Mating strategies of topi bulls: getting in the centre of attention

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In lek-breeding ungulates, only some males defend clustered lek territories, and others defend dispersed territories or are nonterritorial. In this study of lekking topi antelopes, *Damaliscus lunatus*, we measured male mating benefits directly by observing matings and investigated why the alternative mating strategies coexist. A multivariate analysis showed that proximity to the lek centre had an overriding, positive, effect on male mating rate. With increasing distance to the lek centre, proximity of a territory to a drainage line became increasingly important in enhancing male mating success. On the other hand, costs of lekking were suggested by higher hyaena density on leks, relatively poor body condition of lek males, and more frequent agonistic encounters, with central lek males more likely to sustain bleeding wounds than others. Probably as a consequence of the intense competition for central lek territories, males defending such territories were larger than others and, judging from horn wear, they were also older than resource defenders. Not only did males defending central lek territories achieve the highest instantaneous mating rate and resource defenders the lowest, but the same order was also likely for overall lifetime reproductive success when we took territorial tenure into account. These results suggest that male mating strategies are phenotype limited, as demands on male quality increase with proximity to the lek centre.

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In lekking populations of ungulates, as well as in many lekking birds, only some males defend territories on leks, and others defend dispersed territories or are nonterritorial (Höglund & Alatalo 1995). The game-theoretical basis for such coexistence of alternative mating tactics is often unclear (Rubenstein 1980; Dunbar 1982; Gosling 1986). Are payoffs age dependent with individuals switching tactics through life? Or are tactics fixed for each individual? If the latter is the case, do the different strategies yield similar lifetime payoffs through frequency-dependent costs and benefits or do payoffs depend on individual quality, so that low-quality individuals have different optimal strategies from high-quality individuals (phenotype-limited strategy; Parker 1982)?

Different studies have found support for different models, which undoubtedly reflects interspecific variation in evolutionary mechanisms (Höglund & Alatalo 1995; Lanctot et al. 1998). However, the variation might also be partially due to discrepancies in how payoffs are measured. In species where males invest relatively little in offspring and the operational sex ratio is male biased,

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mating opportunities are important in determining payoffs to male strategies (Clutton-Brock & Parker 1992). Male mating opportunities in such species are generally thought to be maximized by mapping on to female dispersion determined by resources (Davies 1991). Based on this logic, female numbers have been used as a proxy for male mating success. However, where females mate preferentially with certain phenotypes or in certain locations, as is typically the case in lekking species (Bradbury 1981; Bro-Jørgensen 2002), female number is a confounded measure of mating success because of variation in female mating probability. In such cases, mating success is more reliably measured as number of matings observed.

We investigated how male traits influence the use of mating strategies in topi antelopes, *Damaliscus lunatus*, and the consequences for mating success, food intake, fighting costs and predation risk. This is the first time that mating success in topi has been assessed directly by observing matings. Because evolution favours strategies yielding high lifetime reproductive success, we also addressed the question of whether the short-term measures of costs and benefits used are likely to reflect lifetime payoffs. To do this, we estimated to what degree individual males may switch tactics over their lifetime.

METHODS

Study Area

Between November 1998 and June 2000, J.B.-J. studied the mating strategies of topi males in the Masai Mara National Reserve in Kenya (1°15′–1°43′S, 34°47′–35°24′E). The study area was covered by open, rolling grassland characterized by red oat grass, *Themeda triandra*, with woody vegetation along drainage lines. The numerous ungulate species in the area also included blue wildebeest, *Connochaetes taurinus*, Burchell's zebra, *Equus burchelli*, Thomson's gazelle, *Gazella thomsoni*, and impala, *Aepyceros melampus*. The main predators of topi in the area were spotted hyaena, *Crocuta crocuta*, and lion, *Panthera leo*, of which the former is presumed to be the more important (see Discussion).

Three topi leks, separated by 6.8–8.6 km, were identified; in between these other males defended large resource defence territories (RDTs). Four survey areas were defined: area A (4.1 km²; four central lek territories, eight peripheral lek territories, nine RDTs), area B (2.5 km²; three central lek territories, eight peripheral lek males, 12 RDTs), area C (1.8 km²; six central lek territories, eight peripheral lek territories, 11 RDTs) and area D (9.2 km²; 21 RDTs). All lek territories were included in the survey areas.

Study Species

The topi is a homeomorphic species in which both sexes are horned and female body mass averages 12% less than that of males (Balmford & Blakeman 1991). Within the study area, topi occur at a density of 7/km² and the adult sex ratio is 1.86 females:males (Bro-Jørgensen 2001). The topi rut, defined as the period during which matings are observed, typically lasts 1.5 months during the long wet season in March–May. Males are also territorial outside the rut but at this time lek males in particular often leave their territories for prolonged periods. While generally only females and calves are accepted on to a male's territory, topi can be found in mixed-sex herds in non-territorial areas. The males in these herds are either territorial males that have temporarily left their territory or nonterritorial males. During the rut, females follow a more or less regular movement pattern in relation to the slopes (so-called catenas) and the leks. After spending the night on the catena top, which presumably has anti-predator advantages, they descend the catena around dawn to feed closer to the drainage lines. This is typically the time when the largest numbers of females pass via the leks (Bro-Jørgensen, in press b). During the rest of the day, female visits to the leks follow a more irregular pattern. In the afternoon females ascend the catena again to spend the night on the catena top. Oestrous females typically mate multiply.

Individual Recognition and Measurements

The following information allowed both males and females to be recognized: shape of the black face-mask, face profile, number of horn ridges and, if present, abnormality in horn ridge pattern, asymmetry in horn curvature or length, horn fracture or deformity, location and shape of ear nicks, abnormal tail morphology, eye damage, albinisms, melanisms, location and shape of scars or lumps. In addition, colour of the scrotum tip was recorded for males and the characteristics of any accompanying calf for females.

Size was measured by shoulder height from the top of the shoulder to the false hoof gland because grass often covered the hooves themselves. The measure was taken from projected slides of individuals standing relaxed calibrated by slides of a 1-m pole taken at the same distance. Distance was measured with a laser rangefinder (Bushnell Yardage Pro 800). Repeatability (calculated following Lessells & Boag 1987) was highly significant ($F_{85,118}=26.64$, $P<0.0001$, repeatability 0.91).

The horns of topi become worn through life by horning the ground (Anthony & Lightfoot 1984). Based on a correlation between horn wear and tooth eruption it has been argued that horn wear can be used to determine age (Jewell 1972). In the present study, the degree of horn wear was scored on a sliding scale from 1 (tips pointed and long) to 9 (tips rounded and worn down to the ridges).

Condition of territorial males was also scored on a sliding scale from 1 (all ribs visible, lumbar region extremely angular) to 9 (no ribs visible, lumbar region well rounded; modified from Riney 1960). This was done regularly during territorial surveys between December 1999 and June 2000. As scores followed a normal distribution, we calculated the monthly condition score of individuals as the monthly mean score, and the average condition score as the mean of the monthly means.

Territorial Surveys and Mating Scans

Between December 1999 and June 2000, J.B.-J. regularly surveyed territories in the four survey areas: area A (84 surveys), area B (40 surveys), area C (27 surveys) and area D (21 surveys). The surveys were evenly distributed between morning (0615–0900 hours), midday (1000–1500 hours) and early evening (1600–1900 hours). During surveys the following data were recorded for each territory: male identity and GPS location, male condition, horn wear, the number of females, calves, hyaenas and lions on the territory, and whether the male engaged in agonistic encounters during a 3-min interval.

During the rut, daytime scans for all matings were carried out on predetermined subsets of territories: in area A 19 territories were surveyed for 10 days in 1999 and 20 territories were surveyed for 6 days in 2000; in area B 21 territories were surveyed for 12 days in 2000; and in area C 25 territories were surveyed for 4 days in 2000. Although males do perform a distinct ejaculation thrust, we assume that fertilization may also take place during intromissions without such a thrust, as sperm often drips from erect penes. Hence, we used intromission as the critical mating event.

Vegetation Monitoring

Forage quality on territories was measured by a green leaf index with a method similar to that described in

Table 1. Independent variables included in the analysis of male mating success

Variable	Description
Lek centre distance	Shortest distance from a territory to the geometrical centre of the lek (measured in ArcView 3.2)
Territory size	Territorial boundaries were defined based on GPS recordings of all relocations of males on their territories (measured in ArcView 3.2)
Green leaf index	An index reflecting food availability
Number of females	Mean number of females recorded on the territory during territorial surveys in the rut
Hyaena density	Mean density of hyaenas recorded on the territory during territorial surveys
Lion density	Mean density of lions recorded on the territory during territorial surveys
Shoulder height	Height of the territorial male from the false hoof gland to the top of the shoulder
Estimated age	Age estimated from horn wear
Index for male display rate	Coefficient assigned to individual males in a GLM of display rate in front of oestrous females (Bro-Jørgensen, 2001). Male topi display in a characteristic high-stepping gait (Estes 1991)
Frequency of agonistic encounters	Proportion of 3-min one/zero intervals during which a male was engaged in agonistic behaviour
Bordering drainage line	Whether a territory bordered a drainage line
Body condition	Whether a male was in poor (score 1–4) or good (score 5–9) condition
Horn asymmetry*	Whether a male had developmental asymmetry in horn curvature; asymmetry caused by wear or breakage was not considered
Horn break	Whether a male had had more than 3 cm of one or both horns broken off
Facemask	Whether a male had full black bridges under the eyes and on the muzzle

The first 10 variables are continuous; the last five are dichotomous.
*In oryx antelopes, *Oryx gazella*, horns show fluctuating asymmetry rather than directional asymmetry or antisymmetry, and scoring of asymmetry in the field reliably reflected measured asymmetry (Møller et al. 1996).

Balmford et al. (1992), which is based on the finding that topi select green leaf in their diet rather than particular grass species (Duncan 1975). On 25 random sites within each territory, J.B.-J. placed a polystyrene tile (21 × 21 cm, 25 g) on the grass and measured the following: greenness (the proportion of the four leaves closest to the corners of the quadrate that 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, we calculated an index of food availability, the green leaf index. Territories were sampled during the rut in May 1999 and May 2000.

Male Mating Success

The mean number of females mated per day by 78 territorial males followed a gamma distribution. We therefore analysed this parameter with a generalized linear model (GLM) with a gamma error distribution. The morphological and ecological variables described above (Table 1) were fitted to the model in a stepwise forward regression to test whether they explained significant variation in male mating success. All interactions with distance from the lek centre were included in this analysis to test for nonlinear changes in the effects of these parameters depending on the proximity to the prime territories in the lek centre. Whenever terms were significant at the 0.05 level, they were included in the model in the order of highest significance. Thus the final model included only significant terms. The males included in this analysis were the territory holders in the three mating scan areas, each of which contained both lek and resource defence territories.

Male Body Condition

Male body condition was normally distributed and hence could be analysed with standard ANCOVAs and ANOVAs. For these analyses independent variables were divided into those that showed variation for individual males during the study and those that varied negligibly.

To investigate the temporally variable factors we modelled mean monthly condition scores of individual males as the dependent variable in an ANCOVA. Monthly rainfall and 'rut' were fitted as independent variables. 'Rut' was defined as 1 when rutting took place during the first half of the month, and 0 when no rutting took place, or when rutting occurred only in the second half of the month. The onset of rutting in the second half of the month was assumed to have limited influence on body

condition. Male identity was also fitted to control for repeated measures of body condition for the same individual across different months.

To investigate factors that showed little temporal variation with male identity over the study period, we modelled mean male condition score between December 1999 and June 2000 as a normally distributed dependent variable in an ANOVA. The variables tested were territory type defended, age estimated from horn wear (relatively young, i.e. category 1–3, versus older, i.e. category 4–9) and whether a territory had been defended for more or less than a year by March 2000.

Nonparametric Statistics

Because observations of kills were rare, the relation between predation risk and mating tactic was assessed by indirect measures similar to Gosling & Petrie (1990). For hyaenas, which are cursorial predators, we tested for correlation between the mean hyaena density on territories and the minimum distance from a territory to the lek centre. For lions, which are stalking predators, we tested for differences across territory types in vigilance of territorial males during uninterrupted grazing bouts, as too few lions were recorded during territorial surveys to determine their mean density. (See Discussion for limitations of this measure of predation risk.) Vigilance was measured as the number of times a grazing male lifted his head above shoulder level during a 5-min interval when the male was alone on his territory. Repeatability of this measure was highly significant ($F_{55,87}=6.07$, $P<0.0001$, repeatability 0.67).

We assessed relative fighting costs by testing for differences between the three categories of territory holders in (1) the frequency of 3-min intervals during which agonistic encounters were observed and (2) the proportion of males observed with bleeding wounds, presumably sustained during severe fights. We also tested for differences in morphological traits across the three territorial categories. For this analysis the data set was expanded to include territorial males for whom direct information on mating success was not available.

Lifetime Reproductive Success

We calculated indices for lifetime reproductive success (LRS) associated with defence of the three territory types by multiplying an index for momentary mating rate by the total duration of tenure. The index used for momentary mating rate was the mean number of females mated per day per male on a given territory type. A minimum value for the LRS index was calculated assuming a single tenure only and a maximum was calculated assuming tenure lasting the entire reproductive life span. The purpose of calculating these hypothetical minimum and maximum values was to determine the degree of overlap between the intervals of possible values for the LRS index relating to the three territory types.

To estimate the mean duration of a single tenure, we calculated the inverse of the turnover rate for each territory type. Because territorial changes were relatively rare, we estimated the turnover rate by the fraction of territories occupied by new territory holders in January 2000 compared to January of the year before ($N=72$ territories).

The duration of male reproductive life span was estimated by the mean time from reproductive maturity, at around 3 years of age (Kingdon 1997) until death. We estimated longevity by the mean age of death of 93 captive topi which had survived until 3 years of age (International Species Information System ISIS; http://www.isis.org). Because predation and periods of food scarcity might lead to lower life expectancy in the wild, the estimate was regarded as a maximum value for topi in the study area.

Because territorial switches were generally rare, we estimated the probability of switching from one territorial strategy to another by the fraction of 72 identified territory holders identified in January 1999 that had changed territorial status in January 2000.

RESULTS

Determinants of Male Mating Success

Modelling the mean number of females mated daily per male as a gamma-distributed dependent variable in a generalized linear model showed that (1) mating success decreased markedly with increasing minimum distance from the defended territory to the lek centre and (2) the further a male was from the lek centre the stronger was the advantage of defending a territory next to a drainage line (Table 2, Fig. 1). Restricting the analysis to the mating rate of lek males also showed a strong effect of proximity to the lek centre, while none of the other variables or their interaction terms with lek centre distance explained significant proportions of the remaining variation (GLM: gamma dispersion parameter 0.60, coefficient estimate 0.0147, deviance 21.07, $F_{1,45}=34.89$, $P<0.001$).

Analysing the three mating survey areas separately showed the same relation between territory type and mating success on all three leks: central lek males were more successful than peripheral lek males, which in turn were more successful than resource defenders (Fig. 2).

Mean female numbers on territories during the rut showed no significant relation with daily mating rates of territory holders (GLM: gamma dispersion parameter 1.40, coefficient estimate 0.171, deviance 2.14, $F_{1,49}=1.53$, $P=0.22$).

Nutritional Costs and Benefits

When monthly scores of male body condition were fitted as a normally distributed dependent variable in an analysis of covariance, significant relations were found with mean monthly rainfall, rut and male identity (ANCOVA: monthly rainfall: $F_{1,401}=16.44$, $P<0.001$; rut:

Table 2. Results of a generalized linear model fitting variation in the mean number of females mated daily by territorial males

Parameter	Main effect					Interaction with lek centre distance			
	df	Coefficient	Deviance	F	P	Coefficient	Deviance	F	P
Lek centre distance (m)	1,75	0.017	74.68	43.66	<0.001		NA		
Bordering drainage line	1,75	0.215	0.99	0.57	NS	6.56×10^{-3}	7.17	4.19	0.044
Territory size (m²)	1,75	5.65×10^{-6}	0.24	0.15	NS	1.79×10^{-8}	0.79	0.48	NS
Green leaf index	1,75	6.91×10^{-4}	0.37	0.22	NS	6.67×10^{-7}	0.001	0.006	NS
Hyaena density/m²	1,75	4.96×10^{-3}	0.10	0.06	NS	1.21×10^{-3}	1.25	0.70	NS
Lion density/m²	1,75	0.185	0.38	0.21	NS	-1.78×10^{-3}		NA	
Estimated age	1,75	-2.92×10^{-3}	0.002	0.001	NS	5.77×10^{-4}	0.30	0.18	NS
Body condition	1,75	3.72×10^{-4}	0.01	0.006	NS	-3.05×10^{-3}	1.27	0.81	NS
Horn break	1,75	0.160	0.20	0.11	NS	0.026	2.68	1.59	NS
Facemask	1,75	-0.094	0.90	0.53	NS	-2.70×10^{-4}	0.01	0.008	NS
Asymmetry in horn curvature	1,74	−0.035	0.05	0.03	NS	-4.71×10^{-3}		NA	
Agonistic encounters	1,69	3.96×10^{-3}	0.09	0.05	NS	-1.27×10^{-3}		NA	
Shoulder height (cm)	1,65	-0.016	0.03	0.02	NS	-5.65×10^{-4}	0.33	0.21	NS
Display index	1,59	0.272	0.14	0.18	NS	1.26×10^{-3}	0.02	0.028	NS
No. of females	1,48	−0.034	1.70	1.88	NS	-3.20×10^{-4}	0.59	0.65	NS

The data were fitted as a gamma distribution with the dispersion parameter estimated at 1.71. The final model, which included only significant variables, was: [Females mated daily]=[0.375+(0.0232−0.0131x)×(distance to lek centre)]$^{-1}$, where x=0 if the territory does not adjoin a drainage line and x=1 if it does. For nonsignificant parameters, the results were obtained by adding them to the final model. The analysis fits the independent variables to the inverse of the dependent variable; thus, variables showing positive correlations are assigned negative coefficient estimates. Although missing values reduced sample sizes in some analyses, lek centre distance and its interaction with proximity to drainage line retained their significance in all sample subsets except in the analysis including agonistic encounters, where the interaction term was not significant (P=0.098). Female numbers were not recorded in area C.
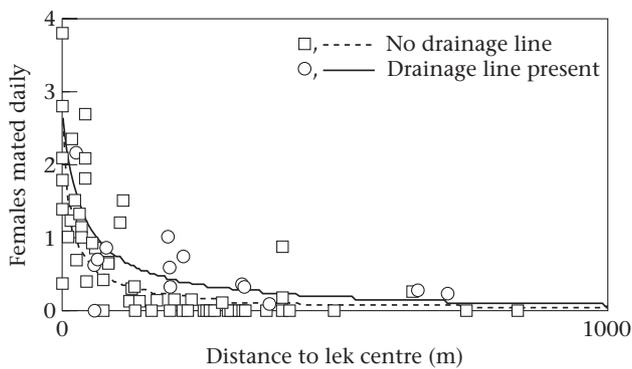

Figure 1. Number of females mated during daytime hours by males in relation to the minimum distance from their territory to the lek centre. Territories were classified according to whether they bordered a drainage line. The curves depict the results of the GLM with gamma errors fitting the number of females mated daily per male.
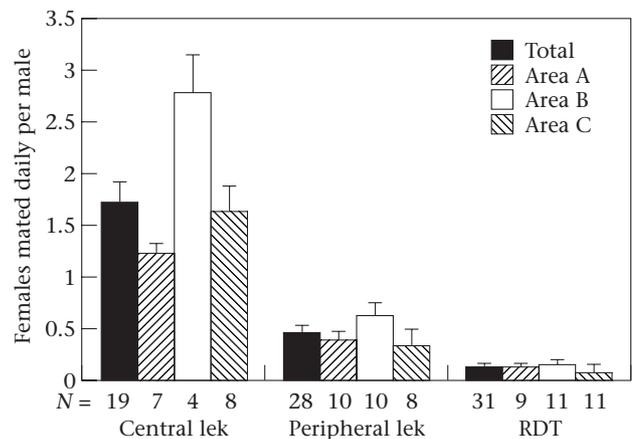

Figure 2. Mean+SE number of females mated per male per day during daytime hours according to territory type. Separate results from three areas with one lek each are shown as well as the average across all three areas. RDT=resource defence territories. N=number of males in each category.

$F_{1,401}$=19.82, P<0.001; identity: $F_{84,401}$=8.64, P<0.001; deviance explained: 65.7%; Fig. 3). Although body condition was relatively poor in the dry months of December 1999 and January 2000, it peaked as the long rains began in March. However, the long rains were also the time of rutting, which explains the drop in body condition in April and May. As the rut ended, males improved their body condition in June in spite of the modest rainfall reflecting the onset of the dry season.

Modelling the mean body condition scores of individual males showed significant effects of territory type defended and estimated age, whereas there was no effect of tenure duration (ANOVA: territory type: $F_{2,91}$=4.60, P=0.012; age score: $F_{1,91}$=7.57, P=0.007; deviance

explained: 17.0%; duration of tenure $F_{1,66}$=0.88, NS; Fig. 4). In two-way comparisons, central and peripheral lek males were both in worse condition than resource defenders, but the two categories of lek males did not differ (Mann–Whitney U test: central lek males versus resource defenders: U=195.5, N_1=14, N_2=58, P=0.003; peripheral lek males versus resource defenders: Z= − 2.25, N_1=23, N_2=58, P=0.027; central versus peripheral lek males: U=125, N_1=14, N_2=23, NS). With age estimated by horn wear, young males were in better condition than older males in all three categories of territory defenders (Fig. 4).
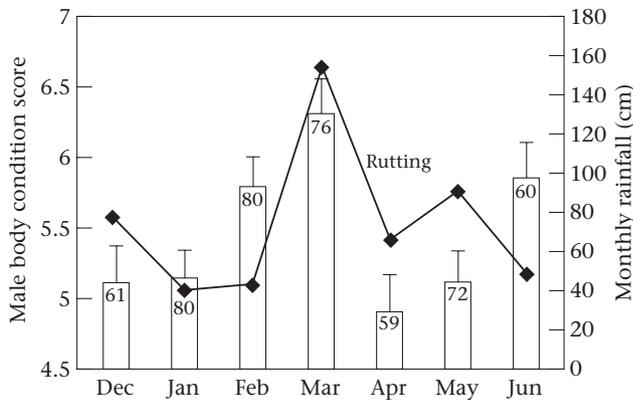
Figure 3. Mean+SE monthly body condition score of territorial males (columns) in relation to rainfall (line) and rutting. Numbers in columns refer to the number of a total of 85 males that were sampled during the month.
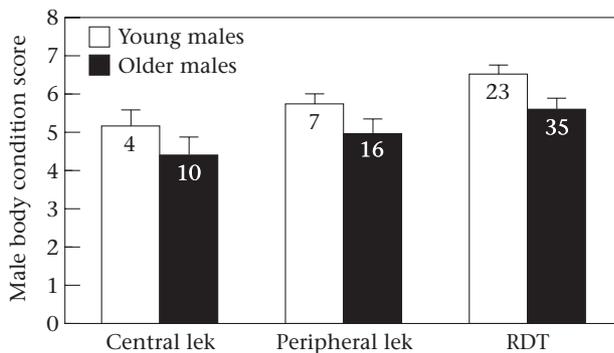

Figure 4. Mean+SE male body condition score between December 1999 and June 2000 in relation to territory type and age. RDT=resource defence territories. Numbers in columns refer to number of males in each category.

Costs of Predation

Territories closer to the lek centre had higher hyaena density (Spearman rank correlation: $r_S = -0.37$, $N=64$ territories, $P=0.002$; Fig. 5). Vigilance of males also differed between territory types (Kruskal–Wallis test: $H_2=23.18$, $N=39$ males, $P<0.001$) and two-way comparisons showed that both central and peripheral lek males had lower vigilance than resource defenders, but the two categories of lek males did not differ (Mann–Whitney U test: central lek males versus resource defenders: $U=4$, $N_1=9$, $N_2=21$, $P<0.001$; peripheral lek males versus resource defenders: $U=16.5$, $N_1=9$, $N_2=21$, $P<0.001$; central versus peripheral lek males: $U=35$, $N_1=N_2=9$, NS; Fig. 6).

Costs of Fighting

Males on leks were more often involved in agonistic encounters than were resource defenders (Kruskal–Wallis test: $H_2=10.80$, $N=63$ males, $P=0.005$; Fig. 7). Two-way comparisons did not show any difference between central
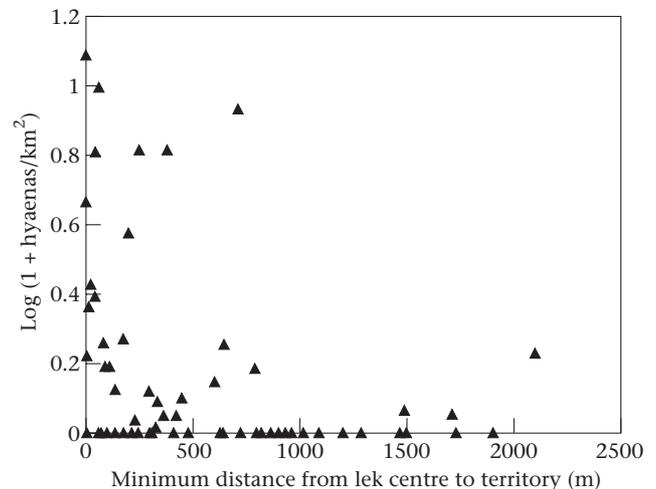

Figure 5. Average density of hyaenas observed on territories in relation to the minimum distance from the territory to the lek centre.
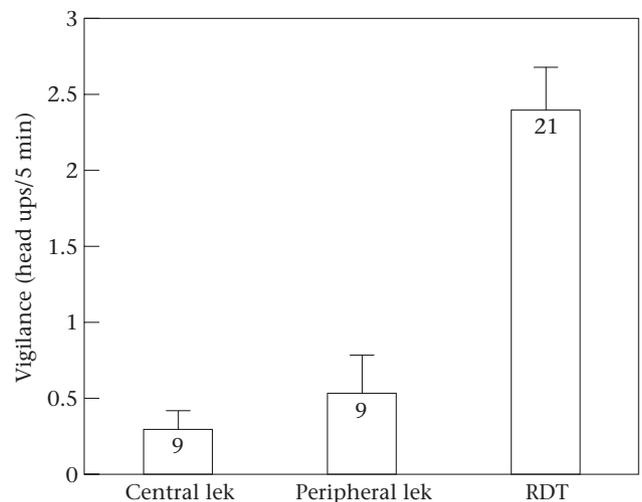

Figure 6. Vigilance of males ($\bar{X}$+SE head ups/5 min) according to the type of territory defended. RDT=resource defence territories. Numbers in columns refer to number of males.

lek males and the other categories, but there was a significant difference between peripheral lek males and resource defenders (Mann–Whitney U test: $U=153.5$, $N_1=16$, $N_2=40$, $P=0.001$). The incidence of open wounds, presumably all caused by intense fighting, was also significantly related to territory type defended (Kruskal–Wallis test: $H_2=16.34$, $N=63$ males, $P<0.001$). Two-way comparisons showed that open wounds were more common in central lek males than in the other two categories of males; no difference was found between peripheral males and resource defenders (Mann–Whitney U test: central versus peripheral lek males: $Z=-2.43$, $N_1=23$, $N_2=32$, $P=0.015$; central lek males versus resource defenders: $Z=-3.44$, $N_1=23$, $N_2=93$, $P=0.001$; peripheral lek males versus resource defenders: $Z=-0.59$, $N_1=32$, $N_2=93$, NS).
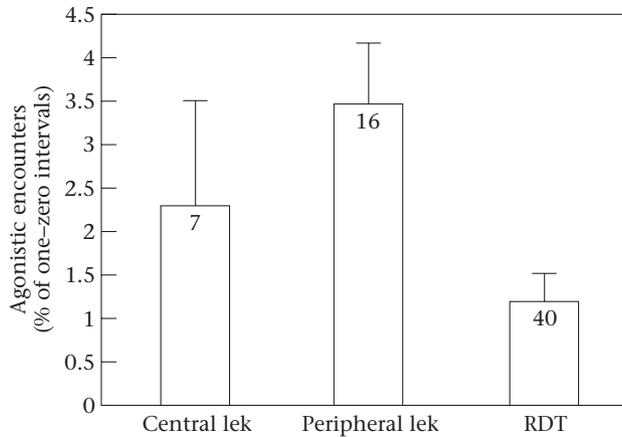
Figure 7. Mean+SE percentage of 3-min intervals during which males defending different territory types were engaged in agonistic encounters. RDT=resource defence territories. Numbers in columns refer to number of males.
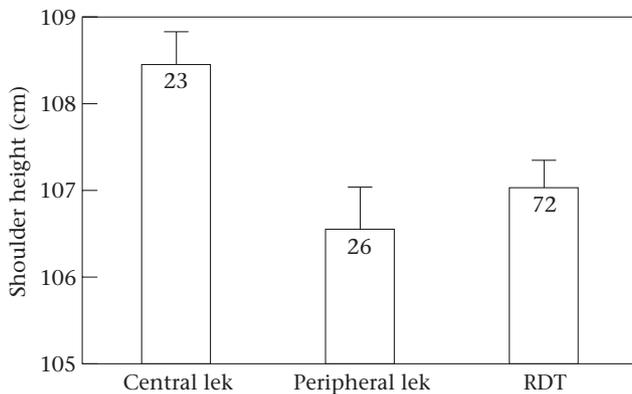

Figure 8. Mean+SE shoulder height (from the false hoof) of males adopting different territorial strategies. RDT=resource defence territories. Numbers in columns refer to number of males.

Male Phenotypic Traits and Mating Strategy

Central lek males were larger than other territorial males (Kruskal–Wallis test: $H_2=9.74$, $N=121$ males, $P=0.008$; Fig. 8).

Age, as estimated from horn wear, also varied significantly with territory type (Kruskal–Wallis test: $H_2=6.98$, $N=150$ males, $P=0.031$; Fig. 9). Although the horns of both categories of lek males were more worn than those of resource defenders, only the difference between central lek males and resource defenders was significant in two-way tests (Mann–Whitney U test: central lek males versus resource defenders: $Z=-2.35$, $N_1=25$, $N_2=93$, $P=0.019$; central versus peripheral lek males: $Z=-0.56$, $N_1=25$, $N_2=32$, NS; peripheral lek males versus resource defenders: $Z=-1.73$, $N_1=32$, $N_2=93$, $P=0.08$, NS). As expected in a species with determinate growth, shoulder height did not vary significantly with age (linear regression: $t_{119}=0.423$, NS).

No other morphological variables varied significantly with territory type defended (Kruskal–Wallis test: asymmetry in horn curvature: $H_2=2.42$, $N=149$ males; black-
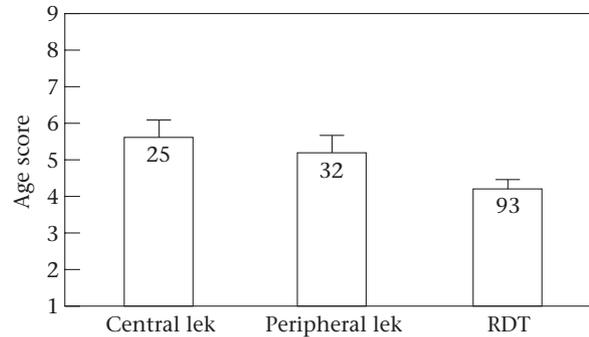

Figure 9. Mean+SE age score of males adopting different territorial strategies. RDT=resource defence territories. Numbers in columns refer to number of males.

ness of facemask: $H_2=2.00$, $N=150$ males; horn breaks: $H_2=0.22$, $N=150$ males; all NS).

Lifetime Reproductive Success

The mean age of death of 36 captive males that had survived until 3 years of age was 7 years and 11 months and for 57 females it was 8 years and 11 months, with no significant difference between the sexes (two-sample t test: $t_{91}=-1.18$, NS). As males reach sexual maturity around the age of 3 years, their mean reproductive life span was therefore estimated to be roughly 5 years.

None of the 72 males followed for a year switched between two territories of the same type. Of 48 resource defenders, 8 (17%) lost their territory within a year, while three (6%) 'upgraded' their territory to a peripheral lek territory by shifting closer to the lek centre. Thus the average duration of tenure for resource defence territories was estimated at 4 years and 4 months. Of 14 peripheral lek males, five (36%) lost their territory within a year, while one (7%) shifted to a central lek position; consequently the average duration of tenure was estimated at 2 years and 4 months for peripheral lek males. Of 10 central lek males, six (60%) lost their territory within a year but two (20%) acquired resource defence territories in new locations; thus the average duration of tenure of central lek territories was estimated at 1 year and 8 months.

The estimated mean duration of tenure for resource defenders nearly equals their mean reproductive life span; however, for peripheral lek males and central lek males, tenures were estimated to last about one-half and one-third of their reproductive life span, respectively, suggesting that multiple tenures could be common. Nevertheless, whether single or multiple tenures were assumed, males acquiring a central lek territory appeared to have higher LRS than males that remained on the peripheral lek, who in turn had higher LRS than resourse defenders (Table 3).

Since our research design focused on monitoring territories, we do not know the fate of males that lost their territory and failed to acquire another. None the less, we did confirm that former lek males could subsequently become nonterritorial and join bachelor herds just as males that acquired both central and peripheral lek

Table 3. The minimum and maximum lifetime reproductive success (LRS) indices for males according to territorial status

	Minimum	Maximum
Central lek male	1.72×1.67=2.87	1.72×5=8.60
Peripheral lek male	0.46×2.33=1.07	0.46×5=2.30
Resource defender	0.12×4.33=0.51	0.12×5=0.60

Minimum LRS index=(Index for momentary mating success)× (duration of a single tenure in years) and maximum LRS index=(Index for momentary mating success)×(reproductive life span in years), where momentary mating success index is the mean number of females mated on a territory per day.

territories in some cases were known to have been non-territorial immediately before.

DISCUSSION

The strongest correlate of male mating success was the distance from a territory to the lek centre: males closer to the centre mated with more females. With increasing distance from the lek there was a growing but modest benefit of defending a territory next to a drainage line. The relatively low territory turnover suggests that momentary mating success might reflect relative lifetime reproductive success, supporting the hypothesis that males gathered on leks for mating benefits. However, lek males incurred several costs as well: they were in worse body condition than resource defenders; hyaenas, their presumed main predator, were found in higher densities on than off leks; and lek males engaged in agonistic encounters more frequently than resource defenders.

Severe fighting was more frequent on the central lek, which could explain why central lek males were larger than other males, because fighting ability often depends on body size (e.g. Davies & Halliday 1977; Jarman 1983; Owen-Smith 1993; McElligott et al. 2001). The food shortage on leks is likely to exacerbate this demand on male quality. Apart from body size, the results suggest that viability may be indirectly favoured by sexual selection because of its association with centrality. Although darkness of the male facemasks did not correlate with male strategy in the present analysis, restricting the analysis to lek males showed a positive association between centrality and darkness of the facemask (Bro-Jørgensen 2002). This finding suggests that dark facemasks may reflect high levels of androgens and higher levels of aggressiveness. For example blackbuck, *Antilope cervicapra*, males turn lighter after castration (Krumbiegel 1955).

The results relating to predation risk mirrored those of Gosling & Petrie (1990) in showing higher hyaena density, but lower vigilance, on than off leks. The lower vigilance of lek males could suggest benefits from sharing vigilance and possibly reducing the risk of lion predation; however, there are other interpretations. For example males may scan primarily for conspecifics, or reduced vigilance on leks could be related to poor feeding conditions. In any case, lion predation is likely to be of less concern than hyaena predation: even though an individual adult lion eats about twice as much per day as an adult hyaena (lion: 5–7 kg, Schaller 1972; spotted hyaena: 3.0 kg, Kruuk 1972), hyaenas in the Masai Mara study area outnumber lions by more than eight to one (Ogutu & Dublin 1998). Furthermore, in a study on a similar ungulate community in Serengeti National Park lions did not prefer topi (Scheel 1993), while hyaenas in the present study area select topi during the first half of the year (Cooper et al. 1999) which includes the months of the rut. Thus the higher hyaena density found on leks suggests that lekking overall leads to increased rather than decreased costs of predation.

Resource-defending males in general did not swap between tactics. While switching might be more common in lek males, it appeared unlikely to even out the large skew in momentary mating success: the indices for life-time reproductive success suggest that resource defenders achieved lower LRS than males capable of acquiring lek territories, especially in the centre. For peripheral lek males and resource defenders, a weak tendency for a centripetal direction of territory shifts suggests that topi males could show an intermediate queue discipline for central territories, resembling the system described for black grouse, *Tetrao tetrix*, where territory position reflects male lifetime performance (Kokko et al. 1998, 1999). In line with the present results, such a system predicts that central territories will be held by older males with superior fighting ability.

Although resource defenders generally seem to be making the best of a bad job, our results suggest that they can improve mating success by holding territories next to drainage lines, an advantage that may be explained by the higher availability of green grass and water, which attract females. Females may mate with resource defenders because of male coercion (Bro-Jørgensen in press a).

Gosling & Petrie (1990) assessed male mating success indirectly by female numbers in Masai Mara National Reserve. Although lek males that attracted many females tended, nonsignificantly, to be large, lek males overall were smaller than resource defenders because lek males that attracted few females were small. In the present study successful males were significantly larger than others; however, we did not observe small, unsuccessful lek males. Between the dates of these two studies topi numbers and lek size have declined in the area (Ottichilo et al. 2000), and an explanation for the different results could be a density-dependent switch in the tactics of small males, which might be poor competitors. At high densities, the costs of acquiring resource defence terri-tories might be relatively high because of intensified competition. Under such conditions, a satellite tactic could be favoured where poor-quality males cluster around leks trying to intercept females moving to the lek centre. However, any clustering of poor-quality satellite males would be a secondary phenomenon that does not explain the origin of lekking: on the smaller leks in the present study, males were not smaller than resource defenders and all lek males were relatively successful, whether central or peripheral.

While the LRS indices presented here allow initial assessment of the game-theoretical basis for coexistence of male strategies, further information on certain critical variables is desirable. Data on paternity would improve the measure of mating success (Lanctot et al. 1997). In addition, following individuals for life would allow determination of the life span of topi in the wild and would provide a more accurate picture of switches in tactics (McElligott & Hayden 2000; McElligott et al. 2002). Furthermore, the calculations assume that the mating rate of males following a nonterritorial tactic is lower than that of territory holders. While that appeared to be the case in our study, as all matings observed involved males showing territorial behaviour, ideally the mating success of nonterritorial males should be assessed through focal watches.

In summary, we propose that the main factor deciding overall male mating success in the study population is how close a male managed to get to the lek centre. Although, once established, a male's position on the lek was relatively fixed, the benefit of centrality might explain the weak tendency for males to shuffle closer to the lek centre as opportunities arose. Larger males, presumed to be superior competitors, were more likely to obtain central positions. Older males may be more likely to establish themselves on the lek, possibly because of more fighting experience. Although lek males could hold resource defence territories at other times in their lives, the main contribution to their lifetime reproductive success was likely to come from the tenure of the lek territory. Resource defenders in most cases stayed with their tactic through life, although the lifetime payoff was lower than for lek males; this might be explained by poorer competitive ability.

Our results suggest that the alternative mating strategies in lekking topi are phenotype limited with males having different optimal strategies according to their quality. High-quality males are able to harvest high lifetime payoffs, because they are able to pay the high costs associated with the high mating benefits on the central lek. Low-quality males achieve lower lifetime payoffs: because they are unable to pay the cost of staying at the lek they have to opt for the alternative strategy of resource defence.

Acknowledgments

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