Mate retention, harassment, and the evolution of ungulate leks

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Current models of lek breeding mostly suggest that males defend clustered mating territories because females show a preference for mating on leks. Here we argue that, in lek-breeding ungulates, males may also gain benefits from holding clustered mating territories because clusters retain does in estrus. We show that in fallow deer (*Dama dama*) harems are commonly disrupted by young males. Bucks that hold territories on the lek that lose their harems quickly regain does as other harems are disrupted, whereas bucks defending isolated, single territories rarely regain does the same day. The risk of harassment may also help to explain why does in estrus leave the large, unstable herds that they usually live in. Does in estrus are frequently chased by young males when outside male mating territories. Benefits of moving to the lek (versus moving to single territories) include reduced risks of long chases. Though intrusions by young bucks are the commonest cause of does leaving male territories in our study population, other factors that cause does to move between neighboring harems (including disturbance by predators and persistent courtship by males) may generate benefits to males holding clustered mating territories. Once clustered mating territories have developed, the additional costs of mate choice are likely to be low, and female preferences for particular male characteristics may be likely to develop. *[Behav Ecol 3:234–242 (1992)]*

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The different types of polygyny found among mammals apparently represent forms of precopulatory or postcopulatory mate guarding (Clutton-Brock, 1989). Food distribution, the risk of predation and disease, and harassment by males affect the distribution of receptive females in time and space, and males distribute themselves so as to maximize their access to mating partners (Bradbury and Vehrencamp, 1977; Clutton-Brock, 1989; Clutton-Brock and Harvey, 1978; Emlen and Oring, 1977; Rubenstein and Wrangham, 1986).

Leks, where males defend small, clustered mating territories in one part of the female range, are not easily interpreted within this framework (Clutton-Brock, 1989). Leks have been reported in bats (Bradbury, 1977; Bradbury and Vehrencamp, 1977), pinnipeds (Fay et al., 1984), and dasyurid marsupials (Lazenby-Cohen and Cockburn, 1988) but are commonest among the ungulates, where they occur in the Cervinae (Clutton-Brock et al., 1988; Schaal, 1986), the Alcelaphinae (Gosling, 1987; Monfort-Braham, 1975), Reduncinae (Balmford, 1990; Leuthold, 1966; Schuster, 1976), and, possibly, the Antilopinae.

A central question concerning the evolution of lek breeding is why male territories should be clustered within one part of the females' range (Balmford, 1991). A priori, one might expect the average mating success of dispersed males to be higher than that of clustered ones because the latter would be likely to share mating access to a relatively small segment of the female population. However, observations of leks in birds and mammals show that this is not the case: large numbers of females typically mate on leks, and females will move to leks from considerable distances (Balmford, 1990). In lek-breeding populations, the frequency of copulations on dispersed, single territories is usually low (Wiley, 1991). In our study population of fallow deer, 94% of observed matings occur on the lek, and the most successful males may mate with more than 50 does during a single rut (Clutton-Brock et al., 1988). In Uganda kob (*Kobus kob thomasi*), copulations on single territories are rare (Balmford, 1990; Leuthold, 1966).

In several lek-breeding ungulates, there is clear evidence that females in or close to estrus are attracted to leks once they have left the large, unstable herds that they usually live in (Balmford, 1990; Clutton-Brock et al., 1988). However, a second reason males may

hold clustered territories is that clusters of territories may retain estrous females more effectively than dispersed territories. For example, during the 6–24 h that precede copulation, female fallow deer usually change territories several times, typically moving from one territory to its closest neighbor. Where females change territories several times before mating and usually move to the nearest territory, this process can generate advantages to males that hold clustered territories, arising from the fact that females that have entered a cluster of territories seldom leave it, subsequently moving between territories within the cluster. As a result, males holding territories in clusters have an improved chance of receiving females that move from other males within the cluster (Stillman et al., in press). In contrast, males holding isolated single territories suffer the disadvantage that, once estrous females leave their territory, they are unlikely to return. This process will operate so long as females leaving territories commonly move to the nearest territory, and it does not depend on any preference in females for remaining on leks, though female preferences for doing so will reinforce the advantages to males holding territories there. In the first part of this paper, we investigate the benefits that males holding territories on the lek may gain from the lek's capacity to retain does in estrus.

This approach to the evolution of lek breeding in fallow deer raises two immediate questions. Why do estrous does move between territories? And why do they leave the herds where they usually live in the first place? In both cases, females might move in order to choose mating partners (see Balmford, 1991; Bradbury, 1981; Gibson et al., 1990; Queller, 1988). However, though female ungulates avoid mating with immature males, there is little unequivocal evidence of female preferences for particular mating partners in ungulates and, in fallow deer, females will mate as readily with unsuccessful adult males as with successful ones (Table 1). In this situation, it is sensible to avoid the common assumption that females move between male territories to assess mating partners and, instead, investigate the reasons for female movements. We have already suggested that harassment by young males is often responsible for movements of females between territories (Clutton-Brock et al., 1989) and that does in estrus may leave the large, unstable herds that they live in for much of the year because individual bucks cannot provide adequate protection from dangerous harassment in unstable herds (Clutton-Brock et al., 1988). In the second half of this paper, we investigate the relationship between harassment and female movements and compare the frequency of harassment at times when females in or close to estrus are on the lek, in single territories, and in feeding herds. To overcome the problem that estrous does are rarely seen outside mating territories, we waited until does on the lek began to allow bucks to mount them (confirming that they were in full estrus) and then gently herded them off the lek and monitored their behavior.

Table 1

Hourly mating rates for female fallow deer (number of observed copulations divided by number of hours spent by does in each buck's territory) in relation to total number of doe/hours spent in the harem of each buck and mean harem size[a]

	Mating rate per doe/h in relation to			
	Total doe hours/buck		Mean harem size of bucks	
Year	r_s	N	r_s	N
1986	−.324 (ns)	22	−.253 (ns)	22
1987	−.235 (ns)	19	−.18 (ns)	19
1990	−.018 (ns)	18	−.155 (ns)	18

[a] Both calculated for all bucks mating on the lek at Petworth during the rut (18–30 October). In 1986 and 1987, about 200 copulations were observed on the lek per year, but in 1990 the sample of observed copulations fell to 90 as a result of reduced time spent in observation.

METHODS

Study area and population

Fallow deer were present in Britain in the Pleistocene, but the present subspecies is thought to have been introduced from the Mediterranean area before or shortly after the Norman conquest. The species is widely kept in deer parks and has established itself in many wooded parts of the country. Coat color is variable, ranging from white through spotted to black. Mature bucks, which develop large, palmated antlers, usually weigh between 50 and 70 kg; mature does weigh from 30 to 55 kg (Chapman and Chapman, 1975; Pemberton and Dansie, 1983). Social behavior also varies. Where density is high, does and younger bucks form large, mixed-sex herds numbering 50 or more but of unstable membership while, in areas of lower density, does are usually seen in small parties of 2–10. Mature bucks are segregated from does throughout much of the year, also forming unstable groups of up to 50 or more animals (Alvarez et al., 1975; Chapman and Chapman, 1975; Schaal, 1986). Breeding is strongly seasonal (Armstrong et al., 1969): In late September, buck groups fragment and bucks move to areas of high doe density where they defend discon-

tinuous mating territories or stands, often on the edge of clearings in the forest (Chapman and Chapman, 1975). Does will only accept mounting for a short period, and in our study area more than 90% only mate once (Asher, 1988; Clutton-Brock et al., 1988). mating peaks in the second half of October and is largely complete by the beginning of November. Single calves are born in mid-June, about 234 days after mating.

Our study area in Petworth Park (Sussex, England) consists of 380 ha of long-established grassland. Trees (mostly oak, sweet chestnut, and beech) are sparsely distributed, either singly or in small clumps. The park contains a population of about 900 fallow deer. Of these, approximately half are does of breeding age (≥1 year old), 20% are fawns of the year, 13% are mature bucks (>5 years), and 14% are young bucks (1–4 years).

As in other fallow deer populations (Apollonio, 1989), bucks at Petworth showed several distinct breeding strategies during the short annual rut (approximately 15–31 October) (Clutton-Brock et al., 1988). These strategies included:

1. Defense of a territory on the lek. About 15 of the largest and oldest males attempt to defend small mating territories, usually 5–10 m in diameter, on traditional sites. Territories are not contiguous and younger males can pass between them. Successful bucks can mate with up to 50 or more females during a single breeding season. Harem size varies among bucks, but harems of more than eight does are unusual, and their average size is between three and five (Clutton-Brock et al., 1989).

2. Defense of an isolated mating territory. A small number (usually <5) of mature bucks temporarily defend isolated mating territories at least 100 m from the lek, which (like territories on the lek) do not contain resources attractive to females. Sometimes these single territories occur in pairs, but, unlike lek territories, they are always separated by at least 50 m and usually by more than 100 m. We refer to these as "single" territories. The number of does on single territories was normally low, ranging from zero to three. The behavior of bucks and does on these territories closely resembles their behavior on the lek: territories are usually less than 10 m in diameter and boundaries are well defined. Does spend little time feeding and much of their time lying down. Estrous does will copulate readily on these territories, and copulation rates per doe/hour do not differ significantly from those on the lek. However, the mating success of bucks holding small territories is seldom high because these territories typically contain does intermittently. When bucks holding these territories lose their does, they often abandon the territory temporarily, either returning to mixed-sex herds or, in some cases, defending resource territories under oak trees (see below).

3. Defense of resource territories. In some years, 10–15 bucks that have not yet reached their full size or that have been defeated in competition for lek territories defend large resource territories around oak trees where females gather to feed on acorns. We refer to these as "resource territories" to distinguish them from single territories. In contrast to lek and single territories, the great majority of females on resource territories are not in estrus, the frequency of copulations per doe/hour is low, and the average mating success of males on resource territories is less than one observed copulation per year. The manipulation of food availability in resource territories affects their attractiveness to does (Clutton-Brock et al., 1988).

4. Harassing does. Juvenile males 1–4 years old are also attracted to the lek or to single territories in substantial numbers and spend much of their time attempting to chase does out of the territories defended by older bucks.

Samples

Buck, doe, or harem groups were watched for varying periods of time by one or more observers equipped with 10 × 50 binoculars and telescopes. We collected data on the results of intrusions in 1990 and based analysis on a sample of 124 intrusions involving the harems of 22 different bucks. Comparisons of intrusion rates, rates of doe loss, and number of changes per minute were based on matched samples collected from 8 to 10 different bucks in 1990, whereas comparisons of animals on single territories versus lek territories were based on unmatched samples of varying size collected in 1990 and 1991. Observation periods varied in this sample from less than 1 h to several hours duration but did not differ between the two samples.

Definitions

Harem: the number of does in a buck's territory at any time.

Single territory: any territory more than 50 m from another territory. In most cases, distances between single territories exceeded 100 m.

Lek territory: any territory within a cluster in either of two traditional sites.

Chases by young bucks: cases where does were chased for at least 5 m by a young buck that approached them to within 1 m.

Chase length: the estimated length of the chase in meters.

Intrusions: any entry into the territory defended by a mature buck by a juvenile or an adolescent male.

Number of young bucks within 20 m: the number of young bucks within 20 m of the periphery of a territory.

Chases of young bucks by mature bucks: any case where a territory holder left his territory to run after a young male.

Number of does gained/lost per minute: the number of does entering or leaving a territory.

Copulation: an observed ejaculation, usually preceded by a sequence of mounts.

Latency till does regained: the number of minutes from the time that a territory was emptied of does until the first doe returned to the territory.

Removal of does from territories

Under normal conditions, does in estrus are rarely seen off the lek, and the degree of harassment suffered by anestrous does provides no indication of the possible treatment of estrous does. To investigate the frequency with which estrous does off the lek would be harassed by young bucks, we waited until a doe on the lek had been mounted repeatedly, then, before copulation, we gently herded her away from the lek and into the closest mixed herd by walking slowly toward her. We subsequently attempted to maintain a continuous record of the doe's behavior over the next half hour, recording her activity, the frequency with which she was chased by juvenile or subadult males, and the length of each chase. The same technique was used in experiments involving the emptying of single territories and lek territories.

RESULTS

Retention of does on lek versus single territories

Both on and off the lek, harems were unstable as does moved from one territory to another. On the lek, the average doe changed territories about four times per hour (Clutton-Brock et al., 1988), whereas, on single territories, the average rate of territory change was about twice per hour (Figure 1a; Mann-Whitney U test, $U = 36.5$, $N = 12, 12$, $p < .05$). Several does commonly left territories in quick succession, and territories often emptied altogether. As a result, bucks holding lek or single territories rarely retained their harems for more than 2 h at a time (Figure 1b). The

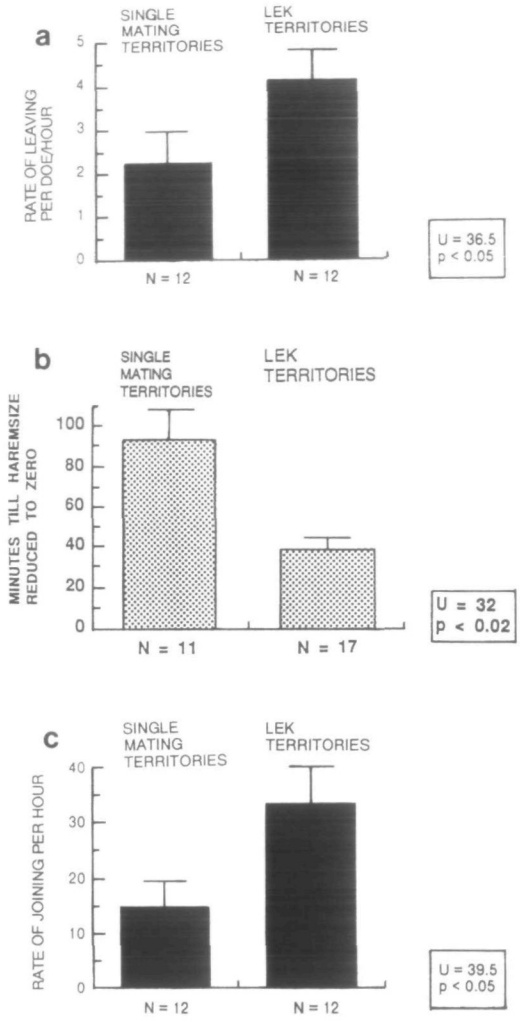

Figure 1
(a) Rate of leaving (per doe/hour) from single mating territories and lek territories. (b) Mean number of minutes until number of does on single territories versus the lek were reduced to zero. (c) Rate of does joining single mating territories and lek territories per hour based on watches of territories already containing does. Numbers of bucks sampled are shown below each histogram. Extending lines show SEs.

frequency with which bucks lost their complete harems was significantly higher on lek territories compared to single territories ($U = 32$, $N = 11, 17$, $p < .02$).

Bucks holding harems on the lek were joined by additional does more than twice as frequently as those holding harems on single territories (Figure 1c; $U = 39.5$, $p < .05$), whereas, among bucks holding single territories, the number of does joining harems per hour increased as the distance to the nearest territory holding does decreased ($r_s = -.58$, $N = 12$, $p < .05$). These comparisons underestimate the advantages of holding lek territories, as bucks holding single territories that lost their does seldom regained them quickly. None of 11 bucks holding single territories that lost their harems failed to regain does within 2 h, whereas, on the lek, bucks that lost their harems usually regained some does within a few minutes and as many does as they originally held within half an hour (Figure 2a; $U = 0$, $N = 11, 15$, $p < .02$).

To confirm the difference in the rate at which does were regained, we experimentally

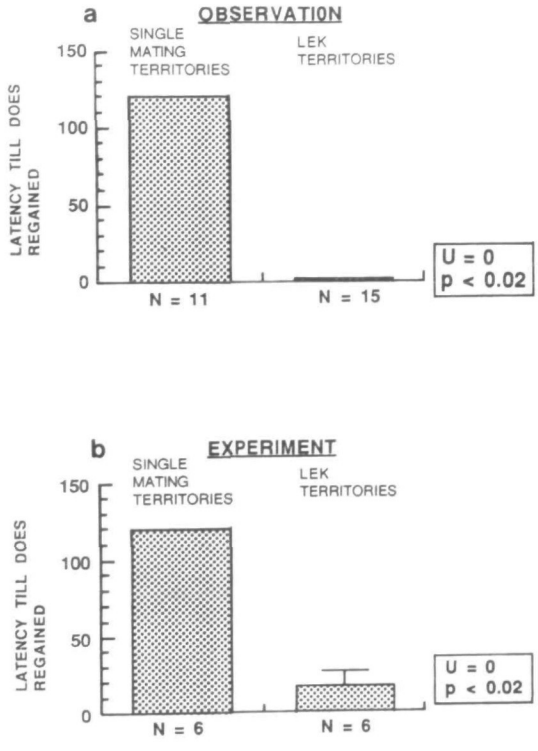

Figure 2
Mean number of minutes from time that a territory wa: emptied of does until it regained one or more does. (a) Observational samples (b) after experimental emptying of a sample of single territories versus lek territories. Extending line shows SE.

emptied six single territories and six territories on the lek by gently herding does off the territories. In this sample, too, bucks holding single territories never regained does in less than 2 h, while bucks holding territories on the lek regained does within 17 min on average (Figure 2b; $U = 0$, $N = 6, 6$, $p < .002$). It was not surprising that the latency until does were regained on the lek was longer in the experimental than the observational samples, as the removal of does from particular territories inevitably caused a measure of disturbance on neighboring territories.

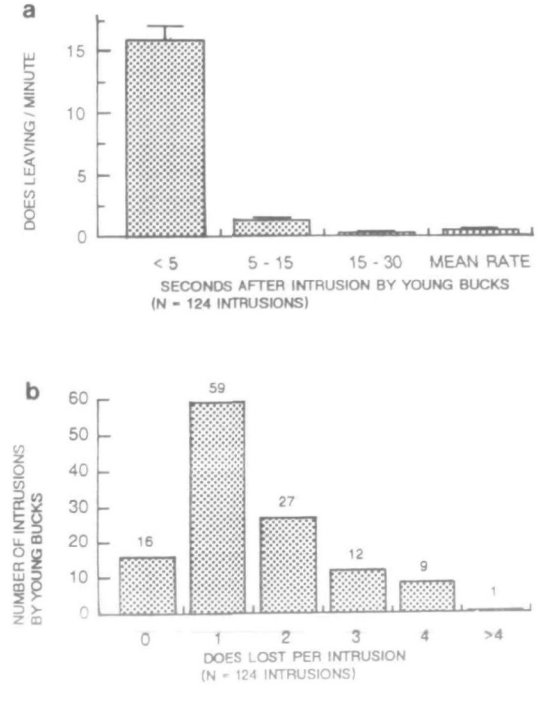

Figure 3
(a) The average number of does lost within different intervals after intrusions by young bucks into the territories of bucks defending does on the lek ($N = 124$ intrusions). Because intervals varied in length, numbers are shown as rates of doe loss per minute. Extending lines show SEs. (b) The frequency distribution of the number of does lost during the first 30 s after an intrusion.

Harassment and the movement of does between territories

Most movements by does between lek or single territories were associated with intrusions by juvenile or subadult bucks (Figure 3a). Of a sample of 244 movements of does between harems on the lek, 144 (59%) occurred in the 5 s after a successful intrusion by a young buck, compared with an expected value of 18 based on the overall rates of intrusion and doe loss ($\chi^2 = 93.2$, df = 1, $p < .001$). In the majority of cases, a single intrusion was associated with the loss of a single doe, but, in some cases, an intrusion led to the loss of several does (Figure 3b). In about 5% of cases, a single intrusion led to the loss of all does in the buck's territory, but one intrusion was often followed in quick succession by others as the harem became dispersed and the buck began to chase intruders. On average, bucks lost all the does that they were defending approximately once an hour on the lek and slightly under once every 2 h when holding single territories (Figure 1b).

The rate at which different bucks lost does rose with the rate of intrusions into their territories by young bucks ($r_s = .82$, $N = 17$, $p < .001$), with the average number of young bucks that were within 20 m of their harems ($r_s = .53$, $N = 17$, $p < .05$), and with the frequency with which they chased young bucks ($r_s = .63$, $N = 17$, $p < .01$). The rate of intrusions increased with the number of young bucks within 20 m of the territory ($r_s = .64$, $N = 17$, $p < .01$), with the proportion of time that young bucks were close to the harem ($r_s = .77$, $N = 17$, $p < .002$), and with harem size (Clutton-Brock et al., 1989). Intrusion rates decreased as the proportion of time the territorial buck spent close to or in his territory increased ($r_s = .53$, $N = 17$, $p < .05$).

Comparisons of the rate at which bucks lost does showed that the number of does lost per minute was higher when the majority of does in the buck's territory were standing than when they were lying down (Figure 4a; Wilcoxon matched-pairs test, $T = 0$, $N = 10$, $p < .01$). The number of young bucks within 20 m of the territory also increased when most does were standing ($T = 0$, $N = 10$, $p < .01$), as did the frequency with which territory holders chased young bucks ($T = 2$, $N = 10$, $p < .01$), whereas the number of intrusions per minute showed a nonsignificant trend in the same direction ($T = 5$, $N = 8$, $p < .1$). Bucks whose does were standing spent about 80% of their time moving, but this proportion fell to 35%

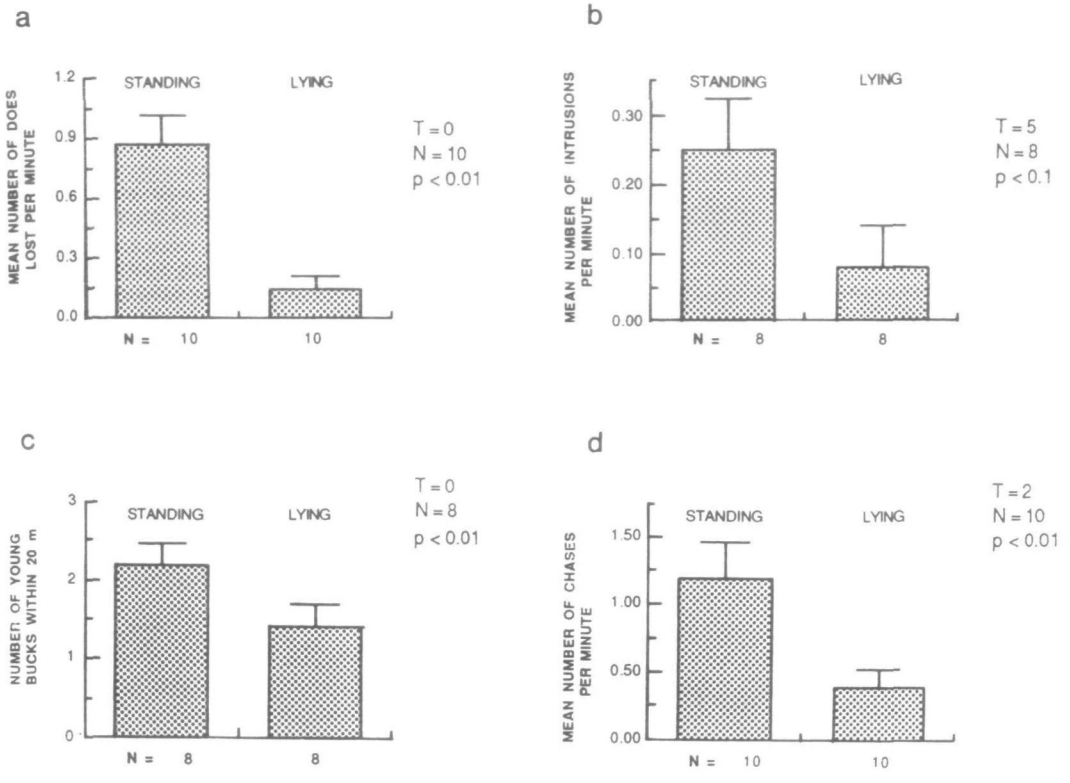

Figure 4
(a) Mean number of does lost per minute, (b) mean number of intrusions by young bucks per minute, (c) mean number of young bucks within 20 m, and (d) mean number of chases involving the territorial buck, calculated for matched samples of 8 and 10 bucks at times when the majority of the does in their territory were standing versus lying down. Extending lines show SEs.

when their does lay down (Wilcoxon matched-pairs test, $T = 1$, $N = 10$, $p < .01$).

Comparisons of lek versus single territories provided no indication that lek territories were less likely to be disrupted by young bucks. On the contrary, the number of young bucks close to the territory and the frequency with which the territorial buck chased intruders was higher on the lek than on single territories (Figure 5a,b; $U = 52$, $N = 12, 22$, $p < .002$; $U = 8$, $N = 5, 18$, $p < .02$). As a result of the high frequency of intrusions on the lek, bucks commonly lost all their does approximately once an hour, and the latency to total doe loss was only half that on single territories (see Figure 1b).

Harassment and the benefits of leaving herds to does

To investigate the benefits of estrous does of moving to mating territories, on 20 separate occasions we gently herded a doe that had begun to allow males to mount her off the lek and into the nearest mixed herd (see above). For 13 of these does we were able to observe the frequency with which the same doe was harassed (1) when she was on the lek, (2) when off the lek but within a single territory, and (3) when not in a territory.

The results of herding does in estrus off the lek were dramatic. Estrous does rapidly attracted the attention of nonterritorial bucks who chased them repeatedly until they ran into the territory of a male holding an isolated territory or back to the lek. The average frequency with which these does were chased was about four times higher than it had been before they left the lek (Figure 6; Wilcoxon matched-pairs test, $T = 1$, $N = 13$, $p < .01$). Does that entered isolated, single territories were chased less frequently than they had been

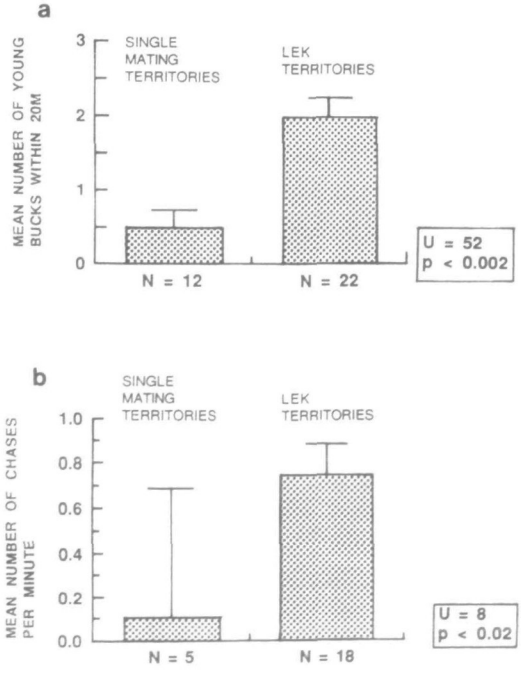

Figure 5
(a) Mean number of young bucks within 20 m of single territories versus lek territories and (b) mean numbers of times (per minute) that bucks defending single versus lek territories chased young bucks.

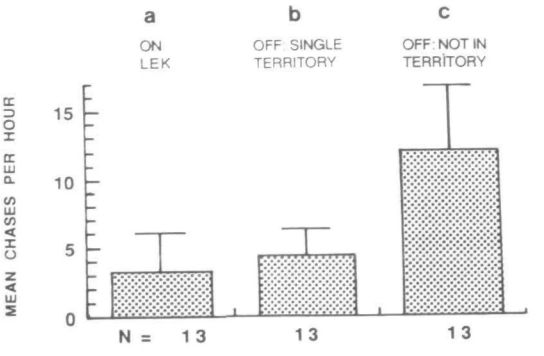

Figure 6
Mean rate (per hour) at which estrous does were chased by young bucks (a) before being herded off the lek, (b) after being herded off the lek when in an isolated single territory and (c) when not in a buck's territory. Extending lines show SEs. Sample based on 13 does observed in each condition.

off the lek (Wilcoxon matched-pairs test, $T = 6$, $N = 13$, $p = .05$), and there was no significant difference in the frequency of chases on the lek versus single territories.

Does that were being chased usually ran to the nearest territorial buck. Because of the clustering of territories on the lek, chases on the lek were shorter than those involving does outside territories or on single territories. Of the 14 chases starting on the lek whose length we were able to estimate, none exceeded 50 m in length, and their average length was less than 10 m, whereas more than half of the 28 chases starting off the lek exceeded 50 m ($\chi^2 = 4.99$, df = 1, $p < .05$). Of these chases, the mean length was 187 m ± 82.8, though this must have underestimated their actual length because the farther a doe was chased, the more likely we were to lose her during the course of the chase.

In more than half of these experiments, does herded off the lek ran in a circle and returned to the lek in less than 10 min. In 4 of the 20 experiments, does that were being chased by young bucks came to a halt and mated with one of the juveniles chasing them—an event we had never seen previously.

DISCUSSION

Our analysis shows that fallow bucks defending clustered territories gained substantial benefits from the ability of the lek to retain does in estrus. At Petworth, both lek and single mating territories were frequently disrupted by intrusions by young males and, in the ensuing melee, bucks commonly lost their entire harems. On the lek, harassment by young males rarely led to estrous does leaving the lek altogether, and bucks holding territories there quickly regained does as other territories were disrupted in their turn. In contrast, when isolated, single territories were disrupted, does were quickly chased far away and bucks rarely regained estrous does the same day. In this study, it was not possible to determine to what extent does that were chased out of a lek territory remained on the lek by preference and to what extent they did so merely because they tended to move to neighboring territories.

Intrusions by young males appeared to be one of the principal causes of the frequent movement of does between mating territories in our study population. Intrusions into mating territories are probably less frequent in lek-breeding ungulates where density is lower, though other factors, including overenthusiastic courtship by resident males and disturbance by predators, may cause females to move between neighboring territories. As we show in a subsequent paper, the rate at which females move between male territories does not need to be high to generate a benefit to males that hold territories in clusters if females usually move between neighboring territories (Stillman et al., in press).

The risk of harassment by multiple males may also help to explain why females in estrus leave the unstable herds that they usually live in. All lek-breeding ungulates live in unstable herds where there is probably no consistent dominance hierarchy among males, who are consequently unable to provide effective protection for females in estrus. Attempts by receptive females to mate within herds are commonly disrupted (Nefdt R, unpublished data), and harassment of this kind is probably dangerous. In other ungulates, there is evidence that females go to considerable lengths to avoid circumstances where they can be courted simultaneously by multiple males (Clutton-Brock, 1989; Clutton-Brock et al., 1988; Rubenstein, 1986; Rubenstein and Wrangham, 1986). By entering a mating territory, estrous does can escape from the intense harassment that they suffer outside territories. Though intrusions by young bucks are more common for lek territories than for single territories, does on the lek can easily escape intruding males by running to the next territory, and chases are short, whereas chases involving does from single territories are likely to be long. A similar difference in the length of chases on and off leks has been found in Uganda kob (Balmford, 1990).

There are at least three functional reasons why estrous females, after leaving their original herds, might be attracted to leks. First, females might be attracted to leks because they contain important resources (Bradbury, 1981; Bradbury and Gibson, 1983). However, both in fallow deer and in Uganda kob, a disproportionate number of females visiting leks are in or close to estrus, and females in this condition spend relatively little time feeding (Balmford, 1990; Clutton-Brock et al., 1988). Although in both species leks are usually located close to areas heavily used by grazing herds, leks are not always sited in areas of

maximal use. In addition, experimental manipulation of resources on fallow deer leks has no obvious effect on the distribution of does (Clutton-Brock et al., 1988).

A second reason for the attraction of receptive females to leks is that they may gain direct or indirect benefits from the opportunities that leks afford for mate choice (Alexander, 1975; Balmford, 1991; Bradbury, 1981, Bradbury and Gibson, 1983; Kirkpatrick and Ryan, 1991). Male mating success is correlated with behavioral and morphological traits in fallow deer and Uganda kob (Apollonio et al., 1989; Balmford, 1990; Clutton-Brock et al., 1988), and differences in male success persist when female preferences for particular territories are controlled for (Balmford, 1990; Clutton-Brock et al., 1989). However, there are empirical reasons for questioning whether females move to leks to select mating partners. If females moved to leks to select mates, females might be expected to be more likely to copulate on the lek than on single-mating territories. However, copulation rates per doe/hour do not differ significantly between the lek and single-mating territories (copulations per doe/hour = 0.167 and 0.120, respectively, $N = 2512$ and 1480 doe/hours, NS). In addition, if does visit the lek to choose mating partners, one might expect that they would be more likely to copulate with successful males, but the number of matings achieved by different bucks is proportional to the amount of time does spend in their harems, and copulation rates per doe/hour are no higher when does are in the harems of successful versus unsuccessful bucks (see Table 1).

A third reason why receptive females might be attracted to leks is that leks are probably the safest places to mate (see Wrangham, 1980). As we have already described, estrous does on the lek are seldom chased far and can easily escape from intruders into neighboring territories. Similar differences in chase length on and off leks have been found in Uganda kob (Balmford, 1990). Where predators are present, females that have left their usual herds may also be safer from predators on the lek than on single territories (Gosling, 1986), though, as yet, there is no direct evidence of the relative susceptibility of female ungulates to predation when on single versus lek territories (see Balmford and Turyaho, in press).

Further investigations of why females are attracted to leks are needed. In the past, studies of the evolution of leks in mammals have commonly assumed that receptive females are attracted to leks to choose mating partners and that female preferences for mating on leks provide the principal reason why males benefit from defending clustered mating territories (see Kirkpatrick and Ryan, 1991; Wiley, 1991). We believe that both assumptions should be questioned. As this study shows, clustered mating territories may have substantial advantages to males that do not depend on female preferences for mating on leks, and receptive females may be attracted to leks for reasons other than the opportunities that they provide for mate choice. Unequivocal evidence of female preferences for mating with particular phenotypic categories of males is not yet available in lek-breeding mammals, and the extent to which female preferences are responsible for generating differences in male mating success is not yet known. Finally, even clear evidence of female preferences for particular male phenotypes (e.g., Höglund et al., 1989) would not exclude the possibility that receptive females are attracted to leks for some other reason. Once females are on the lek, the costs of mate choice are likely to be low, and it would be surprising if some preference did not evolve (Reynolds and Gross, 1990).

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