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Site-specific asymmetries in male copulatory success in a fallow deer lek

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Abstract. In a fallow deer, *Cervus dama*, lek in central Italy, most copulations occurred in a few male territories on one side of the lek. Individual territories were fixed in space between years, and most maintained their relative rank in terms of numbers of copulations in successive years. High-ranked territories were peripheral, near paths used by females to enter the lek area. Successful territories were defended more often than territories where few or no copulations were seen, but their defence did not involve a greater frequency of fighting. The turnover of males on territories was unrelated to the number of copulations seen there. Females appear to choose mates partly on the basis of location, and thus males should compete for ownership of territories preferred by females.

There is normally a skewed distribution of matings on leks: a small proportion of males perform the majority of copulations and the majority of males do not mate at all (Wiley 1973; Bradbury & Gibson 1983; Clutton-Brock et al. 1988). While it is generally believed that females on leks choose their mates, the criteria they use to select mates are not clear (Bradbury & Gibson 1983). In particular, some studies have suggested an effect of territory position upon copulatory frequency (Wiley 1973), while others have found no evidence of this (Lill 1974; Shepard 1975). In this paper, we analyse the distribution of copulations, fights and females among territories in a fallow deer, *Cervus dama* lek over 3 years. Comparisons between years, with different males holding the same territories, should help distinguish between site-specific and male-specific characters that appear to attract females.

If females chose mates solely by phenotypic cues, there should be no reason for successful territories to be the same in different years, unless preferred males consistently returned to the same territories. However, if some territories were favoured by females independently of the phenotype of the male, the same territories should be preferred in different years. If males competed for territories preferred by females, they may be distributed in the lek according to their competitive ability. Territories preferred by females would probably be occupied by more competitive males, and the cues used by females to select mates would be difficult to discern in a single season. A similar problem would arise if territories are not fixed in space from year to year. Neither problem, however, arises in our study, because it covered three consecutive rutting seasons and was carried out on a lek with territories fixed in space in different years.

The discovery of leks in fallow deer is relatively recent (Schaal 1986; Pemberton & Balmford 1987; Clutton-Brock et al. 1988). In our study area, lek territories are fixed in space, possibly because the rutting pits dug and scent-marked by territorial bucks during the rut (see Gosling 1987) remain for many months in the sandy soil. At the beginning of each rut, bucks dig and mark the same pits used in previous ruts. It is therefore possible to determine if the relative attractiveness of territories for females remains the same in different years. Here we test the hypothesis that central territories are preferred by females, so that few matings occur in peripheral territories (Buechner & Schloeth 1965; Wiley 1973; Bradbury & Gibson 1983; Schall & Bradbury 1987; Clutton-Brock et al. 1988). We also test the hypothesis that the turnover of males and the frequency of escalated fights are correlated with the average number of females and number of copulations observed in each territory (Floody & Arnold 1975; Fryxell 1987). Such a correlation would suggest that males compete for territories that are preferred by females.

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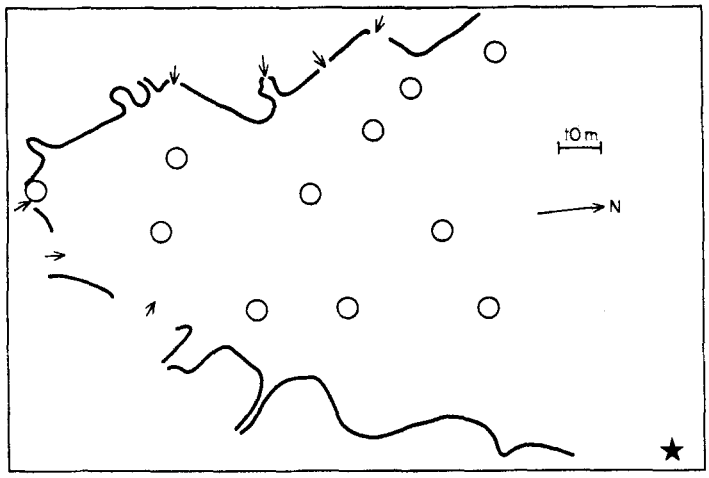

Figure 1. Map of the fallow deer lek. ○: centre of male territories; →: paths used by females entering the lek; ———: the approximate boundary of thick scrub; ★: the observation blind.

METHODS

The study area (39 km^2) near Pisa, Italy (43°43′N, 10°19′E), included woodlands (*Pinus* spp., *Quercus* spp. and mixed), open pastures and cultivated fields. It is bounded by the Tyrrenian Sea to the west, the Serchio and Arno rivers to the north and south, and a fence to the east.

Fallow deer have been in this area for several hundred years. The deer population, estimated from spring censuses, declined due to a culling programme from 1124 in 1984 to 807 in 1987.

We observed one of three leks in the study area, in an old pine forest with a high canopy. The other leks were in dense forest where it was not possible to see the entire lek from one point. Areas immediately off the lek were mostly covered with thick scrub (*Erica* spp.; Fig. 1). The deer used traditional paths through the scrub to the lek, particularly a large opening at the southern end of the lek. Two or three observers watched from an elevated blind (Fig. 1). Observations were conducted on each day of the rut, usually from dawn (about 0600 hours) to dusk (about 1800 hours). Observation times were 185 h in 1985 (5–25 October), 259 h in 1986 (2–24 October) and 172 h in 1987 (8–24 October). Each year, the lek site was visited every 1–3 days for 1 week before and after the dates reported above, to check for the presence of territorial males. Observations began when territorial defence was first detected, and ended when defence ended. The rut was defined as the time between the first and the last day on which copulations were recorded each year.

All males that held territories on the lek for 3 h or longer were individually identified from their antlers and coat colour patterns. Photographs of these males were taken with an 800 mm lens to aid in subsequent identification. Several males were also marked with numbered and coloured plastic ear tags. Thirty-seven tagged males were seen on the lek, of which nine held territories.

During observations, the lek was scanned every 30 min. For each territory we recorded the identity of the territorial buck (if any), and the number of does. We also recorded all copulations and fights. With one exception, matings involved courtship displays and several (usually 10–30) mounting attempts before ejaculation. Therefore, it is very unlikely that any copulations were missed during observations. Ejaculations were identified by the characteristic leap of the male, typical of cervid species (Clutton-Brock et al. 1982). In this paper, the term 'copulation' refers to matings where ejaculation was recorded. For fights, we recorded the identity of the combatants, the territory (or territories for border fights) where the fight took place, the duration (s) of the fight and its outcome (identity of winner and loser, or draw). We distinguished between escalated fights and border clashes. The latter occurred when two neighbouring territorial males locked antlers and wrestled for less than 1 min, with no clear winner or loser. Escalated fights either lasted over 1 min or ended with one

Table I. Details of the fallow deer lek during the study

	Year		
	1985	1986	1987
No. of territories*	10	13	7
No. of territorial bucks†	13	24	13
Date of first copulation	8 October	6 October	10 October
Date of last copulation	25 October	24 October	22 October
No. of copulations seen	166	228	77
No. of escalated fights‡	—	79	75
No. of border clashes‡	—	124	121

*Defended for over 3 h.
†Bucks that defended territories on the lek for over 3 h.
‡See text for definitions.

buck chasing away the other. Most escalated fights were between neighbours and 28% ended in draws. Fights were not recorded in 1985.

In 1986 and 1987, we recorded to the nearest minute any changes in territory ownership, including the arrival and departure of bucks from the lek, and instances when bucks moved from one territory to another. In 1985, we reconstructed changes in territory ownership from an analysis of 30-min scans and other observations (e.g. time of copulations). We assumed changes occurred at the mid-point between two observations, so our calculations were accurate to within 15 min or less. Since changes in ownership were infrequent, the 1985 data are comparable with data collected in the following 2 years.

We analysed data for 10 lek territories that were occupied for a minimum of 3 h during 1985, and that were clearly recognizable from the presence of rutting pits, about 30–60 cm deep. We chose 3 h as a cut-off because that was the minimum time on the lek after which territorial bucks were seen to copulate. All 10 territories were occupied by a buck for some time in each of the 3 years. We also considered one territory established in 1986 that became the highest-ranked territory in 1987 in terms of number of copulations. Two other territories were defended for over 3 h in 1986, with no copulations recorded. In 1987, only seven of the 11 territories were defended for over 3 h; analyses of 1987 data were restricted to those seven territories, except for between-year comparisons, when all 11 territories were considered. Each year, territories were ranked at the end of the rut according to the number of ejaculations recorded, with top rank assigned to the territory with the largest number of ejaculations.

Most variables were not normally distributed among territories, therefore we used non-parametric statistics (Siegel 1956) with two-tailed probability values. Most analyses were restricted to the rut (defined above), and repeated for each year of the study.

RESULTS

The lek was in an old *Pinus pinea* wood, traversed by several deer paths (Fig. 1). Copulations were seen on similar dates each year (Table 1). Active and prolonged territorial defence by bucks (continuous presence during daylight hours) began 1 or 2 days before the first copulation, and ended 1 or 2 days after the last copulation was seen. Rutting continued through the night. We collected data only during daylight hours, and had no reason to suspect that nocturnal behaviour was significantly different from diurnal behaviour (see also Clutton-Brock et al. 1988). About 15 individually recognizable females were seen to copulate on the lek, and none copulated more than once. Apparently, most females copulate only once (Clutton-Brock et al. 1988). Marked females did not remain in the lek for more than 36 h.

Copulations were not normally distributed among territories; successful territories remained the same in different years, despite usually being held by different bucks (Fig. 2). A Kendall coefficient of concordance calculated both excluding the southernmost territory, not defended in 1985 and highest in rank in 1987, and including it

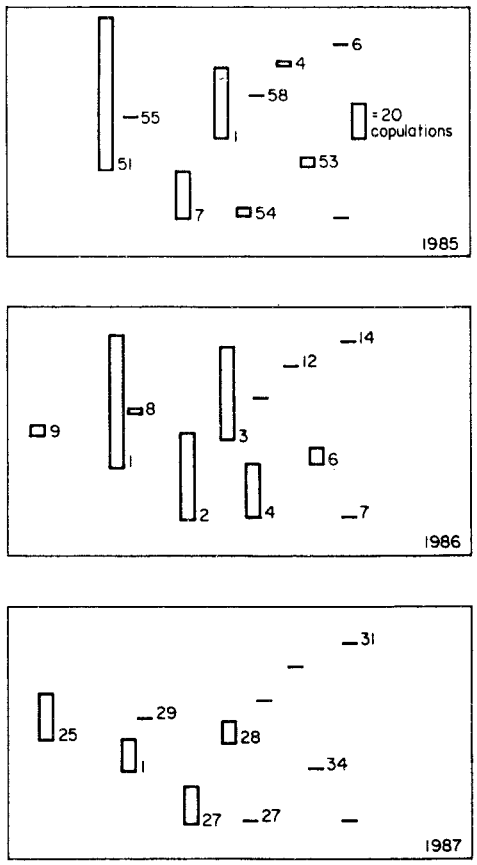

Figure 2. The number of copulations seen during observations in different lek territories. The height of the bars is proportional to the number of copulations seen there. Short horizontal lines indicate territories where no copulations were seen. The southernmost territory was not present in 1985. Numbers to the right of territories indicate the identity of the buck that held each territory for the longest time each year. Territories with no buck identification number were not defended by any single buck for more than 3 h in that year.

(with a rank corresponding to zero copulations in 1985) was significant ($W=0{\cdot}857$, $N=10$, $P<0{\cdot}01$ and $W=0{\cdot}693$, $N=11$, $P<0{\cdot}05$). Each year, bucks first occupied territories at the southern end of the lek, which were the most successful, and bucks that arrived later settled to the north. The copulatory rank of the territory was correlated with the date of occupancy in 1985 and 1986 ($r_s=0{\cdot}623$ and $r_s=0{\cdot}554$, $P<0{\cdot}05$) but not in 1987 ($r_s=0{\cdot}49$, $P<0{\cdot}25$), except when the southernmost territory was excluded from the analysis ($r_s=0{\cdot}884$, $P<0{\cdot}05$) which tested whether males followed the pattern of the females' access to the lek in the previous year when they occupied the territories. All territories where copulations were seen were occupied by a buck within 2 days of the start of the rut in 1985 and 1987, and within 4 days in 1986.

Before the rut, does entered the lek in the morning from the south, moved along the edge of the scrub, and left to the west. In the evening, does followed the same paths in the opposite direction (Fig. 1). To enter the lek from the south, almost all does used two relatively wide openings in the vegetation, while the western access included several narrow paths. After the rut began, most does appeared to enter from the south, then to remain on the lek. The southernmost territory achieved the highest copulatory rank in 1987 after a bulldozer widened a path to the lek in spring 1987. Does used the widened path, which led directly to the southernmost territory (Fig. 1).

Territories where copulations took place were defended more frequently (Table II), and each year the copulatory rank of a territory was correlated with how long it was defended (1985: $r_s=0{\cdot}93$; 1986: $r_s=0{\cdot}97$; 1987: $r_s=0{\cdot}79$, $P<0{\cdot}005$ in all years; Table II).

Given that successful territories were occupied for longer, it is not surprising that they also had more escalated fights: the overall number of copulations and the overall number of fights seen in each territory were correlated in both 1986 ($r_s=0{\cdot}7$, $P=0{\cdot}008$) and 1987 ($r_s=0{\cdot}84$, $P=0{\cdot}001$). The average hourly frequency of escalated fights while territories were occupied, however, did not differ between territories where copulations were seen (0·09) and those where no copulations were seen (0·47, $P=0{\cdot}1$. Mann–Whitney U-test). It is unlikely that these results were affected by our definition of escalation, because the numbers of escalated fights and border clashes in each territory were closely correlated (1986: $r_s=0{\cdot}97$; 1987: $r_s=0{\cdot}98$; $P<0{\cdot}001$). Territorial bucks often appeared able to repel other bucks by threat displays without antler contact. Threat displays included one buck approaching another while grunting, holding up his head and tail, sometimes walking, other times at a trot. After approaching the opponent, a buck often lowered his antlers towards him.

Successful territories were held by one buck for over 70% of the time that they were held by any buck (Table II). The turnover of bucks was not greater in successful territories than unsuccessful territories.

Table II. The percentage of observation time during the rut when lek territories were defended by territorial bucks, and the percentage of total defence time by the buck that held the territory the longest

		% Time defended		% Defence by one buck	
Copulations	Territories	Mean	Range	Mean	Range
>20	9	69	39–87	72	33–97
10–20	3	63	43–98	71	43–94
1–9	6	40	17–53	78	43–96
0*	12	10	2–37	65	37–100
0†	21	6	0·3–37	66	37–100

The results are summarized according to the number of copulations seen in each territory. The pooled data are from 1985 to 1987.
*Territories defended for over 3 h.
†Territories defended for over 15 min.

Table III. The average number of fallow deer females seen in lek territories during the rut, according to the number of copulations recorded in each territory

	Year		
Copulations	1985	1986	1987
>10	3·9 (3)	2·5 (5)	2·4 (4)
1–9	0·3 (3)	0·4 (3)	— (0)
0	0·0 (4)	0·0 (5)	0·0 (3)

The number of territories is given in parentheses.

Does were seldom seen in territories where no copulations took place (less than 0·05 does per scan on average; Table III). From 0 to 18 does were seen in lek territories during the rut during instantaneous scans. The average number of does was correlated with the number of copulations seen in territories during all years of the study ($r_s > 0{\cdot}9$, $P < 0{\cdot}001$).

In 1985, we first had the impression that many does mated in the first territory they encountered upon entering the lek. To test this possibility, we measured the distance between the centre of each territory (i.e. the most central rutting pit) to the largest opening used by does to enter the lek from the south (Fig. 1). This distance was negatively correlated with the number of copulations in the 11 territories in 1986 ($r_s = -0{\cdot}7$, $P < 0{\cdot}02$) and 1987 ($r_s = -0{\cdot}63$, $P < 0{\cdot}02$). In 1985, this correlation was significant only if the southernmost territory (not present in 1985) was excluded ($r_s = -0{\cdot}58$, $N = 10$, $P = 0{\cdot}04$).

Clearly, the best test of whether does choose bucks or territories would be to compare the copulatory success of the same buck in different territories. Most bucks defended only one territory, and a few bucks switched between two or more territories where no copulations were recorded. A switch between territories of different rank was accompanied by the expected change in ejaculation rate in four of six cases (Table IV). In 1986, buck 60 switched from a territory where no copulations were seen to one where very few copulations were seen, and did not copulate there during a short (8 h) tenure. Also in 1986, buck PA had a greater ejaculation rate in the second-ranked than in the first-ranked territory (Table IV).

We observed nine cases where individual males defended different territories in successive years, and one case where a male defended the same territory in two consecutive years. In all cases where a switch occurred, the territory occupied in year 2 ranked higher that year than the territory occupied in year 1 had ranked the previous year ($P = 0{\cdot}011$, binomial test). These changes in territory rank, however, may be partly due to a positive effect of age on male copulatory success. In only five cases the territory defended in year 2 had a higher rank in year 1 than the territory defended in year 1.

DISCUSSION

Copulations were not distributed randomly among lek territories. With the exception of the southernmost territory, the copulatory rank of territories

Table IV. Copulatory rate (ejaculations per h) of fallow deer bucks while defending lek territories of different copulatory rank during the same rut

		Territory 1			Territory 2		
Buck	Year	Rank	Time defended (h)	Rate	Rank	Time defended (h)	Rate
SL	1985	5	74	0·05	1	10	0·63
10	1985	4	53	0·00	3	40	0·10
W	1986	5	10	0·10	2	44	0·35
PA	1986	2	14	0·42	1	124	0·31
60	1986	9	16	0·00	5	8	0·00
W	1987	3	14	0·14	1	17	0·23

Territory 1 = lower rank; territory 2 = higher rank.

was similar in different years. The available evidence (Table IV) suggests that bucks may improve their reproductive success by moving to territories that are traditionally successful. We interpret these results as support for the hypothesis that female fallow deer choose mates at least partly on the basis of their territories. Warner (1987) recently reported that female bluehead wrasses, *Thalassoma bifasciatum*, selected spawning territories independently of the identity of the defending male. In this species, eggs enter the plankton immediately after spawning, so, as in the deer lek, the success of a territory depends not on its trophic resources but probably on the protection from predators it gives the female. Warner (1987) suggested that females may use the male's bright colour and displays to judge site quality, and that elaborate secondary sexual characters do not necessarily imply selection for mate quality.

Other studies of the distribution of copulations on leks have found that central territories tend to be more successful than peripheral ones (Buechner & Schloeth 1965; Wiley 1973; Bradbury & Gibson 1983). That was not the case in our study area (Fig. 2). Females appeared to prefer to mate in territories at or near the southern end of the lek, close to where they entered it. We believe this was a major factor in determining the relative success of a territory. The southernmost territory achieved top rank after an apparent shift in the does' routes caused by artificial cuts in the vegetation.

The local structure of the habitat may explain why central territories were not very successful. Females apparently preferred to mate near where they entered the lek. If females selected for quick escape, they should prefer to remain near the wider openings in the vegetation at the southern end of the lek, rather than near the narrow trails in the western side. It was not possible for males to set up additional territories anywhere but north of the most successful territories. The latter were occupied first, and subsequently territories were set up to the north in the available open habitat. Most other ungulate leks have been studied in open habitats (Buechner & Schloeth 1965; Buechner & Roth 1974; Schuster 1976; Clutton-Brock et al. 1988), where males could establish territories all around successful ones. Therefore, the central location of successful territories in other leks may be a result and not a cause of their success (Bradbury & Gibson 1983).

Contrary to our expectations, we found neither more frequent fights nor greater turnover of males in successful than in unsuccessful territories. Most successful territories were defended by one buck for over two-thirds of the rut, and their defence entailed only about one escalated fight every 11 h. The proportion of time each territory was defended was correlated with the number of copulations seen there. Females preferred the territories where most copulations were seen and spent little time in other territories (Table III). Surprisingly, male–male competition, at least as measured by frequency of fights, did not seem to intensify about successful territories. This result runs counter to what Fryxell (1987) saw during 32 h of observations of a white-eared kob, *Kobus kob leucotis*, lek. The relative number of fights may have had little importance for a male's ability to hold a successful territory. Males of superior fighting ability may occupy the best territories before the start of, or early in, the rut, and their dominance may be established in a few

aggressive interactions (Robel & Ballard 1974). These males may then be able to defend preferred territories until they become exhausted towards the end of the rut, then leave without much fighting, to avoid injuries that would compromise their survival and ability to breed again in the following year. Ownership of a successful territory over most of the rut was still costly, however, because the long tenure resulted in more escalated fights. Fighting in cervids is dangerous (Geist 1986), and at least two bucks were killed in fights during our study.

The high degree of between-year predictability of relative copulatory success of different lek territories has several implications for male and female mating strategies. Males should compete for the best territories, and this competition may occur before the rut begins. In our study area, the most successful territories were defended by bucks before the first copulation was observed. Males could employ the same cues used by females to select territories (e.g. proximity to escape routes). Alternatively, males could remember from previous experience which territories were most successful, and attempt to settle in them.

Males should also not defend territories that are traditionally unsuccessful. Our data indicate that territories where no copulations were seen were defended less frequently, but the frequency of escalated fights during the defence of unsuccessful territories was still one every 2 h. Non-breeding males on these territories may have been establishing a dominance hierarchy possibly because they are young and on the lek for the first time. The relative dominance rank they achieve may affect their chances of breeding in later years. Females may select territories partly by environmental cues that are independent of the characteristics of the male occupying the territory. In our study site, the most likely cue appeared to be distance from travel routes. Intrasexual competition among males, however, is likely to produce a situation where the most competitive males occupy the territories preferred by females. Because we did not know the exact age of most territorial males, we are unable to analyse the effects of male age on territory rank. Our data suggest that older males tend to occupy high-ranking territories, but also that territory rank may be partly affected by the age or other attributes of the male defending it. Clearly, location is not the only characteristic of a territory that determines the number of females that will copulate in it. Nevertheless, our data indicate that location is important, especially given that males that switched territories within the same year experienced predictable changes in copulation rate. If characters of males that allow success in intrasexual competition are those that also confer a selective advantage to females, there would be no need for females to choose among males according to male phenotype. Females could simply choose the best territories, and male–male competition would ensure that those territories were occupied by the best males. However, it is possible that females would gain by choosing males according to characteristics other than those important in intrasexual competition. A conflict may then exist because the preferred males would not necessarily be in the preferred territories. The results of our study cannot therefore falsify the hypothesis that females also select territories partly because of the characteristics of defending males.

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