jhala, 1991). The primary predators of blackbuck in this area are wolves (*Canis lupus*) and village dogs. Fawns are preyed on by jackals (*Canis aureus*) as well.

During a survey of the Park at the beginning of the study, four leks were located. Of these, only one was studied intensively. This has traditionally been the largest lek in Velavadar, and its location has not changed since it was first reported in the late 1970s (Ranjitsinh, 1989). The lek studied is located towards one end of a large grassland, and is bordered by a road and a mud track on two sides. Of the other three leks, one had a maximum of sixteen males in December and eight in April. The other two never had more than four males during the study period.

## Methods

This study lasted from November 1994 to April 1995 and covered both low levels in rutting activity (December to February) and a major rutting peak (March-April).

### *Individual identification*

Males were individually identified using their horn morphology. Following Mungall's (1978) classification, we defined an adult male as an animal sporting at least three horn spirals. Males with one or two spirals were classified as sub-adults and those with short straight horns as juveniles. The thickness of the horns and the length of each spiral varied, often quite markedly, among individuals and helped in identification. The angle between horns was estimated visually and the animal was placed in one of three classes:  $< 30^\circ$ ,  $30\text{--}45^\circ$ ,  $> 45^\circ$ . The tips of the right and left horns were rarely similar in shape and often pointed in different directions. Breaks in horns were common and were also used for individual identification.

### *Dispersion of territorial males on the lek*

An area of 25.75 ha on the lekking ground was gridded into  $50 \times 50$  m blocks, using two 50 m ropes and a compass. Short stakes were used to mark the corners of these blocks. Since we were unable to map all territories using behavioural observations, we used dung piles as a measure of the dispersion of territorial males. Dung piles, formed by the repeated defecation by males at specific sites, are focal points of territories (Mungall, 1978; Prasad, 1989) and serve well as territory markers. The majority of mating and territorial activity (except border encounters) and displays are focussed around dung piles. A territory usually has one or two large dung piles towards the centre and several smaller ones at the periphery or scattered at other points within the territory (Mungall, 1978; this study). At the beginning of every month, from January to April, all the dung piles on the lek were mapped. All lekking males were represented on a map by their principal dung piles. Apart from this, at least once a week, and up to four times in a week, the following data were recorded on these maps: the territories (represented by dung piles) occupied, the number of males present on the lek, the presence or absence of identified males, changes in territory ownership, and movement of males from one territory to another. Horn diagrams of new males were also recorded. These data were also gathered during breaks in behaviour sampling.

### *Male behaviour*

To identify possible costs of lekking we studied the behaviour of both bachelors (which are usually not involved in reproductive activity) and lekking males. To examine the relationship between territory location and the costs of lekking, we identified a 'lek centre' at the onset of the study, which was a period of low rutting activity. We defined this as the area on the lek where territories appeared to be most clumped. In contrast to the surrounding areas this area was almost totally devoid of grass. The centre does not refer to the geometric centre of the lek but rather to the area with the greatest density of territories at the time of designation. We continued to regard this area as the lek centre for all sampling purposes throughout the study and did not in any way modify it based on patterns in territory additions recorded during the course of the study. To investigate the relationship between territory location and

male behaviour only two classes of lekking males were studied: central males — those with territories located inside the designated centre, and peripheral males — those with no or only one territory peripheral to them. Males intermediate in position were not sampled.

Continuous focal animal sampling was used to estimate time-activity budgets of central and peripheral lekking males, and bachelor males. In each category, individuals were chosen at random from among males that could be individually identified. Each animal was sampled once (one focal day). The focal animal was followed from around 30 minutes before sunrise to 30 minutes after sunset. The activities recorded were (1) foraging — which included feeding and searching, (2) lying, (3) moving, (4) standing, and (5) displays associated with territorial defence and reproduction (for a description of these displays see Mungall, 1978). The last category also included fights, and these were classified into ritualised fights (display walks, parallel walks) and clashes (where horn contact was recorded). On a few occasions, the animals were disturbed by human intrusion onto the lek. If the disturbance lasted for over half an hour, sampling was abandoned. The focal animal was then located the next day and sampling was completed. To evaluate the association between the level of rutting activity and male behaviour, two focal sampling series were conducted: one in November-December during low levels of rutting activity, and one in March-April during the rutting peak.

Group scans were conducted during March-April to quantify the variation in time spent on the lek by males during the rutting peak. The day was divided into three time periods — morning (0700-1030 hrs), midday (1030-1530 hrs) and evening (1530-1900 hrs). Five scan sessions were conducted in each time period. During each scan session (which consisted of 11-18 scans), at least 10 central and 10 peripheral individually identified males were scanned every 15 minutes. The behavioural categories recorded were the same as in the focal samples. In addition, if the animal was not present on the lek during a scan, it was noted as being 'absent' and animals were not followed outside the lek. All males that could be individually identified were scanned. A similar series of group scans was conducted to study patterns in female visits to the lek and the activity of females while on the lek. The same three periods of the day were used. During each session (which consisted of 7 to 16 scans), the lek was scanned every 15 minutes and the number of females present on each lek-territory and their activity were recorded. Female movement on the lek increased sharply from the first week of February. Subsequently, daily watches were conducted for female visits and matings.

Matings were recorded whenever possible, and their location and the identity of the male were noted. Males typically mount a female several times before ejaculating. An ejaculation can be identified by the characteristic sharp arch of the lower back which nearly throws the male off balance (Mungall, 1978; Ranjitsinh, 1989). Only clearly identified ejaculations were recorded as copulations seen. Whenever possible, the behaviour of both the male and the female during and after copulation was recorded.

### *Analyses*

We examined the relationship between the behaviour of lekking males and (1) lek-territory position, and (2) the level of rutting activity. Time-activity budgets were calculated for each individual sampled. For every focal day, the proportion of time spent in different activities was calculated. The more a lekking male invests (in terms of energy and time) in territorial and reproductive activities, the less he can invest in maintenance activities. Hence, the reduction in time spent foraging, and the increase in time spent displaying were used as potential measures of the cost of lekking. The actual loss in foraging time was not estimated; instead, bachelors

(non-reproductive males) were used as a baseline and compared with central and peripheral lekking males. Display rates (all displays) and fighting rates, calculated from focal samples, and the proportion of daylight hours spent on the lek, calculated from group scans, were also used as measures of the cost of lekking. We should emphasise that because our measures of cost are purely behavioural they may not necessarily reflect an equivalent reduction in future fitness. For example, a high quality male incurring heavier behavioural costs may, in fact, experience lower fitness costs than might a male of lower quality.

From the data on scans of females at the lek, the mean number of females per scan for each of the three time periods was calculated; the number of females observed on the lek was first averaged across scans for each session and then averaged across sessions for each time period. Due to low sample sizes and uncertain distributions of the sampled variables, non-parametric tests were used. For comparisons between two means, the Mann-Whitney  $U$  test was used. For those involving three samples, the Kruskal-Wallis ANOVA was initially used to test for significance; if results were significant, pairwise comparisons were made among the three samples using the Mann-Whitney  $U$  test. All  $p$ -values reported are two-tailed.

## Results

### *Territorial behaviour*

Territories were maintained on the main lek throughout the study period. Their numbers increased from a mean of 16 (SE = 1.7) in November to a mean of 48 (SE = 1.5) in April. The lek centre designated at the onset of the study remained the area with the greatest density of territories throughout the study.

Lek territories were focussed around dung piles (see Methods). Dung piles seem to play an important role, as visual and olfactory landmarks, in territorial defence. A large proportion of territorial displays and of courtship and mating activities was carried out on dung piles. All focal animals and animals scanned on the lek rested on dung piles and all mating observed occurred on or within two metres of the principal dung piles in a territory. Interestingly, few large, principal dung piles were added during the study period. Instead, new occupants tended to use the dung piles maintained by previous owners. For example, of the 62 territorial males present on the lek during the first fortnight in April, 90% used old dung piles that were already in use in January.

Female and mixed herds did not move regularly through the lek. Herds passing by the lek usually moved along its periphery. This is not surprising given that there was hardly any forage on the lek, especially in the centre. However, a water hole in the centre attracted several blackbuck, mostly

females. Males from mixed or bachelor groups attempting to use the water hole were invariably chased off the lek by territorial males. Female groups visiting the water hole did not visit or remain on territories but left the lek immediately.

### *Behaviour of females visiting the lek*

During the rutting peak, females visited the lek singly or in pairs. The average number of females on the lek tended to be greater in the evening than in the morning or at midday (Table 1; Kruskal-Wallis ANOVA:  $\chi^2 = 6.856$ ,  $N = 54$ ,  $df = 2$ ,  $p = 0.032$ ; Mann-Whitney  $U$  tests: morning vs midday  $z = -0.0413$ ,  $N_1 = 15$ ,  $N_2 = 16$ ,  $p = 0.967$ , midday vs evening  $z = -2.319$ ,  $N_1 = 16$ ,  $N_2 = 23$ ,  $p = 0.020$  and morning vs evening  $z = -2.045$ ,  $N_1 = 15$ ,  $N_2 = 23$ ,  $p = 0.041$ ). Despite herding attempts by males, females were observed to move freely from one territory to another. On entering a territory, they moved directly to dung piles and appeared to smell them. This behaviour was repeated frequently during a female's stay on a territory. Several females lay on dung piles on the territory following repeated mounting attempts by the territory owner. Females spent most of their time on the lek standing (mean = 32%; SE = 3%) or lying (mean = 37%; SE = 4%) and spent very little time feeding (mean = 6%; SE = 3%). This supports the idea that females were not attracted to the lek by feeding opportunities (one of the characteristic features of the lekking system).

TABLE 1. *Patterns in female visits to the lek through the day during the rutting peak (March-April)*

Time period	Average number of females on the lek (per scan)
Morning 0700-1030 hrs ( $N = 15$ )	1.36 ( $\pm 0.41$ )
Midday 1030-1530 hrs ( $N = 16$ )	1.10 ( $\pm 0.25$ )
Evening 1530-1900 hrs ( $N = 23$ )	2.49 ( $\pm 0.41$ )

$N$  = number of scan sessions (each session ranged from 7 to 16 scans). Numbers in the table represent means ( $\pm 1$  SE).

*Distribution of copulations among lekking males and lek-territories:  
a position effect*

A total of 36 copulations was observed between March 1 and April 28. Matings occurred predominantly in the evening (28 of 36 copulations) even after accounting for differences in sampling effort through the day (Chi-square goodness-of-fit test:  $\chi^2 = 19.24$ ,  $df = 2$ ,  $p < 0.001$ ).

Matings were not distributed at random among the lekking males. Of a total of at least 104 males that defended territories on the lek for a day or longer between the days the first and last copulations were seen, only twenty were observed to mate. Of these, 15 mated once, four mated thrice, and one mated nine times.

Matings were also spatially clumped; the number of matings in the lek-centre was disproportionately higher than those in the periphery and in intermediate territories (Fig. 1). While there were, on average, 12 (SE = 0.53) central, 10 (SE = 0.79) intermediate and 23 (SE = 1.10) peripheral territories on a given day during the rutting peak (March 1 to April 30), 89%, 6% and 6% of observed matings occurred on central, intermediate and peripheral territories respectively.

Matings were observed on only 13 territories. Females continued to visit and mate on eight of these territories even after the original successful owner was replaced. Two males, each of whom mated thrice, successively occupied the same territory, and all their matings occurred on that territory. A similar pattern was observed on seven other territories. In addition, there was a tendency of males to move towards the lek-centre when shifting territories. Of the 26 males that shifted territories during the study period, eighteen moved towards or into the lek-centre while seven were last seen on territories that were further from the centre than their original territories.

Territory turnover, defined as the number of males that defended a particular territory for at least a day during the rutting peak, varied among central (mean = 7.3, SE = 0.51), intermediate (mean = 6.2, SE = 0.47) and peripheral (mean = 3.2, SE = 0.60) lek-territories. Turnover was higher on central than on peripheral territories (Mann-Whitney  $U$  test:  $z = -3.797$ ,  $N_1 = 15$ ,  $N_2 = 13$ ,  $p < 0.001$ ) and lower on peripheral than on intermediate territories ( $z = -3.133$ ,  $N_1 = 13$ ,  $N_2 = 13$ ,  $p = 0.002$ ). Although there was no significant difference between central and intermediate territories, the trend was in the expected direction ( $z = -1.664$ ,  $N_1 = 15$ ,  $N_2 = 13$ ,  $p = 0.096$ ).

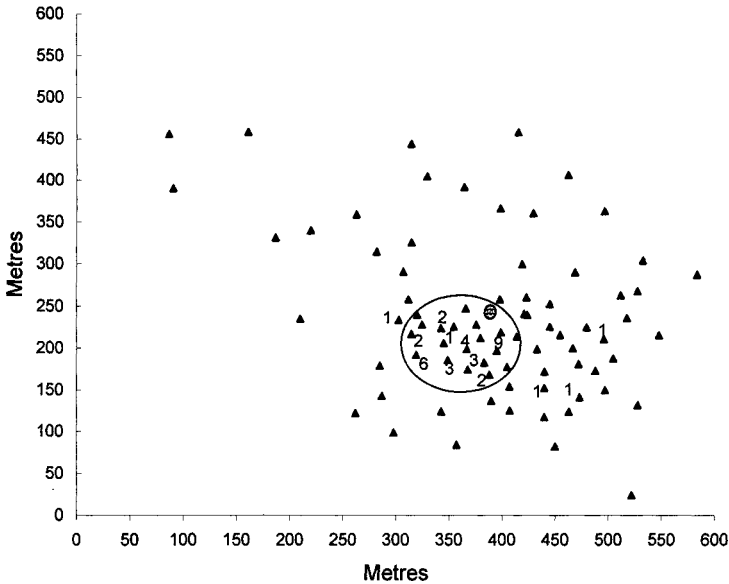
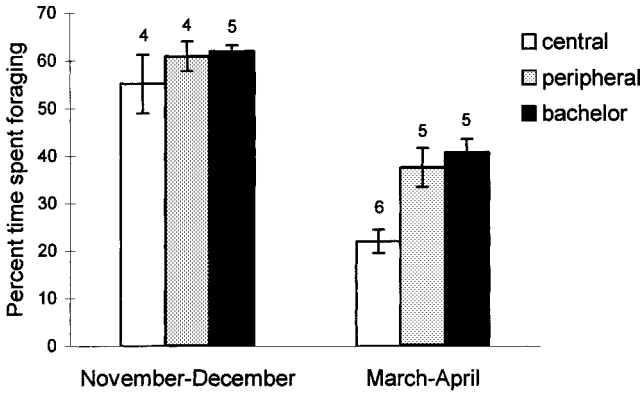


Fig. 1. Spatial distribution of matings on the lek. All territories occupied for two days or more during the rutting peak (March-April) are represented by their principal dung piles (denoted as solid triangles). Numbers next to territories indicate the number of matings that occurred on those territories; territories on which no matings were observed are not numbered. The large circle denotes the lek-centre designated at the onset of the study (see Methods); the smaller stippled circle represents an artificial water hole.

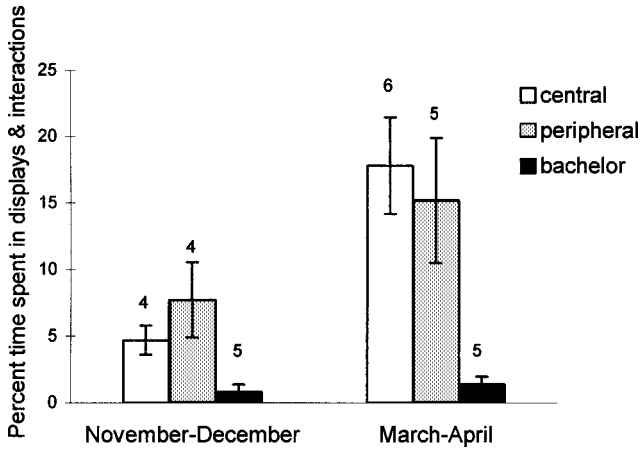
### *Cost of lekking: effects of rutting activity and lek-territory position*

The behaviour of lekking males differed both according to the positions of their territories on the lek (central *versus* peripheral) and according to the level of rutting activity.

The level of rutting activity was low in November-December and there was little female movement on the lek. During this period, central, peripheral and bachelor males did not differ much in their use of daylight hours. Bachelors and both classes of lekking males spent a similar proportion of their day foraging (Fig. 2a; Kruskal-Wallis ANOVA:  $\chi^2 = -0.515$ ,  $N = 13$ ,  $df = 2$ ,  $p = 0.773$ ). However, bachelors tended to spend less time in displays and social interactions than either central or peripheral lekking males (Fig. 2b; Kruskal-Wallis ANOVA:  $\chi^2 = 7.044$ ,  $N = 13$ ,  $df = 2$ ,  $p = 0.03$ ; Mann-Whitney  $U$  tests:  $z = -1.96$ ,  $N_1 = 5$ ,  $N_2 = 4$ ,  $p = 0.063$  and  $z = -2.205$ ,  $N_1 = 5$ ,  $N_2 = 4$ ,  $p = 0.032$  respectively) while there was no difference



(a)



(b)

Fig. 2. Time spent (a) foraging and (b) in displays and social interactions, by central and peripheral lekking males and bachelor males during low (November-December) and high (March-April) levels of rutting activity. Error bars represent  $\pm 1$  SE. Sample sizes ( $N$ ) given above bars are the number of focal follows.

between central and peripheral males in the time spent in these behaviour patterns (Mann-Whitney  $U$  test:  $z = -0.577$ ,  $N_1 = 4$ ,  $N_2 = 4$ ,  $p = 0.686$ ).

During the rutting peak (March-April), the time spent foraging by the three classes of males differed (Fig. 2a; Kruskal-Wallis ANOVA:  $\chi^2 = 8.86$ ,  $N = 16$ ,  $df = 2$ ,  $p = 0.012$ ). While bachelors and peripheral males spent similar proportions of the day foraging (Mann-Whitney  $U$  test:  $z = -0.731$ ,  $N_1 = 5$ ,  $N_2 = 5$ ,  $p = 0.548$ ), both classes of males foraged more than



Fig. 3. A comparison of the display and agonistic behaviour of central ( $N = 6$ ) and peripheral ( $N = 5$ ) lekking males during the rutting peak. Error bars represent  $\pm 1$  SE. Rates for 'all displays' are reported per hour, while those of 'ritualised fights' and 'horn clashes' are reported per 12 hours.

central bucks (Mann-Whitney  $U$  tests: bachelor vs central  $z = -2.556$ ,  $N_1 = 5$ ,  $N_2 = 6$ ,  $p = 0.009$  and central vs peripheral  $z = -2.373$ ,  $N_1 = 6$ ,  $N_2 = 5$ ,  $p = 0.017$ ). Bachelors spent less time in displays and social interactions than either central or peripheral lekking males (Fig. 2b; Kruskal-Wallis ANOVA:  $\chi^2 = 9.85$ ,  $N = 16$ ,  $df = 2$ ,  $p = 0.007$ ; Mann-Whitney  $U$  tests: bachelor vs central  $z = -2.739$ ,  $N_1 = 5$ ,  $N_2 = 6$ ,  $p = 0.004$  and bachelor vs peripheral  $z = -2.611$ ,  $N_1 = 5$ ,  $N_2 = 5$ ,  $p = 0.008$ ) and bachelors did not engage in any horn clashes. Central males tended to have higher rates of horn clashes than peripheral males (Fig. 3; Mann-Whitney  $U$  test:  $z = -1.838$ ,  $N_1 = 6$ ,  $N_2 = 5$ ,  $p = 0.066$ ). However there was no significant difference in the rates of ritualised fights, overall display rates or in the time spent in displays and social interactions (Fig. 3; Mann-Whitney  $U$  tests:  $p > 0.09$  in all cases), although for all these behaviours, the trend was in the predicted direction (central greater than peripheral males).

Central and peripheral males differed in the proportion of daylight hours spent on the lek (another measure of the cost of lekking). Scan data (all three time periods pooled together) revealed that central males (mean = 77.55%, SE = 2.46%) spent more time on the lek than peripheral males (mean = 66.22%, SE = 3.09%; Mann-Whitney  $U$  test:  $z = -2.4725$ ,  $N_1 = 15$ ,  $N_2 = 15$ ,  $p = 0.0134$ ). When a similar comparison was made within each time period, finer differences emerged (Fig. 4). Central males spent more time on the lek than peripheral males during the morning and

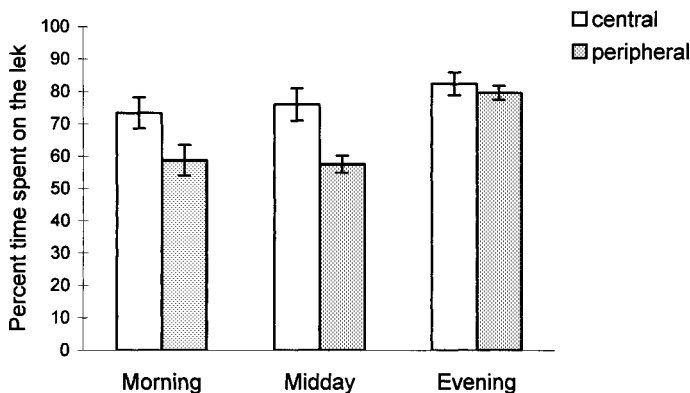


Fig. 4. Temporal patterns in the time spent on the lek by central and peripheral lekking males during the rutting peak (March-April). Error bars represent  $\pm 1$  SE. Five scan sessions were conducted in each time period.

midday sessions (Mann-Whitney  $U$  tests: morning  $z = -1.991$ ,  $N_1 = 5$ ,  $N_2 = 5$ ,  $p = 0.047$  and midday  $z = -2.522$ ,  $N_1 = 5$ ,  $N_2 = 5$ ,  $p = 0.012$ ). However, in the evening session, there was no difference between the two classes of males (Mann-Whitney  $U$  test:  $z = -0.808$ ,  $N_1 = 5$ ,  $N_2 = 5$ ,  $p = 0.419$ ). This is because peripheral males spent more time on the lek in the evening than in the morning or at midday (Fig. 4, Kruskal-Wallis ANOVA:  $\chi^2 = 9.994$ ,  $df = 2$ ,  $p = 0.007$ ), while central males spent similar proportions of time on the lek in all three time periods (Kruskal-Wallis ANOVA:  $\chi^2 = 0.759$ ,  $df = 2$ ,  $p = 0.684$ ).

## Discussion

We found that a male blackbuck's lekking behaviour varied according to the level of rutting activity and according to the position of its territory on the lek. During periods of low rutting activity and low numbers of oestrous females, lekking males and bachelor males followed similar time-investment strategies. However, during the rutting peak, the costs of lekking were elevated. Lekking males foraged much less and spent much more time in displays and social interactions than did bachelor males. Direct mortality of males due to territorial disputes, though rare in blackbuck, has been observed (Y.V. Jhala, unpubl. data).

As predicted, we found that lekking costs and time-investment strategies varied according to the position of a male's territory on the lek. Central males

spent more time on the lek and foraged less than did peripheral males. Also, central and peripheral males showed different temporal patterns in their time spent on the lek. There were more females on the lek in the evening than in the morning or in the afternoon, and most observed matings occurred in the evening. Corresponding to this, peripheral males spent more time on the lek in the evening than either in the morning or in the afternoon. Thus, they seem to be tailoring their time spent on the lek to suit temporal patterns in female activity on the lek. On the other hand, central males showed fairly uniform levels of lekking throughout the day. Central males also tended to have higher fighting rates than peripheral males, although central and peripheral males spent similar amounts of time in displays and in social interactions.

While variation in time-investment strategies of males within ungulate leks has not been previously described, differences among lekking males associated with displays and agonistic interactions have been studied in topi, kob (*Kobus kobus*), lechwe (*Kobus leche*) and fallow deer leks. For example, Gosling & Petrie (1990) observed that male topi on the edge of the lek had lower fighting rates than males in territories further within the lek. In contrast, Apollonio *et al.* (1992) did not find any variation in the number of escalated fights among lekking male fallow deer. Further, on several avian leks, differences in foraging behaviour, display rates, display repertoire and fighting ability related to territory location have been described (Gibson & Bradbury, 1985; Kruijt & de Vos, 1988; Vehrencamp *et al.*, 1989; Alatalo *et al.*, 1991).

Corresponding to spatial variation in lekking costs, we found similar differences in male mating success. Our results suggest that female blackbuck prefer to mate with males holding territories in the lek-centre and may use indirect cues (like territory location) to choose mates. Several observations support this conclusion. Firstly, most matings occurred in the lek-centre (which included only ten percent of the entire lek area). Secondly, many central territories continued to be successful even after the original successful males were replaced. A similar pattern has been observed on Uganda kob leks (Deutsch & Weeks, 1991). Thirdly, although three of the five most successful male blackbuck originally held several territories outside the lek-centre, they were not observed to mate on any of their previous territories. Similar changes in male mating success accompanying changes in territory position have been recorded on a fallow deer lek (Apollonio *et al.*, 1990).

Fourthly, throughout the study, males tended to move towards the lek centre while shifting territories. Since this trend was observed even during low levels of rutting activity and before the first matings were observed, it seems that males too may prefer the centre. This might occur if males were responding to a general female preference for central territories. Finally, competition for central territories seemed to be greater than that for peripheral territories since territory turnover was higher among central than among peripheral territories. Studies of other lekking ungulates have also reported the importance of the characteristics of territories to female choice, although the actual cues that females use may differ among species and even among populations of a species (Clutton-Brock *et al.*, 1988; Apollonio *et al.*, 1989; Deutsch & Weeks, 1991).

The observed female mating patterns on the lek may explain the differences among males in their lekking behaviour. If females consistently preferred certain sites, then males would be expected to fight for and maximise their stay at those sites. Males occupying territories in the lek-centre where most matings occurred should try to maximise encounters with females in oestrus. This can be done by cutting down on foraging time (since foraging entails moving out of the lek) and increasing the time spent on the lek. Thus, males on central territories, where the benefits of lekking are the greatest, should invest heavily in lekking. Peripheral males following a similar strategy would face the same heavy costs but reap meagre benefits. A better strategy for peripheral males would be to avoid compromising on foraging time, to maintain condition and to try to oust central males when the latter lose condition. Thus male blackbuck may adjust their investment in lekking to the potential benefits (mating opportunities) associated with the positions of their territories. Lekking males may be sensitive even to variation through the day in potential gains; the data on time spent on the lek suggest that peripheral males take part in lekking activities at times of the day when female activity on the lek is high, and that they shift to maintenance activities at other times.

An alternative explanation for the behavioural differences we found is that they might reflect intrinsic differences in male phenotype (Clutton-Brock *et al.*, 1988; Vehrencamp *et al.*, 1989). Peripheral males may be younger, weaker or older individuals that cannot afford to invest much in lekking behaviour. Instead, they might establish territories around successful males and attempt to intercept females attracted to these males. Such a strategy

would result in a similar spatial pattern in the distribution of copulations: a cluster of successful territories surrounded by unsuccessful ones. Although we did not directly assess male phenotype (other than behaviour), our data on male movement towards the centre, and the change in male mating success with territory location suggest that it is likely that females pay more attention to indirect spatial cues than to direct phenotypic cues while making mating decisions. Thus, our results are consistent with the hypothesis that, among lekking males, variation in lekking costs is related to differences in mating benefits: central males, whose gains from lekking were high, faced apparently heavy costs, while peripheral males, whose mating success was low, incurred lower costs, especially in relation to a reduction in foraging. The potential role of male phenotype in explaining the patterns we found remains to be studied.

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