

Comparison of reproductive success in fallow deer males on lek and single temporary stands

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Abstract. Lek is a territorial mating strategy which is widely spread amongst males in the fallow deer, *Dama dama* high density population. A group of fallow deer in Březka park, Czech Republic, was studied where males exhibit a mixed mating system with territorial (single temporary stands, leks) and non-territorial strategies during the rut. Reproductive success was estimated indirectly by counting females/minute held per male both on the lek and single temporary stands. A total of 636 records were analysed (281 on leks and 355 on temporary stands). In contrast to other reports, males on leks were accompanied with significantly less females (LSMEANS \pm S.E., 3.80 ± 1.10 does present per minute of observation) compared to those on single temporary stands (6.74 ± 1.10 does present per minute of observation). The results suggest that under specific conditions (over-abundance of adult males compared to females) attracting females on the lek need not be the most effective one.

Key words: lek, reproductive success, rutting behaviour

Introduction

This communication is a supplement to the parallel publication (Fričová et al. 2007) dealing with bucks' encounters and presence of females.

Plasticity of mating strategies during the rutting season is rare in fallow deer (Schaal & Bradbury 1987, Clutton-Brock et al. 1988, Langbein & Thirgood 1989). The only other deer species similarly adaptive in mating is sika deer, *Cervus nippon* (Balmford et al. 1993, Bartoš et al. 1998, 2003). In fallow deer, males can adopt different mating strategies even within one mating system. There is a broad scale of territoriality in rutting bucks: from non-territorial males on one side through single stand holders to defenders on the multiple territories on the other side. In the terminology of Langbein & Thirgood (1989), observed males adopted both nonterritorial (harem holding, following group of females) and territorial (temporary stand, multiple stand and lek) tactics. Harem and following were not included in this study. Individual territorial tactics when more than one rutting buck aggregate on a short distance from each other are difficult to distinguish. Therefore, any situation when two and more bucks defended reproductive territories which did not preserve the geographical separation from neighbours

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(Langbein & Thirgood 1989) was considered as a lek. For the purpose of this study we recognized two tactics: lek and temporary stand.

Lek could be characterized as a cluster of small territories, which do not contain food resources and are visited by females for the single purpose of mating (e.g., Bradbury & Gibson 1983, Schaal 1986, Clutton-Brock et al. 1988). In fallow deer, leks were observed mostly in high-density populations (Clutton-Brock et al. 1988, Langbein & Thirgood 1989), although high male density is one of the major factors, other factors such as environmental heterogeneity and resource distribution may determine lekking behaviour (Apollonio 1989).

Leks exhibit greater variance in male mating success than expected by chance (Mackenzie et al. 1995). Joining lek offers high potential benefit for a few males (Apollonio et al. 1989). With exceptions (e.g., Apollonio et al. 1989), within the lek, usually central males have higher mating success and face higher costs than peripheral males. While central males invest heavily in lekking, peripheral males try to gain central territories in blackbuck, *Antilope cervicapra* (Isvaran & Jhala 2000).

In lekking populations, males may also adopt alternative mating tactics (Clutton-Brock et al. 1988, Apollonio et al. 1992). In that case, comparisons between alternative tactics have shown that lekking is a high cost-high benefit strategy (Apollonio et al. 1992). As shown by Clutton-Brock et al. (1988), mating success was higher on leks than on isolated territories. Equally, the majority of copulations occurred on leks rather than on single territories, because oestrous females tended to visit lek (Clutton-Brock et al. 1988, Apollonio et al. 1990). Potential male benefits of higher mating rates on lek is believed to be compensated by costs in terms of fighting rates, which are higher than on single territories (Gosling et al. 1987, Thirgood et al. 1999), although Pélabon et al. (1999) suggested spatial stability on lek attenuates aggressions among males. Compared to single-territory defence, lekking is a strategy, which only few males can afford (Apollonio et al. 1992), whilst alternative tactics are chosen by inferior competitors (Apollonio 1998). Consequently, a hypothesis was set in this study that reproductive success would be higher in lekking fallow deer males compared to those defending single temporary stands.

Reproductive success is not easy to determine in natural conditions, notably in populations where the maximum of mating activity occurs in night time. As in the previous study (Fričov et al. 2007), an indirect method of reproductive success measurement was therefore used: number of females in imminent proximity of focal male per minute of observation was calculated for each observed male.

Material and Methods

Observations were carried out in Březka deer park (N49°54', E014°32'), a 2.06 km² park located in Kostelec u Křížk, Czech Republic (property of Forestry and Game Management Research Institute, Jlovišt – Strnady). There were between 100 and 150 fallow deer bucks in the park and approximately 100 adult females during the observation period, which included four rutting seasons (2000 to 2003). As in the parallel study (Fričov et al. 2007) data were collected by several observers. At the beginning and at the end of the rut (first decade of October), observations occurred almost every other day, whilst during the peak of the rut (approximately from 10th to 20th October) observations were conducted on a daily basis.

Observation of the rutting activity took place from 16:00-19:00 when the frequency of activity was highest. Records were taken simultaneously from 1 to 5 hides. The park is closed to the public. Therefore, no human disturbance occurred during the observations. For each focal male, the observers recorded: the date and location, if there was a lek or temporary stand and the proximity of females up to 20 m from the buck (number and duration of sojourn) during three rutting seasons. The data was analysed using the general linear mixed model (PROC MIXED, SAS). 'Number of does present/minute of observation of the focal male' (Number of does) was dependent variable. The fixed effects tested were categorical 'lek' (focal male presented on lek - yes or no) and 'season' (three levels). To account for the repeated measures on the same site, the analysis was performed with the 'Location' as a random factor. Least squares means (LSMEANS) were calculated by computing the mean of each treatment and averaging the treatment means. These means of means are then used to compare the factors. In this way, the means are adjusted for the number of observations in each treatment. This estimate is unbiased because the unequal number of observations is taken into account (Welsh et al. 2000).

Results

In total, there were 636 records analysed (281 on leks and 355 on single temporary stands) from five locations. Number of does present was dependent on if they were observed on a lek or on a temporary stand ($F_{(1,636)} = 6.34, p < 0.01$). Effect of the season was nearly significant ($F_{(1,636)} = 2.48, p = 0.08$) and therefore it was not dropped from the final model. In contrast to expectations, lekking males were accompanied with significantly less females than males on single temporary stands (Fig. 1).

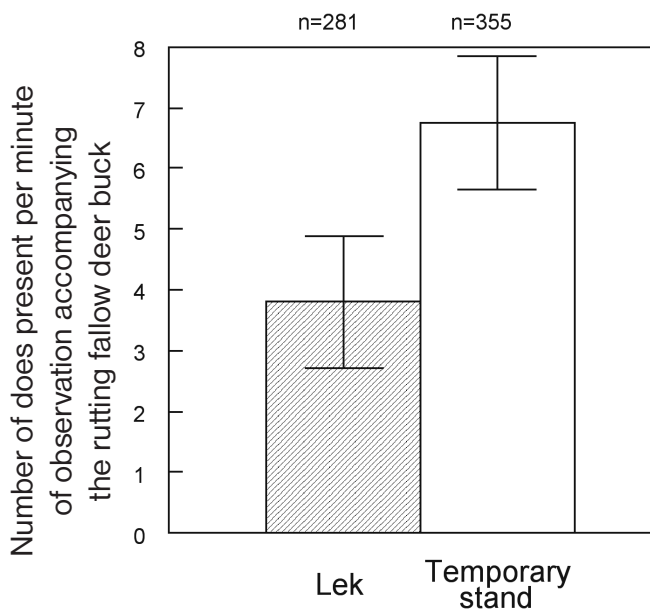


Fig. 1. Number of does present per minute of observation accompanying the rutting fallow deer buck if he was on the lek or on a single temporary stand (Least square means \pm S.E.) with the effect of a season eliminated statistically.

Discussion

Although mating success was described higher on leks than on isolated territories (Cuttone-Brock et al. 1988), our results showed that the number of females in imminent proximity of focal male per minute of observation was significantly lower in the group of lekking males than in males on single temporary stands. This finding is inconsistent both with expectations and with the literature cited above. High population density (particularly adult male density) might support forming of lek in fallow deer (Langbein & Thirgood 1989). Nevertheless, where sex ratio is diverted on the side of males, as was the case in this study, the tactics of lekking perhaps fails to be the most efficient. In general, among lek-breeding populations of fallow deer (and other ungulates), majority of copulations occur on leks rather than on single territories or in mixed-sex herd (Thirgood et al. 1999). But in some populations, males that are unable to defend central lek territories may achieve more copulations on single territories than on the periphery of leks (Gosling & Petrie 1990, Thirgood 1991). In fallow deer populations with a sex ratio strongly biased towards females, lek formation could be difficult because of the lack of mature bucks (Apollonio 1989). In Březka park, the population density was high (over 100 adult animals/100 ha), but there was also noticeable over-abundance of adult males: sex ratio was biased towards males (up to 1:0.67). On this locality, lek was mentioned by Chapman (in Apollonio 1989) already (although during that period the density was only 48.5/100 ha and sex ratio was 1:1). Lekking is thus traditional in Březka park. If mating success was strongly correlated with the number of females in a male's territory (Apollonio et al. 1989), reproductive success in this particular case of high population density and sex ratio biased towards males was higher out of the lek. Either non-territorial strategies or defending isolated territory brought presumably a higher chance of reproductive success to rutting bucks. However, a question remains how accurate is the common method of indirect measurement of reproductive success. Since most matings in the study area occurred during the night (Fričov et al. 2007), it is also possible that by attending the single temporary stands during the day time, the females just avoided harassment from the males outnumbering them markedly.

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