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Correlates of copulatory success in a fallow deer lek

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Summary. We studied the behavior and copulatory success of fallow deer (*Cervus dama*) males at a lek. We recorded 471 copulations in 3 years. Most males did not copulate. The top three males accounted for between 60 and 90% of copulations each year. Lek attendance time was the major determinant of male copulatory success, but territory location also affected the number of copulations achieved. Copulatory success was correlated with the number of females in a male's territory and possibly with dominance status, but not with fighting success or fighting rate. All males that defended lek territories were 5 years of age or older. Copulatory success may improve with age. Body condition appears to be an important determinant of male copulatory success, because only males in superior condition could defend a lek territory for up to 2 weeks. Males do not feed while defending lek territories. Foraging ability during the year probably determines condition at the onset of the rut. Females appear to choose mates at least partially on the basis of location, preferring males located near traditional routes. Females may ultimately select mates in the best body condition.

Introduction

Bradbury and Gibson (1983) defined a lek as an assembly of territorial males visited by females for mating. Males do not provide paternal investment other than gametes, and territories do not contain other resources useful to females. Leks are ideal for the study of whether females select mates according to phenotype, but few attempts to identify the criteria used by females in mate selection have been successful. Among ungulates, leks occur in antelopes of the genera *Damaliscus* and *Kob* (Buechner 1961; Montfort-Braham 1975; Schuster 1976; Gosling 1987), and in fallow deer *Cervus dama* (Schaal and Bradbury 1987; Pemberton and Balmford 1987; Clutton-Brock et al. 1988). In this study we analyze the behavior of fallow deer males at a lek during three breeding seasons. We identify correlations between individual traits and copulatory success and measure the relative importance of some traits through multivariate analyses. Lande and Arnold (1983) recommended a multivariate approach to mate selection criteria,Gibson and Bradbury (1985) have applied multivariate techniques to copulatory success of males in a lek.

The characteristics of males that we consider here include lek attendance, location, fighting success, age, courtship duration, and number of females in territories. Previous analyses (Apollonio et al., in press) indicated that some lek territories were more successful than others. It is important to determine whether a male's location influences its reproductive success. If some territories were preferred by females, males should compete for those territories, and fighting success should be a determinant of copulatory success.

Fighting success, dominance, and age are correlated with male reproductive success in many polygynous mammals (Geist 1971; LeBoeuf 1974; Clutton-Brock et al. 1982). Lek attendance time was expected to correlate with copulatory success, as reported for other lekking species (Gibson and Bradbury 1985; Halliday 1987). Finally, we investigated the possibility that females preferred males with long courtship. Presumably, a male could only afford a long courtship when firmly in control of its territory. Females other than the one being courted may use courtship duration as an indication of mate quality.

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From the viewpoint of the male's strategy, we also present our analyses of the effects of harem size on male copulatory success. We tested the hypothesis that success increases asymptotycally with harem size, because large harems may be more difficult to defend than small ones (Clutton-Brock et al. 1982).

Methods

Study area and population

The study was conducted in the San Rossore estate in central Italy (43°43'N, 10°19'E). The estate includes 46 km^2, of which 39 km^2 are accessible to the deer. The orography is plain and the climate submediterranean. About 70% of the estate is forested, with pine (*Pinus* spp.), oak (*Quercus* spp.), and other deciduous plants. Marshes and open pastures are also present. Apart from fallow deer, wild boars (*Sus scrofa*) are the only wild ungulates in the area. Large predators are absent. The estate is closed to the public except for designated areas open on Sundays. The lek is outside the area open to the public.

Spring censuses indicated that deer numbers declined from 1100 in 1984 to 750 in 1987. The decline was due to culling. Sex ratio estimates during the same period ranged from 1:1.2 to 1:1.7. Deer were culled through shooting and live captures in winter; 245 were marked with plastic ear tags and released.

During the rut, males defended either single, isolated territories or lek territories. We observed rutting behavior in one of three large (>5 territories) leks in the study area.

Observations

Observations were conducted by two or three observers from an elevated blind (Fig. 1). The lek was monitored from 1 to 26 October 1985, 30 September to 2 November 1986, and 30 September to 27 October 1987. Intensive observations began when prolonged territorial behavior by males was detected (2–4 days before the first copulation was seen) and ended the day after the last copulation. The rut was defined as the period between the first and the last copulation seen. During the rut we observed the lek daily, usually from dawn to dusk. Observations lasted 185 h in 1985, 259 h in 1986, and 172 h in 1987.

Lek territories were mapped and given identification numbers. Territories were fixed in space from year to year; therefore, we used the same map in all years and assigned males to specific territories during observations.

All males that defended territories on the lek for more than 3 h were recognized individually, either through ear tags or combinations of antler size, shape, and coat color. All unmarked males that copulated were photographed with an 800 mm lens, to facilitate identification between years.

The lek was scanned every 30 min. For each territory, we recorded the identity of the defending male (if any) and the number of females. All fights and matings were recorded, except in 1985 when we did not collect data on fights. For fights, we noted their location, identity of combatants, duration, and outcome (winner, loser, or draw). Fights were classified as escalated if they lasted longer than 1 min or if a clear winner chasing away the loser was identified. All other fights were between neighboring males and were classified as border clashes. Each year there was a strong correlation between the two classes of fights for individual males ($rs > 0.83$, $P < 0.001$). In 1987 we also recorded interactions where one male displaced another without contact. We recorded all details noted for fights. For matings, in 1985 we recorded the identity of the male and the territory where they took place. In 1986 and 1987 we also noted the duration of courtship (first mount to ejaculation) and number of mounts. Ejaculations were recognized through the characteristic leap of the male (Clutton-Brock et al. 1982).

In 1986 and 1987 we recorded changes in territory ownership to the nearest minute, including arrival and departure of males from the lek and movements from one territory to another. In 1985 we reconstructed temporal changes from scans and other observations (e.g., times of copulations). We assumed that changes in ownership occurred at the mid-point between observations. Breeding continued through the night. We assumed that nocturnal behavior was not different from diurnal behavior.

Age was known of males tagged before they were 5 years old. Unmarked males could be aged by antler size and shape as yearlings, 2- or 3-year-olds, and 4 years or older.

Definitions

Territorial male: Any male that held a lek territory for more than 3 h, the minimum time after which a new territorial male was seen to copulate.

Reproductive success: The number of ejaculations seen performed by a male during one rut.

Mating rate: The number of ejaculations per hour by a male during observations.

Lek attendance: The time during observations that a male defended any lek territory.

Position index: In 1985 and 1986, most females appeared to enter the lek from one wide opening in the thick *Erica* scrub that surrounded it (Fig. 1). We measured the distance in meters from the center of each territory to the females' main entrance. The position index was the average distance of a territorial male from that entrance. It was calculated by multiplying the fraction of lek attendance that a male spent defending each territory by the distance from the females' entrance of that territory, and summing the products.

Fighting success: The index suggested by Clutton-Brock et al. (1979) to measure dominance in red deer (*Cervus elaphus*). Only fights with a clear outcome were considered in 1986. In 1987, the index was also calculated including interactions where one male displaced another without contact.

Fighting rate: The sum of border clashes and escalated fights divided by lek attendance for each male.

Daily harem size: The sum of the numbers of females seen during scans in the territory held by a male, divided by the number of scans during which the male held a territory during a day.

Mean harem size: The average daily harem size for all days during the rut when a male held a territory in the lek.

Analyses

Most variables were not normally distributed; therefore, we initially employed non-parametric statistics. After establishing simple correlations, we attempted multivariate analyses. The latter were often inappropriate because most independent vari-

ables were correlated ($rs > 0.85$) with each other (Lande and Arnold 1983). Position index and lek attendance were independent and were entered into a stepwise multiple regression (Sokal and Rohlf 1981). Variables in this analysis were transformed (square root) to approximate a normal distribution. Other transformations (log, arcsine) were attempted, but square-root resulted in the lowest values of the g1 and g2 statistics for skewness and kurtosis.

Most analyses were repeated for each year, first considering all territorial males, then only males that copulated. The multiple regression included data from all copulating males from all years; year-by-year analyses were inappropriate because of small sample size. The 29 cases were collected from 17 males; two males were observed for 3 years and three for 2 years. To account for yearly differences in number of ejaculations, we used the percentage achieved by each male of the total seen each year. Similarly, we used percent lek attendance to account for differences in observation time.

Results

Description of behavior and lek structure

The 1-ha lek (Fig. 1) was in an old pine (*Pinus pinea*) wood. The ground was covered with dead pine needles. The almost complete lack of ground vegetation was apparently due to the use of this lek for several decades (as reported by local game wardens). Monfort-Braham (1975) recorded similar modifications of the vegetation in topi (*Damaliscus korrigum*) leks. Dense *Erica* scrub surrounded the area, and the deer used traditional paths to enter the lek.

Before the rut, females entered in the morning from the southeast, moved along the edge of the scrub and exited to the west, following the same path in the reversed direction in the evening. This was the traditional route to and from feeding areas. During the rut, most females entered from the southeast and remained in the lek for some time. A summary of descriptive statistics is provided in Table 1.

Lek territories were centered around 2–14 ($X = 5.7$) rutting pits, dug and scent-marked by territorial males. Gosling (1987) reported a similar behavior for topi in a lek. The pits, 30 to 60 cm deep, remained in the sandy soil. Before and during each rut, males re-pawed the same pits, beginning the late August. By the end of September 1986 and 1987, all territories that later were defended showed fresh signs of pawing. These data were not collected in 1985.

Males began to defend territories 2–4 days before the first copulation was seen. Female presence in the lek was then strongly bimodal, with peaks at dawn and dusk and no females at midday. During the rut, females were present at all hours. Breeding ended abruptly; the day after the last copulation was seen, females no longer stopped at the lek, and only two or three males were present for 1 or 2 h at dawn and dusk. These males continued to use the lek as a resting place until the end of October.

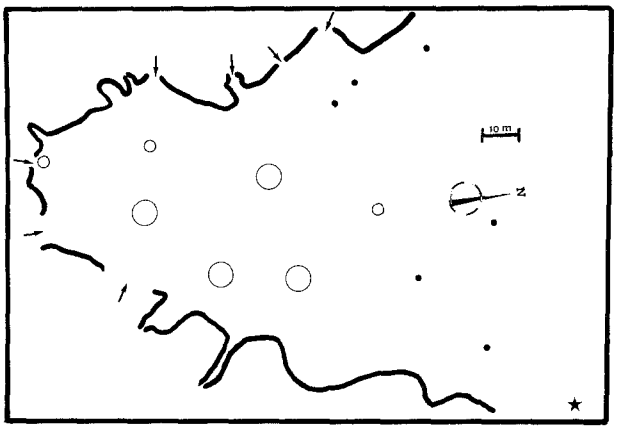

Fig. 1. Map of fallow deer lek in 1986. Large circles indicate territories where >10 copulations were seen; small circles are territories where 1–9 copulations were seen; dots indicate territories that were defended for >3 h, but where no copulations were seen. Arrow indicates the main path used by females to enter the lek; broken line represents the approximate boundary of thick scrub; star shows the location of the 5-m high observation blind

Table 1. Characteristics of the fallow deer lek, 1985 to 1987

	Year		
	1985	1986	1987
Territories[a]	10	13	7
Territorial males	13	24	13
Copulating males	7	13	10
First copulation	Oct 8	Oct 6	Oct 10
Last copulation	Oct 25	Oct 24	Oct 22
Copulations seen	166	228	77
Escalated fights	n/a	79	75
Border clashes	n/a	124	121

[a] Defended over 3 h

Switches between territories were infrequent. Each year males that copulated spent on average 72–80% of lek attendance defending one territory (interquartile range: 65–94%, $N = 29$). In 20 cases, males performed more than 90% of ejaculations in the territory they held for the longest time. The other nine males appeared to wait for another territory to be vacated, then took it over. All but one of these nine ranked below the median reproductive success for copulating males.

Behavior during the rut included territorial defense by males, scent marking, frequent vocalizations, and chasing of non-territorial males. Upon

entering the lek, females usually visited two or more territories, despite herding attempts by territorial males. Males with no females in their territory spent many hours lying idle. Attempts to herd females from other territories were not systematically recorded, but appeared to be very uncommon. Fights occurred mainly between neighboring territorial males. Escalated fights were frequently interrupted by lateral antler displays and parallel walks, and 72% ended with an obvious winner. Losing a fight did not necessarily imply loss of territory ownership. As in other Cervids (Geist 1986), escalated fights were dangerous; most territorial males had neck wounds, breaking of the main antler beam occurred in at least five cases, and at least two males were killed in fights. Males engaged in escalated fights always lost any females that were in their territories.

On average, territories where copulations took place were held by one male for 74.5% of the observation time; this turnover of successful males was lower than reported by Clutton-Brock et al. (1988) in a larger lek. In 1986, the 13 males that copulated left the lek 1.2 times per day on average, usually for 5–10 min. We suspect that they visited water holes, because they often returned with wet legs and underbelly. Males did not feed while defending lek territories, with the rare exception of a few bites at the bark of pine trees or dry pine needles. Females also did not feed while in the lek.

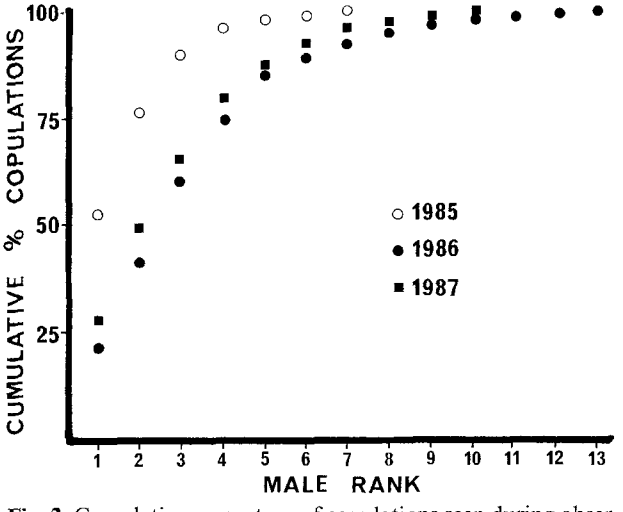

Fig. 2. Cumulative percentage of copulations seen during observations of the fallow deer lek, according to male copulatory rank, 1985 to 1987

Male reproductive success

The distribution of ejaculations among territorial males was skewed. The most successful male achieved 52% of all ejaculations seen in 1985, 21% in 1986, and 27% in 1987 (Fig. 2).

Each year the distribution of ejaculations was different from a Poisson distribution (Kruskall-Wallis test, $P<0.01$).

Each year reproductive success and mating rate of individual males were correlated (Spearman rank correlation, $P<0.01$). In 1985 and 1987, the most successful male had the highest mating rate. Most successful males held territories for several days and copulated almost every day (Table 2).

Lek attendance

In all years, males that copulated stayed in the lek longer than those that did not (Mann-Whitney

Table 2. Number of copulations achieved by different fallow deer males in the lek during October 1986. Males did not defend territories in days when no numbes are indicated. All males that copulated are included

Male I.D.	Date																						
	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
PA	0	0		0	1	0	1	1	2	1	6	3	8	5	2	6	4	3	4	0			
NY	0										1	3	4	7	14	7	7	3		0	0	0	0
W				0					0	1	1	11	7	10	8	2	2	0	0	0	1	2	0
29										0			0	7	7	4	3	1	7	0	0	1	0
F4															0				4	9	5	9	0
FA										0				1	3	1	1	1	1	0	0	0	
UC	0			0	0			0		4	3												
70										0	2	1	1	0	0	0	0	0	2	0			
AA									0	0	0	1	1	2	2	0	0	0					
UN																			0				2
NP														1	1	0							
IN		0		0			1	0	0	0	0				0			0		0		0	
FO										1	0												

Table 3. Average percent of observation time during the rut, 1985 to 1987, when fallow deer males defended lek territories. Males are subdivided according to the proportion of copulations that they achieved each year. Numbers in parentheses indicate sample size. Only males that defended territories for more than 3 h are included

Year	Copulations		
	0	<10%	>10%
1985	12.6 (6)	51.7 (3)	74.2 (3)
1986	4.5 (11)	19.3 (8)	52.2 (5)
1987	2.2 (3)	19.2 (6)	44.6 (4)
Toal	6.6 (20)	25.0 (17)	56.0 (12)

Table 4. Spearman rank correlation coefficients between the number of copulations achieved by fallow deer males in the lek and their average distance from the main female entrance (see text), 1985 to 1987. Only territorial males are included. Sample sizes in parentheses

Year	All males	Males that copulated
1985	−0.39 (12)	−0.95** (6)
1986	−0.24 (24)	−0.03 (13)
1987	−0.73** (13)	−0.41 (10)

** $P<0.01$

U tests, $P\leq 0.045$). Males that stayed for <3 h, none of which copulated, were not included in these tests. For males that copulated, reproductive success was correlated with lek attendance each year ($rs=0.59$ to 0.89, $P=0.03$ to $P<0.001$; Table 3).

Position effects

Males close to the main female entrance had greater reproductive success than males whose territories were located further from this entrance. In 1985 and 1986 the most successful male was the one that defended the territory closest to the female entrance for the longest time. In 1987, the pattern of female access to the lek changed, with several females using an artificially widened path. The most successful male in 1987 held a territory near the entrance from the enlarged path, whereas the male that held the most successful territory in 1985 and 1986 ranked second.

Distance from the main female entrance appeared to be negatively correlated with reproductive success, but most correlations were not significant (Table 4). The strong negative correlation between position index and reproductive success in 1985 may be explained by the relatively low variance in lek attendance among successful males in 1985. Variance in lek attendance was 3.1 times greater in 1986 than in 1985, and 1.5 times greater in 1987 than 1985. Therefore, differences in lek attendance did not have as strong an effect on the position index in 1985 as in the following 2 years.

Position and lek attendance

Three transformed variables were considered in this analysis: the percentage of ejaculations achieved by each copulating male in 1 year, the position index, and the percentage lek attendance, obtained by dividing lek attendance by observation time during the rut. Data from 29 male-years were available for these analyses. Percent copulations and percent lek attendance were correlated ($rp=0.69$, $P<0.001$), but percent copulations and position index were not ($rp=-0.25$, $P=0.2$), nor were position index and percent attendance ($rp=0.08$, $P=0.7$).

Partial correlation revealed a stronger correlation of lek attendance and copulations when position index was controlled ($r=0.74$, $P<0.001$). When lek attendance was controlled, the position index was correlated with copulations ($r=-0.43$, $P=0.02$). Lek attendance and position index contributed significantly to a multiple regression with copulations as the dependent variable. Percent attendance explained 49% of the variance in percent copulations; the two variables together accounted for 58% of the variance (F 2,26=17.95, $P<0.0001$).

Age

All males of known age or known minimum age that held lek territories were 5 years or older. One ejaculation was performed by a non-territorial yearling that mounted a female and ejaculated on its first attempt. Reproductive success may increase with age; of 13 males followed for 2 or more years, copulatory success rank improved with age in nine cases, decreased in two, and remained the same in the other two cases.

Fighting success

There was no relationship between fighting success and reproductive success, regardless of whether the analysis included all territorial males or only those that copulated. In 1987, when interactions involving threat by a dominant and withdrawal by a sub-

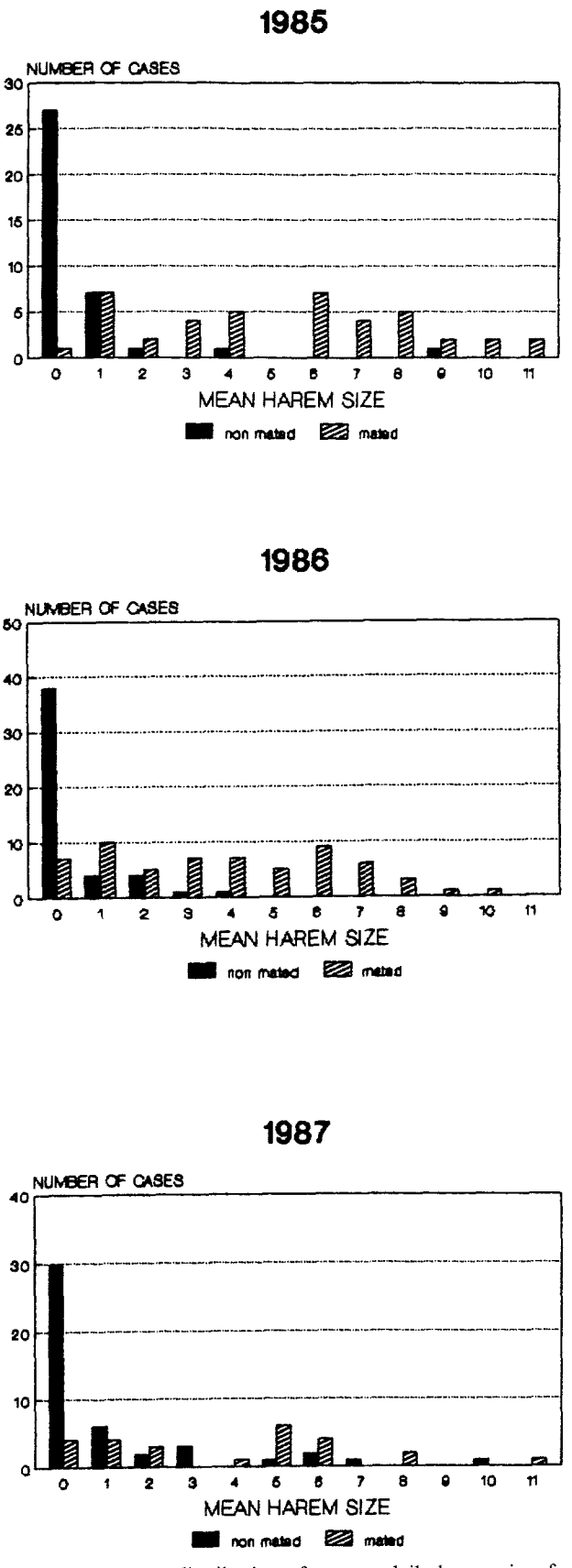

Fig. 3. Frequency distribution of average daily harem sizes for fallow deer males at the lek, 1985 to 1987

ordinate were included in its calculation, the fighting success index was correlated with reproductive success ($rs=0.65$, $N=13$, $P=0.01$) and with lek attendance ($rs=0.76$, $N=13$, $P=0.001$). The correlation with reproductive success was not significant when only males that copulated were considered ($rs=0.35$, $N=10$, $P=0.16$). The number of fights was correlated with lek attendance and reproductive success ($rs>0.9$, $P<0.001$). Fighting rate was independent of mating rate or reproductive success.

Courtship duration

The mean time from first mounting to ejaculation varied among males (1986: 7.15 min, range 2.17–15.38, $SD=4.26$; 1987: $X=7.17$ min, range 2.41–17.27, $SD=7.62$) and was correlated with the number of mounting attempts (1986: $rs=0.5$, $P=0.04$; 1987: $rs=0.98$, $P<0.001$). The number of mounting attempts during a courtship sequence varied from 1 to 225. Courtship duration and number of mounting attempts were not correlated with reproductive success.

Harem size

In all years, mean harem size was correlated with reproductive success ($rs>0.84$, $P<0.001$), and males that copulated had a greater average daily harem size in days when they copulated than in days when they did not, except in 1985 (Wilcoxon matched-pairs test, 1985: $P=0.07$; 1986: $P=0.003$; 1987: $P=0.005$; Fig. 3).

For males that copulated in 4 or more days and that achieved at least 10% of all copulations in 1 year, there was a significant correlation between the daily number of ejaculations and daily harem size in eight of nine cases. Mean harem size of males, during days when they were seen to copulate, did not vary among years (Mann-Whitney U tests, $P>0.07$); it was 6.3 in 1985, 4.8 in 1986, and 5.6 in 1987. The maximum daily harem size was 11 females each in 1985 and 1987, 10 females in 1986.

Discussion

Lek attendance was the most important determinant of male reproductive success. Only a few males had long lek attendance times, suggesting that it is costly to remain in the lek. It is likely

that a male's ability to remain in the lek was dependent upon body condition (Halliday 1987).

We did not measure the cost of defending a lek territory, but suspect that it would be considerable (Gosling et al. 1987). Red deer males lose about 20% of body weight during the rut (Clutton-Brock et al. 1982), and successful fallow deer males likely experience a similar or greater weight loss. Successful males spent 10–17 days defending territories. During this time they never ate, slept very little and were often engaged in strenuous activities.

Our data suggest that the most vigorous males began to defend successful territories early in the rut, then held them for most of the rut. Other males may have waited to move into preferred territories when the most successful males became exhausted towards the end of the rut. Ripping and Boag (1974) provided experimental evidence for this strategy in sharp-tailed grouse (*Pedioecetes phasianellus*). Less successful males spent only a few days in the lek and obtained few copulations (Table 2). Most males defended territories for short times and did not copulate. Extrapolating from the proportion of tagged males that did and did not copulate, we estimate that as many as 77% of males that appeared in the lek never copulated. This percentage excludes males less than 5 years of age, since these animals were excluded from copulating in the lek. The same age threshold has been reported for red deer (Clutton-Brock et al. 1982) and sika deer (*Cervus nippon*; Miura 1984). Moreover, circumstantial evidence suggested that reproductive success increased with age. Therefore, lifetime reproductive success should be greatly influenced by survival to social maturity (5 years or more) and subsequent survival.

As previously mentioned, some lek territories were more successful than others, regardless of the identity of the defending male. Successful territories were defended more often, a situation analogous to that found in blue grouse (*Dendragapus obscurus*, Lewis and Zwickel 1980). Copulatory ranks of territories in successive years were correlated, and when males switched from a low-ranking to a high-ranking territory, their mating rate increased (Apollonio et al., in press). Location is important for a male's reproductive success. Males had more copulations if they held territories close to the females' main entrance to the lek. Position, however, explained only about 10% of the variance in reproductive success; lek attendance was more important.

Other studies of lekking ungulates report that central males are more successful (Buechner and Schloeth 1965; Floody and Arnold 1975; Clutton-Brock et al. 1988). That, however, was not the case in the lek we studied, where successful males defended territories near the site where females entered the lek. We suspect that less successful males clumped their territories near those of successful males, but because of the thick scrub (Fig. 1) were unable to set up territories all around the most successful ones.

Fighting success was not correlated with reproductive success, and the outcome of fights did not always determine territory ownership. In at least two cases, successful males lost escalated fights after having fought, in succession, two to four other males. They left their territory for up to 1 h, then returned and easily displaced their opponent by threatening it. When all territorial males in 1987 were considered, the dominance index calculated including non-contact interactions was correlated with reproductive success. However, its contribution to variance in reproductive success could not be assessed, because comparable data were not collected in the first 2 years and also because the strong correlation of dominance and lek attendance did not allow us to examine these two variables together, particularly since the sample was so small.

Floody and Arnold (1975) and Fryxell (1987), working with different subspecies of kob (*Kobus kob*) reported an association between fighting frequency and indirect measures of reproductive success, such as number of females in territories. Clutton-Brock et al. (1988) found a relationship between copulatory success and dominance in fallow deer in a lek larger (about 20 territorial males) than the one we observed, with faster male turnover. We suspect that dominance was important in determining a male's reproductive success, but that the number and frequency of interactions in the lek were not very important. It is likely that dominance was established before the rut. Males may be able to assert their dominance without many overt aggressive interactions during the rut. The lek system may collapse if frequent escalated fights were necessary to maintain dominance relationships. Escalated fights always led to a loss of all females from the fighters' territories and attracted nonterritorial males that chased and scattered the females. Courtship sequences of territorial males were never disrupted by aggression from other males, supporting the contention that this mating system requires respect for established social relationships.

The low turnover of successful males is somewhat surprising, especially when contrasted with

the high turnover reported by Clutton-Brock et al. (1988). Differences between the two studies may be due to unequal deer densities (less than 40/km^2 in our study area vs 300/km^2 in that of Clutton-Brock et al.). Dewsbury (1982) pointed out that at high population density dominance hierarchies should be unstable.

Why do some unsuccessful males leave the lek without much fighting? We strongly suspect that very few copulations occur off the lek (Clutton-Brock et al. 1988). Males should take considerable risks to obtain access to estrous females. Possibly, most of the unsuccessful males are young and may have a greater chance of reproducing in later years. By challenging older males, they would expose themselves to risk of injury and also their chances of winning may be very low. Alternatively, males may forfeit years of reproduction if they do not reach a sufficient body condition by the onset of the rut, particularly if this would improve their chances of being in better condition the following year. Obviously, foraging ability must play a pivotal role in this process.

Male and female mating strategies in the lek may at times conflict. Our data suggest that the larger the harem, the more copulations achieved by a male. Therefore, males should attempt to hold large harem. Yet, average and maximum harems sizes did not vary among years, despite changes in population size, number of copulations seen, and probably number of females visiting the lek. Females may be reluctant to join large harems, possibly because they may have a lower chance of mating during the short estrus (Asher 1985). Females in large harems may also be more harassed by young, non-territorial males. If our hypothesis is correct, some females may select suboptimal males in order to avoid harems larger than optimal.

Our study was not without shortcomings. We do not know whether the lack of predators affected the behavior of the deer or the survival of territorial males. We assumed that each ejaculation was worth the same in terms of reproductive success, but we do not know if all males were equally able to impregnate females, or if the females they mated with had on average the same reproductive ability. For example, copulations late in the rut may have been mostly with younger females and, therefore, possibly less likely to result in viable offspring. The value of holding a lek territory may vary during the rut, thereby affecting the selective pressures operating on males.

In conclusion, we suggest that females may select males that defend certain preferred territories. In so doing, they may produce a situation where males in the best condition occupy those territories. Body condition partly reflects the male's ability to forage effectively and avoid parasites and pathogens. If any of these characteristics have an inheritable component, by choosing according to spatial cues, females may ultimately transmit some genetic advantage to their offspring.

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