

CHARLES UNIVERSITY, PRAGUE
Faculty of Science
Dept. of Zoology



Ph.D. Thesis

Agonistic encounters of fallow deer (*Dama dama*) males during the rut



Mgr. Barbora Fričová

Supervisor: Prof. Ing. Luděk Bartoš, DrSc.

Praha 2008

AUTHORS´ STATEMENT

Hereby I state that all the co-authors are cited properly and my part on each publication included in this thesis is not lesser than that corresponding to the number and order of the authors. I have not submitted neither this thesis nor any substantial part of it to obtain identical or another academical degree. I agree with public exposure of this thesis in the library.

Barbora Fričová

ACKNOWLEDGEMENT

Although this thesis was written in English, I decided to use Czech for an Acknowledgement, because it sounds more sincerely and nicely to me.

PODĚKOVÁNÍ

Na tomto místě bych ráda poděkovala všem, kteří mi přímo či nepřímo pomohli s realizací mé dizertace.

V první řadě patří můj dík Prof.Ing. Ludřkovi Bartošovi, DrSc., který celý tým vedl. Jeho trpělivost, nadhled a optimismus při překonávání mnohých překážek neznal mezí. Velice si vážím času, který jsem s ním měla možnost společně strávit pozorováním daňků, ale i zajímavými diskusemi nad výsledky a metodikou. Cenné byly veškeré rady, které mi v průběhu času ušetřil. Neméně si však vážím jeho vstřícného, ochotného, přátelského a osobního přístupu ke studentům, který je, žel, v současnosti spíše světlou výjimkou. Děkuji mu také za laskavé zapůjčení obrázku daňků.

Dále bych ráda poděkovala Ing. Jitce Bartošové, PhD., která zvládla brilantně mimo jiné také práci se statistickými výpočty i při současné a nepřetržité péči o své potomstvo, což ve mně vzbuzuje upřímný úžas a obdiv.

Tátovi děkuji za mnohé konzultace, připomínky, knížky a nejen technickou podporu.

Mé poděkování patří také všem lidem z oddělení etologie VÚŽV, kteří pomáhali se sběrem dat, starali se o technické zázemí a zajišťovali logistiku, zejména Pietrovi, Vráťovi, Lídě, Pavlovi, Josému, Jitce, Gudrun, Dominice, Heleně, Iloně, Honzovi a Robertovi.

Zvláštní poděkování bych ráda věnovala Honzovi, který mne soustavně duševně podporoval, s mírnou dávkou ironie toleroval moje stavy beznaděje i hysterie, a přesto mne nepřestal milovat.

Poděkovat chci také svým synům Jakubovi, Matoušovi a Kryštofovi, že mi pokreslili pouze některé separáty, dovolili mi střídat se s nimi u počítače a nepřekročili limitní hranici mého nervového systému. (Nemalý dík patří i společnosti Lego za vynález geniální stavebnice, která dokáže zcela nenásilnou cestou udržet děti celé hodiny v soustředěném klidu.)

Finančně byla tato práce podpořena zejména prostředky doktorského grantu GA ČR (206/05/H012); dále grantem GA AV ČR (IAA6307201) a grantem MZe ČR (MZe 0002701402).

CONTENT

Introduction.....5

1. Bartoš L., **Fričová B.**, Bartošová-Víchová J., Panamá J., Šustr P. and Šmídová E.:
Estimation of the Probability of Fighting in Fallow Deer (*Dama dama*) During the Rut.
Aggr. Behav. 33:7–13 (2007)
2. **Fričová B.**, Bartoš L., Bartošová J., Panamá J., Šustr P. and Jozífková E.: Females
presence and males agonistic encounters in fallow deer, *Dama dama* during the rut.
Folia Zool. 56(3): 253–262 (2007)
3. **Fričová B.**, Bartoš L., Bartošová J., Panamá J., Šustr P. and Chaloupková H.:
Comparison of reproductive success in fallow deer males on lek and temporary stands.
Folia Zool., in press (2008)

Discussion.....15

Literature.....17

INTRODUCTION

Social organization and behaviour in fallow deer (*Dama dama*) varies strongly among different localities. Important factors affecting particular configuration seem to be population density, habitat type, human activity, type of climate, food resources availability and sex ratio (Chapman and Chapman 1975, Clutton-Brock 1989, Apollonio et al. 1989).

Similarly to sika deer (*Cervus nippon*) or red deer (*Cervus elaphus*), fallow deer form herds that transform during the year. Seasonal cycles of social grouping and disintegration are closely related to males antler cycle: except the reproductive period females associate with yearlings and fawns, while males gather in smaller separate groups or live solitary (Chapman and Chapman 1975, Gould & Werts 1979). Adult males are thus separated from females when new antlers develop and when fawns are born, adult sex-mixed groups tend to appear during the rut only. The onset of the rut is daylight dependant. It arises after velvet shedding (August-September in central Europe), culminates in October and runs out in November. Deer groups dissociate during that period. Adult males either defend a territory or move dependently on females in accordance to different mating strategy adopted (Langbein & Thirgood 1989, Thirgood 1991). Females leave the herd and search mating partners.

To prevent and minimize conflicts in adult ungulates, assessment of social relationships among all animals is fundamental. In adult fallow deer males (bucks), the hierarchy is complicated and may change distinctly during the year.

As for a male's territoriality, we can find three different types of strategies in Cervidae. To compare native examples, red deer is non-territorial species, whilst roe deer (*Capreolus capreolus*) is strictly territorial during extended part of the year and fallow deer represents the last strategy type: it may be territorial, but only during the rut.

In different ungulate species, divers repertoire of behavioural pattern could be found which males use to maximize their reproductive success. In contrary, females ungulates spend maximum of time selecting mating partner before copulation. Most of fallow deer females copulate once per breeding season (Clutton-Brock et al. 1988). Plain behaviour of females is in contrast to striking males behaviour during the rut. This is because females have to invest heavily into both prenatal and postnatal development of their offspring, whilst males' investment terminates by successful copulation. Energetically strenuous and exhausting

mating behaviour of males partly balances biased distribution of parental investment. Reproductive behaviour in fallow deer bucks includes above all harem or territory defence, scent marking (Stenstrom et al. 2000), vocalization (groaning) and chasing non-territorial bucks away (Apollonio et al. 1989).

Plasticity of mating strategies during the rutting season is outstanding in fallow deer (Schaal & Bradbury 1987, Clutton-Brock et al. 1988, Langbein & Thirgood 1989). Bucks can adopt different mating strategies even within one mating system. Besides, during a single rut, bucks can maximize their fitness by switching among different tactics according to changes of benefit-cost proportion (Hirth 1997). Huge capacity of relatively quick switches of mating tactics in fallow deer is in opposite to e.g. red deer, where tactics of adult males are not mixed. Fallow deer bucks can, for example, may adopt territorial tactic at the beginning of the rut, while non-territorial in the end of the rut. Such shift in mating behaviour from territorial to opportunistic following was associated with a decline in the availability of oestrous females (Hirth 1997). In general, we can distinguish two basic types of mating strategies: territorial and non-territorial.

Non-territorial strategies are independent on certain area and the shift of males is driven by the movements of female groups. Principal model is represented by harem defence, where one buck defends group of females and obtains exclusive access to receptive females. Other type is following, where bucks associate with group of females but do not defend them actively. The less common strategy is dominance group, where one buck is dominant over all others in multimale mixed-sex group and achieves exclusive access to oestrous females, but does not defend neither territory, nor females (Thirgood et al. 1999).

Territorial strategies are bound up with an area, which is defended by a male. 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. An extreme example of multiple stand is a lek. A territory in fallow deer has a reproductive function and mostly contains no important food resources. Bucks seem to know the value of individual territories. In contrast to other lekking ungulates, an alternative to lek is not a large territory rich on food resources, but a small expositional area close to females' traditional routes in fallow deer (Apollonio et al. 1992).

Lek could be characterized as a cluster of small territories, which do not contain food resources and are visited by females for a single purpose of mating (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 few central males (Apollonio et al. 1989). Within the lek, 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 adopt also 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, 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 temporary stands.

According to evolutionary theory, each male in mixed-mating system should choose the very tactics which brings him the highest average reproductive success (Apollonio et al. 1992). Selection of mating tactics is affected by particular circumstances of potential costs and benefits in actual time. Any tactics is more favourable than the others under certain conditions; on the contrary it brings increased risks in another respect. Some tactics mark out with low probability of potential benefit (successful mating) but risks and costs are extremely low. For example, non-territorial following of females is the least effective tactics for dominant males (low rate of mating), however it is also the least exigent tactics from different point of view (the competition among mating males is low, mating success does not depend on vocalization which is energetically very costly, and finally males have an opportunity to feed while following). For the reason given above, following is adopted when number of oestrous females is lowest – at the very end of the rut (Hirth 1997). Conversely, lek is a high cost – high benefit strategy and therefore is chosen only by small proportion of males. Risks

and costs resulting from high frequency of fighting, costly vocalization and territory defence concern all lekking males regardless their reproductive success, but only few of them achieve benefit (successful mating). Those lucky who finally mate on lek would likely become fathers of great proportion of offsprings in the population, because several dominant males provide 60-90% of all copulations (Apollonio et al. 1989, 1992). On the imaginary scale, costs and benefits are highest on lek, medium on individual territories, lower competition among males but less females are attracted (Apollonio et al. 1992), and lowest in non-territorial tactics.

Presumably most important factors affecting adoption of particular mating tactics are population density (Schaal & Bradbury 1987, Clutton-Brock et al. 1988, Clutton-Brock et al. 1993, Stillman et al. 1996), sex ratio of adult animals (Apollonio 1989), availability, spatial distribution and preferences of receptive females (Schaal 1985, Schaal & Bradbury 1987, Apollonio 1989, Gosling & Petrie 1990, Apollonio et al. 1992, Deutsch & Nefdt 1992, Clutton-Brock et al. 1992, Clutton-Brock & McComb 1993, Mackenzie et al. 1995, Carranza et al. 1995, Hirth 1997, McElligott & Hayden 1999), distribution of food resources (Clutton-Brock et al. 1988, Carranza et al. 1995), body condition of adult males (Schaal 1985, Apollonio et al. 1992), age and hierarchy rank (Thirgood 1991), structure and heterogeneity of environment (Schaal 1985, Schaal & Bradbury 1987, Apollonio 1989).

- Population density: Higher population density supports lekking behaviour in general (Clutton-Brock et al. 1988, Langbein & Thirgood 1989). Clustered small territories are advantageous both for dominant males because of large number of oestrous females attracted to lek and for receptive females (they have chance to compare several dominant males at once). Under these conditions it is difficult to defend individual territories and non-territorial tactics are less effective.
- Sex ratio: In wild populations, sex ratio of adult animals in fallow deer could be balanced or biased towards females. Lek formation could be difficult because of the lack of mature bucks in population where sex ratio is strongly biased towards females (Apollonio 1989). However, most fallow deer live in parks nowadays. Thus man, his activity and regulation interventions affect sex ratio fundamentally. We can find populations where sex ratio is strongly biased towards adult males corresponding to demand on antler trophies. Such disproportion radically affects social behaviour of whole population and causes e.g. scarce occurrence of harem holding. The most serious consequence is social stress of overwhelming majority of adult bucks, which have only subtle chance for successful copulation in such strong competition. Frequently,

no rutting behaviour occurs by them due to low testosterone level as a reaction to social stress.

- Availability, spatial distribution and preferences of receptive females: Adoption of particular mating tactics is frequently affected by female preferences for few specific territories on lek. Extent of females joining the territory increases with harem size despite increasing frequency of harassment from non-territorial males (Carbone & Taborsky 1996). Females could be attracted to particular successful territories by olfactory cues from soil (experimental manipulation of soil cover between successful and unsuccessful territories in lek-breeding antelopes (*Kobus kob* and *Kobus leche*) caused increase of matings on unsuccessful territory (Deutsch & Nefdt 1992). Females tend to associate into small groups, which can be caused by copying of others females, gathering on hotspots (attractive areas with extremely low risk of predation, containing rare food resources or with limited occurrence of male harassment). High concentration of females on hotspots can lead to settle the lek on such localities. Transforming availability of receptive females during the course of the rut causes changes in males' behaviour – e.g. switching from territoriality in the peak of the rut to non-territorial tactics at the end of the reproductive season.
- Food resources distribution: Distribution of female groups is often determined by food resources distribution. This can affect settling males' territories on areas containing scarce food or along paths used by females to get to food resources. Changes in food resources distribution can induce territoriality in harem holders even in otherwise non-territorial species such as red deer (Carranza et al. 1995).
- Body condition: Territory (does not matter if solitary or on lek) defence is physically very costly activity. Therefore, territorial tactics are adopted mostly by bucks of high body condition, with sufficient disposition to take up the costs of territory defence (Apollonio et al. 1992). Weaker bucks have no chance to become successful in the competition with top-class males at least during a great part of the rut and they adopt less exigent tactics. Lek as the most exigent tactic is occupied only by elite males in the peak of the rut, which can be however replaced by bucks with lower physical condition especially at the end of the rut when the first are exhausted after a fight and defending their territory for up to couple of days. Most important factors affecting males' assessment of body condition seem to be antler symmetry and size, body size, hair condition, posture and vocalization.

- Age, body size and rank position: Most of territorial bucks recruit from 5 years class and older. Such limitation is related to body growth which is terminated between 4 and 5 years. Thus, adoption of particular mating strategy is at least partly correlated with age. Body size and weight is remarkable factor affecting not only a female choice, but also an intrasexual comparison of opponents. If an encounter among two bucks escalates in a fight, distinctly lighter opponent has practically no chance of winning, because fight contains mostly pushing where body weight plays a fundamental role. Experience can be also advantageous, but this increases with age, too. Thus, age and body size are intimately correlated and affect choice of mating strategy similarly to fitness. On the top of the hierarchy stand obviously elite males with best phenotype, optimal age class and perfect body condition. After an experimental removal of some dominant bucks a shift of mating tactics occurred (Thirgood 1991, Apollonio et al. 1992). Hierarchy rank therefore complements age and body-size with the same effect. It should be mentioned here that hierarchy rank is probably a key factor affecting age of the first reproduction in bucks (Komers et al. 1997).
- Environment structure: Fallow deer occupy a broad spectrum of habitat from open outdoors to areas with thick ground cover. However, for simultaneous occurrence of different mating tactics heterogeneity of habitat seems to be important. It should be also noticed here that after experimental change of food distribution in ungulate population a shift from harem holding to territory defence can be artificially induced in few days (Carranza et al. 1995).
- Predation: As for predation risk, it is still not clear which tactics is more dangerous – territory defence or lekking. But it seems to be comprehensible when lekking itself is more exhausting than territory holding, it makes bucks after the rut also more vulnerable to predators (Apollonio et al. 1992).

Mating system works more efficiently when oestrus of females is synchronized. This means majority of does are in oestrus simultaneously. When the number of receptive does is low (both because the end of the rut comes or does density is low from the very beginning), it is more advantageous for bucks to leave their territories and search for does, especially when other bucks do so. In other words, on the calculation of potential risks and benefits it is more effective to tempt oestrous females to territory when they are abundant and to search for them actively, when number of receptive females is low (Hirth 1997). The strongest bucks began to defend their territories early at the onset of the rut and they remained for almost whole rut,

while others waited for an offset of the rut to occupy the most favourite territories when top-males were exhausted enough to defend them (Apollonio et al. 1989).

The duration of the rut can be significant factor affecting assessment of different mating system or tactics advantages and disadvantages. Lack of seasonality in tropics induces prolongation of the rut. On the other hand, in ungulates of temperate zone reproductive season is very short. In the second case, lek is obviously the most efficient tactics, whilst in tropics it is impossible to defend leadership on the lek for the whole rut (Apollonio 1998).

Since rutting behaviour in fallow deer bucks includes above all harem or territory defence and chasing non-territorial bucks away, encounters between adult bucks are inevitable and common. Encounter may (but does not have to) escalate into a physical combat. However, fighting between males as a frequent component of the rutting behaviour in Cervidae is exhausting, may be risky and can lead to serious injuries or even death (Wilkinson & Shank 1976, Geist 1986). Loss of the harem females after the fight is also common (Clutton-Brock et al. 1988, Apollonio et al. 1989, Nefdt 1995). In an environment with predators, costs of conflict may also include increased risk of predation (Jakobsson et al. 1995). To avoid the risk of injury, males can assess their opponent's fighting ability before a physical fight, as it has been shown in red deer. Through vocalization and parallel walk, red deer stags can avoid any physical engagement with their opponent when the chances to win are uncertain (Clutton-Brock et al. 1979, 1982). Clutton-Brock et al. (1979) described the circumstances under which red deer stags began to fight. The course of the agonistic interaction between two adult red deer stags has quite stable phases, which are relatively strictly respected by each opponent: firstly vocalization (roaring) occurs, then parallel walk occurs, and finally the encounter escalates into a fight. Conflict can be terminated after any of these phases. Many similar, if not identical, elements of fighting behaviour can also be seen in the fallow deer. The hierarchy between adult fallow deer bucks is established mostly by non-contact interactions, even before the reproductive period (Apollonio et al. 1989, McElligott et al. 1999). Outlasting of the hierarchy from the pre-rut up to the rut and the tendency of adult fallow deer males to solve conflicts without antler contact contribute to a lower frequency of fights and decreased risk of serious injury (McElligott et al. 1998). Vocalization (groaning), parallel walk and physical combat during the breeding season have been described by several authors (Apollonio et al. 1989, Festa-Bianchet et al. 1990, Reby et al. 1998, McElligott et al. 1998, 1999, Mattiangeli et al. 1998, McElligott & Hayden 1999, Mattiangeli et al. 1999, Jennings et al. 2002, 2003, 2004, 2005). These authors have examined various aspects of rutting combats, such as vocalization rates (McElligott & Hayden 1999), fighting tactics and techniques and

factors affecting the duration of fights (McElligott et al. 1998, Mattiangeli et al. 1998, 1999, Jennings et al. 2004). Authors have also demonstrated that the lateral presentation of the palmate antlers during a fight does not necessarily signify dominance (Jennings et al. 2002) and that the parallel walk between competing male fallow deer does not indicate a lateral display of individual quality (Jennings et al. 2003). In a study included in this thesis (Bartoš et al. 2007), we focused on a simple process of assessment of the opponent's fighting ability and the escalation of the combat, as described originally for red deer (Clutton-Brock et al. 1979), estimating the probability of fighting based on the encounter components.

The duration, frequency and intensity of fighting behaviour during the rut may be affected by various factors, of which the probability of getting access to does seems to be the most important. Clutton-Brock et al. (1979) described that the course of the agonistic interaction between two adult red deer stags has quite stable rules with a clearly defined behavioural sequences: vocalization (roaring) occurs first, then parallel walk and finally a physical fight escalates. Conflict can be terminated after any of these phases. Fallow deer bucks also use such efficient tactics, which minimize the chance of injury while fighting and allow bucks to avoid fighting (Bartoš et al. 2007). Encounters between males in either red or fallow deer go on both in the presence and in the absence of nearby females. In the study by Clutton-Brock et al. (1979), hinds (red deer females) were present in two-thirds of the total sample of fights. Similarly in fallow deer, most fights (70 %) between bucks took place in the presence of does (Alvarez 1993, Mattiangeli et al. 1998). In red deer, fights between two harem holders were found to be significantly longer than combats between solitary stags (Clutton-Brock & Albon 1979). In fallow deer, the duration of fights also depended on the presence of females (Mattiangeli et al. 1998). Nevertheless, Jennings et al. (2004) reported no relationship between the number of matings recorded on any day during the rut and fight duration. Interestingly, the highest rates of groaning were produced by males that were in the presence of females (McElligott & Hayden 1999). The frequency of fights between bucks has been found to be closely related to the number of mating opportunities (McElligott et al. 1998). Furthermore, on those days when most of the matings occurred, the highest frequency of combats during the rut also occurred (Clutton-Brock et al. 1988, McElligott et al. 1998). Additionally, the frequency of fallow deer matings and fights on lek territories has been found to be positively correlated (Apollonio et al. 1990). Lastly, red deer stags have been found to fight more frequently and intensively during the time period when females were likely to conceive (Clutton-Brock et al. 1979). This contrasts the findings of Festa-Bianchet et al. (1990) who reported that the number of fights observed in fallow deer were not correlated

with mating success and that bucks did not fight more frequently during those days when many copulations occurred compared to those days with few matings. According to previous literature, the course of an encounter between two male deer seems to be affected by three main proximate causes from the point of view of a female: presence of females, mating frequency and conception probability. To test this predictions, it was examined how decisive the presence of females is for the course of an encounter between bucks. The prediction was that when females are present, bucks should be motivated to show their status. Hypotheses were set that the presence of females near males enhances the frequency of encounters as well as the occurrence of fights and groaning compared to the situation when females are absent. Furthermore, the presence of females should also increase the number of incidences where there is a clear outcome of the fight.

If there are some females with one or both opponents at the beginning of an encounter, they have the opportunity to leave the place or join the opponent during or after the encounter. The movement of females from one opponent to another should partially indicate female choice based on the course of the encounter and its result. In red deer, reproductive success of stags (estimated indirectly by counting females/days held per season) has been found to be closely related to fighting success (Clutton-Brock et al. 1979). In fallow deer, fighting success has been correlated with mating success (Clutton-Brock et al. 1988, Moore et al. 1995, Hayward et al. 2005). Furthermore, it has been demonstrated that winning fights, whilst defending a harem, can be decisive for reproduction success (Apollonio 1998). In contrast, in the study of Apollonio et al. (Apollonio et al. 1989) fighting success was not found to be correlated with mating success in fallow deer. Despite this, non-contact, aggressive interactions between adult fallow deer males can play an important role in determining access to a mate (Festa-Bianchet et al. 1990). In general, fighting success likely rules reproductive success according to various studies both on red and fallow deer (Clutton-Brock et al. 1979, Festa-Bianchet et al. 1990, Moore et al. 1995, Apollonio 1998). Therefore, it was attempted to determine if the result of an encounter affects the choice of a female (i.e. the shift of females between opponents). Those factors that may affect the probability of a female's desertion from one buck to his opponent during an encounter were examined. Assuming that the result of a fight is relevant for those present females, the following hypotheses were tested: 1. Females will stay in the harem of the winner of an encounter and will abandon the loser. 2. Females will desert to a buck with females rather than to a buck that is without them.

Three publications enclosed above deal with different aspects of rutting behaviour in fallow deer. To summarize shortly, we tried to explain the process of escalating an encounter,

similarly to that one described for red deer stags. We specified factors affecting probability of physical combat (Bartoš et al. 2007). We investigated the role of fallow deer does by the bucks encounters and circumstances influencing females' tendencies to stay with or leave the buck (Fričová et al. 2007). We also examined the special strategy of lek and compared a reproductive success of bucks defending a lek territory and those defending temporary stands by an indirect method (Fričová et al. 2008).

DISCUSSION

Our study compares at first the process of opponents' assessment between red deer stags and fallow deer bucks. We found that in 83% of the encounters of two adult bucks, at least one of the phases of displayed rivalry was utilized to estimate the opponent's ability (Bartoš et al. 2007). This result is very similar to that found in red deer study (Clutton-Brock et al. 1979). Frequency of vocalization and parallel walk was even higher than in red deer. This suggests that adult bucks used non-contact techniques for reciprocal comparison of strength even more than the red deer stags in the aforementioned study. Unlike red we found that fallow deer would interrupt a fight and switch into another parallel walk. In agreement with other reports (e.g., McElligott et al. 1998, Mattiangeli et al. 1999), our results suggest that fallow deer males use efficient tactics to avoid combat situations that may result in physical injury (Bartoš et al. 2007). The probability of a fight was lowest in those situations where the males displayed asymmetric behavior. Higher symmetry of the contestants' behavior was strongly correlated with a higher probability of a fight. A high proportion of fights without an obvious winner rejected our expectation that fights would mostly be terminated by the victory of one male (e.g., Jennings et al. 2004). On the contrary, we found that for most encounters with a clear outcome, the encounter ended without the fight rather than escalating into a fight. Perhaps an evident victory of one male is not really that important in this reproductive system. This would confirm the supposition that fighting is just a complement to vocalization and parallel walk, which are most important for establishing hierarchy during the rut. The fights in fallow deer may not be as severe as those that occur in red deer since parallel walk often occurred after combat. In agreement with earlier studies (e.g., McElligott et al. 1998) we believe that vocalization, parallel walk as well as fighting are suspiciously about clearing up the dominance relationships. During the course of the rut, as body condition declines, the fighting ability of individual deer male changes. Individuals vary in the timing of their decline, so inter-relationships among the males is most likely highly dynamic. Consequently, any assessment of criteria that do not vary with changes in body condition during the rut can result in incorrect conclusions.

As for females, they were only present during half of the encounters between bucks. Furthermore, most of the fights escalating from encounters occurred in the absence of females. Vocalization and incidence of clear victory was not affected by the presence of

females. This study failed to support the prediction that bucks are highly motivated to show their status in the presence of females (Fričová et al. 2007). It is more likely that bucks did not reflect if there were any females nearby them during the encounters. Again, it can be concluded that encounter components and fights were directed to other fallow deer bucks in order to monitor the current competitive abilities of their opponents, as previously suggested, rather than to decide about direct access to receptive females. Under the given social conditions, encounters between bucks did not lead to any imminent gain of females and, thus, mate choice was realized in some other way. Since we observed very few matings during the daytime throughout the four observation seasons in our study, it strongly suggests that males decided about access to receptive females soon before mating, which typically occurred during the night time (ibid.).

Our data supports the idea that the outcome of an encounter impacts the decision of a fallow deer female to stay with or leave the male whom she accompanied prior to the encounter. This might suggest that the fighting success of males is important for mating success. On the contrary, it was found that the probability of a female to desert her buck was generally low. Therefore, this indicates that fighting success was not essential or exclusive for mate choice. However, our finding that the presence of any females with the opponent decreased the probability of female desertion opposes the mate-copy theory.

Although mating success was described higher on leks than on isolated territories (Clutton-Brock et al. 1988), our results showed that 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 temporary stands (Fričová et al. 2008). 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, in Březka population, sex ratio was diverted on the side of males, and therefore tactics of lekking perhaps fails to be the most efficient. Either non-territorial strategies or defending isolated territory brought presumably higher chance of reproductive success to rutting bucks. We conclude that potential reproductive success of lekking fallow deer bucks is definitely affected by the population density, but sex ratio might be the fundamental factor determining effectiveness of different mating tactics.

LITERATURE

- Alvarez, F., 1993: Risks of fighting in relation to age and territory holding in fallow deer. *Can. J. Zool.*, 71: 376-383.
- Apollonio, M., 1989: Lekking in fallow deer - just a matter of density. *Ethol. Ecol. Evol.*, 1: 291-294.
- Apollonio, M., 1998: Relationships between mating system, spatial behaviour, and genetic variation in ungulates, with special reference to European cervids. *Acta Theriol.*, 155-162.
- Apollonio, M., Festa-Bianchet, M. & Mari, F., 1989: Correlates of copulatory success in a fallow deer lek. *Behav. Ecol. Sociobiol.*, 25: 89-97.
- Apollonio, M., Festa-Bianchet, M. & Mari, F., 1990: Effects of removal of successful males in a fallow deer lek. In: Myrberget, S. (ed.), Transactions XIXth IUGB Congress, Volume I: Population dynamics. *NINA, Norwegian Institute for Nature Research, Trondheim*: 68-69.
- Apollonio, M., Festa-Bianchet, M., Mari, F., Mattioli, S. & Sarno, B., 1992: To lek or not to lek - mating strategies of male fallow deer. *Behav. Ecol.*, 3: 25-31.
- Apollonio, M., Festa-Bianchet, M., Mari, F. & Riva, M., 1990: Site-specific asymmetries in male copulatory success in a fallow deer lek. *Anim. Behav.*, 39: 205-212.
- Apollonio, M., Festa-Bianchet, M. & Franco, M., 1989: Effect of removal of successful males in a fallow deer lek. *XIXth IUGB-Congress, Trondheim 1989, Abstracts*, 3.
- Bartoš, L., Fričová, B., Víčová, J., Panamá, J., Šustr, P. & Šmídová, E., 2007: Estimation of the probability of fighting in fallow deer (*Dama dama*) during the rut. *Aggress. Behav.*, 33: 7-13.
- Bradbury, J.W. & Gibson, R.M., 1983: Leks and mate choice. In: Bateson, P. (ed.), *Mate Choice. Cambridge University Press, Cambridge, New York, New Rochelle, Melbourne, Sydney*: 109-138.
- Carbone, C. & Taborsky, M., 1996: Mate choice or harassment avoidance? A question of female control at the lek. *Behav. Ecol.*, 7: 370-373.
- Carranza, J., Garcia-Munoz, A.J. & Vargas, J.D., 1995: Experimental shifting from harem defence to territoriality in rutting red deer. *Anim. Behav.*, 49: 551-554.
- Chapman, D.I. & Chapman, N.G., 1975: Fallow deer: Their history, distribution and biology. *Terence Dalton, Lavenham, Suffolk*.
- Clutton-Brock, T.H., 1989: Mammalian mating systems. *Proc. Roy. Soc. Lond. B*, 236: 339-372.
- Clutton-Brock, T.H. & Albon, S.D., 1979: The roaring of the red deer and the evolution of honest advertisement. *Behaviour*, 69: 145-170.
- Clutton-Brock, T.H., Albon, S.D., Gibson, R.M. & Guinness, F.E., 1979: The logical stag: Adaptive aspects of fighting in red deer (*Cervus elaphus* L.). *Anim. Behav.*, 27: 211-225.
- Clutton-Brock, T.H., Deutsch, J.C. & Nefdt, R.J.C., 1993: The evolution of ungulate leks. *Anim. Behav.*, 46: 1121-1138.
- Clutton-Brock, T.H., Green, D., Hiraiwa-Hasegawa, M. & Albon, S.D., 1988: Passing the buck: resource of defence, lekking and the mate choice in fallow deer. *Behav. Ecol. Sociobiol.*, 23: 281-296.
- Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D., 1982: Red deer, behavior and ecology of two sexes. *The University of Chicago Edinburgh University Press, Edinburgh*.
- Clutton-Brock, T.H. & McComb, K., 1993: Experimental tests of copying and mate choice in fallow deer (*Dama dama*). *Behav. Ecol.*, 4: 191-193.

- Clutton-Brock, T.H., Price, O.F. & MacColl, A.D.C., 1992: Mate retention, harassment, and the evolution of ungulate leks. *Behav. Ecol.*, 3: 234-243.
- Deutsch, J.C. & Nefdt, R.J.C., 1992: Olfactory Cues Influence Female Choice in 2 Lek-Breeding Antelopes. *Nature*, 356: 596-598.
- Festa-Bianchet, M., Apollonio, M., Mari, F. & Rasola, G., 1990: Aggression among lekking male fallow deer (*Dama-dama*) - territory effects and relationship with copulatory success. *Ethology*, 85: 236-246.
- Fričová, B., Bartoš, L., Bartošová-Víchová, J., Panamá, J., Šustr, P. & Chaloupková, H., 2008: Comparison of reproductive success in fallow deer males on lek and temporary stands. *Folia Zool.*, in press.
- Fričová, B., Bartoš, L., Bartošová-Víchová, J., Panamá, J., Šustr, P. & Jozífková, E., 2007: Females presence and males agonistic encounters in fallow deer *Dama dama* during the rut. *Folia Zool.*, 56: 253-262.
- Geist, V., 1986: New evidence of high frequency of antler wounding in cervids. *Can. J. Zool.*, 64: 380-384.
- Gosling, L.M. & Petrie, M., 1990: Lekking in topi: a consequence of satellite behaviour by small males at hotspots. *Anim. Behav.*, 40: 272-287.
- Gosling, L.M., Petrie, M. & Rainy, M.E., 1987: Lekking in topi: a high cost, specialist strategy. *Anim. Behav.*, 35: 616-618.
- Gould, M.S. & Werts, J.M., 1979: Influence of the buck on social behavior of captive female fallow deer (*Dama dama*). *Behav. Process.*, 4: 253-263.
- Hayward, L.S., Satterlee, D.G. & Wingfield, J.C., 2005: Japanese quail selected for high plasma corticosterone response deposit high levels of corticosterone in their eggs. *Physiological and Biochemical Zoology*, 78: 1026-1031.
- Hirth, D.H., 1997: Lek breeding in a Texas population of fallow deer (*Dama dama*). *Amer. Midland Natur.*, 138: 276-289.
- Isvaran, K. & Jhala, Y., 2000: Variation in lekking costs in blackbuck (*Antilope cervicapra*): Relationship to lek-territory location and female mating patterns. *Behaviour*, 137: 547-563.
- Jakobsson, S., Brick, O. & Kullberg, C., 1995: Escalated fighting behaviour incurs increased predation risk. *Anim. Behav.*, 49: 235-239.
- Jennings, D.J., Gammell, M.P., Carlin, C.M. & Hayden, T.J., 2002: Does lateral presentation of the palmate antlers during fights by fallow deer (*Dama dama* L.) signify dominance or submission? *Ethology*, 108: 389-401.
- Jennings, D.J., Gammell, M.P., Carlin, C.M. & Hayden, T.J., 2003: Is the parallel walk between competing male fallow deer, *Dama dama*, a lateral display of individual quality? *Anim. Behav.*, 65: 1005-1012.
- Jennings, D.J., Gammell, M.P., Carlin, C.M. & Hayden, T.J., 2004: Effect of body weight, antler length, resource value and experience on fight duration and intensity in fallow deer. *Anim. Behav.*, 68: 213-221.
- Jennings, D.J., Gammell, M.P., Payne, R.J.H. & Hayden, T.J., 2005: An investigation of assessment games during fallow deer fights. *Ethology*, 111: 511-525.
- Komers, P.E., Pélabon, C. & Stenström, D., 1997: Age at first reproduction in male fallow deer: Age-specific versus dominance-specific behaviors. *Behav. Ecol.*, 8: 456-462.
- Langbein, J. & Thirgood, S.J., 1989: Variation in mating systems of fallow deer (*Dama-dama*) in relation to ecology. *Ethology*, 83: 195-214.
- Mackenzie, A., Reynolds, J.D., Brown, V.J. & Sutherland, W.J., 1995: Variation in male mating success on leks. *Amer. Natur.*, 145: 633-652.
- Mattiangeli, V., Mattiello, S. & Verga, M., 1998: Factors affecting the duration of fights in fallow deer (*Dama dama*) during the rut. *Ethol. Ecol. Evol.*, 10: 87-93.

- Mattiangeli, V., Mattiello, S. & Verga, M., 1999: The fighting technique of male fallow deer (*Dama dama*): an analysis of agonistic interactions during the rut. *J. Zool., Lond.*, 249: 339-346.
- McElligott, A.G. & Hayden, T.J., 1999: Context-related vocalization rates of fallow bucks, *Dama dama*. *Anim. Behav.*, 58: 1095-1104.
- McElligott, A.G., Mattiangeli, V., Mattiello, S., Verga, M., Reynolds, C.A. & Hayden, T.J., 1998: Fighting tactics of fallow bucks (*Dama dama*, Cervidae): Reducing the risks of serious conflict. *Ethology*, 104: 789-803.
- McElligott, A.G., O'Neill, K.P. & Hayden, T.J., 1999: Cumulative long-term investment in vocalization and mating success of fallow bucks, *Dama dama*. *Anim. Behav.*, 57: 1159-1167.
- Moore, N.P., Kelly, P.F., Cahill, J.P. & Hayden, T.J., 1995: Mating strategies and mating success of fallow (*Dama dama*) bucks in a non-lekking population. *Behav. Ecol. Sociobiol.*, 36: 91-100.
- Nefdt, R.J.C., 1995: Disruptions of matings, harassment and lek-breeding in kaffue lechwe antelope. *Anim. Behav.*, 49: 419-429.
- Pélabon, C., Komers, P.E. & Hoglund, J., 1999: Do leks limit the frequency of aggressive encounters in fallow deer? Linking local male density and lek occurrence. *Can. J. Zool.*, 77: 667-670.
- Reby, D., Joachim, J., Lauga, J., Lek, S. & Aulagnier, S., 1998: Individuality in the groans of fallow deer (*Dama dama*) bucks. *J. Zool., Lond.*, 245: 79-84.
- Schaal, A., 1985: Variation of mating system in fallow deer (*Dama d. dama*). Abstr. 19th Int. Ethol. Conf. Toulouse. 277.
- Schaal, A., 1986: Evidence of lek mating behaviour in the European fallow deer (*Dama d. dama*). *C. R. Acad. Sci. Ser. III-Vie*, 303: 729-732.
- Schaal, A. & Bradbury, J.W., 1987: Lek breeding in a deer species. *Biol. Behav.*, 12: 28-32.
- Stenstrom, D., Dahlblom, S., Fur, C.J. & Hoglund, J., 2000: Rutting pit distribution and the significance of fallow deer *Dama dama* scrapes during the rut. *Wildlife Biology*, 6: 23-29.
- Stillman, R.A., Deutsch, J.C., Clutton-Brock, T.H. & Sutherland, W.J., 1996: Black hole models of ungulate lek size and distribution. *Anim. Behav.*, 52: 891-902.
- Thirgood, S., Langbein, J. & Putman, R.J., 1999: Intraspecific variation in ungulate mating strategies: The case of the flexible fallow deer. In: Slater, P.J.B., Rosenblat, J.S., Snowden, C.T. & Roper, T.J. (eds.), *Advances in the Study of Behavior*, Vol. 28. *Academic Press Inc, 525 B Street, Suite 1900, San Diego, CA 92101-4495 USA*: 333-361.
- Thirgood, S.J., 1991: Alternative mating strategies and reproductive success in fallow deer. *Behaviour*, 116: 1-10.
- Wilkinson, P.F. & Shank, C.C., 1976: Rutting - fight mortality among musk oxen on Banks Island, Northwest Territories, Canada. *Anim. Behav.*, 24: 756-758.