Territoriality as a mating strategy in red deer

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Abstract. The mating behaviour of red deer stags, *Cervus elaphus*, has been extensively described as harem defence. However, it appears that territoriality may be chosen as a mating strategy when certain conditions are met. In a study area in southwestern Spain, early on in the rut, about 58% of adult males established territories in preferred areas, defended the territory against other males even in the absence of females, and courted females only within territorial boundaries. The mean territory size was about 2·3 ha. The later a male settled on his territory during the rut the fewer the females he was able to keep. The preferred areas where males established territories were also extensively used by females even before the start of the rut. The number of females per ha before the onset of the rut was positively correlated with the cumulative number of hinds that each male kept later on. Hence the reproductive success of males was largely influenced by the location of their territory. Such intensive use by females of a highly productive area for feeding and daily passage in an otherwise low-resource environment appears to promote the defence of territories located in the richest area. This paper provides the first evidence for territorial defence of mates in red deer and may contribute to the understanding of the dynamic nature of mating behaviour in ungulates.

Reproductive strategies in male ungulates are mainly designed to maximize their access to receptive females. Gosling (1986), in a review of reproductive strategies of different antelope species, showed that males can adopt a variety of strategies including following a group of females over their foraging range or staying in one part of the females' range and defending it against other males. The average reproductive success derived from adopting one strategy or another depends mainly on the ecological factors that influence the social and spatial behaviour of females. A considerable lability of mating systems is thus expected between populations of a given species living under different environmental conditions (Emlen & Oring 1977). Although there is little evidence for intraspecific variability in ungulate mating systems, recent reports suggest that between-population variation may be greater than usually assumed (see Gosling 1986 for antelopes; Rubenstein 1986 for horses and zebras; Schaall & Bradbury 1987; Pemberton & Balmford 1987 for fallow deer, *Dama dama*; Knight 1970; Geist 1982 for North American elk, *Cervus canadensis*).

Rutting cervids are reportedly non-territorial, definite evidence of territoriality in the family being available only for the roe deer, *Capreolus capreolus*

(Kurt 1968; Bramley 1970) and the sika deer, *Cervus nippon* (Miura 1984) whereas the general tendency for most species is for males to mate by joining a group of females and following them over their foraging range (Bützler 1974; Owen-Smith 1977). Nevertheless, there are some early suggestions of territoriality in cervids, including red deer, *Cervus elaphus*. Thus, Graf (1956) indicated that territoriality in the family Cervidae had apparently been overlooked. He predicted that evidence for territoriality would be forthcoming when more species had been studied. Burkhardt (1958) considered the existence of territoriality and scent-marking behaviour when observing a population of red deer in Switzerland but provided no data to demonstrate it. Reproductive behaviour of red deer has been extensively studied on Rhum (Scotland) by T. H. Clutton-Brock and colleagues (Clutton-Brock et al. 1982). In the early rut, males move to traditional rutting grounds, attempt to form harems and, once associated with hind groups, they move as their harems do to new feeding areas or to sheltered positions. Although Darling (1937) seemed to recognize some territorial behaviour by rutting stags, further studies on Scottish red deer demonstrated only a tendency to concentrate rutting activities in particular areas, mainly for

prime stags, but without any defence of the terrain in the absence of a harem (Lincoln et al. 1970; Lincoln & Guinness 1973; Gibson & Guinness 1980; Clutton-Brock et al. 1982). Nevertheless, information from other populations, in particular those inhabiting markedly different habitats like those of the Mediterranean region, may bring a new perspective to the adaptive plasticity of mating behaviour in the species.

Our aim in this study is to investigate whether territories are held by rutting males in a population of red deer living in Doñana National Park, in the extreme southwestern edge of the species' European range.

STUDY AREA

Doñana National Park lies in the estuary of the Guadalquivir river, in southwestern Spain. The dominant feature of the Park is a seasonal marshland bordering the western shore of the river. This zone is limited to the west by an area of meadows and sands, the latter being covered by low Mediterranean shrub.

The climate is typically Mediterranean, with hot dry summers and mild wet winters. Annual rainfall is about 530 mm (513·7 mm in the 12 months before this study started in 1986). The rains fall mostly in winter, and temperatures range from 5°C in January to 35°C in July and August. Seasonality is therefore the most typical feature in this habitat.

After winter rains, and throughout summer and early autumn, the waters recede and all the habitat types dry up. At this time, the narrow strip of meadows between the lower dry marsh and the higher area of shrub is the only zone remaining relatively moist, due to reserves from a higher water table. This area of complex pasture mosaics (Allier et al. 1974; Rogers & Myers 1980) is where red deer traditionally gather at the time of rutting in September. The meadows are also regularly used (particularly at dawn and dusk) by the hinds in their daily movements between the shrub area where they spend the day and the marsh where they spend the night (Braza et al. 1984).

For observation purposes at Doñana, we chose the less disturbed zone, the inner reserve, and, within it, an area of 500 ha (Fig. 1) comprising low shrub (17·0%), bracken (8·1%), meadows (6·0%), meadows with rushes (10·2%) and dry marsh (58·5%). For more details of habitat types and vegetation composition see Allier et al. (1974) and Rogers & Myers (1980).

METHODS

We collected data mainly in September of 1986, 1987 and 1988. The first step in the study consisted of identifying individual adult males by video-recording stags, then observing the differences in size and branching pattern of their antlers. Most adult stags visiting the area could be recognized in this way.

From 1 September to 3 October 1986, and from 15 August to 24 September 1987, we censused deer in the study area from 0600 to 0900 hours and from 1600 to 1930 hours; the position of any animal sighted was located on a 1:4000 map divided up into 1-ha squares. We also recorded harem size, defined as the number of females older than 1 year less than 50 m away from each adult male or within known territorial boundaries. When several adult males were accompanying females, the latter were ascribed to the bigger stag since body size in red deer is correlated with fighting success (Clutton-Brock et al. 1979) and dominance (Suttie 1979).

During 1987 and 1988, some selected sedentary stags were observed focally from 1600 to 1930 hours at the peak of the rut, in order to record their rutting behaviour, as well as that of the females and neighbouring males in the zone. Samples of behaviour were taken in 1-min units, for sequences as long as possible without interruption (typically 20–40 min). Only sequences lasting up to 20 min, without any changes in the number of females in the territory, were used for the analysis; a change in number of females or a sequence longer than 20 min we considered sufficient conditions to guarantee independence between samples. Since each sample was then the mean of several 1-min units of observation, data on rates of behaviour of focal males fulfilled normality criteria, hence parametric Student's *t*-tests were used for testing differences between means. Most of the remaining data were not normally distributed, hence appropriate non-parametric tests were used for analysis (Zar 1984).

From all sightings of each individual, an approximation to his rutting area was obtained by connecting the outer locations (complete convex polygon). We obtained 90% convex polygons by removing the 10% of locations furthest from the geometric centre (Michener 1979). The actual territory within
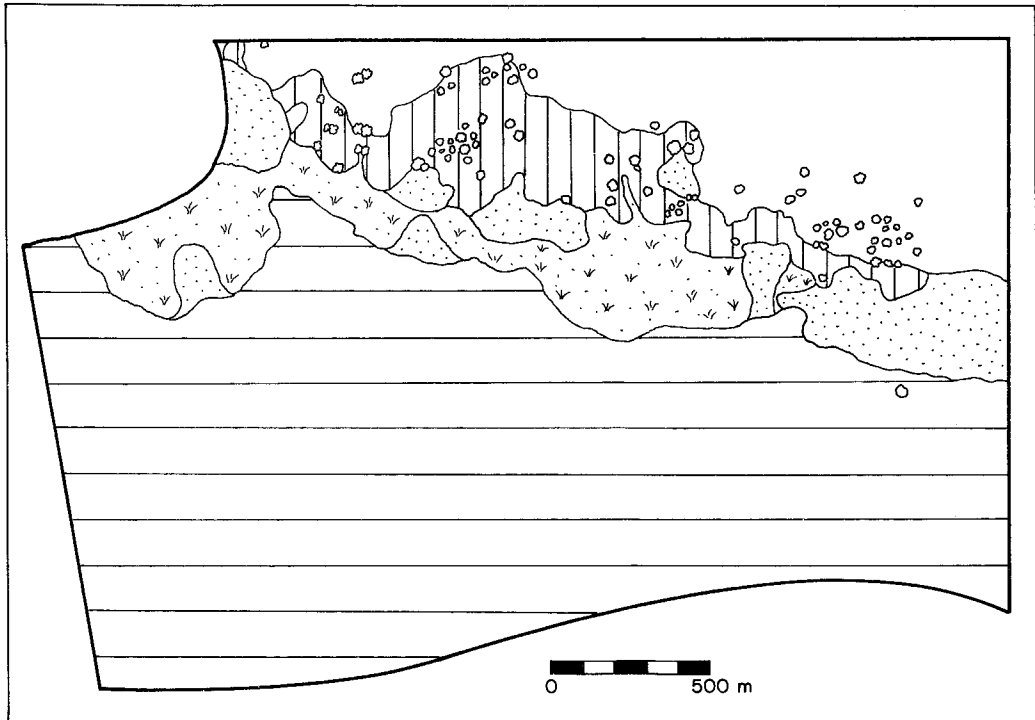
Figure 1. Map of the study area showing the distribution of habitat types. ○ cork oak, ☐ shrub, ☐ bracken, ▨ meadows, ▨ meadows and rushes ☐ dry marsh.

this area was obtained on the basis of the behaviour patterns that indicate the existence of boundaries (see below). The rutting area occupied by a male over the breeding season was larger than the territory at any one time because the boundaries usually changed during the rut.

Since harem size and harem-holding duration (number of days that the stag was seen with a harem) are known to be correlated with breeding success in red deer (Gibson & Guinness 1980), we computed an individual index of reproductive success by adding up for each stag the number of hinds seen with him over the whole rutting period. Such an estimate of reproductive success had the undesirable property of being correlated with the number of days that a male was seen in our study area, a variable that was also influenced by a male's date of settlement. Date of settlement was measured from the first day a male was spotted on the rutting area (day 1). Since we were interested in whether settlement dates affected reproductive success, we ran non-parametric partial correlation analyses (Conover 1980) between these two variables holding constant the number of observation days for a male.

To determine whether stags defended territories the following behaviour patterns were considered.

(1) Defensive activities (for a more detailed description see Clutton-Brock et al. 1982): displacing: forcing young stags to withdraw; chasing: running to other males and often pursuing them; thrashing (considered only if directed towards another male): raking the vegetation with antlers; initiating: lowering antlers, inviting contact; parallel walk: tense walking parallel to other; fighting: antler fighting.

(2) Behaviour towards females: herding: driving females towards the centre of the harem or the territory; points where a male starts to herd an approaching female; points where a male stops following females.

RESULTS

Settlement of Rutting Males

In our study area, the rutting activities were concentrated along the ecotone between marsh and shrub. During our daily censuses, we could recognize a number of rutting adult males that remained
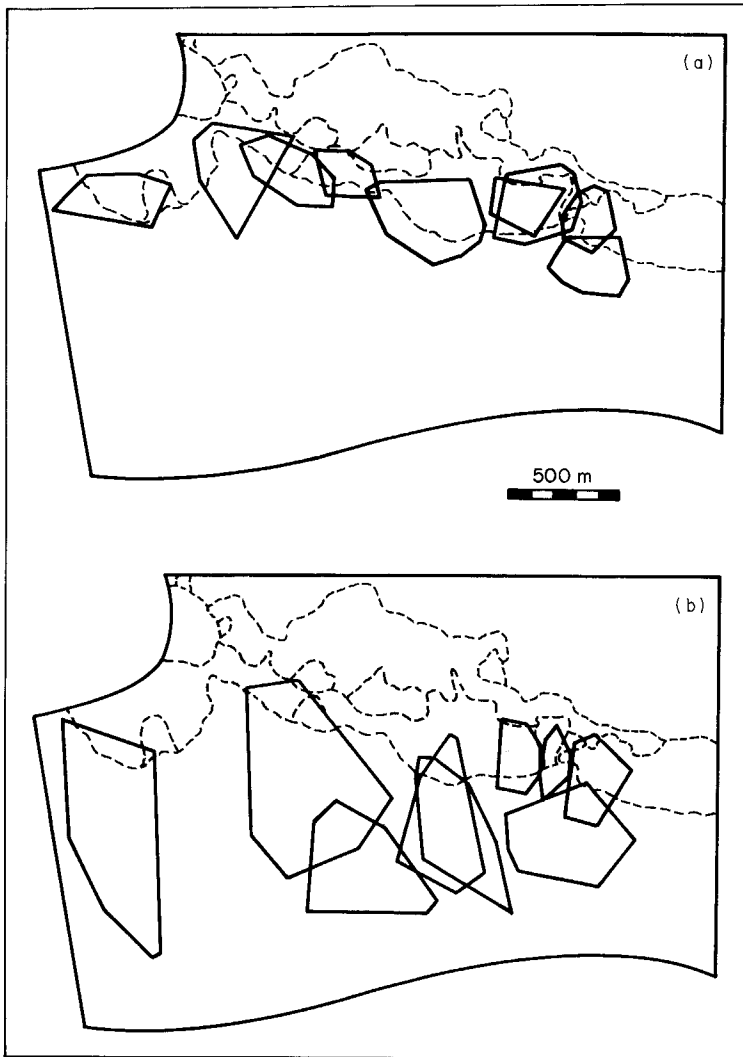
Figure 2. Rutting areas (90% convex polygons) of the nine sedentary stags that remained the longest in the area (more than 15 and 10 days for (a) 1986 and (b) 1987, respectively).

in the study area for several days (ranging from 2 to 24). Such males always concentrated their activities at particular zones in the area, which could be roughly delimited by drawing convex polygons around the places where each male had been seen on different days. Such activity areas were spaced along the ecotone, a preferred area being shared by those males that remained the longest (Fig. 2). Convex polygons resulting from cumulative data from several days overlapped to some degree. This is caused by variations in both the shape and the daily localization of the actual territory (see below).

The timing of settlement at rutting areas varied among males. Some of them settled at the onset of the rut, whereas others arrived during it. Some of the earliest established males left the area before the end of the observation period. Despite the fact that not all the early established males remained through to the late rut, the cumulative number of females kept in harems by each male was negatively correlated with their date of first settlement, keeping constant the number of days he remained at the study area (partial non-parametric correlation coefficients for 1986: $r = -0.509$, $df = 21$, $P < 0.01$; for

Table I. Mean harem size of sedentary and wandering males

Year	Harem size		Sample size (days)	Z^*	P
	$\bar{X}$	SD			
1986					
Sedentary males	1·22	0·83	33	1·39	0·081
Wandering males	0·89	0·42	20		
1987					
Sedentary males	2·79	1·23	24	4·97	<0·001
Wandering males	0·92	0·73	22		
Total (1986 + 1987)					
Sedentary males	1·88	1·27	57	4·30	<0·001
Wandering males	0·90	0·59	42		

*Mann–Whitney test.

1987: $r = -0.355$, $df = 24$, $P < 0.05$; i.e. late-settling males had few hinds.

From all the observations of adult males, 67·6% and 49·6% were sedentary in 1986 and 1987, respectively. Most hinds were seen accompanying sedentary males. For each day of observation, sedentary males had larger harems, on average, than wandering ones (Table I).

Territory Defence and Limits

Males under observation performed a number of behavioural patterns that indicated actual defence and/or the acceptance of fixed spatial limits.

Focal males engaged in defence activities towards the neighbouring established males, the satellites (adult and subadult males around the territory trying to sneak females) and non-satellite subadult males. Rates of defensive behaviour varied greatly, probably because such behaviour was triggered by the occasional approach of intruders. When this occurred, the focal male reacted aggressively, regardless of the presence of females within his territory ($\bar{X} \pm$ SD number of defensive activities per min: 0.06 ± 0.06 with females versus 0.10 ± 0.07 without females; matched-pairs t-test, $t = 0.93$; $df = 4$, NS), indicating that he was defending not a harem but an area. Defensive activities were restricted mainly to the spatial borders within which males displayed most of their rutting activity (see below).

Females were not individually marked, but when a group of females arrived in the area under observation, we recorded some instances of individual females crossing through one or several territories and the subsequent response of the focal males.

Territory owners did not start courting and herding females until hinds came within their spatial limits. They then followed them through the defended area, and gave up when the females went outside the border, sometimes at the same point where a neighbouring male started herding them. Territory owners did not follow females beyond their spatial limits, even when the hinds entered an area where no neighbouring male was established. This suggests that the attachment of a male to an area was not the result of constraints imposed by neighbouring stags. We sometimes observed the arrival of a typical mobile harem (a group of females followed by a herding male) at one of the territories. In such cases, the herding male always left the females alone while they crossed through the territory, and waited for them at the opposite side, just in case they decided to continue on their way (despite the effort of the territory owner to retain them). Occasionally, both satellite and neighbouring territorial males were observed to trespass into an alien territory to steal some females. Such incursive behaviour always occurred when the owner was engaged in some activity, far enough away at the opposite part of the territory. On two occasions, a pair of subadult males were observed walking together to the territory, one of them teasing the owner, while the other one tried to approach the females.

The locations where territorial males started herding an approaching female, and the points where they stopped following females and came back, can thus allow us to define the territory's limits (Fig. 3). If we use the data from a single day the border of a territory is clear and overlaps little
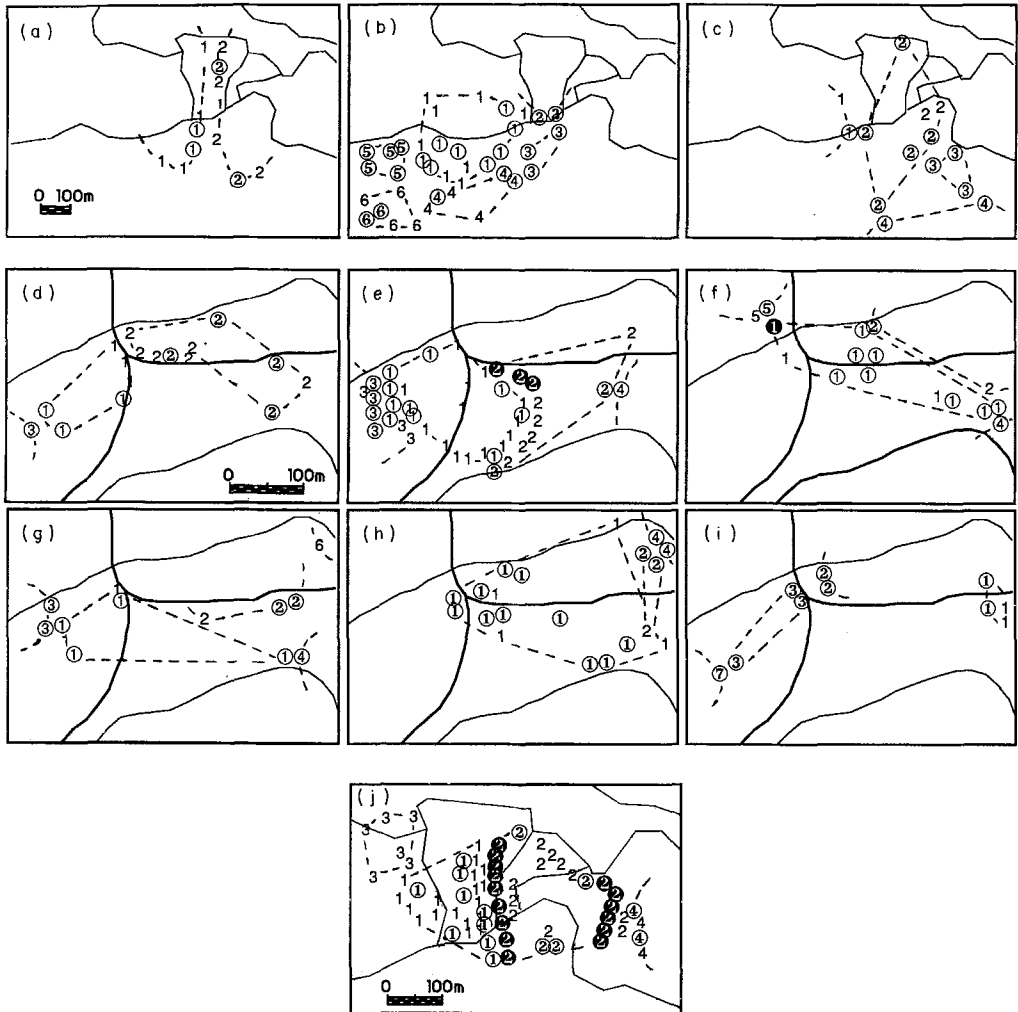
Figure 3. Territorial limits of the observed sedentary stags. Three sets of maps are shown: a–c represent three 8-day consecutive periods throughout the rut in 1987; d–i correspond to 6 consecutive days at the peak of the 1988 rut; and j shows the cumulative locations from 5 days at the peak of the 1988 rut. Numbers correspond to individual males within a set of maps. Dashed lines represent our estimate of the shape of the territories. —— Limits between vegetation types. —— Paths. Territorial behaviour: 1 behaviour towards females. ① Defensive activities. ● Defensive activities without females in the territory.

with neighbouring ones (i.e. Fig. 3d–i). Nevertheless, territorial limits could differ between successive days, so in the cumulative set of points from several days (Fig. 3a–c, j) it is possible to see some overlap or more than one border-like line of points. Likewise, some overlap is expected for convex polygons, since they included the different positions of territories during the whole observation period. The mean territory size of the observed males, estimated from territorial boundaries, was $2 \cdot 29 \pm 1 \cdot 84$ ha ($N = 14$).

Territorial males advertised themselves by roaring at higher rates when females were present than when they were not ($\bar{X} \pm$ SD $= 2 \cdot 04 \pm 0 \cdot 07$ roars per min versus $1 \cdot 56 \pm 0 \cdot 47$, respectively; matched-pairs t-test, $t = 4 \cdot 74$, $df = 4$, $P < 0 \cdot 01$). Nevertheless, roaring occurred when the male was engaged in both threatening males and courting females, and there is no significant difference between these rates ($\bar{X} \pm$ SD $= 2 \cdot 30 \pm 0 \cdot 51$ roars per min versus $2 \cdot 05 \pm 0 \cdot 63$, respectively; $t = 0 \cdot 16$, $df = 4$, NS), although both rates were higher than that in the absence of

both courtship and contest activities ($1·49 \pm 0·54$; $t = 3·48$ and $t = 3·05$, respectively, $df = 4$, $P < 0·05$).

Urine spraying was frequently observed in association with thrashing, either with apparently no external stimulation or during aggressive encounters at the territory limits. Also, urine was sprayed over objects or vegetation; although it might function as a mechanism for scent marking, we did not attempt to verify this point.

Space use by Females

Daily censuses showed that the cumulative number of females in the study area increased early in the rut ($\bar{X} \pm$ SD $= 34·71 \pm 13·70$ sightings per day before the start of the rut versus $64·08 \pm 17·91$ during the rut; $t = 3·99$, $df = 29$, $P < 0·001$; data from 1987 only). Females did not use the area uniformly; instead, there were some zones of higher density. The localization of these areas, or 'hotspots', roughly coincided with the position of the most successful male territories (i.e. those with the majority of females) and appeared to be constant from one year to another. Also, such a distribution pattern of females was not caused by the positioning of males, since their distribution was very similar even before the rut began (Fig. 4).

The density of females in the area where a rutting male defended a territory largely affected the number of females he kept (1986: $r = 0·73$, $N = 22$, $P < 0·01$; 1987: $r = 0·74$, $N = 27$, $P < 0·001$). Moreover, we found a high positive correlation between the cumulative number of females that each male gathered in his harem, and the density of females in his area during the 15 days before the start of the rut, when almost no adult male was yet in the study area ($r = 0·71$, $N = 27$, $P < 0·001$; data from 1987).

DISCUSSION

Until now, the mating strategy of red deer stags has been described as the male joining a group of females and following them over their foraging range, trying to keep them together by restricting their movements, and defending the harem against other males (Lincoln et al. 1970; Gibson & Guinness 1980; Clutton-Brock et al. 1982). Our data from Doñana, however, show a quite different situation. At the start of the rut, some adult males settled at some strategic areas, defending them against neighbours and non-established males. Sedentary males

did not attempt to court females outside spatial boundaries, and defended the area even when no females were inside it. These findings indicate defence of the space itself for reproductive purposes, hence territoriality (sensu Noble 1939).

Territorial boundaries were well defined at any one moment, although they were susceptible to being moved from one day to another. Such a displacement may be due to changes in the relative resource-holding potential of neighbouring males (exhaustion, injuries from fights, etc.) as the rut goes on, and/or to the shifting of the main 'hotspots', determined by variations in the use of space by females as the relative food availability of different habitats changed during the rut (Valverde 1960).

Territorial stags should advertise ownership. The acoustic self-advertisement of red deer stags by roaring is well known, broadcasting information about resource-holding potential (Clutton-Brock & Albon 1979). In this sense, roaring may play a major role in ownership advertisement for territorial males since it provides clues about both the location and the quality of the owner. Olfactory advertisement is also expected for a territorial mammal. Urine spraying in red deer has been extensively described in the literature (e.g. Lincoln et al. 1970). Urine smelling is more pronounced for rutting males (Lincoln et al. 1970) and it probably provides reliable information about a male's physical condition, indicated by metabolic by-products excreted (Coblentz 1976). Hence, it could be used as a territory marker as for other ungulates (review in Gosling 1982). Skin glands also play a role in social communication in red deer (preorbital glands: Bartos 1983). Such glands are used in territory marking by sika deer (Miura 1984) although little is known about spatial marking in red deer (but see wiping behaviour in Clutton-Brock et al. 1982). We have not observed such behaviour in Doñana stags, although urine spraying was common and often associated with thrashing at the territory boundaries.

We found a negative correlation between dates of settlement and the cumulative number of females held by territorial males, hence males seem to benefit from arriving early at rutting areas. Non-territorial stags have also been reported to travel to rutting areas early in the rut, before attempting to establish a harem (Lincoln & Guinness 1973; Clutton-Brock et al. 1982). Early-settled males have to invest in territory defence for longer prior
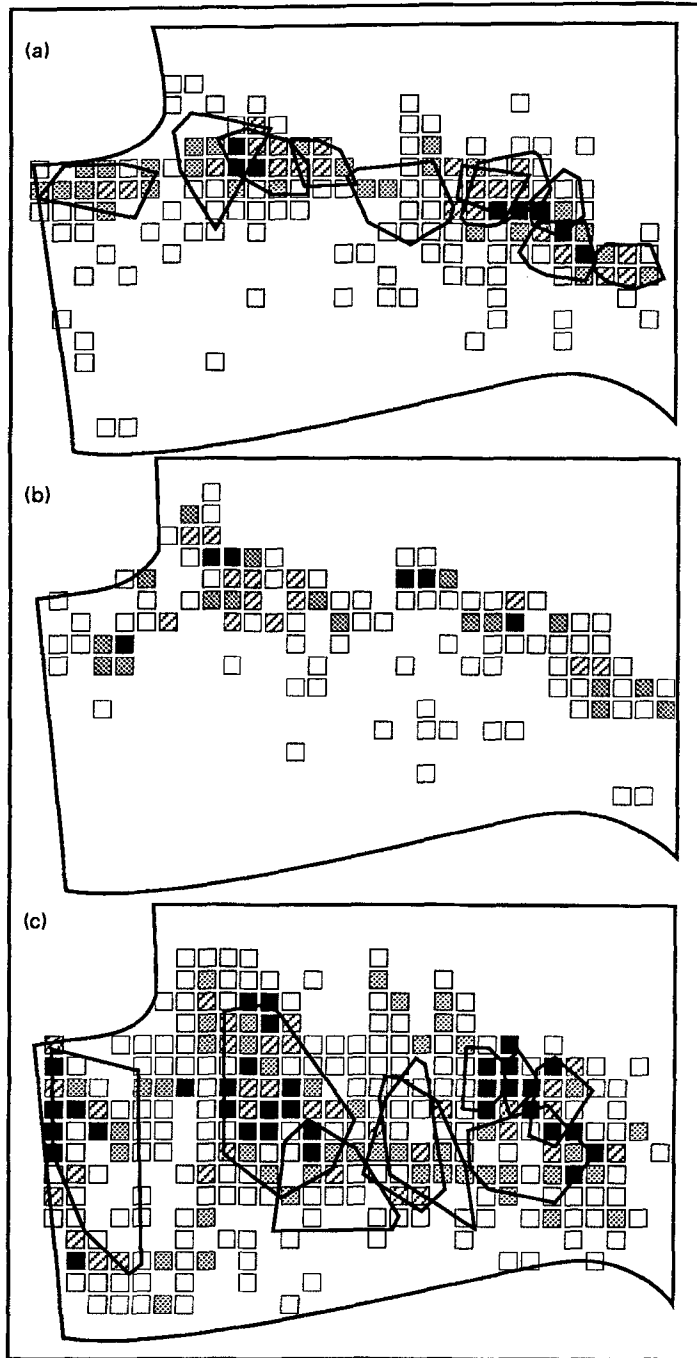
Figure 4. Density of hinds in the study area superimposed upon male rutting areas during the rut for 1986 (a) and 1987 (c) and during the 15 days before the start of the 1987 rutting period (b). Females per ha: ■ 15–30, ▨ 10–14, ▦ 6–9, □ 1–5.

to the peak of oestrus. In return they might benefit from favoured positions in dominance relationships due to prior-residence effects later on, when most females come into heat and competition between males for high-quality territories is most intense (see Gosling 1986).

While some stags in our study area defended a territory, others would follow a group of females (the latter may be young males, though this point could not be verified). Nevertheless, the mean number of females kept in harems by territorial males was higher than that kept by non-territorial ones, which suggests that, in our study area, following females or harem defence is a 'best of a bad job' strategy, used by males with a low resource-holding potential when economically defensible areas have already been occupied by the highest ranking stags.

A polygynous mating system based upon territoriality may be related either to resource defence or to a lek system, depending on whether females use the area for obtaining resources or for the single purpose of mating (Emlen & Oring 1977). Our data apparently support the first possibility, since females in Doñana concentrate along the meadows of the shrub–marsh ecotone even before the beginning of the rut, and since the success of males in gathering females in harems depends largely on such high densities of females. In Doñana the females cluster in an area defined in previous studies as very productive due to its high humidity, caused by the flow of water from a higher water table at the shrub area (Allier et al. 1974; Rogers & Myers 1980). The presence of food resources in some wet areas is especially important in Mediterranean ecosystems, where the rut coincides with a period of food scarcity for herbivores. Food is scarce from August to the rains of October–November because of the very dry summer but remains available in especially wet areas which may explain the concentration of females in the ecotone of our study area (Fig. 4). It is possible that such a circumstance renders the space economically defensible for red deer males in many parts of their Mediterranean range. On the other hand, the daily passage of females through the ecotone of Doñana in their movements to and from the shrub and marsh areas (see Braza et al. 1984) brings an additional advantage for males placing themselves in such a strategic area, thus enhancing their chances of mating.

Apart from the positive correlation between females in harems and densities before the start of the rut, which suggests the females use the area for foraging, the number of females sighted increased as the rut went on. This may be due to at least two very different but not mutually exclusive reasons: (1) the restriction of the areas with available food resources as the dry season goes on, and (2) the arrival of females from adjacent areas with the purpose of mating in a highly competitive area for males. These two reasons would, respectively, lead to a resource defence or a lek-like mating system but we lack sufficient evidence to decide between these possibilities at present.

To date, there is no evidence for female choice in red deer, although there are some suggestions in the literature supporting it (e.g. Lincoln & Guinness 1973; Bartos 1982; Bubenik 1983). A mating system based upon territoriality would probably make it easier for females to exercise choice, since male site tenacity allows females to play a major role in deciding with whom to mate. If so, it is interesting to question the relative importance of epigamic-selected traits in different populations with varying mating strategies.

The pattern of territoriality described here for red deer is very similar to that reported by Miura (1984) for sika deer. We feel that mating strategies based upon territorial defence could be found for more cervid species, as reports from different populations are gathered, if mating strategies are in fact largely determined by environmental conditions. Further studies might focus on the relative contribution of resource defence versus female choice as determinants of male mating success in territorial strategists. Other topics deserving further attention are the individual plasticity to switch between resource and harem defence and the evolutionary implications of the relative frequency of each strategy which would model the direction and intensity of sexual selection. Such topics may bring further insight into the dynamic nature of ungulate mating behaviour.

ACKNOWLEDGMENTS

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