Lekking, resource defense, and harassment in two subspecies of lechwe antelope

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For lek-breeding in ungulate populations to continue, benefits to males defending lek territories and to females visiting leks must outweigh the costs. In this study, Kafue lechwe males on leks gained higher mating rates than nonlekking males, a result of sexually receptive females leaving herds and aggregating on leks. When the numbers of females on leks were experimentally reduced, benefits to males decreased, resulting in males gradually abandoning lek territories. A comparison with a population of nonlekking, resource-defending black lechwe showed that mating attempts by estrous females in herds were disrupted by harassing males eight times more frequently in a population of lek-breeding Kafue lechwe than in the nonlekking black lechwe. Despite the fact that there were fewer Kafue lechwe females on single territories, harassment of estrous females by males was greater on single territories of Kafue lechwe than on leks and greater than on black lechwe resource territories. Females were also absent on Kafue lechwe single territories for long periods because of erratic, widespread movements of compact herds resulting from unpredictable distributions of resources. In contrast, black lechwe females were more evenly dispersed over homogeneous resources and for a given territory, females were likely to be present most of the time. Therefore, unlike black lechwe, male Kafue lechwe find it uneconomical to defend resource territories. Thus, costs to estrous females mating off leks and the absence of benefits to males attempting to defend resource-based territories may be important cofactors in the appearance of lek-breeding in some ungulate populations. *Key words:* harassment, lechwe, leks, mating strategies, resource defense. *[Behav Ecol 8:1–9 (1997)]*

Among the ungulate mating systems, leks are the most unusual, consisting of relatively tiny territories clustered close together, usually at traditional sites (Bradbury, 1971). Lek-breeding is a relatively rare mating system and has only been reported in detail in a dozen species of mammals, including several species of ungulates (Höglund and Alatalo, 1995). Most other ungulate species exhibit resource-defense polygyny, harem-defense polygyny, monogamy, or dominance hierarchies within herds (Clutton-Brock, 1989). Within lekking species, different populations may adopt different mating systems, and even within the same population mating strategies may be variable (fallow deer: Apollonio, 1989; Langbein and Thirgood, 1989; Thirgood 1991; topi: Balmford and Blakeman, 1992; Gosling, 1991; Montfort-Braham, 1975). The question arises, therefore, of why males in only some populations and only in a fraction of species defend tiny lek territories, when by doing so they are likely to incur heavier costs via intense aggression and lack of food than males that adopt other mating strategies.

The most important and immediate benefit to males defending clustered territories is high mating rates. In most studies of lek-breeding mammals, males on leks achieve higher mating rates than males off leks in the same population (topi: Gosling and Petrie, 1990; white-eared kob: Fryxell, 1987; fallow deer: Apollonio et al., 1992; Clutton-Brock et al., 1988; Uganda kob: Balmford et al., 1992; Kafue lechwe: Nefdt, 1992, 1995; Schuster, 1976). This is because females, particularly those in estrus, actively travel to and settle on leks (Balmford, 1992; Balmford et al., 1993; Clutton-Brock et al., 1993; Nefdt, 1995). In addition, leks are sometimes visited by herds, which rest on lek-sites and leave estrous females behind when the herd moves on (Apollonio et al., 1990; Monfort-Braham, 1975). In fallow deer (Clutton-Brock et al., 1993), Uganda kob (Deutsch, 1994b), and Kafue lechwe (Nefdt, 1995), clustered territories may also retain larger numbers of females than single, isolated territories. Such retention of females among clustered territories may generate additional benefits to males that defend territories close together (Stillman et al., 1993).

Why then do females prefer to mate on lek territories? By analogy with bird leks, the most widely held view is that by traveling to leks, female ungulates benefit from opportunities to choose particular males that will provide them with offspring that have better survival rates or sons that are more attractive to females (Kirkpatrick and Ryan, 1991). Evidence in favor of the "good-genes" hypothesis normally involves the demonstration that, within leks, the majority of females mate with the most competitive males (Balmford, 1991; Balmford and Read, 1991; Clutton-Brock et al., 1989). By visiting leks, females may mate with bigger and fitter males. For example, female Uganda kob nearly always mate with lekking males, which are larger than average nonlekking males (Balmford et al., 1992). This does not, however, preclude the possibility that females could still choose genetically superior males among hundreds of males concentrated together and therefore potentially available at low cost in herds, as in Kafue lechwe (Nefdt, 1995), or among males defending resource territories, as in puku (Rosser, 1992), red lechwe (Williamson, 1994), or black lechwe (Thirgood et al., 1992). Furthermore, even if females do gain genetic benefits from mating on leks, it does not necessarily follow that mate choice is the sole cause of lek formation.

It is also possible that females may gain direct benefits from mating on leks through decreased predation risk or increased mating rates (Kirkpatrick and Ryan, 1991). Studies of ungulates have shown that (1) estrous female fallow deer are harassed by males when off leks (Clutton-Brock et al., 1992), (2)

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in Kafue lechwe, successful mating rates are depressed by disruptions by nonterritorial males in herds (Nefdt, 1995), and (3) Uganda kob prefer high-visibility leks, possibly to avoid predation (Deutsch and Weeks, 1992). Once estrous females leave herds due to harassment, they may be attracted to harems of females already ensconced within lek territories, either to avoid further harassment, to reduce the risks of predation, or to settle on comfortable resting sites (Clutton-Brock et al., 1992; Deutsch and Weeks, 1992; Gosling and Petrie, 1990; Nefdt, 1995).

Environmental factors such as resource distribution and terrain, which influence female movements and distribution, may also determine whether it pays males to defend lek territories. Current dogma holds that lek breeding is a default strategy, where it does not pay males to defend harems or resource-based territories when female groups are unstable and resources are spatially unpredictable (Clutton-Brock, 1989; Deutsch, 1994a). If during the mating period, females are consistently attracted to areas of good-quality resources, it might pay males to defend these resources, as reported in red lechwe (Williamson, 1994) and puku (Rosser, 1992). In contrast, if females are not attracted consistently to any food-resource patches, then encounter rates with single territorial males would be low due to an erratic distribution of females, and it would be uneconomical for males to defend food resources, as reported for Uganda kob (Deutsch, 1994a).

In this paper we compare the mating systems of the lek-breeding Kafue lechwe *(Kobus leche kafuensis)* with the resource-defending black lechwe *(Kobus leche smithemani)*. The comparison between these two subspecies provides a valuable opportunity to investigate which proximate factors determine whether an ungulate population adopts resource-defense polygyny or a lek-breeding mating system. To conduct this comparison, we first examined the costs and benefits to Kafue lechwe males on leks to determine why only a small fraction of males in a population defend lek territories. We then tested whether Kafue lechwe males defend lek territories because females visit leks by experimentally reducing the numbers of females traveling to leks. If harassment is an important factor leading to lek formation, then greater rates of harassment would be expected in Kafue lechwe herds and single territories than in black lechwe herds and resource territories, respectively. Thus, we also compared the harassment rates of estrous females of Kafue lechwe with black lechwe. Finally, by comparing female dispersion in the two subspecies, we examined whether erratic distributions of females make defending resources an uneconomic mating strategy for Kafue lechwe.

METHODS

Study populations

Kafue lechwe are restricted to the central region of the Kafue Flats, a wetland area in southern Zambia. We studied the population in Lochinvar National Park on the south bank of the Kafue River, estimated at 25,000 animals, from April 1989 to June 1991 (Nefdt, 1992). Kafue lechwe provide opportunities to investigate the costs and benefits of mating on and off leks because they adopt a number of different mating strategies within one population. Mating attempts are seen in herds, but the majority are unsuccessful due to disruptions by nonterritorial males (Nefdt, 1995). Males also defend single territories up to 3 ha, which are often near leks, and generally decrease in size the closer they are to leks. Finally, males defend tiny territories on lek sites, some of which shift with changes in floodline (Nefdt, 1996; Schuster, 1976). Females of Kafue lechwe also have resting sites, usually located on slightly raised ground or on headlands jutting into water. Groups of 1–300 females lie on these sites, and in some cases, single males defend them against other males. However, mating on these sites is rare because few females are sexually receptive (Nefdt, 1992).

Black lechwe are endemic to the Bangweulu Swamps, a wetland area in northern Zambia. Current estimates put the population size at 30,000 animals (Thirgood et al., 1994). During the dry season, when water levels are low, the population is spread across some 2,000 km^2 of flood plain. At this time, the lechwe occur in large herds of up to 2000 individuals. When water levels rise during the wet season, the population splits into several subpopulations (Grimsdell and Bell, 1975). One of these, consisting of about 13,000 individuals, was centred in the Chikuni Game Management Area on the southern Bangweulu floodplains. We studied the mating system and ecology of this population from January to March 1991. A proportion of male lechwe defend a network of more than 1000 contiguous, resource-based territories of approximately 2 ha in size. Most copulations occur on these resource territories, and during this study no leks were identified (Thirgood et al., 1992).

Costs and benefits to Kafue lechwe males mating on and off leks

We compared average mating rates of males on five different leks with those of males holding single territories, those in herds, and those on resting sites by scan sampling for periods of 1–3 h. By watching from the roof of the vehicle, we could observe all males on leks (130 h of scan sampling), and up to 40 single territory males (40 h) in one scan. Single territories were >2 ha and >1 km from the nearest lek. Similar data were collected from males defending groups of females on resting sites (11 h), as well as from males in herds >100 animals (18 h). Resting sites and herds were >2 km from the nearest lek. During scan sampling, we recorded the number of males and females standing, lying down, feeding, and moving every 5 min. During each scan, the following agonistic and sexual behavior was recorded: (1) number of threats (noncontact agonistic interactions between males); (2) number of fights (physical agonistic contacts between males); (3) number of mounting bouts (unsuccessful mating attempts); and (4) number of ejaculations (successful mounting bouts). By dividing the rate of each of these activities by the total number of males in the scan, the per capita rates could be compared between males on and off leks.

Scan sampling only gave average rates of mating and fighting for all males, irrespective of whether estrous females were present. We therefore conducted 3-h focal watches of individual males to examine males in the process of defending estrous females. The categories of agonistic and sexual interactions were the same as those used in scan sampling. We recorded the number of agonistic and sexual interactions during each minute and the activity of each male on the minute. Only males defending one or more females were watched in order to compare the ejaculation rates and fighting rates of males holding lek (n = 20 males) and single territories (n = 12), and males defending estrous females in herds (n = 20). In addition the mating and fighting rates of subadult males were recorded on leks (n = 20) and on single territories (n = 11).

Experimental reduction of Kafue lechwe female numbers on leks

We conducted an experiment to test whether reduction of the number of females traveling to leks caused males to abandon lek territories. Observations conducted before the experiment demonstrated that large mixed-sex herds of 100–800 lechwe regularly moved during the evening from their feeding areas 3 km inland to two leks (Channel and Mainde leks) on the edge of Chunga Lagoon. We assumed that numbers of lechwe on each lek were independent of each other because the distance between the leks was 3 km. Herds traveled down well-worn paths, some of which passed directly through Mainde and Channel leks. We counted the number of males and females on each lek on a daily basis between 21 August 1990 and 25 June 1991. In the first manipulation, from 8 September to 29 September 1990, we erected a 300-m long fence 130 m east of Channel lek, across the route females took to the lek. During this period, the Mainde lek remained unfenced. The treatments were reversed during the second manipulation from 29 September to 25 October 1990 by removing the fence from Channel lek and erecting it 120 m east of Mainde lek. The fence consisted of ten 2-m high poles approximately 30 m apart, with a single strand of 2-mm wire attached to the poles 80 cm above the ground. The wire strand was not visible to the human eye from the lek, and lek males ignored it. Two lek males were seen jumping the fence after being frightened off the lek by people, but both returned within 20 min. Lechwe in mixed-sex herds noticed the wire once they were within 10–20 m and in the majority of cases would walk along the fence. A few animals were seen jumping over the wire, particularly when there were animals on the other side.

Harassment rates in Kafue and black lechwe

We compared harassment and disruption rates of estrous Kafue lechwe and estrous black lechwe during continuous watches of up to 3 h. Continuous watches entailed identifying individual estrous females using natural coat or ear markings and recording particular behavioral acts and interactions with males within 10-s intervals. The proportion of mating bouts disrupted by harassing males was calculated from 24 estrous black lechwe in mixed-sex herds (50.3 h of continuous watches), 49 estrous black lechwe on resource territories (18.7 h), 24 estrous Kafue lechwe in mixed-sex herds (51.0 h), and 10 estrous Kafue lechwe on single territories (30.0 h). We divided the causes of terminations of mating bouts into the four categories [described by Nefdt (1995)]: (1) the male voluntarily stopped the mating bout; (2) the male stopped the mating bout after successfully ejaculating; (3) the female terminated the mating bout by running away or lying down; and (4) mating disrupted by harassment from other territorial or nonterritorial males.

Female encounter rates in Kafue and black lechwe

We examined the advantages to males of the two subspecies of lechwe defending large nonlek territories by comparing potential encounter rates of females by territorial males on the Kafue Flats with potential encounter rates of females by territorial males on the Bangweulu flood plains. The distribution of Kafue lechwe females was calculated from a series of ground transects conducted between August 1990 and May 1991 (Nefdt, 1992). We divided the transects into a total of one hundred fifty-two 25-ha squares. The number of female lechwe in each square was censused every 2 weeks from a motor cycle. Similar data for black lechwe were collected from a series of ground transects conducted between January and March 1991. These transects were divided into a total of thirty-two 25-ha squares. We counted the number of female lechwe in each square three times each week from the roof of a vehicle. From these data the proportion of time that squares were vacant and the mean densities of females on squares could be calculated and used as an indicator of whether males would find it economical to defend large territories.

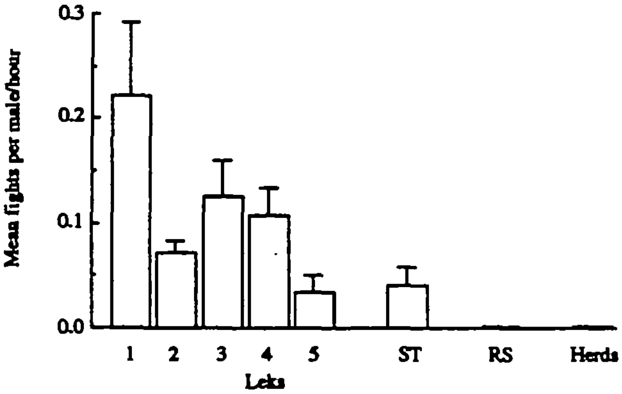

Figure 1
Mean number of fights per adult male per hour on five different leks. These estimates are compared with mean per capita fighting rates per hour of adult males defending single territories (ST), adult males on resting sites (RS), and adult males in herds.

RESULTS

Lekking in Kafue lechwe

Large numbers of estrous Kafue lechwe females on leks resulted in frequent competition between territory holders. During 130 h of scan sampling of leks, two males were killed by neighboring lek males. Scan sampling showed that mean fighting rates on different leks varied between 0.03 and 0.22 fights/male/ h (Figure 1; Kruskal-Wallis test = 18.64, $p < .01$). The average fights/male/h for all leks did not differ from a mean of 0.04 for males on single territories ($n_1 = 419$, $n_2 = 37$, $z = -1.322$, ns). Only on two leks was the number of fights/male/h greater than on single territories (Figure 1). No fights were recorded for resting sites during 11.21 h of scan sampling, nor for herds during 18.33 h of scan sampling.

Temporal increases in the number of males on one lek resulted in increases in per capita fighting rates, with a positive correlation between mean number of males on different days and the number of fights/male/h on those days ($r_s = 0.734$, $n = 22$, $p < .001$). Most males defended lek territories for only 1–3 days, but having occupied a territory, they seldom left it unattended. A number of males joined the lek on a temporary basis, usually defending territories farthest away from successful territories. One-third of all lek males occupied territories for 1 day, 62% for 1–2 days, and only 17% spent more than 10 days on the lek. Once males had occupied lek territories, they seldom left, with 62% of males spending 90%–100% of their time on their territories, and a further 19% spending 80%–90% of their time on their territories. Only 9% spent less than 50% of their time occupying their lek territories.

To examine whether popular territories were more costly to defend than unpopular ones, we examined the relationship between the time males spent on the lek and the mating success of males which achieved one or more ejaculations. Within this subsample of males, those that achieved higher mating rates remained on the lek for fewer days ($r_s = -.79$, $n = 8$, $p < .05$). This suggests that the costs are greater for more successful males.

There were no differences in threat rates of 20 males with estrous females on leks and 12 males with estrous females on single territories (threats/h on leks: mean = 1.88, SD = 1.90,

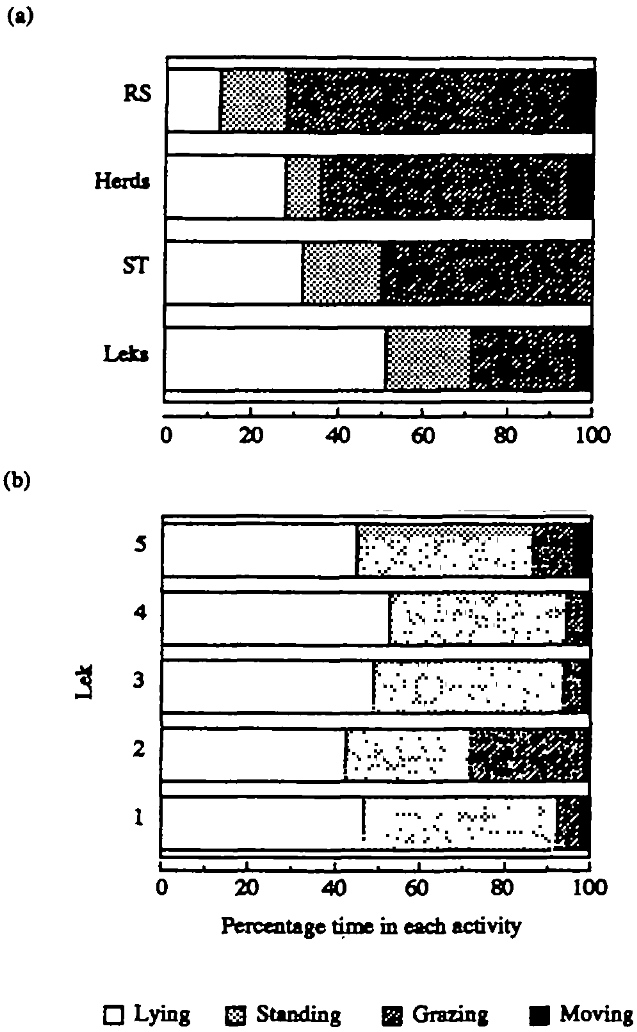

Figure 2
Percentage of time spent lying down, standing, grazing, and moving by (a) males defending lek territories (five leks combined) or single territories (ST), on resting sites (RS), and males in herds and (b) territorial males on five different leks.

threats/ h on single territories: mean = 3.5, SD = 4.21, z = 0.489, ns). There were also no differences in the rates of fights between the same 20 lek males versus the same 12 single-territory holders (fights/h on leks: mean = 0.65, SD = 1.09, fights/h on single territories: mean = 0.33, SD = 0.49, z = 0.49, ns). The rates of threats and fights/ h of lek males did not differ from those of males defending estrous females in herds (threats/h on leks: mean = 1.88, SD = 1.90, threats/h in herds: mean = 1.10, SD = 2.11, $z = -1.67$, ns; fights/h on leks: mean = 0.65, SD = 1.09, fights/h on single territories: mean = 0.28, SD = 0.47, $z = -0.767$, ns). Subadult males, however, seldom managed to defend females, and this was reflected in an average rate of retreats from threats of 1.2 on leks and 1.9 in herds. The frequency of fights was even lower for subadult males, and in all cases resulted in the subadult male losing.

An additional cost to males on leks was reduced time spent feeding (Figure 2). Males on all five leks spent less time feeding than males on single territories, in herds, or on resting sites (Mann-Whitney tests, all $p < .05$). The time spent lying down did not differ between the five leks (Kruskal-Wallis = 8.85, $p > .05$), but there were differences in time spent feeding (Kruskal-Wallis = 128, $p < .0001$), a result of variation in grass cover between leks.

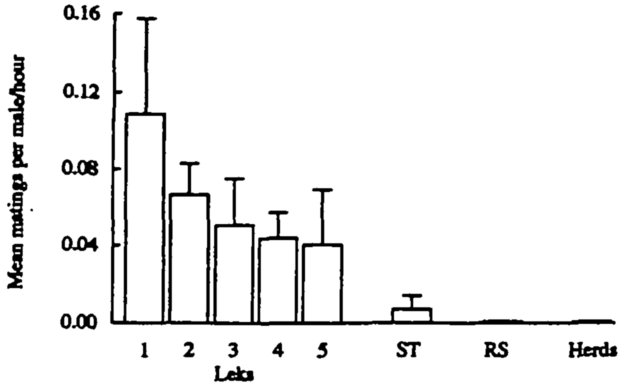

Figure 3
(a) Mean numbers of matings per adult male per hour on five different leks. These estimates are compared with per capita mating and fighting rates of adult males defending single territories (ST), adult males on resting sites (RS), and adult males in herds.

The costs of increased competition and lower feeding rates among lek males were offset by high mean per capita mating rates. Mating rates varied from 0.04 to 1.08 matings/male/h across the five leks (Figure 3). Fewer than 0.01 matings/male/h were recorded on single territories. No matings were recorded in herds or on resting sites. Despite no records of ejaculations off leks, unsuccessful mating bouts were seen, with a mean of 0.87 mounts/h in herds, and 0.35/h on single territories, suggesting that most mating attempts off leks were unsuccessful. Focal watches of adult males with estrous females showed that males on single territories mounted females more frequently than males on leks did (Figure 4a; leks: mean = 6.21, SD = 4.59, n = 20; single territories: mean = 19.50, SD = 12.65, n = 12, z = 3.25, $p < .005$), but did not achieve more ejaculations (Figure 4b; leks: mean = 0.26, SD = 0.30, n = 20; single territories: mean = 0.083, SD = 0.150, n = 12, $z = -1.65$, ns).

Experimental reduction of female numbers on Kafue lechwe leks

Experimental reduction of females traveling to leks caused males to gradually abandon their territories (Figure 5). In the first manipulation, erection of a fence across the route to Channel lek caused an overall reduction of the number of females on the lek (n_1 = 11, n_2 = 18, t = 3.07, $p < .005$), whereas on the unfenced Mainde lek, there was no significant decrease in the number females (n_1 = 30, n_2 = 16, t = 1.73, ns). The reduction of females on Channel lek resulted in a decrease in the number of males holding lek territories (n_1 = 11, n_2 = 18, t = 2.45, $p < .05$), whereas on Mainde lek there was an increase in males (n_1 = 30, n_2 = 16, $t = -3.20$, $p < .005$). The fence was unlikely to have caused males to leave territories because, during the first few days, males remained on the lek despite the reduction in females. The decline in males was gradual, in contrast to the immediate decrease in females, suggesting that the absence of large numbers of females on the lek caused many males to leave their territories. Observations clearly revealed that the reduction of females was immediate, whereas males only abandoned their territories after several days of few or no female visits to their territories. Individual males only left after the number of females had been low for more than 3 days. This was statistically

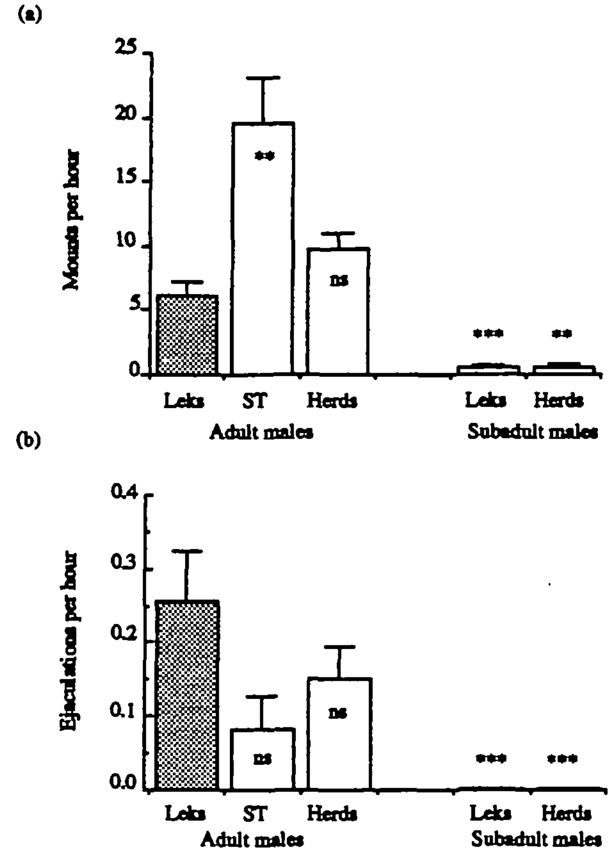

Figure 4
Mean number of (a) incomplete mounts per hour and (b) ejaculations per hour of adult and subadult males defending estrous females on leks, single territories (ST), and in herds.

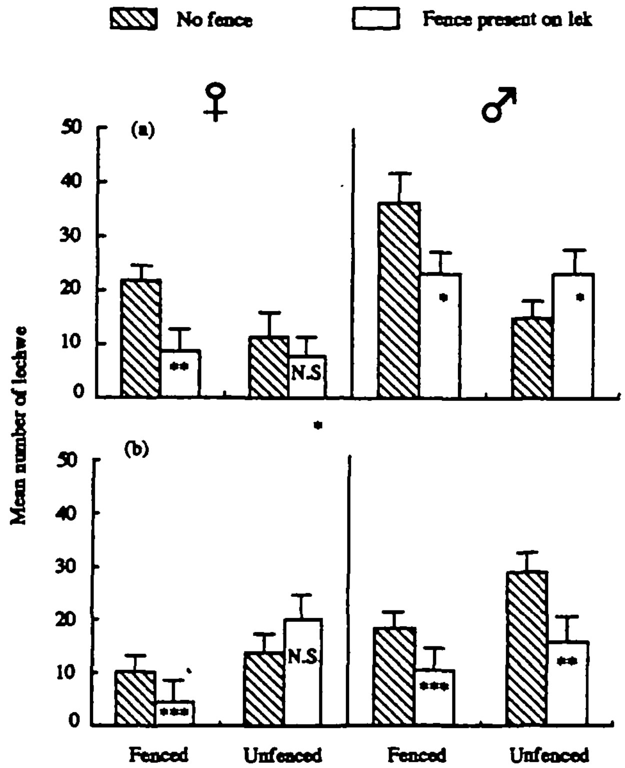

Figure 5
Numbers of male and female lechwe on a pair of neighboring leks before and after erecting fences. (a) In the first manipulation, on the experimental lek (Channel lek), the number of females was reduced by erecting a fence across the route females took to the lek, and the control lek (Mainde lek), 3 km away, remained unfenced. (b) In the second manipulation, treatments were reversed: the fence was erected across the route females took to the Mainde lek, and the control lek (Channel lek) remained untreated. Lines above bars give 95% confidence intervals for daily numbers of males and females on all leks.

supported by no correlation between numbers of females each day on the lek and the number of days after treatment ($r_s = -.163$, $n = 18$, ns), whereas males gradually abandoned their territories on the fenced lek ($r_s = -0.603$, $n = 18$, $p < .01$). A two-way ANOVA showed that after controlling for differences between leks, female numbers decreased significantly after treatment ($F = 19.86$, $p < .0001$), but there was no significant interaction between the effects of treatment (fenced or not fenced) and time (before and after) on the number of females ($F = 0.003$, ns). The numbers of males and females covaried strongly (males; coefficient = .745, females; coefficient = .493).

Reversing the treatments resulted in similar responses of males to experimental reduction of females settling on the lek (Figure 5). The presence of a fence across the route to Mainde lek caused an immediate decrease in number of females ($n_1 = 46$, $n_2 = 22$, $t = 4.297$, $p < .0001$), while on Channel lek there was no significant change ($n_1 = 29$, $n_2 = 20$, $t = -1.097$, ns). The reduction in females numbers on Mainde lek caused another gradual decline in males; the mean numbers were significantly lower after treatment than before treatment ($n_1 = 46$, $n_2 = 22$, $t = 4.16$, $p < .0001$). That this decrease was gradual was evident again from an inverse correlation between number of males and the number of days after treatment ($r_s = -.768$, $n = 14$, $p < .01$). Over the same period, the number of females did not decline gradually because there was no correlation between number of females and days after treatment ($r_s = -.283$, $n = 14$, ns). A two-way ANOVA showed that treatment resulted in a decrease in females ($F = 8.383$, $p < .005$). But in contrast to the first manipulation, there was a significant interaction between the effects of treatment and time ($F = 24.173$, $p < .0001$). As in the first manipulation, the numbers of males covaried (males on females: .803; females on males: .586). In spite of no change in female numbers on the control lek, there was an unexpected decrease in males ($n_1 = 29$, $n_2 = 20$, $t = 3.26$, $p < .005$). One possible reason for this is that males may have abandoned the Channel lek because access to water was reduced; the waterline had receded more than 200 m. This was not the case with Mainde lek, which was located next to a steeper-sided water edge, and the water only receded 30 m. At the end of the experiment, both males and females abandoned the Channel lek, whereas the males on Mainde lek continued to defend territories.

Comparison between black and Kafue lechwe

Whereas the major cause of terminations of mating attempts in Kafue lechwe mixed-sex herds was disruptions by other males, the majority of mating terminations in black lechwe mixed-sex herds resulted from the mating male discontinuing his mating bout (Table 1). There were no differences between black and Kafue lechwe herds in the percentage of termina-

Table 1

Comparison of the causes of terminations of mating bouts (percent) of 23 different estrous Kafue lechwe and 23 estrous black lechwe in herds

Cause of mating termination	Black lechwe (%)	Kafue lechwe (%)	z	p
Female running away	19.40	14.30	0.37	ns
Male stops mating	59.63	39.09	−0.85	ns
Ending as ejaculation	17.39	7.76	−0.85	ns
Disrupted by males	5.43	38.83	3.69	<.0001

Causes of mating terminations were divided into four categories: (1) mating bouts that were stopped by the female running away, (2) those where the male voluntarily stopped mounting the female, but not because of any interaction with another male, (3) mating bouts that ended as an ejaculation, and (4) bouts ending as a direct result of disruption by other males. Mann-Whitney test statistics given.

tions caused by estrous females running away nor by males stopping the mating sequence voluntarily. However, there was a large difference between black and Kafue lechwe in the proportion of mating bouts terminated by immediate disruptions by other males. In black lechwe herds, a mere 5% of mating bouts were disrupted, compared to nearly 40% of all mating attempts by estrous Kafue lechwe. Because of the lower rates of disruption in black lechwe herds, 17% of mating attempts ended successfully as an ejaculation, in contrast to 8% in Kafue lechwe, but due to small numbers of ejaculations this was not significant.

There was also evidence that estrous Kafue lechwe in mixed-sex herds were subjected to more frequent chases than sexually receptive black lechwe females (Table 2). Estrous Kafue lechwe in herds were chased more frequently, and consequently their mating bouts lasted only 1.57 min compared to 7.47 min for black lechwe estrous females. Despite more frequent chases in Kafue lechwe herds than in black lechwe herds, however, there were no detectable differences in ejaculation rates, the number of different males interacting with each estrous female, or in the percentage of time spent lying down, standing, grazing, or moving.

Estrous females on single territories defended by Kafue lechwe males were harassed more persistently than estrous females on resource territories defended by black lechwe (Table 3). Estrous females were chased on average 0.45 times/h on black lechwe resource territories, in contrast to a mean chase rate of 2.05 times/h on Kafue lechwe single territories. Although the mean number of males interacting with an estrous female was greater in black lechwe, this was not due to greater harassment rates, but rather due to females traveling across a number of resource territories unhindered from harassing males. Estrous black lechwe spent less time lying down and moving than estrous Kafue lechwe on single territories. However, there were no significant differences between time spent standing and grazing between the two subspecies on resource and single territories. As a result of the lower harassment rates on black lechwe resource territories, mating bout rates appeared to be greater than on Kafue lechwe single territories. There were more mating attempts in black lechwe than in Kafue lechwe. Black lechwe estrous females received 0.33 ejaculations/h versus 0.13 ejaculations/h in Kafue lechwe, but because of the small number of ejaculations these were not significantly different.

The potential female encounter rates for black lechwe males defending large nonlek territories would be expected to be much higher than for Kafue lechwe. Large herds of

Table 2

Mating rates, chase rates, and male turnover rates of 24 estrous black lechwe in herds compared with those of 24 estrous Kafue lechwe in herds

	Black lechwe	Kafue lechwe	z	p
Ejaculations per hour	0.29	0.18	−0.175	ns
Male turnover rate per hour	2.11	3.91	0.853	ns
Chases per hour	2.34	3.00	2.079	<.05
Mating bouts per hour	3.99	4.65	0.794	<.01
Mating bout lengths (minutes)	7.47	1.57	7.201	<.001

Mann-Whitney tests used to test for significance between samples.

Kafue lechwe were frequently observed to have diurnal movements over large areas of *Vossia* grassland and then move 3–5 km to the flood waters to drink. A herd of 700 animals would, on average, cover an area of approximately 2 ha, but over several weeks the herd would wonder over an area 50–100 km². In addition, at certain times, a large proportion of females (groups of >300) would settle for long periods on resting sites on the edge of the lagoon, further reducing the number of potential mates on any areas inland. Consequently, males attempting to defend large areas away from leks found their territories vacant most of the time.

Transect counts of lechwe demonstrated that, whereas black lechwe were relatively evenly distributed and most transect squares contained females, Kafue lechwe were unevenly distributed and females were absent in most squares for long periods (Figure 6). The frequency distribution of Kafue lechwe female numbers on 25-ha squares was highly skewed, with 69% of the squares vacant. In contrast, the number of female black lechwe on 25-ha squares was not as skewed (Kolmogorov-Smirnov test, $\chi^2 = 631.71$, $z = 12.57$, $p < .005$), and less than 5% of the squares contained no females. The low encounter rates of females by nonlek territorial males on the Kafue Flats may contribute to males abandoning resource-defense polygyny and predispose the population to mating on leks.

DISCUSSION

Male Kafue lechwe gained substantial benefits by defending lek territories because they were more likely to obtain higher mating rates as a result of disproportionately large numbers of estrous females aggregating on leks. Experimental reduction of females on the leks caused males to gradually abandon their territories, suggesting that female presence on the lek was the most important factor determining whether males stay or leave. We believe it is unlikely that reduction in the number of females resulted from male departure because observations and statistical evidence revealed that female reduction was im-

Table 3

Mating rates, chase rates, and male turnover rates of estrous black lechwe on resource territories compared with those of Kafue lechwe on single territories

	Black lechwe	Kafue lechwe	z	p
Ejaculations per hour	0.33	0.13	−0.54	ns
Male turnover rate per hour	1.39	0.50	4.13	<.001
Chases per hour	0.45	2.05	−2.76	<.01
Mating bouts per hour	3.86	2.03	−2.58	<.01

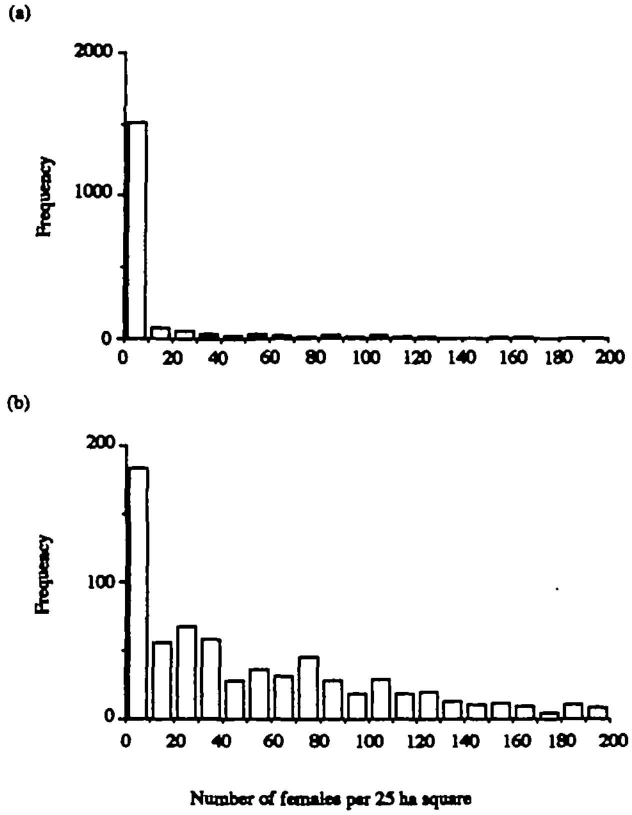

Figure 6
Frequency distribution of (a) female Kafue lechwe and (b) female black lechwe in 25-ha squares.

mediate and a result of the fence blocking the path down which they traveled. Males, on the other hand, only began to leave their territories several days after reduction in females, and the number of males (but not females) was negatively correlated with days after treatment. Observations revealed that males with few or no females on their territories were the first to abandon the lek. The results also suggest that female traffic and resting sites may play a role in the location of lek sites because altering the number of females entering leks affects male numbers. Moreover, the observations of anestrous Kafue lechwe settling on resting sites and the defense of these areas by single males is further evidence that particular sites may function as nonsexually active hotspots. These hotspots on resting sites determined the location of female groups and single males, but did not cause lek formation. As the distribution of the anestrous female population is likely to influence the movements and settling patterns of estrous females, overall population movements are likely to influence the location of leks. The importance of female traffic on lek location was also shown convincingly in fallow deer, where after parts of a forest were cleared, females changed their daily route to feeding grounds (Apollonio et al., 1990). A lek located on the former route disintegrated and re-formed at another site on the new route.

Because disproportionately large numbers of females visiting leks are in estrus (Balmford et al., 1993; Nefdt, 1992), male lechwe had, on average, both higher mating and fighting rates than males on single territories, on resting sites, or in herds. Thus, it is both costly and beneficial for males to defend lek territories. As the number of males on one lek increased, however, the per capita fighting rates increased. As lek size increases beyond a certain threshold, it may become less beneficial for additional males to defend lek territories (Höglund and Alatalo, 1995), and the balance between per capita costs and benefits may be important in determining the maximum size of leks.

There are a number of possible advantages to female Kafue lechwe that mate on leks. They may obtain genetic benefits by visiting leks that provide low-cost opportunities for mate choice. A more direct benefit to Kafue lechwe females of mating on leks may be avoidance of harassment and disruption of their matings when away from leks. Comparisons with black lechwe clearly showed that harassment rates of estrous females in herds were much higher in Kafue lechwe, and that 40% of all mating attempts by estrous females were unsuccessful due to disruptions by aggressive interactions with other males. Moreover, female rejection of courting males in Kafue lechwe herds only accounted for 14% of all terminations of mating attempts and did not differ from female rejection rates in black lechwe. Estrous females on the Kafue Flats have already been shown to reject males just as frequently in herds as on leks, suggesting that female preferences for particular males (if there are any) are similar both in herds and on leks (Nefdt, 1995). These higher levels of harassment of estrous females and large proportion of matings ending unsuccessfully as a result of disruptions by males may explain why females avoid mating in herds in Kafue lechwe, but readily mate in black lechwe herds.

The question nonetheless arises as to why females prefer lek territories more than single territories. Estrous female Kafue lechwe may also avoid mating on single territories because the territory owners are unable to defend them from disruptions and harassment from other males. Our results showed that despite females attempting to mate three times more often with Kafue lechwe holding single territories than with lek males, there were almost four times as many successful ejaculations on leks. One in 200 mating attempts by single-territory males defending estrous females was successful, compared to a success rate of 1 in 23 mating attempts by lek males with estrous females. This was because the majority of mating attempts on leks were successful, whereas on single territories, few culminated successfully as an ejaculation. The main factor that reduced mating success rates on single territories was premature termination of a mating bout by other disrupting males.

Male Kafue lechwe may not find it economical to defend resources because of unpredictable encounter rates of sexually receptive females away from leks. If male Kafue lechwe defended comparatively large territories away from the lek, they would encounter estrous females less frequently than male black lechwe. Even in 25-ha squares, which were 10 times larger than the average lechwe resource territory, Kafue lechwe females were present less than 5% of the time. A Kafue lechwe male which set up a 2 ha territory randomly in the area normally inhabited by lechwe would have to wait several days for the appearance of any females on his territory. As only a tiny proportion (<1%) of females in a herd are in estrus, the probability of a male on a large, randomly located territory gaining a sexually receptive female would be extremely low. Another reason higher instability of groups of Kafue lechwe may reduce the benefits of resource-defense polygyny is that when a large herd enters a resource territory, the single male attempting to defend any estrous females may be overwhelmed by hundreds of males in the herd. Any attempts to mate by the owner of the territory are likely to be aborted by intense harassment and disruptions by nonterritorial males. Thus, in Kafue lechwe, males defending large resource-based territories will have no access to females for most of the time, as their territories will remain vacant, but when a herd passes through the resource territory, he will be unable to compete with the other males in the herd for estrous females.

There are probably a number of reasons why Kafue lechwe female encounter rates are lower away from leks, but most important is that in the variable flood plain habitat, males are unable to defend patches of resources that predictably attract females, and mixed-sex herds travel erratically over a vast area. Seasonal floods, which vary from year to year, cause movements of Kafue lechwe of more than 15 km (Nefdt, 1992). Annual differences in flooding patterns, which recently have been made more unpredictable by the construction of hydroelectric dams, also cause changes in the distribution of vegetation communities (Nefdt, 1992). As female distribution is strongly affected by habitat preferences, seasonal and annual changes in vegetation are likely to make territorial defense of resources used by females even more difficult for males. Another major cause of unpredictable resources are spatial factors such as distance to the waterline, grass height, fire, and whether the ground is dry or wet (Nefdt, 1992).

If unpredictability of resources make it uneconomical for male Kafue lechwe to defend resource territories, then why do male black lechwe defend resources used by females? On the Bangweulu flood plains, females are distributed relatively evenly, in response to the homogeneity of the vegetation (Thirgood et al., 1992). Thus, resource distribution is predictable during the 4-month mating season. Female group sizes are consequently much smaller than on the Kafue Flats. Rather than a few large herds moving rapidly over large areas, female black lechwe groups moved relatively slowly and remain on shallow-water flood plain vegetation, which has a relatively high protein content (Grimsdell and Bell, 1975). Under these circumstances, male lechwe would find it economical to defend a network of more than 1000 contiguous, resource-based territories on the flood plain (Thirgood et al., 1992).

Black lechwe are an example of resource defense on a homogeneous flood plain, where females are distributed evenly both in space and time during the mating period. In red lechwe, *L. l. leche*, a third subspecies living in the Linyanti Swamp, Botswana, males defend patches of discrete resources (Williamson, 1994). Here the food resources are not distributed homogeneously, but in discrete patches. Group sizes in red lechwe are small in comparison to Kafue lechwe, and females are present in a male territory for more than 60% of the time (Williamson, 1994). Thus, both homogeneous and spatially consistent discrete food patches can lead to circumstances favoring resource-defense polygyny. But in circumstances where food patches do not consistently attract females and female distribution is erratic, as in Kafue lechwe, lek formation may result.

In conclusion, the results of this study show that proximate environmental and social factors affecting female dispersion and behavior play important roles in determining which mating system different populations adopt and may help explain the evolution of lek-breeding in ungulates. When it is uneconomical for males to defend resources used by females, ungulate populations may be predisposed to mating on leks. An unpredictable environment and changing distribution of food patches may lead to erratic movements of large mixed-sex herds, resulting in high rates of harassment and mating disruptions of estrous females off leks by nonterritorial males. In Kafue lechwe, therefore, it pays estrous females to avoid such costs in herds and on large territories, whereas in black lechwe, estrous females receive greater mating benefits on resource-based territories. The distribution and consistent movements of females on the Kafue Flats may determine the location of leks, but female preferences for lek territories resulting from avoidance of harassment, female gregariousness, mate choice, and antipredator behavior help generate substantial benefits to males defending lek territories.

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