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The impact of lekking on the spatial variation in payoffs to resource-defending topi bulls, *Damaliscus lunatus*

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In mating systems research it is often ignored that the spatial relationship between individuals adopting alternative mating tactics may influence the intensity of their interactions and therefore also their tactical payoffs. I here take a novel approach to investigating the coexistence of lek territoriality and resource territoriality in male topi antelopes by including territorial distance from a lek centre as a continuous variable. Using the body size of territory holders as a proxy for territorial payoffs, I show that the attractive force of lek centres impact negatively on payoffs from surrounding territories only within an 1800 m radius. Thus, lek males are significantly larger than resource defenders inside, but not outside, this impact zone. The impact zones encompass the ranges during oestrus of 91% of the females mating on leks, and because female topi are highly promiscuous, the impact zone corresponds roughly to the area within which resource territorial males experience sperm competition with lek males. These results can be explained by a preference of oestrous females for mating with central males inside, but not outside, the 1800 m zone. The study illustrates how taking spatiality into account can reveal significant differences in tactical payoffs within behavioural categories that are traditionally regarded as uniform.

Keywords: alternative mating strategies; *Damaliscus lunatus*; lekking; mate choice; sexual selection; territoriality; topi; ungulates

Several studies have highlighted how the payoffs of alternative mating tactics may depend on the frequencies in which they are found in a population (e.g. Maynard Smith 1982; Sinervo & Lively 1996; Shine et al. 2005). However, it is often overlooked that also the continuous spatial distribution of individuals adopting the alternative tactics is likely to have a profound effect on tactical payoffs if proximity enhances the intensity of interaction. In lek-breeding species of ungulates, males either defend small lek territories void of resources or larger territories containing significant resources; both tactics are aimed at securing matings with nonterritorial, group-living females (Gosling 1986; Isvaran 2005). Research into the game-theoretical basis for coexistence of these alternative male territorial tactics has so far concentrated on comparing payoffs between lek males and resource defenders, treating these as discrete categories (e.g. Gosling et al. 1987; Balmford & Turyaho 1992; Nefdt & Thirgood 1997) and/or comparing payoffs within lek males only (e.g. Clutton-Brock et al. 1989; Apollonio et al. 1990; Isvaran & Jhala 2000). In contrast, variation in payoffs within resource defenders has been neglected. To address this issue, I here take a novel approach to clarify the coexistence of resource and lek territoriality in male topi antelopes by analysing spatial variation in territorial payoffs as a continuous function of the territorial distance to a lek centre.

The ranging patterns of receptive females are widely believed to be crucial in determining the spatial distribution of males and hence the payoffs of male territoriality (Ims 1988; Clutton-Brock 1989). In topi, females are known to concentrate on leks when they come into oestrus (Bro-Jørgensen 2003b), a pattern that can be attributed to a preference for mating on leks rather than efforts to avoid harassment or predation (Bro-Jørgensen 2002). Once on leks, females have been shown to prefer central males as mating partners (Bro-Jørgensen 2003a). Thus in topi, the two separate questions of why females

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move to leks and which factors determine their mating patterns on leks (Clutton-Brock et al. 1996) can both be answered by a preference for mating with central lek males. However, how this female mate preference in topi affects the spatial variation in territorial payoffs within resource-defending males has been obscured by the treatment of resource defenders as a uniform category in previous studies (Gosling & Petrie 1990; Bro-Jørgensen & Durant 2003).

I here test two alternative hypotheses on the impact of leks on the spatial variation in territorial payoffs. One possibility is that the preference of oestrous females for centrality is all-important in determining territorial payoffs in which case payoffs are predicted to decline monotonously with lek centre distance throughout the population range. Alternatively, it may be hypothesized that if only the subset of oestrous females mating on leks shows the preference for centrality, then it is only within the range of these females during their oestrus that territorial payoffs are positively related to centrality. I use the body size of territory holders as a proxy for territorial payoffs, building on the assumptions that (1) male competitive ability correlates positively with body size (e.g. Davies & Halliday 1977); and (2) the intensity of competition for a given territory depends on its likely payoffs (Gosling & Petrie 1981).

A lek is defined as 'an aggregated male display that females attend primarily for the purpose of fertilization' (Höglund & Alatalo 1995), and to determine spatial patterns in territorial payoffs relative to leks, it is necessary first to clarify whether the less contracted ('weak') territorial clusters, which are observed alongside classical leks in topi, qualify as 'exploded leks' (Emlen & Oring 1977). Exploded leks share the properties of classical leks, only the degree of aggregation is less spectacular. Since the critical feature distinguishing territorial clusters as leks is that male mating success is not explained by resource availability, I predict that if the weak territorial clusters in topi are, indeed, exploded leks, male mating success will be uncorrelated, or correlated negatively, with resource availability. Furthermore, I would expect any exploded leks in topi to share the characteristic of classical topi leks that male mating success is highest in the lek centre (Bro-Jørgensen & Durant 2003).

METHODS

Study System

The data were gathered from a 300 km^2 study area within the Masai Mara National Reserve and the Olare Orok Conservancy in Kenya over two periods, 1998–2000 and 2004–2006. The landscape is generally open savannah with good visibility. The population of topi in the study area was estimated at 2000–2500 individuals. Adult male topi are highly territorial, territorial tenure being all-important to achieve reproductive success (Bro-Jørgensen 2003a). Females, whose home ranges average at least 50 km^2 (Bro-Jørgensen 2003b), come into oestrus during a rut which lasts around 2 months and takes place between January and May, the exact timing depending on rainfall (Bro-Jørgensen 2001). During their oestrus, which usually last less than a day, individual females typically mate repeatedly with several males (Estes 1991; Bro-Jørgensen 2001). Oestrous females visiting leks may arrive either in groups with anoestrous females or alone.

Territorial Mapping

Topi were recognized individually from combinations of natural marks, primarily horns, ear nicks, coloration, and scars; the reliability of identification was confirmed independently by repeatability of size measurements (see later). Using a Garmin GPS receiver, the positions of males showing territorial behaviour (i.e. marking, intrasexual aggression, mating display and herding) were recorded while driving regular transects covering the entire study area. The territorial boundaries were identified based on resightings and boundary encounters between neighbouring males.

Based on the map of territories, territorial clusters were defined as territorial mosaics within which territory size showed a decreasing trend towards a centripetal point, the cluster centre. Altogether seven clusters were identified, the centres of which were separated by a minimum of 3000 m. Four of the clusters were 'classical leks' with minimum territory sizes of 0.135, 0.145, 0.165 and 0.245 ha, while three were 'weak clusters' with minimum territory sizes of 0.670, 1.05 and 1.39 ha. I use the term 'clusters' to refer to classical leks and weak clusters collectively. 'Centrality' of a male's territory was defined as the minimum distance from the territory to a cluster centre, measured as a nonpositive value, and for the 539 males sampled, it ranged between 0 and 6740 m with the median at 374 m. Lek males are here defined relative to resource defenders as males who defend a territory which is at least partly situated within a 400 m radius of a lek centre. The relative proportion of territorial males in each territorial category within the study area is roughly reflected in the sample sizes given in the results.

Resource Availability

Topi select green grass blades (Murray & Brown 1993) and territorial resource availability was therefore assessed by measuring a green leaf index following Balmford et al. (1992). On 25 random sites within each territory, a polystyrene tile (21 × 21 cm) weighing 25 g was left to rest on the grass and the following three measures were taken: greenness (the proportion of the four leaves closest to the corners of the quadrate which was scored as green rather than withered), grass cover (cover under the translucent tile estimated to the nearest 5%), and sward height (the distance from the ground to the centre of the tile). By multiplying the three measures and taking the mean of the 25 products, an index of food availability, the green leaf index, was calculated. Altogether 18 territories in one weak cluster were sampled during December 1998.