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Female aggression in red deer: Does it indicate competition for mates?

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Abstract

Female–female competition over mates is often considered of minor importance, particularly in polygynous species. In red deer (*Cervus elaphus*), female–female aggression within harems during the breeding season has not been studied to date. Herein, we examined if oestrous female red deer in harems show elevated aggression rates, compared to when they are in harems but not in oestrous, and also when they are in foraging groups outside of the breeding season. Any increased levels of aggression involving oestrous females, could indicate the potential for female–female competition for mates in this species. We found that aggressive interactions among female red deer were clearly evident. The most common forms of aggression were displacements, nose threats and kicking. Biting and ear threats occurred less frequently, and chases were rare. There were no differences in the proportion of the different aggression types in the three social contexts. More importantly, we found that the highest overall rates of aggression were for oestrous females in harems, and for females in foraging groups. The lowest rates of aggression were found in harems (when the focal female was not in oestrous). If high rates of aggression also occur when several females are simultaneously in oestrous within single harems, then it is possible that this aggression could affect either mate choice or mating order. These results suggest that female–female competition over mates could play a role in the mating behaviour of red deer.

Key words: *Cervus elaphus*, female-female competition, mating

Introduction

Female–female competition over mates is often overlooked or considered of minor importance, particularly in polygynous species. This is because males are usually the competing sex and females the choosing sex. Males also often compete in dramatic and conspicuous ways for access to mating opportunities (Andersson 1994; McElligott et al. 1998; Rosenqvist and Berglund 1992). However, underestimating female–female competition over mates means underestimating an important aspect of sexual selection (Cunningham and Birkhead 1998).

Females may compete either for access to mates or for reproductive resources such as nest sites or food, and it is often difficult to distinguish between the two types of competition (Jennions and Petrie 1997; Rosenqvist

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and Berglund 1992). Females can be expected to compete over males under several different conditions. For example, if males and females have similar parental roles, if the operational sex ratio is female biased, or if male quality varies so that high-quality males are rare (Berglund et al. 1993).

In polygynous ungulates, females may actively and passively select for potential males on the basis of food resources, safety from predators, avoidance of harassment, or male phenotype (Clutton-Brock 1989; Saunders et al. 2005). In pronghorns (*Antilocapra americana),* females employ mate-sampling tactics by visiting different males before eventually mating with one (Byers 1997; Byers et al. 2005). Red deer are highly polygynous and usually have a harem mating system (Clutton-Brock et al. 1982a, b). In rarer cases, where food resources are clumped in space, red deer males may be territorial (Carranza et al. 1995; Sánchez-Prieto et al. 2004). In the case of harems, males herd females and compete among themselves for control of the resulting groups. No firm evidence has been found to show that females actively select mating partners, and male–male competition is assumed to be more important than female–female competition in determining which individuals mate in this species (Carranza 1995; Clutton-Brock et al. 1982a; Gibson and Guinness 1980). However, in an experimental study, McComb (1991) suggested that red deer females choose mates with high roaring rates. In addition, female red deer can discriminate between the roars of their current harem-holding male, and those of neighbouring males, and they move between different harems when they are in oestrous (Pemberton et al. 1992; Reby et al. 2001).

In polygynous ungulates, female–female competition over mates was considered unlikely. However, recent evidence showed that female topi (*Damaliscus lunatus*) competed aggressively with each other in order to mate with preferred males on central lek territories. It is thought that females do this to avoid mating with exhausted and sperm-depleted males at times of high mating activity. In addition, females were more likely to actively disrupt the matings of others in the lek centre than anywhere else (Bro-Jørgensen 2002). In Soay sheep (*Ovis aries)*, large rams can become sperm depleted as the mating season progresses, and this may also occur in other polygynous ungulates (Preston et al. 2001). Therefore, seasonal or short-term sperm depletion of high-quality males may be another important factor that results in the evolution of female–female competition over mates.

Aggressive interactions among red deer females are common and they usually result from female competition over food resources (Thouless 1990; Veiberg et al. 2004). Additionally, dominance relationships among females are usually clearly defined, and winning agonistic interactions is related to age and experience (Thouless and Guinness 1986). There are no data available on female aggression rates in harems and the potential for female–female competition in this context has been overlooked. The operational sex ratio of this species is usually strongly female biased, as females mate at an age of 2 years old and males rarely mate before the age of 5 years. Additionally, there are large differences in male quality and high rates of mating and other mating-related activities can result in males becoming exhausted (Clutton-Brock et al. 1982a). Male red deer and males of other polygynous deer lose a large proportion of their body weight during the breeding season (McElligott et al. 2003; Yoccoz et al. 2002).

In this study, we examined if oestrous female red deer in harems experience elevated aggression rates, compared to when they are not in oestrous, and in other social contexts. In order to distinguish between female aggression over food and resting places, and potential female aggression over mates, we compared aggression rates of females in foraging groups, with aggression rates of females in harems. We also compared the aggression rates of females in harem groups that were either in oestrous or not. If the aggression rates of females in harems and in oestrous are significantly higher than the aggression rates of females in harem groups but not in oestrous, then it could indicate that intrasexual female competition over mates occurs in red deer.

Materials and methods

Study site and population

This study was carried out in a valley called Val Trupchun (46°35′N/10°04′E) in the Swiss National Park (SNP). The SNP is situated in southeast Switzerland. Val Trupchun is 20 km^2 in size, and the vegetation consists of forests and Alpine meadows. The forest has an open structure with regular avalanche aisles and the most dominant tree species is the larch. The tree line is situated at 2200 m a.s.l. and grass meadows are found above this altitude. The red deer population of Val Trupchun only spend the summer in that area and leave in winter (Haller 2002). The breeding season normally lasts in Switzerland from early September until mid-October (Merkel 1995). In summer 2003, the population in Val Trupchun consisted of approximately 215 stags, 228 females and 114 calves.

Observations

We carried out fieldwork from June 25 until October 4, 2003. We conducted our observations 5 days per week while the deer were on their summer range, and every day during the breeding season. Observations were carried out from dawn to dusk. Dawn occurred at approximately 5.00 at the beginning of the study period and 7.00 at the end. Dusk occurred between 22.00 and 20.00. We used telescopes (Kowa and Swarovski, ×20–60 lens magnification) and all data were recorded using dictaphones. All observations were carried out from the walking tracks or from one of the three rest areas. This was in accordance with park regulations.

In 2003, the first harem was observed on August 28 and we used this as an indication of the start of the breeding season. Rutting grounds were the sites where harem-holding stags were observed with their harems and where matings took place. They were situated at and below the tree line.

Focal watches of females

We carried out continuous focal watches of randomly chosen females. For each focal watch we recorded the date and the social context. We defined three social contexts; foraging group, harem with the focal female not in oestrous, and finally harem with the focal female in oestrous. Later in the text these are referred to simply as foraging group, harem group and oestrous group. During focal watches, the time and type of every aggressive interaction were recorded and if the focal female was the aggressor or the receiver. The following definitions were used for the differentiation of the types of aggressive interactions: mild threats such as nose threats, ear threats and displacements and severe threats such as kicking, biting and chasing (Clutton-Brock et al. 1982a). In addition, changes in group size or harem size of the focal female were continuously recorded. The females were observed for 422 h and the total number of focal watches was 213. The focal watches lasted as long as the focal female could be seen, which was between 10 and 422 min (mean $\pm$ SE $=$ 120.13 $\pm$ 7.86).

Data analysis and statistics

All data were organized in Excel and statistical analyses were performed in SPSS 11.0 and SAS. All tests are 2-tailed and factors were considered to have a statistically significant influence if $P \leqslant 0.05$. Means are given with standard errors.

Aggression types and aggression rate

We used a χ^2 test to check for differences in the proportions of the six different aggression types between foraging groups, harem groups and oestrous groups. We calculated aggression rates as the number of aggressive interactions per hour. The overall aggression rate was used for all the statistical analyses. This includes the aggressive interactions both when the focal female was the aggressor and when it was the receiver.

Aggression rate and percentage time inactive

We first checked if a significant difference existed in the percentage time inactive between females in foraging groups, females in harem groups and females in oestrous groups. This was carried out with a random sample ($n = 24$; $n = 8$ from each social context) out of the whole data set. First, we used the Levene's test to examine the homogeneity of variances. We then carried out a univariate general linear model (GLM). If this GLM showed a significant difference, then only the percentage time a focal female was active could be used for the calculation of aggression rates.

Aggression rate and group size

Group sizes were generally much larger in foraging groups than in harem groups. Therefore it was necessary to test if differences in aggression rates were due to differences in group size. During a focal watch, the group size also often varied.

Therefore, we first divided the 213 focal watches into several periods with different group sizes. This resulted in 320 periods for which aggression rates were calculated. We then removed periods in which the aggression rate was zero ($n = 205$) and four extreme values to improve the distribution of the residuals. In addition, both the aggression rates and the group sizes were log transformed. We examined the relationship between group size and aggression rate using Pearson correlation. The Pearson correlation was carried out once for the whole data set and once for each social context separately.

Aggression rates in different social contexts

We tested for significant differences in overall aggression rates between females in foraging groups, harem groups and oestrous groups. We carried out a GLM with a log link function and an assumed Poisson distribution of the error. The criteria for assessing goodness of fit showed that the aggression rate data had an almost perfect Poisson distribution (Pearson $\chi^2 = 1.68$). Therefore it was appropriate to use this GLM. The model also took into account the different observation durations. The influence of the observation duration on the number of aggressive interactions observed was, as expected, significant ($\chi^2_{1,316} = 50.32$, $P<0.001$). The estimate ($=0.0049$) showed that there are 5/1000 more aggressive interactions per minute, i.e. 30% more aggressive interactions per additional hour. Within this GLM the three categories of the independent variable (foraging groups, harem groups, oestrous groups) were contrasted against each other to check for a significant difference. We also report the numbers and proportions of aggressive interactions given and received by females in the three social contexts. However, these could not be analysed in detail.

Results

Observation durations and group sizes

It was possible to observe the females for longer periods in their foraging groups ($\text{mean} = 195.95 \pm 15.45\,\text{min}, n = 73$) than in harem ($\text{mean} = 75.5 \pm 6.72\,\text{min}, n = 126$) and oestrous groups ($\text{mean} = 112.36 \pm 24.44\,\text{min}$, $n = 14$). The group sizes in foraging groups ($\text{mean} = 38.33 \pm 4.57$) were much larger than in harem ($\text{mean} = 5.16 \pm 0.26$) and oestrous groups ($\text{mean} = 5.67 \pm 0.62$).

Types of aggression and overall aggression rate

The most common form of aggression in all three social contexts was displacement (Tab. 1). Nose threats were also very common and often occurred simultaneously with displacements. The occurrence of ear threats and chases was, however, very low in all three social contexts. There were no significant differences in the proportion of the 6 different aggression types between females in foraging groups, harem groups and oestrous groups ($\chi^2 = 14.05, P = 0.25$). The overall aggression rate ranged from 0 to 22.5 interactions per hour (median = 0).

Aggression rate and percentage time inactive

The percentage time that females were inactive in foraging groups ($\text{mean} = 0.61 \pm 0.06$), harem groups ($\text{mean} = 0.57 \pm 0.07$) and oestrous groups ($\text{mean} = 0.46 \pm$

Table 1. Numbers and proportions of aggressive interactions for each aggression type and each social context.

Aggression	Foraging group		Harem group		Oestrous group		Total
	n	%	*n*	%	*n*	%	*n*
Ear threat	21	4.3	4	3.5	0	0	25
Nose threat	147	29.9	36	31.3	19	35.2	202
Displacement	199	40.5	46	40.0	24	44.4	269
Kicking	79	16.1	14	12.2	11	20.4	104
Biting	40	8.1	15	13.0	0	0	55
Chasing	5	1.0	0	0	0	0	5
Total	491	100	115	100	54	100	660

0.05) was not significantly different (GLM: $F_{2,0.87} = 1.63$, $P = 0.22$, $r^2 = 0.14$). Therefore, any difference in aggression rate between the three social contexts was not because the percentage time that females were inactive was different in each context, and the total observation time was used for calculating aggression rates.

Aggression rate and group size

There was a significant negative relationship between overall aggression rate and group size for the whole dataset (Pearson correlation: $r = -0.38$, $P < 0.001$, $n = 111$). However, the relationships between overall aggression rate and group size for each social context considered separately (foraging groups, Pearson correlation: $r = -0.15$, $P = 0.27$, $n = 58$; harem groups, Pearson correlation: $r = 0.01$, $P = 0.97$, $n = 40$; oestrous groups, Pearson correlation: $r = -0.13$, $P = 0.67$, $n = 13$) were not significant. Therefore the aggression rate is influenced by the different social contexts and not by the group size.

Female aggression rates in the different social contexts

There were significant differences in the overall aggression rates between the three social contexts (Fig. 1, Tab. 2). Oestrous females in harems had the highest rates of aggression, along with non-oestrous females in foraging groups. The lowest rates of aggression were found in non-oestrous females in harems. The number of aggressions given is higher than those received in all three contexts (Tab. 3). However, there is some evidence to suggest that oestrous females receive proportionately more aggressions than they give, compared to non-oestrous females in the other two social contexts (Tab. 3).

Discussion

Aggressive interactions among female red deer were clearly evident and common in the study population. The most common forms of aggression were displacements, nose threats and kicking. Biting and ear threats occurred less frequently, and chases were rare. These results are generally consistent with the findings of others (Clutton-Brock et al. 1982a, 1986; Thouless 1990). There were no differences in the proportion of the different aggression types in the three social contexts. More importantly, we found that the highest aggression rates were for oestrous females in harems, and for females in

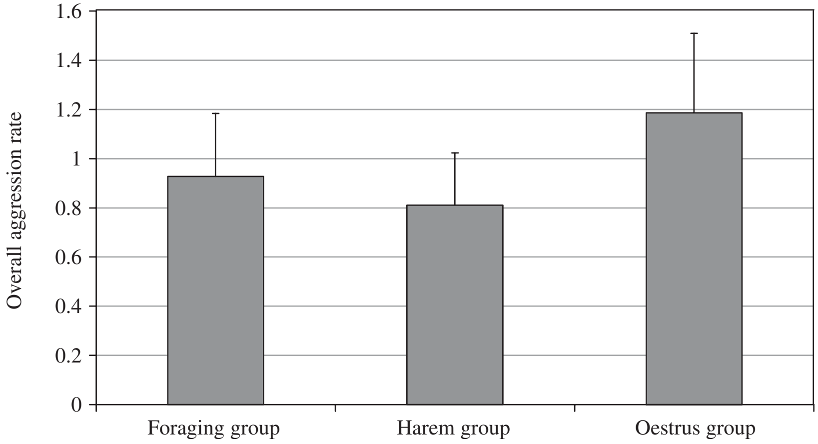

Fig. 1. Overall aggression rate per hour (mean ± SE) for the focal females in foraging groups (mean $= 0.93 \pm 0.26, n = 92$), harem groups (mean $= 0.81 \pm 0.21, n = 198$) and oestrous groups (mean $= 1.19 \pm 0.32$, $n = 30$).

foraging groups. In addition, some evidence suggests that oestrous females receive proportionately more aggressions than they give, compared to females in the other two social contexts. The lowest rates of aggression were found in harems (when the focal female was not in oestrous). These results suggest that female–female competition over mates could play a role in the mating behaviour of red deer. If high rates of aggression also occur when several females are simultaneously in oestrous within single harems, then it is possible that this aggression could affect either mate choice or mating order, as is the case with topi (Bro-Jørgensen 2002).

We found that the mean overall aggression rate among females in foraging groups was 0.93 interactions per hour. This is similar to the only other population that is available for comparison (Clutton-Brock et al. 1982a, 1986; Thouless 1990). The aggression rate of females in foraging groups was significantly higher than for females in harem groups (0.81 per hour). This could result from foraging groups being larger than harem groups, and nearest neighbour distances decline as group size increases (Clutton-Brock et al. 1982a). However, our results showed that there was no relationship between group size and aggression rate, when each social context was considered separately. These results are contrary to the theory that aggression rate should increase as group size increases (Clutton-Brock et al. 1982b). The aggression rate in foraging groups may be higher than in harem groups because related females tend to be found in the same harems (Clutton-Brock et al. 1982b). Therefore as a result of kin selection, the degree of competition could be reduced if rivals are related to one another (Griffin and West 2002; Rosenqvist and Berglund 1992).

Table 2. GLM analysis with overall aggression rate as a function of the three social contexts. Contrasts of the three categories of the explanatory variable with overall aggression rate as the dependent variable are shown.

Contrast	$F_{1,316}$	P
Foraging group – harem group	10.71	0.001
Harem group – oestrous group	25.16	<0.001
Foraging group – oestrous group	0.08	0.78

The mean aggression rate of females in oestrous was 1.19 per hour and this was significantly higher than for females that were in harems, but not in oestrous. This aggression consisted of similar numbers of aggression both given by oestrous females, as well as received from other females by oestrous females. Unfortunately, no other data on female aggression rates in harems are available in the literature for comparison. We suggest that this high rate of aggression involving oestrous female red deer could be new evidence for female competition for mates in a polygynous ungulate (Bro-Jørgensen 2002). This competition could have two important results. Firstly, certain females could be excluded from mating with particular males (Berglund et al. 1993; Foster 1983). It is already known that females can be highly aggressive to one another when foraging, and the most dominant females have access to better quality forage as well as higher overall reproductive success (Clutton-Brock et al. 1984, 1986; Veiberg et al. 2004). Females also move between harems (Pemberton et al. 1992) and aggression from other females could be a factor that influences the

Table 3. Numbers and proportions of aggression given and aggression received by focal females for each social context.

Social context	Total aggression	Aggression given		Aggression received	
	n	n	% of total	n	% of total
Foraging group	171	124	72.5	47	27.5
Harem group	52	35	67.3	17	32.7
Oestrous group	25	14	56.0	11	44.0

occurrence of these movements. Secondly, even if females are not excluded from mating with a particular male, the order in which they mate may change, and thus there is greater risk of a female being receptive when a male is exhausted or sperm depleted (Bro-Jørgensen 2002; Preston et al. 2001).

Harems with more than one female in estrus at the same time were only observed on three occasions during the current study. The summer of 2003 was extraordinarily hot and dry (Schweizerischer Nationalpark Geschäftsbericht 2003), and therefore a substantial part of the population (N. Bebié, personal observation) had left the study site at an early stage in the breeding season and moved to lower valleys for better foraging. This usually occurs later in the year, after the breeding season (Haller 2002). Therefore the potential for female–female aggression within harems was less likely in the year in which this study was carried out, due to environmental conditions. The fact that we found the highest aggression rates for oestrous females despite the reduction in the population due to environmental influences further emphasizes the potential importance of aggression involving oestrous females in harems.

Strong evidence showing that environmental or human influences affect the occurrence of female–female competition in polygynous ungulates already exists. In the critically endangered saiga antelope (*Saiga tatarica tatarica*), a catastrophic drop in the number of adult males due to poaching led to a strongly female-biased operational sex ratio. After the reduction in male numbers, dominant females aggressively excluded subordinate females from the males (Milner-Gulland et al. 2003). Therefore the mating behaviour of female ungulates can be very flexible and change depending on local conditions. If the number of mature males in our study population decreased or the number of females increased, one would also predict a change in the occurrence of female–female aggression within harems, if competition for males occurs. Other aspects of the breeding of red deer, such as mating skew, have already been shown to be sensitive to population density and sex ratio changes (Clutton-Brock et al. 1997).

Higher aggression rates involving oestrous female red deer suggest that female–female competition over mates could play a role in the mating behaviour of red deer. New research involving identifiable females is needed in order to determine if the aggressive behaviour or dominance status of oestrous females affects either mate choice or mating order in this species.

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Zusammenfassung

Aggressives Verhalten bei Rotwildkühen: Ein Zeichen für Konkurrenz unter Weibchen um potentielle Paarungen?

Die Konkurrenz unter Weibchen um potentielle Paarungen wird oftmals als nicht relevant erachtet, vor allem bei polygynen Arten. Beim Rothirsch (*Cervus elaphus*) wurden bis heute keine Studien über weibliche Aggressivitäten in Harems während der Paarungszeit durchgeführt. In unserer Studie haben wir untersucht, ob Rothirschkühe im Harem und im Oestrus höhere Aggressionsraten aufweisen als Kühe im Harem, die aber nicht im Oestrus sind, oder Kühe in Kahlwildrudeln ausserhalb der Paarungszeit. Erhöhte Aggressivität bei Rothirschkühen, die im Oestrus sind, kann als

Zeichen für Konkurrenz unter Weibchen um potentielle Paarungen gedeutet werden. Aggressive Interaktionen zwischen Rothirschkühen fanden häufig statt während unserer Studie. Die meistverbreiteten Aggressivitäten waren Verdrängungen, Drohgebärden mit dem Äser und Tritte. Bisse und Drohgebärden mit den Ohren fanden weniger häufig statt und Verfolgungen waren selten. Wir fanden keinen Unterschied in der Häufigkeit der verschiedenen Aggressivitätsformen zwischen den drei verschiedenen sozialen Kontexten. Es konnte jedoch gezeigt werden, dass Rothirschkühe im Harem und im Oestrus sowie Kühe in Kahlwildrudeln ausserhalb der Paarungszeit die höchsten Aggressionsraten aufweisen. Die tiefsten Aggressionsraten wurden in Harems gefunden, wenn das Fokustier nicht im Oestrus war. Falls hohe Aggressionsraten auch auftreten, wenn mehrere Weibchen gleichzeitig im Oestrus sind innerhalb eines einzelnen Harems, dann ist es möglich, dass diese Aggressivität die Partnerwahl oder die Reihenfolge der Paarungen beeinflusst. Diese Studie zeigt auf, dass die Konkurrenz unter Weibchen um potentielle Paarungen eine wichtige Rolle beim Paarungsverhalten des Rotwildes spielen kann.

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