

Females presence and males agonistic encounters in fallow deer, *Dama dama* during the rut

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A b s t r a c t. Similarly to other Cervidae, conflicts and fights are frequent during the rut of fallow deer. The part of does (female fallow deer) during buck (male fallow deer) encounters was examined in this study. Encounters between adult bucks were recorded during the rut. The numbers of encounters with and without females present were nearly equal with similar proportions of encounters when females accompanied one or both of the males. Fighting occurred in 39.5% of the encounters only. Female presence seemed to have a negligible effect on the probability of an encounter between two bucks escalating into a fight. However, fights tended to escalate more frequently when there were no females present compared to when females were present. Vocalizations were recorded in most encounters and occurred irrespectively of female presence / absence. Bucks were more likely to engage with conspecific with female consorts. When both opponents had female consorts with them, the probability of desertion of the females was significantly lower compared to when the male had some females while his opponent did not. Results in this study suggest that the presence of females did not affect male agonistic behaviour during the rut.

Key words: female choice, fighting, rutting behaviour

Introduction

As in other deer species, conflicts and fights are frequent during the rut of fallow deer. These occur despite the fact that they are energetically expensive and may result in serious injuries (Wilkinson & Shank 1976, Geist 1986), loss of harem (Clutton-Brock et al. 1988, Apollonio et al. 1989, Nefdt 1995), and increased risk of predation (Jakobsson et al. 1995). The duration, frequency and intensity of fighting behaviour may be affected by various factors, of which the probability of getting access to does seems to be the most important despite the fact Festa-Bianchet et al. (1990) reported that individual fighting success was not correlated with individual mating success.

Escalation of encounters as influenced by the presence of females

Clutton-Brock et al. (1979) described that the course of the agonistic interaction between two adult red deer (*Cervus elaphus*) stags has quite stable rules with a clearly defined

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behavioural sequence: vocalization (roaring) occurs first, then parallel walk and finally a fight escalates. Conflict can be terminated after any of these phases. Further, 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 bucks in either red or fallow deer go on both in the presence and in the absence of nearby females. In a 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.

Female choice

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 (A p o l l o n i o 1998). In contrast, in the study of A p o l l o n i o 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 (F e s t a - B i a n c h e t et al. 1990). In general, fighting success likely rules reproductive success according to various studies both on red and fallow deer (C l u t t o n - B r o c k et al. 1979, F e s t a - B i a n c h e t et al. 1990, M o o r e et al. 1995, A p o l l o n i o 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 who is without them.

Material and Methods

Observations were carried out in Březka deer park (N49°54', E014°32'), a 2.06 km² park located in Kostelec u Křížků, Czech Republic (property of Forestry and Game Management Research Institute, Jíloviště – Strnady).

During the observation period, which included four rutting seasons (2000 to 2003), there were between 100 and 150 fallow deer bucks in the park and approximately 100 adult females. Twenty adult bucks from different age groups were individually marked. Several authors (A p o l l o n i o et al. 1992, C i u t i et al. 2004, D a v i n i et al. 2004) have described variability in mating strategies as result of high population density. Similarly, the fallow deer bucks studied in Březka adopted a mixed mating system with lekking males, probable single territory defenders and followers of female groups. Most of the fighting activities occurred on the leks. Therefore, as in the parallel study (B a r t o š et al. 2007), we only used the data that came from the lek. For the purposes of this study observation focused on the agonistic behaviour of fallow deer bucks during the rut and the presence of females near the encounters regardless of which mating system the bucks were utilizing.

Data were collected over four seasons by several observers. At the beginning (first decade of October) and at the end of the rut, 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. During pilot observations (1999), it was noted that the rutting activity in the park was not evenly distributed throughout the day. For this reason 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. For each encounter between two opponents, following was recorded: the date and location, the time of the buck's arrival and departure from the location, the duration at the location, the proximity of females up to 20 m from the buck (number and duration of sojourn), which of the bucks was the resident, initiator, attacked, winner and loser, and if the encounter contained groaning of the opponents, parallel walk, and a physical fight. Only adult males (more than 4 years old) were considered for these observations.

Definitions

Encounter components were recognized according to the definitions set out in Table 1. For the statistical analysis, all these activities were classified categorically if occurring (YES/NO). Furthermore, the date, place, time and duration of all the agonistic interactions were recorded.

Table 1. Definitions of encounter component.

Encounter	meeting of two bucks (which may or may not result in a fight)
Victory	a clear outcome of an encounter (one buck remained at the place of an encounter, while the other left) regardless of whether a fight occurred or not
Ritualized behaviour	non-contact display which allows contestants to assess their opponents' fighting ability (e.g., groaning and parallel walk – C l u t t o n - B r o c k et al. 1979)
Groaning	vocalization of an adult fallow deer male during the rutting period
Parallel walk	ritualized display, when two bucks walked side by side (2–10 m apart) with a stiff-leg gait (C l u t t o n - B r o c k et al. 1979). When parallel walk occurred after a previous parallel walk or after a fight, it was termed parallel walk ₂
Retreat	a situation when one of the bucks escaped from the place of encounter after a threat by an opponent or when a buck was driven away by another one. A retreat indicated the end of an encounter
Fight	physical contact between two bucks, including having their antlers locked. The opponents pushed each other vigorously until one of them was defeated or until consequential parallel walk ₂ occurred
Initiator	the buck who initiated the beginning of an encounter by approaching an opponent
Attacked	the buck who was challenged by the initiator
Winner	the buck that remained on the place of encounter after the retreat of the loser (regardless of whether or not the encounter escalated into a physical fight)
Loser	the buck who left the place of encounter apparently as a consequence of agonistic activity of the opponent
Gain or loss of the females after encounter	the number of females accompanying the winner or the loser after the encounter minus the number before the encounter

Statistics

All of the data were analyzed using the SAS System V 9.1 (SAS Inst. Inc., Cary, NC). The effect of female presence on the probability of an encounter between two fallow deer bucks resulting in a fight was tested by fitting a binomial logistic regression model using the GENMOD procedure. The explanatory variables tested were categorical: 'female presence' (presence of females during an encounter: yes or no), 'displayed behaviour' covering six possible combinations of vocalizations (one buck groaning, no display, both bucks groaning, one buck groaning during parallel walk, no groaning during parallel walk, and both bucks groaning during parallel walk) and parallel walk (yes or no), and the interaction 'female presence' * 'displayed behaviour'. (The particular results of this model referring to the behaviour of the males have been described in a parallel paper (B a r t o š et al. 2007)). There was no significant effect of the individual observers; therefore, data were combined across observers. The tests for specific hypotheses concerning the model parameters and odds ratio for explanatory variables were constructed using the ESTIMATE statement. The odds ratio compares the odds of the outcome in one level of explanatory variable to the odds of the outcome in another level; odds are the ratio of the probability of the outcome to the probability of no outcome.

The probability of a clear outcome of an encounter ("clear outcome" = one of the males was recognized as a clear winner of the encounter – yes/no) when females were present or not was fitted using a logistic regression model (PROC GENMOD). The explanatory variables tested were categorical: 'female presence' (presence of females during an

encounter: yes or no), 'fighting' (an encounter of two males resulting in a combat or not), and the interaction 'female presence' * 'fighting'.

A binomial logistic regression model (PROC GENMOD, SAS) was fitted to model the probability that a female would desert the buck that she had accompanied before encounter. The tested factors were: result for the buck the female came with (winner, loser, or tie when a clear winner of an encounter could not be assessed), initiator of the encounter (yes/no), physical fight (yes/no), presence of females with the opponent (yes/no) and all of the first order interactions. Dependencies in pair type of data were treated as repeated measurements on the same encounter using the REPEATED statement.

The probability that an initiator of an encounter would win was predicted using a binomial logistic regression model (PROC GENMOD, SAS), with one factor covering which of the bucks had any female accompaniment: the initiator, the opponent or both of them.

Further associations between categorical variables were tested using a chi-square test for equal proportions (PROC FREQ, SAS).

Results

Presence and absence of females at the encounters

During 270 hours of observations 205 encounters between adult bucks were recorded. The proportions of encounter components when females were present with at least one of the contestants or absent are shown in Fig.1. Encounters with (n = 100) and without (n = 105) females present were nearly equal in frequency. Similar proportions of encounters occurred when females accompanied one or both of the males (52.0 vs. 48.0 %, respectively, $\chi^2_{(1)} = 0.16$, NS).

Physical fighting only occurred in 39.5% of the encounters, whereas in all the other cases the opponents avoided a fight. Females presence seemed to have a negligible effect on the probability of an encounter between two fallow deer bucks escalating into a fight (logistic regression model, 'female presence': $\chi^2_{(1)} = 2.89$, $p = 0.09$; interaction 'female presence' * 'displayed behaviour', $p = 0.78$). However, fights tended to rise more frequently without any females at the place of an encounter compared to encounters when females were present (44% vs. 35 %, odds ratio = 1.78, $p = 0.09$). The factor 'displayed behaviour' contributed significantly to the final logistic regression model ($\chi^2_{(5)} = 54.33$, $p < 0.0001$), as described in details previously (B a r t o š et al. 2007).

Vocalizations were recorded in most cases, regardless if females were present or not (70.5 %, 81 % respectively, $\chi^2_{(1)} = 0.43$, NS).

The initiator of an encounter between two bucks could be recognized in 167 cases by the observers. In eighty of these cases, the bucks were accompanied by females. Among these, similar proportions of encounters were found whether females came with the initiator, an attacked one, or both of the bucks (30.0, 33.7, and 36.3 %, respectively, $\chi^2_{(2)} = 0.48$, NS). In other words, initiators primarily attacked opponents who were accompanied by females compared to those without females (70.0 vs. 30.0 %). Furthermore, in most cases (66.3 %), males were accompanied by females. There does not seem, therefore, to be any general rule by which the bucks commence an encounter based on the presence of females with one or both of the bucks.

Fig. 2 shows the termination of encounters between two opponents resulting in either victory (encounter with a clear outcome) or with no apparent winner. The presence of

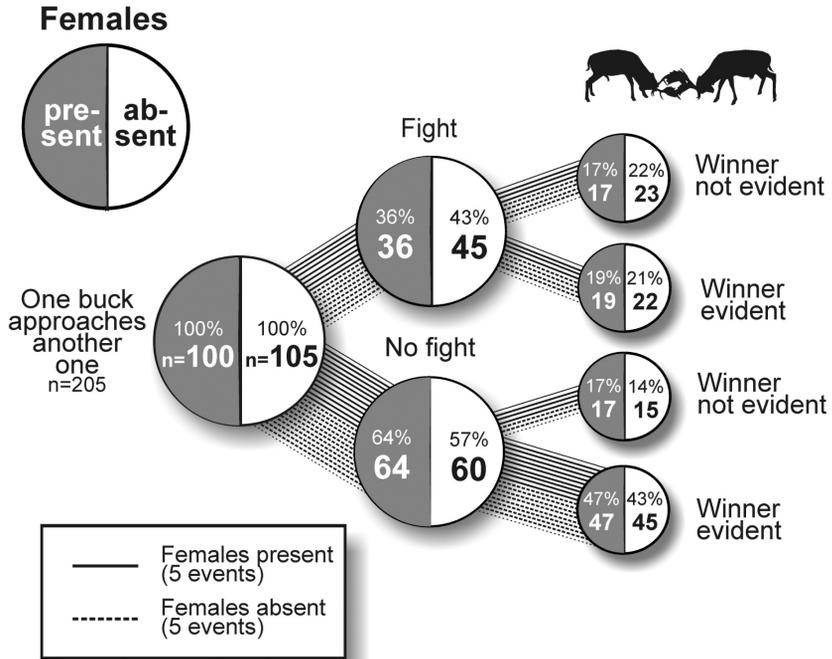


Fig. 2. The termination of encounters of two opponents by victory of one of them (encounter with a clear outcome) or without an apparent winner. (Females present = white numbers on a dark background, females absent = black numbers on a white background. Numbers are a proportion of all events and n for each category.)

If a fight occurred, there was a clear winner in 61.1 % of those cases with females compared to 55.6 % without females.

The initiator of an encounter also most frequently won the encounter, regardless if females were present or not with any of the bucks (63.8 vs. 64.6 %, respectively, $\chi^2_{(2)} = 1.63$, NS). The probability of an initiator's victory differed according to which of the bucks had female accompaniment prior to an encounter (logistic regression model, $\chi^2_{(2)} = 7.19$, $p < 0.03$). Those initiators accompanied by females attacking an opponent without females had considerably greater probability to win (0.79) than the reverse situation when an initiator without female accompaniment attacked an opponent who was with females (0.44, odds ratio = 4.75, $p < 0.02$). When both of the bucks were accompanied by females, the probability that the initiator would win was 0.69.

The initiator gained one or more females (in terms of the number of females accompanying the initiator) in 10 of 56 (17.9 %) encounters where the opponent had female accompaniment. Further, the frequency by which the initiator won the encounter did not differ if the buck gained or did not gain a female (70.0 % vs. 54.4, $\chi^2_{(1)} = 0.82$, NS).

Female choice

The probability of desertion by a female was affected by the outcome of an encounter ($\chi^2_{(2)} = 7.44$, $p < 0.03$) and by the presence of females with the opponent ($\chi^2_{(1)} = 10.15$, $p < 0.01$) (Fig. 3). Female desertion was more probable in losers (0.26) than in winners (0.07) or in encounters without a clear outcome (0.16, $\chi^2_{(2)} = 7.44$, $p = 0.0242$). When both

of the opponents had some female accompaniment, the probability of desertion by a female was significantly lower (0.04) compared to when one male was with some females while his opponent was not (0.41, $\chi^2_{(2)} = 10.15$, $p = 0.0014$). Regardless, the probability of a female to desert was generally low. Further, neither the initiation of an encounter, nor the escalation of an encounter into a physical fight affected probability of desertion by a female.

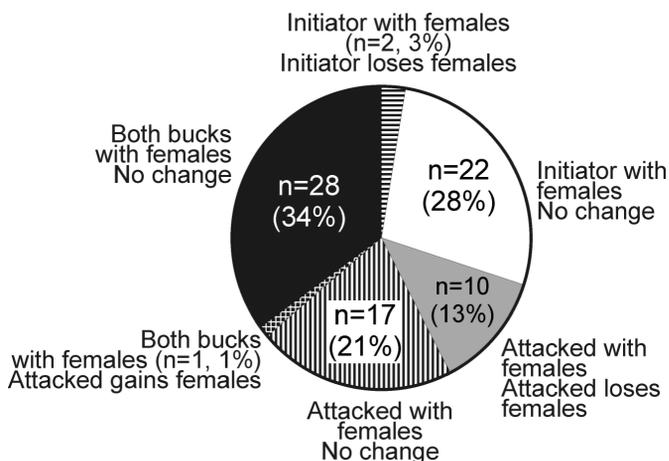


Fig. 3. The proportion of cases when the initiator and presence of females before and after the encounter were recognized.

Discussion

Females were only present during half of the encounters between bucks. Furthermore, most of the fights escalating from encounters occurred in the absence of females. Vocalizations occurred at the majority of encounters and were not affected by the presence of the females. A clear winner was recognized after approximately two thirds of the encounters, regardless if females were present or not. The incidence of a clear winner after a fight was only slightly higher when females were present. Thus, in this study, the presence of females did not appear to affect the frequency of male fallow deer fighting behaviour.

This study failed to support the prediction that bucks are highly motivated to show their status in the presence of females. It is more likely that bucks did not reflect if there were any females nearby them during the encounters. The presence of females was not decisive for the frequency of encounters which escalated into fights. Therefore, 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 (McElligott et al. 1998, Bartoš et al. 2007), rather than to decide about direct access to receptive females. As indicated by the non-significant trend ($p = 0.09$), it could also well be so that females might induce fighting avoidance to reduce the costs of female losses and increase motivation in males to accompany them.

Our results suggest that, 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. This is in agreement with Festa-Bianchet et al. (1990) who did not find any correlation between individual fighting success and individual mating success. In a non-lekking population Moore et al. (1995) reported that mating success was only

weakly related to fighting success. 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.

This 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. However, once the encounter escalated into fighting, the presence of females could give the attacking male a stronger motivation. This may be supported by the study of Mattioli et al. (1998) who reported that fallow deer fight duration was affected by the presence of females, though to a lesser extent than by rank, presence or absence of parallel walk in the fight sequence. 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.

The finding that the presence of any females with the opponent decreased the probability of female desertion opposes the mate-copy theory (Clutton-Brock et al. 1989, Gibson & Höglund 1992, Marks et al. 1994, McComb & Clutton-Brock 1994). This theory suggests that a female might have a higher chance to reproduce with a male who does not have any female accompaniment. It is possible that a more detailed analysis needs to be done on female oestrus assessment and synchronization to properly understand the mechanisms controlling female desertion and perhaps to bring an alternative explanation based on differences between oestrous and anoestrous females as in McComb & Clutton-Brock (1994).

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