Etología, 2: 83-90 (1992)

Lekking in red deer? - A comment on the concept of lek

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ABSTRACT. *Lekking in red deer? - A comment on the concept of lek.*- A case of clustered, small mating territories of rutting red deer (*Cervus elaphus hispanicus*) is described. The assembly could be called a lek by following the current definition of the term, and would be the first case described for this species. Nevertheless, it would be too confusing to call it a lek because some components of both resource defence and lekking are involved. The case is used to review the current concept of lek and to propose a way of agreement in the use of the term.

KEY WORDS. Lekking, resource defence, mating, territoriality, red deer, *Cervus elaphus*.

Introduction

Lekking is considered a highly specialized mating system in which males congregate on display grounds, defending small individual territories where females obtain neither resources nor parental care (Bradbury, 1977, 1981; Emlen & Oring, 1977). Lek-like situations have been described for a wide variety of taxa (reviews in Bradbury, 1985; Bradbury & Davies, 1987; Krebs & Harvey, 1988; Höglund, 1989; Balmford, 1990).

With more information available about mating strategies for species and populations, the dynamic nature of mating systems has become quite clear. In the Cervidae, recent studies have shown the existence of previously unknown mating strategies such as territorial resource defence in sika deer *Cervus nippon* by Miura (1984) and in red deer *C. elaphus* by Carranza et al. (1990), and several other mating strategies including different lekking situations in fallow deer (*Dama dama*: reviews in Apollonio, 1989 and Langbein & Thirgood, 1989). Lekking has also been recently described for sika deer (Bartos et al., 1990; Balmford et al., in press). The cluster of territories presented here for red deer fits the current definition of the term lek, and would be the first case in this species. Nevertheless, the proper assignment of the term lek may be more complicated than would seem at first sight. An example from red deer is used here as a starting point for a discussion on the concept of lek.

Methods

The study area was located in Sierra de San Pedro (Cáceres - Spain). The typical vegetation cover is pastureland with scattered oaks (*Quercus rotundifolia* and *Q. suber*) and some areas of scrub (*å*, etc.). The area was visited at the peak of the rut in 1990, and observations were focused on a particular zone where a number of male territories were concentrated. Males can be individually recognized on the basis of the shape of their antlers. There focal-group data on male interactions at the territory boundaries were recorded, together with scan-sampling data for female behaviour, number of females per male, etc., and focal data on roaring rates.

The presence of a territorial male was recorded on the basis of both his defence of the area, and the restriction of his courtship behaviour towards females within territorial boundaries (Carranza et al., 1990). Three types of 'territorial' activities were considered: 1) gathering females; 2) threatening males when there were females in the territory; and 3) threatening males with the absence of females on the territory. This last case is of crucial importance to differentiate the actual defence of the terrain from any eventual defence of a 'space' around a harem.

Results and Discussion

Figure 1 shows the distribution of territorial males in the observed area. The males were highly clustered, in the densest aggregation of territories ever described for red deer. Males defended very small territories, maintaining only 50-80 metres between neighbouring males. Territories were defended against occasional intruders (roving young males) and neighbouring males even in the absence of females inside, and owners did not pay any attention to females outside territorial limits (fig. 1), these being the criteria considered in describing territoriality in red deer (Carranza et al., 1990).

Let firstly consider the territories 9 to 35. Females did not obtain resources inside them (only 12.3% of females engaged in feeding activities in the territories vs. 71.0% outside in feeding areas; test of comparison between percentages $p<0.001$). In fact the soil there was completely bare and dusty. Territorial males maintained a basal roaring rate of 2.6 roars per minute in the absence of females, and increased the rate when with females in the territory (mean: 6.2 roars per minute, $p<0.001$, Mann-Whitney U-test). The situation appears to correspond to a lekking system.

Moving on to consider the whole assembly of territories, there is an obviuos reason for the location of territories numbers 1 to 8, which are in an artificial feeding area. Resources are scarce at the end of the summer in Mediterranean ecosystems, and many estates provide deer with extra feed at this season, which includes the rut. On such feeding sites, one commonly sees (pers. observ.) the establishment of territorial males defending an area which concentrates a high number of females every day at the moment when the feed is delivered. In the present area, the density of deer is very high (about 0.7 deer per hectare), and during the artificial feeding an area as small as 4 ha. concentrates about 500 animals. Deer came to the feeding area along several main paths which roughly follow smooth stream beds leading to the site. Typically, territorial males did not go to feed but remained on their territories. After 20-30 minutes of feeding, females and young males started leaving the feeding area back along the same paths. The movement of female groups along these paths, passing through several territories, caused a wave-like variation in the activity of territorial males. Each one tried to keep the females within his territory and interacted with neighbouring males at the boundaries. There were two kinds of territories: i) at the feeding area (numbers 1 to 8), and ii) along the main paths leading to the feeding area (the remaining territories).

The circular line at the top of figure 1 indicates the track on which a vehicle spread the feed every day. The other three lines show approximately the main routes used by females moving to and from the feeding site. Territories at the feeding area are clearly placed on the site of resource concentration, this being therefore a case of resource defence. But what about the remaining territories? Females would probably pass along the main routes attracted by the feed irrespective of the presence of territorial males. In this example we see a case in which some of the territories contain food resources, and the remainder do not, even though their location is also explained by food resources. Should this assembly of territories be called a lek or is it rather a case of resource defence?

There are several recent examples in the literature about ungulates where the location of what is described as a lek can be explained by routes of female

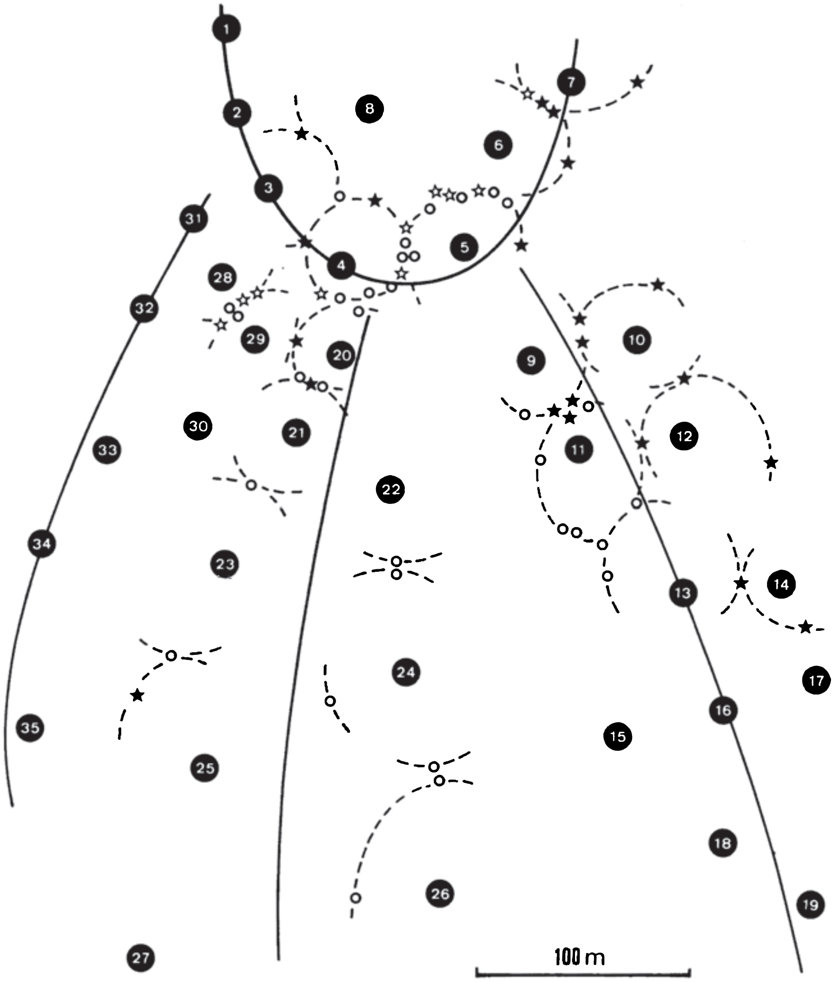

FIGURE 1. Location of territorial males. The circular line at the top indicates the track on which a vehicle spread the feed every day. The other three lines show aproximately the main routes used by females moving to and from the feeding site. Interactions at the territory boundaries: ○ towards females, ☆ towards males when females were on the territory, ★ towards males when females were absent from the territory.

[Localización de los machos territoriales. La linea circular en la parte superior indica el camino por donde un vehículo distribuía cada día la comida. Las otras tres líneas muestran aproximadamente las principales rutas utilizadas por las hembras en sus desplazamientos hacia y desde el lugar de alimentación. Interacciones en las fronteras entre territorios: ○ hacia hembras, ☆ hacia machos cuando había hembras en el territorio, ★ hacia machos cuando las hembras estaban ausentes del territorio.]

traffic independently of the presence of the males (e.g. fallow deer: Apollonio et al., 1990), or places where females cluster for anti-predator reasons (e.g. topi *Damaliscus lunatus*: Gosling & Petrie, 1990). Moreover, this has been one of the classical hypotheses for understanding lek placement based on the clustering of males near "hotspots through which the largest number of females are likely to pass" (Bradbury & Gibson, 1983). There might seem to be a paradox between the hotspot model for lek placement and the main feature of a lek that "females only go there for the purpose of copulation". However, the paradox is solved - as Bradbury (1981) and Bradbury & Gibson (1983) note - if we consider two separate kinds of question, i.e. one concerning lek formation and placement, and the other concerning the distribution of matings among territories in the lek. If resources are involved in the first but not in the second questions, the situation would still be different from resource defence with respect to the role of sexual selection.

One first question regarding the use of the term lek is whether it should be restricted to a particular kind of mating system or not. Early definition of lek mating (Bradbury, 1977, 1981) restricts the use of the term to such cases where: a) there is no parental care, b) there is an arena or lek where males congregate, c) the display sites of males contain no significant resources required by females, and d) the female has an opportunity to select a mate. Later on, Bradbury (1985) reviewed lek breeding in insects and vertebrates, and proposed using the term less restrictively. The idea was to represent mating territories by points in a four-dimensional space with the former conditions as continuum variables. Opinions may differ on which part of such a four-dimensional space may be referred to as lekking, from the whole space to only one extreme point. This semantic question may be of importance because one can find this term used differently in the literature. There are studies in which the use of the term lek tends to be restrictive in some of Bradbury's variables but not in others. Most authors agree with the absence of parental care as a prerequisite for lekking. The question of the resources involved is not so clear. Alexander (1975) coined the term resource-based leks, as against non-resource-based leks. In both cases the males are clustered, but they differ in whether the females obtain resources from the male territories or not. It seems that resource-based leks may be better referred to as resource defence polygyny (Emlen & Oring, 1977). Other studies suggest that the role of resources in determining the success among territories varies continuously and it is artificial to impose a boundary between the two extremes (Leuthold, 1966; Bradbury, 1985). Nevertheless, most studies focusing on particular questions about lek evolution assume that females only obtain "genetic benefits" from leks (Gibson & Bradbury, 1983; Krebs & Harvey, 1988; Kirkpatrick & Ryan, 1991; among others).

As referred to above, resources may determine why females go to the lek while not influencing the distribution of females among territories within it. Clutton-Brock (1989), reviewing mammalian mating systems, sets those cases where the clustering is related to some kind of resources (including food, movement routes and antipredator protection), but in which the resources do not influence the distribution of matings among territories, as intermediate between resource defence and classical leks. This resembles the idea of some axis along a gradient of resource influence. Bradbury (1985) also considers an axis of this kind, but the agreement is not complete. To Bradbury, variation along this axis would reflect the degree to which the males' control over the resources influences the distribution of the matings; so, whether the location of the whole assembly is related to any resources or not would not move the point along the axis.

Another component to deal with, according to the four-dimensional model of Bradbury (1985), is the degree of male clustering. The Swedish word 'lek' was originally taken to refer to a cluster of male territories; in the same way, the Spanish word 'arena' also refers clearly to the place or theatre where the action takes place. Nevertheless, the degree of clumping is highly variable from the classical leks to the exploded leks (Bradbury, 1981; Oring, 1982; Bradbury & Gibson, 1983; Bradbury et al., 1986).

This leaves the fourth feature: the degree of free choice by females. It is expected that females are able to choose a mate freely in leks - i.e. when no resources influence the mating decision. Nevertheless, taking this as a condition for using the term is highly impractical. Firstly, most studies failed to prove actual choice (see Bradbury & Davies, 1987; Krebs & Harvey, 1988), and secondly, the influence of male activities (forcing, disruption, etc.) further confounds the issue (Bradbury & Gibson, 1983; Foster, 1983; Clutton-Brock, 1989).

At this point there are two options. Firstly, the term lek can be considered in a broad sense, for all kinds of mating territories, as proposed by Bradbury (1985). In this case it could be out of place to seek questions about the evolution of lekking, since they would not be different from questions about the evolution of mating territories. The term would become meaningless. Secondly, it could be restricted to the sense it takes in most papers on sexual selection in leks. This may not imply a restriction in all four components, but only in those a priori considered to affect sexual selection and which differentiate lekking from others, already described, mating systems. It seems that most authors agree to use the term lek to mean those cases where there are almost no resources determining the distribution of matings among males, although they realize that it may be artificial to set a boundary. They are more flexible with respect to male clustering and female choice, although it is likely that female choice is related to the absence of resources. These are the cases which lead to the 'paradoxical' evolution of males' odd features used in attracting females. The distinction seems to be important to understand their evolution, because sexual selection can drive it in a different direction - and probably is less intense (see Payne, 1984 and Höglund, 1989 for birds) - when resources are involved in mating decisions.

But even if an agreement is reached in the use of the term lek when resources are few or nil, another controversial problem still remains: the meaning of 'resources'. It typically means food resources, but other kinds of 'resources' may also produce the same effect with respect to the conditions under which sexual selection can operate. For example, a main route (to food, water, rest sites, etc.) can attract as many females as a feeding point. Oviposition or nesting sites (e.g. Howard, 1978; Cartar, 1988), or places for antipredator protection (e.g. Gosling & Petrie, 1990), may also be examples of "resources" which can gather females at an area defendable by males. Again, the important question is whether the resources of this kind affect the distribution of females among territories in the assembly. Two aforementioned ungulate examples fall into both cases: 1) territories of topi (*Damaliscus lunatus*) at Mara Game Reserve are situated in an area of antipredator protection, but within which differences in the mating success cannot be explained by differences in the degree of protection (Gosling & Perie, 1990); 2) territories of fallow deer Dama dama at San Rossore, in which the relative success among territories depends on the proximity to the paths used by females for purposes other than mating (Apollonio et al., 1990). If food, routes to food, antipredator protection, etc., are considered as a type of resource, the topi example would be called a lek but not that of the fallow deer - although other populations of fallow deer have "true" leks where mating success has been proved to be related to males' features regardless of the site (Clutton-Brock et al., 1988, 1989).

From this viewpoint, both the defence by males of a resource territory or a route to resources, and insect nuptial gifts or spermatophores, would depart from the conditions for lekking, since every female visit would decrease the male's attractiveness for the following female by depleting the "resources" on which such attractiveness is based. The process here would be better approached by following some model of resource defence (e.g. Orians, 1969; Parker, 1978).

Returning now to the case of red deer presented here, there are as yet no measurements of relative success among territories. So, it is important to stress that the discussion is speculative, but the case could be used to illustrate the general point. Territorial males situated along the various routes used by females can expect to have a higher rate of encounters the nearer they are to a main route. Therefore, the distance to a main route would be one component factor which could explain differences in success among territories. But now let's consider the territories placed exactly on a main route (distance = 0). As almost all the females using this route will pass through all these territories, this probably enables them to choose one of the males to mate with, without any reason related to resources. In this sense two components in the varying success among territories can be imagined: 1) the distance to the nearest main route (e.g. territories 15, 16 and 17; fig. 1), which could be related to resource defence (i.e. resource control under male-male competition), and 2) the position along the main route (e.g. territories 9,11,13,16), which could be related to a male's characteristics but have no effect on the resources obtained. In other words, mate choice among territories distinguished by the first component would involve a cost of leaving the main route (which, although probably very small in the present case, may not be so in others). There would be no cost, however, for the second component, which would be typical of a lek situation - i.e. females enter the zone because it is on a main route (hotspot theory), but there are neither resources nor parental care which might determine an eventual choice among territorial males. Furthermore, one may wonder about the differences between various main routes: these differences could be mainly resource-based ones if there were different intensities of female traffic. Finally one may also wonder about differences among territories situated along a line parallell to a main route: these would be lek-like as they are equal with respect to control of resources (i.e. proximity to the main route), and therefore eventual differences in mating success can be due to female choice. So, as it can be seen, the situation in this example may be quite complex and it would be too confusing to call it a lek. Therefore I would call it simply an assembly of mating territories, realizing that it may have some components of both resource defence and lekking.

A mating assembly can have very different origins. We need to introduce some factor which can unite the situation in functional terms, and thus allow for comparisons in a search for the adaptive explanation or consequences of lekking (e.g. Krebs & Harvey, 1988; Apollonio, 1989; Höglund, 1989; Langbein & Thirgood, 1989). This factor could be the variance in the mating success among males, which cannot be explained by differences in the resources obtained by females. And there needs to be agreement in the way any form of 'resource' -such as food, routes to food, ovoposition or nesting sites, anti-predator protection, etc.- is considered when it plays a similar role in sexual selection.

Acknowledgements

I would like to acknowledge the helpful comments of J. Bradbury, L.M. Gosling, T.H. Clutton-Brock, A. Balmford and M. Festa-Bianchet. Juliana Valencia helped in field observations. Financial support came from Project PB 87 - 0316 DGICYT.

Resumen

Lekking en el ciervo? - Un comentario sobre el concepto de lek.

Recientes estudios han puesto de manifiesto la gran flexibilidad de los sistemas de apareamiento en ungulados, habiéndose descrito nuevas estrategias para especies tan bien conocidas como el gamo o el ciervo. El aumento en la información sobre distintas poblaciones, incluyendo diferentes estrategias de los machos, hace necesario revisar las definiciones sobre las que basamos la clasificación de los sistemas de apareamiento. El sistema tipo lek es probablemente el de orígenes menos claros, y uno de los que más estudios han producido, encaminados en su mayoría a esclarecer las causas ecológicas, sociales, etc. que provocan su existencia. La precisión en el uso del término lek no es una mera cuestión semántica, ya que la experiencia demuestra que la inclusión dentro de esta categoría de sistemas de apareamiento de diferente origen impide el éxito de los trabajos que, basados en la comparación entre poblaciones, pretenden dilucidar las causas adaptativas de la aparición de los leks.

En este artículo describimos un caso de territorialidad de machos de ciervo durante el período de apareamiento. Los territorios en el área observada eran extremadamente pequeños para esta especie (unos 50 m de diámetro) y la agregación de territorios era la más numerosa y densa jamás descrita para el ciervo. La mayor parte de los territorios no poseían ningún recurso en su interior, con lo cual podría considerarse que formaban un lek de acuerdo con la definición actual del término, y sería el primer caso para esta especie. No obstante, algunos de los territorios esta-

ban situados en la zona donde diariamente se proporcionaba alimento artificial. Estos territorios responden a un sistema de defensa de recursos, pero además explican la presencia de los demás territorios situados en las zonas de paso hacia el área de alimentación. Dado que unas zonas de paso pueden ser mejores que otras por razones ecológicas, topográficas, etc., serán utilizadas por las hembras con distinta intensidad, lo cual puede afectar al éxito de los machos que defiendan territorios en ellas.

Basándonos en este caso, y en otros en la bibliografía en los que se llama lek a conjuntos de territorios situados en zonas de paso hacia áreas de alimentación, proponemos que el término lek se utilice para aquellos casos en los que la varianza en el éxito reproductivo de los machos territoriales no pueda explicarse en base a diferencias en el uso que las hembras hacen de la zona independientemente de la presencia de los machos.

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(Recibido: 24 febrero 1992)