The role of females in red deer matings

Diploma thesis

Nicole Bebié
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Institut de zoologie, Université de Neuchâtel
Zoologisches Institut (Verhaltensbiol.), Universität Zürich

Supervised by:

Dr. Alan McElligott
Zoologisches Institut (Verhaltensbiol.), Universität Zürich

Prof. Claude Mermod
Institut de zoologie, Université de Neuchâtel

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Abstract

The role of females in mate choice has been increasingly acknowledged, but there are still many open questions as to how female behaviour influences sexual selection. For example, there may well be important, but as yet underestimated consequences of female-female competition over mates as a special form of female choice. In red deer, the potential of female-female competition has largely been ignored. In my study, I examined the aggressive behaviour of females in a red deer population in the Swiss National Park. In order to separate female contest competition over food and other resources from female-female competition over mates, I examined the aggression rates of hinds in foraging groups and hinds in harems that were either in oestrus or not. The aggression rate for hinds that were in a harem and in oestrus was significantly higher than for hinds that were in a harem but not in oestrus. This suggests that female-female competition over mates may play a role in the mating behaviour of red deer. Furthermore, I examined if hinds move between harems and if there are any factors related to those movements. I found that the hinds moved freely between harems, but it is not possible to tell if the observed movements were mate sampling actions. The order in which the hinds visited the different harems was not related to mating success, dominance rank or antler size of the harem-holding stags. However, my study suggests that female behaviour plays a more important role in red deer matings than previously assumed.

Zusammenfassung

Die Rolle der Weibchen bei der Partnerwahl wurde in den letzten Jahren generell immer stärker betrachtet, aber es gibt immer noch viele offene Fragen zum Einfluss des weiblichen Paarungsverhaltens auf die sexuelle Selektion. Zum Beispiel zieht die Konkurrenz unter Weibchen als eine besondere Form der Partnerwahl sehr wahrscheinlich wichtige, aber bisher unterschätzte Konsequenzen nach sich. Beim Rothirsch wurde das Potential dieser Konkurrenz unter Weibchen bis jetzt weitgehend ignoriert. In meiner Studie habe ich das aggressive Verhalten der Weibchen in einer Rothirschpopulation im Schweizerischen Nationalpark untersucht. Um die Konkurrenz betreffend Nahrung und anderer Ressourcen von der Konkurrenz betreffend potentieller Paarungen zu unterscheiden, habe ich die Aggressionsraten der Hirschkühe in den Kahlwildrudeln und der Hirschkühe in den Harems untersucht. Die Aggressionsrate für die Kühe, die im Harem und im Oestrus waren, war signifikant höher als für die Kühe, die zwar auch im Harem, aber nicht im Oestrus waren. Dies könnte bedeuten, dass die Konkurrenz unter Weibchen betreffend potentiellen Paarungen von Bedeutung ist beim Paarungsverhalten der Rothirsche. Des Weiteren habe ich untersucht, ob die Kühe Harems wechseln während der Brunftzeit und welche Faktoren bei diesen Haremswechseln eine Rolle spielen. Ich konnte zeigen, dass die Kühe sich frei zwischen den verschiedenen Harems bewegen, aber mit meinen Daten war es nicht möglich zu bestimmen, ob diese Haremswechsel in direktem Zusammenhang mit der Partnerwahl stehen. Die Reihenfolge, in der die Kühe die verschiedenen Harems besuchten, stand in keiner Beziehung zu Paarungserfolg, Dominanz oder Geweihgrösse der Platzhirsche. Abschliessend lässt sich sagen, dass meine Studie Hinweise darauf liefert, dass das Verhalten der Kühe eine wichtigere Rolle bei den Rothirschpaarungen spielt, als bisher angenommen wurde.

1. Introduction

1.1 Sexual selection

According to Darwin (1871), sexual selection arises from differences in mating success caused by competition for mates. It therefore requires sexual reproduction; the combination of genetic material from two parents in the progeny. For polygynous species, in which some males mate with several females and others with none, success in competition for mates is crucial for the fitness of males. Therefore these species are often sexually dimorphic in body morphology, weaponry and ornaments (Jarman 1983; Andersson 1994). When Darwin (1859) first proposed the possibility of sexual selection, he identified two mechanisms of competition for mates; male-male competition (=intrasexual selection) and female mate choice (=intersexual selection).

There are two main kinds of sex traits that differ between males and females. Primary sex traits are directly connected with the act of reproduction; gonads and copulatory organs. But males and females also differ in secondary sex traits, such as the greater size of the male, his weapons, colors, various ornaments, song and other such characteristics. These secondary sex traits evolve by sexual selection, often in opposition to natural selection (Darwin 1871; Andersson 1994). Such conspicuous, costly male traits may become targets of female choice because they indicate high heritable viability (Zahavi 1975; Zahavi 2003). The role of females in mate choice has been increasingly acknowledged, but there are still many open questions as to how female behaviour influences sexual selection. For example, there may well be important, but as yet underestimated consequences of female-female competition as a special form of female choice (Berglund et al. 1993; Ahnesjö et al. 1993).

1.2 Female mate choice

1.2.1 Definitions

Wiley & Poston (1996) distinguished two forms of mate choice; direct and indirect. Direct mate choice requires discrimination among the features of possible mates. Any behavioural or morphological features could serve for such discrimination. However, discrimination among possible mates is not necessary for mate choice. Any other behaviour that makes it less likely to mate with certain individuals of the opposite sex than with others, is called indirect mate choice. Direct female mate choice decisions are individually variable. They depend on mating preferences, which are defined as the sensory and behavioural properties that influence the propensity of individuals to mate with certain phenotypes (Jennions & Petrie 1997). Mating preferences are further subdivided into two properties; preference functions and choosiness. Preference functions are defined as the order in which an individual ranks prospective mates (Jennions & Petrie 1997). Choosiness is defined as the effort or energy that an individual is prepared to invest in assessing mates, both in terms of the number of mates sampled and the amount of time spent examining each mate (Jennions & Petrie 1997). There are a number of potential benefits and costs to female mate choice. Direct benefits may include fertilization assurance, nutritional content of the ejaculate and avoidance of disease or disruption of copulation. The most important indirect benefit is increased offspring viability. The costs of female mate choice may include time, energy, predation risk and competition with other females (Rosenqvist & Berglund 1992). If there is costly competition for mates, the poorest competitors might be better off avoiding the highest-quality mates, so that they minimize the costs they incur. Thus, variation in competitive ability generates variation in both the strength and direction of mating preferences (Fawcett & Johnstone 2003).

1.2.2 Female mate choice in ungulates

In polygynous species, females may actively and passively select for potential males on the basis of, for example, food resources, safety from predators, avoidance of harassment, or male phenotype (Clutton-Brock 1989). However, female topi antelopes (*Damaliscus lunatus)* mainly based their mate choice on lek centrality as a way to assess male quality. Females were more likely to mate, and to mate sooner after arrival on central lek territories than elsewhere (Bro-Jørgensen 2002). In pronghorns (*Antilocapra americana),* females move between harems. Most of these movements are referred to as mate-sampling actions. Females often returned to and mated with a male that they had previously visited (Byers 1997). One study on fallow deer (*Dama dama)* showed that the proportion of time that males spent vocalizing during the rut was highly correlated with mating success. Therefore, it was suggested that females could assess males based on their long-term investment in vocal display during the breeding season (McElligott et al. 1999). However, experiments are required to determine the mating preferences of female fallow deer.

Red deer are highly polygynous and usually have a harem mating system. A harem is defined as a group of hinds defended by a stag at a particular time on a given day during the breeding season (Clutton-Brock et al. 1982). Female red deer aggregate during the rut more than at other times of the year (Clutton-Brock et al. 1982). Males herd females and compete among themselves for control of the resulting harems. The aggregation by females might have consequences unrelated to mating. For instance it appears to be advantageous for optimal grazing in autumn. Nevertheless, behaviour by females that facilitates herding by males is a form of indirect mate choice (Wiley & Poston 1996). On Rum, Scotland, no firm evidence was found that hinds actively selected particular breeding partners (Gibson 1978; Gibson & Guinness 1980; Clutton-Brock et al. 1982). For territorial rutting red deer in Spain, Carranza (1995) also suggested male-male competition to be the main component of sexual selection and not female mate choice. However, several other studies indicated the existence of female mate choice in red deer, for example, based on roaring rates (McComb 1991; Reby et al. 2001) or antler size (Lincoln 1992).

1.3 Female-female competition

1.3.1 What is female-female competition?

Females may compete either for access to mates or for reproductive resources such as space, nest sites or food, and it is often difficult to distinguish between the two types of competition (Rosenqvist & Berglund 1992; Jennions & Petrie 1997). However, female-female competition over mates can also sometimes take subtle and indirect forms that do not involve overt aggressive interactions. Mate guarding by females is one of these forms (Jennions & Petrie 1997). Females can be expected to compete over males under three conditions. Firstly, if males and females have similar parental roles. Secondly, if the operational sex ratio is female biased, and thirdly, if male quality varies so that high-quality males are rare (Berglund et al. 1993; Andersson 1994).

At least four hypotheses have been invoked to explain female-female competition over mates (Berglund et al. 1993). According to the first hypothesis, females are kept waiting for the preferred males, and competition for precedence occurs because the costs of fighting are lower than the cost of making a second choice or postponing mating (Avery 1984; Barnard & Markus 1989; Gibson & Bradbury 1986). The second hypothesis states that females reduce the fitness of other females by preventing them from mating with high-quality males (Foster 1983). A third possibility is that by reducing the number of other females or offspring present, competition for food and other resources is reduced. Finally, it was suggested that by being the first to mate, sperm depletion and ensuing risks of unfertilized eggs are avoided (Avery 1984; Barnard & Markus 1989).

The fitness consequences of female-female competition over mates are virtually unknown. This is because males are usually the competing sex and females the choosing sex, and males also often compete in dramatic and conspicuous ways for females (Rosenqvist & Berglund 1992). However, underestimating this aspect of the behaviour of female animals means underestimating an important aspect of sexual selection.

1.3.2 Female-female competition in ungulates

For ungulates, it was believed that female-female competition over mates does not exist. However, there is recent evidence to suggest that this is not the case. Female topi antelopes compete aggressively with each other in order to mate with the preferred males on central lek territories. In addition, females were also more likely to actively disrupt the matings of others in the lek center than anywhere else (Bro-Jørgensen 2002).

In red deer, aggressive interactions among hinds are common (Clutton-Brock et al. 1982). However, these aggressive interactions are mostly due to female competition over food resources. There are no data available on female aggression rates in harems of red deer. The potential of female-female competition as a form of female choice in red deer has largely been ignored. In red deer, the operational sex ratio is strongly female biased, as hinds mate at an age of two years whereas stags rarely mate before the age of five years. In addition, there is a high genetic variability in the red deer population in the Swiss National Park (Haller 2002). Therefore there are also potential high differences in male quality (Shellman-Reeve & Reeve 2000). Due to these two reasons and because hinds are known to be aggressive towards each other, female-female competition is likely to occur in the red deer population of the Swiss National Park.

In order to separate female contest competition over food and other resources from female-female competition over mates, it is necessary to examine aggression rates of hinds in foraging groups and hinds in harem groups. If the aggression rates of hinds in harems are significantly higher than the aggression rates of hinds in foraging groups, then it could indicate that female-female competition over mates exists in red deer.

1.4 Aims of this study

The main aim of my study was to examine female-female competition over mates in red deer und use it as a potential indicator of active mate choice. In particular, I compared the aggression rates of hinds in foraging groups and hinds in harem groups that were either in oestrus or not. The movements of hinds between harems were also used as an indicator of active mate choice. In addition, I investigated the dominance relationships and the mating success of the mature stags.

I investigated the following questions:

1. Can female-female competition be observed in the red deer population of Val Trupchun in the Swiss National Park?
2. Is there a difference in female aggression rates between the three social contexts (foraging groups, harem groups, oestrus groups)?
3. Is there a difference in aggression rates between milk hinds, yeld hinds and female yearlings?
4. What influence has dominance rank and antler size on the mating success of the stags?
5. Do hinds move between harems and are there any factors related to those movements?
6. Is there a relationship between the mating success, the dominance rank and the antler size of a certain stag and the number of days a hind spends in his harem?

2. Materials and methods

2.1 Study animal

2.1.1 Species description

Red deer (*Cervus elaphus L.*) belong to the order of the Artiodactyla, to the suborder of the Ruminantiae and to the family of the Cervidae. Red deer populations extend from Western Europe to Central Asia (Clutton-Brock et al. 1982). The lifespan of red deer in Switzerland varies between 15 and 20 years under natural conditions (Merker 1995). Red deer males are called stags and females are called hinds.

Red deer are sexually dimorphic with large differences in body size and weight. In addition, males have antlers. In Switzerland, males weigh between 150 and 250kg, and females weigh between 90 and 150kg (Merker 1995). The antlers are deciduous and the males cast their antlers each year between February and March. They are fully regrown by July or August (Merker 1995). The number of tines increases with each new set of antlers for some years after maturity (Jarman 1983). The maximum number of tines varies between 8 and over 20 for Alpine red deer (Merker 1995). Red deer live in separate male and female foraging groups except during the breeding season. This sexual segregation outside the breeding season is related to different factors, such as activity budgets, predation risk or body-size-related forage selection (Bonenfant et al. 2004).

The oestrus cycle length for female red deer ranges from 5 to 25 days with a mean of 18.53 days (Jabbour et al. 1997). Although most hinds are successfully fertilized at their first oestrus, some cycle a second and even a third time (Clutton-Brock et al. 1982). The gestation length for red deer is 34 weeks (approximately 7½ months). The time of birth is in

May and June and the number of calves is almost always one. The lactation length varies between five and seven months (Merker 1995; Jabbour et al. 1997).

2.1.2 Reproduction

Sexual maturity occurs in both sexes at an age of 18 months but stags rarely mate before the age of five years (Merker 1995). Male mating success in red deer is highly skewed. In any year on Rum, nearly 50% of stags over four years old failed to breed, and only the most successful individuals (approximately the top 5% of breeders) sired more than four calves (Clutton-Brock et al. 1982). Red deer males in Switzerland have their mating success peak between 10 and 13 years of age (Merker 1995).

The breeding season normally lasts in Switzerland from early September until mid October (Merker 1995). At the onset of the breeding season, mature stags begin to leave their normal ranges and associate with hind groups, becoming progressively intolerant of the presence of other mature and immature stags. As far as possible, the harem-holding stag tries to prevent hinds from leaving the harem wherever possible by herding them back to the group. The harem-holders roar repeatedly and defend their harem by chasing away other stags and by fighting them if they have approximately the same strength (Bützler 1986; Clutton-Brock et al. 1982).

2.2 Study site and population

This study was carried out at Val Trupchun (46° 35’ N / 10° 04’ E) in the Swiss National Park (SNP). Val Trupchun is 20km^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 2200m a.s.l. and grass meadows are found above this altitude. At 2900m a.s.l. the nival zone with little vegetation starts. One walking track follows the valley floor on each side (Haller 2002).

The Swiss National Park (SNP) is situated in southeast Switzerland and borders Italy. The SNP covers an area of 172km^2 and its altitude ranges from 1400 to 3173m a.s.l. Its climate is continental (Buchli 1979). The SNP was established in 1914 and is classified as a Ia Nature Reserve. This means that agricultural, hunting and forestry practices are strictly prohibited within the reserve and visitors must remain on the walking tracks. The park is closed from approximately October to April due to snow cover (Haller 2002).

Red deer (*Cervus elaphus L.*) were extinct in Switzerland at the end of the 19th century due to overhunting. They immigrated again from Austria and have been observed in the SNP since 1918 (Schloeth 1972). Other ungulate species in the study area are chamois (*Rupicapra rupicapra*) and ibex (*Capra ibex*). The red deer population of Val Trupchun only spend the summer in that area and leave in winter. There are two reasons for these separate summer and winter home ranges. First, the SNP provides a suitable habitat for the deer in summer. Second, snow cover in the SNP is usually between one and two meters in height from November to April. Red deer start returning to Val Trupchun during May, and at the beginning of June most of the population has returned (Haller 2002).

The red deer population in the SNP and in Val Trupchun steadily grew until the 1970s. At this time, the population size had reached its estimated carrying capacity; 750 individuals in Val Trupchun in 1975 (Haller 2002). The population increase was mainly due to the Ia Nature Reserve status. In addition, the main hunting season in Graubünden takes place during three weeks in September when most of the deer are not yet outside the park. One other reason is that large natural predators of deer are lacking. As the population increased, intraspecific competition over food resources also increased. In the 1970s, a higher number of hinds shot resulted in a population decrease (Figure 1). The results were reduced intraspecific competition, better individual food provisioning, higher calving rates and higher survival rates during winters. The deer population in the SNP and in Val Trupchun decreased slightly since that time (Haller 2002). The population size and structure in Val Trupchun for 2003 are given in Table 1.

The sex ratio of the deer in Val Trupchun decreased from almost 2.5 ♀ : 1 ♂ in 1960 to approximately 1 : 1 in the 1990s (Figure 2) and in 2003 (Table 1). One of the reasons for this drop was the increased numbers of hinds shot. Another reason was that hunting of stags with a crown at the end of each main beam has not been allowed since 1992 (Haller 2002).

Table 1: Population size in Val Trupchun in 2003

	Count	+ 20% Approximation	**Estimated Total**
Stags	179	36	**215**
Hinds	190	38	**228**
Calves	95	19	**114**
Total	464	93	**557**

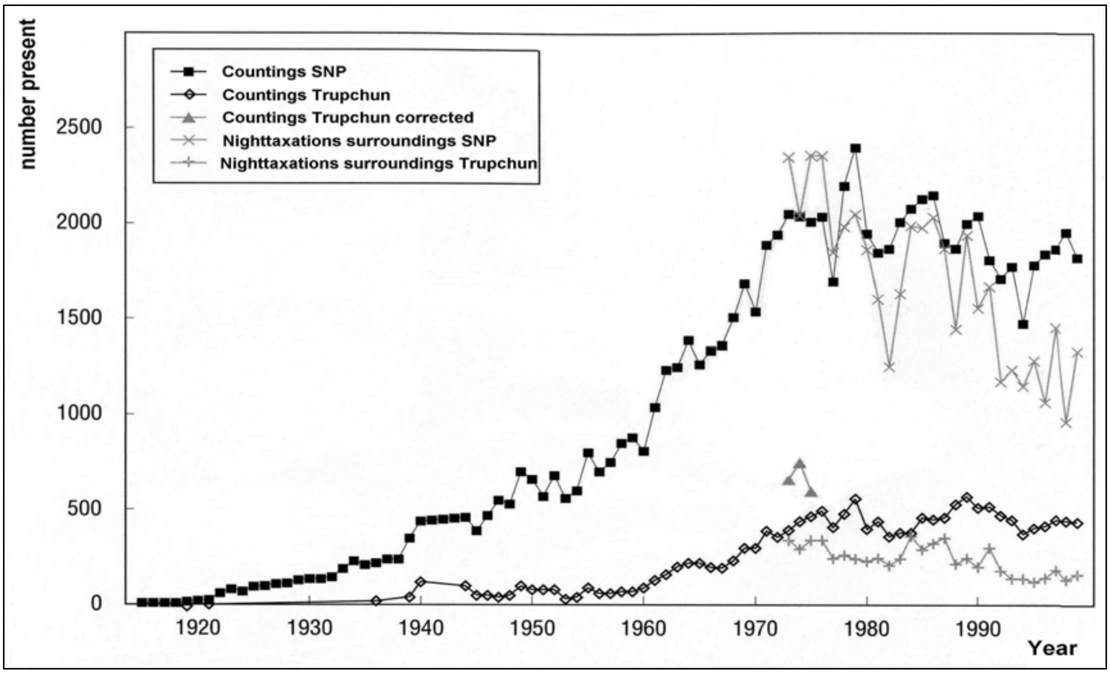


Figure 1: Population numbers (summer maxima) for red deer in the SNP since 1915 and in Val Trupchun since 1919, including corrected data for the years 1973 - 1975. Further results of night-time counts with halogen beams since 1973 are shown (Haller 2002).

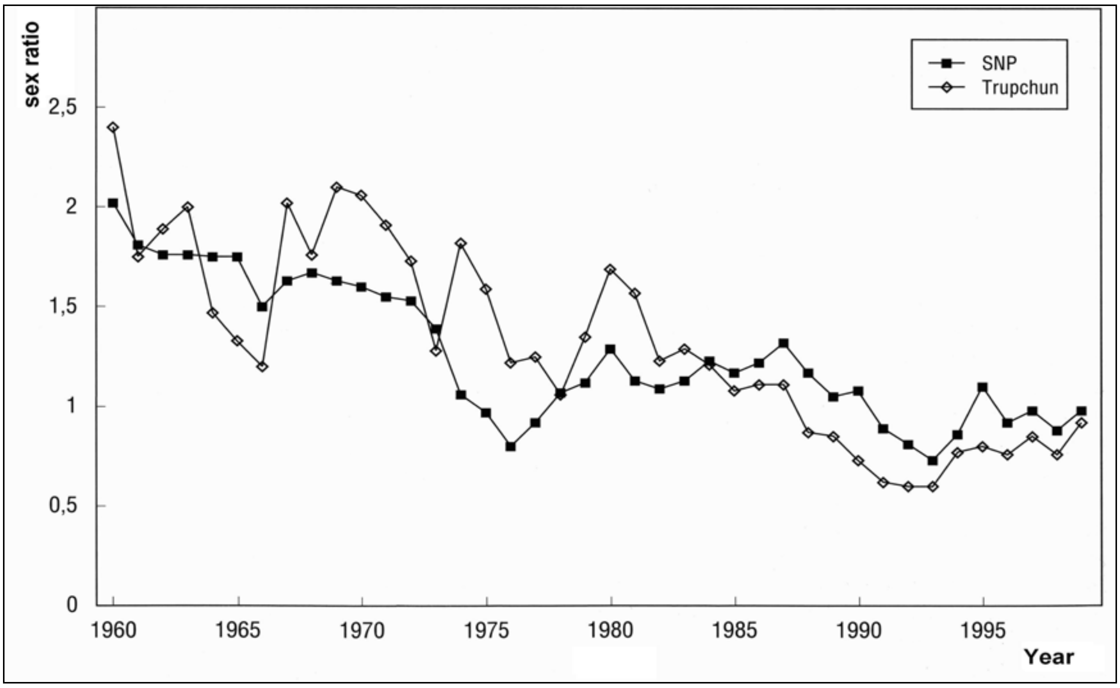
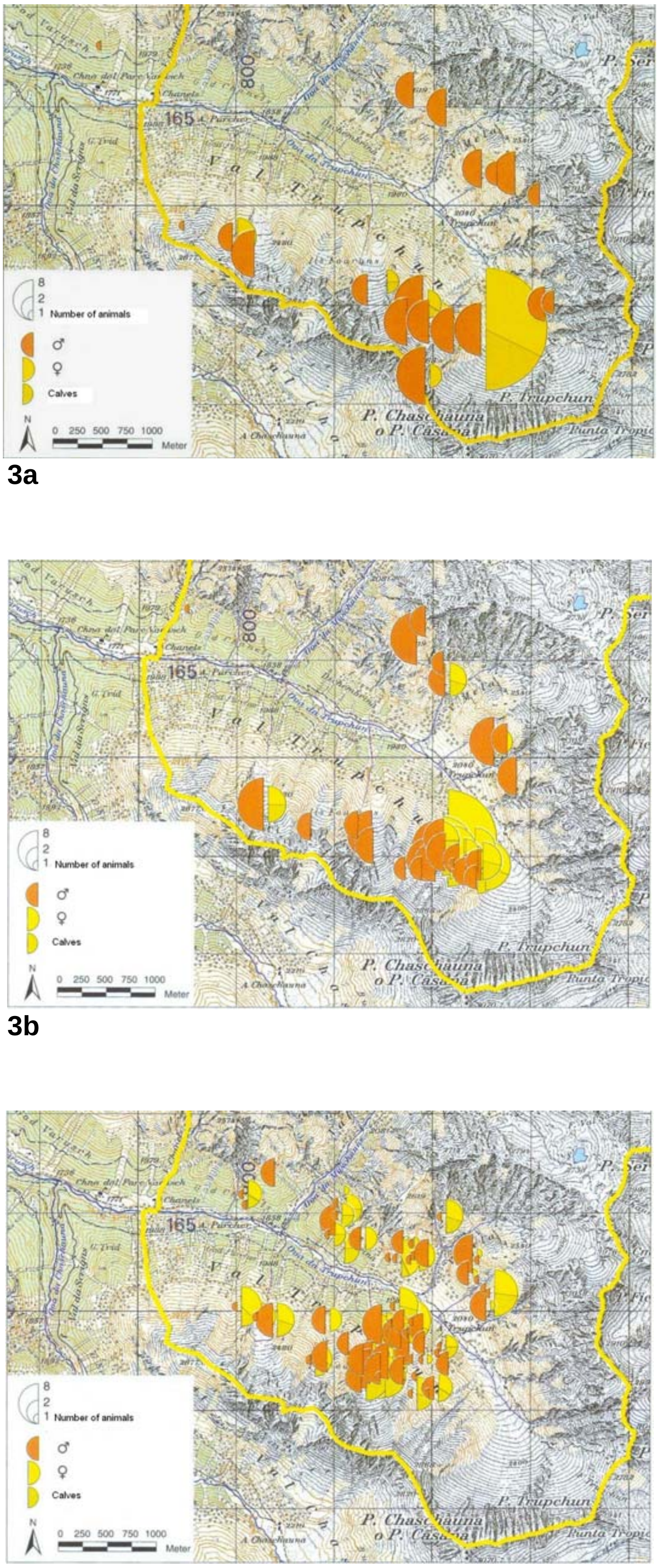


Figure 2: sex ratios (♀ : ♂; proportion ♂ = 1) of red deer in the SNP an in Val Trupchun, 1966 – 1999 (Haller 2002).

2.3 Observations

I carried out fieldwork from June 25 until October 4, 2003. Most observations were conducted with one other observer. We carried out observations five 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. In addition, we were in radio contact and organized to maximize coverage of all animals. All observations were carried out from the walking tracks or from one of the three rest areas. This was in accordance with park regulations.

The study population has its main summer home range at the southeastern end of the valley. The summer home range of the hinds is only on the southern side of the valley, whereas the home ranges of the stags are evenly distributed on both sides of the valley (Figure 3a, Haller 2002). 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. During the first week of the breeding season, approximately one third of the hinds changed at night to the northern side of the valley. The remaining ones were distributed evenly on the whole length of the southern side of the valley (Figure 3b+c). Also, some stags that were observed during summer on the southern side were seen on rutting grounds on the northern side and vice versa. At the end of the field season, a large proportion of the study population had already left Val Trupchun.



3a

3b

3c

Figure 3: Distribution of red deer in Val Trupchun (Haller 2002)
a: August 4 1997 (n = 380), **b:** September 1 1997 (n = 406),
c: October 3 1997 (n = 326)

2.3.1 Focal watches of females

We carried out continuous focal watches of randomly chosen females. The hinds were not individually recognisable with the exception of five tagged hinds. For each focal watch we recorded the date and the social context. I defined three social contexts; in a foraging group, in a harem and not in oestrus, and finally in a harem and in oestrus. In the text these are referred to simply as foraging group, harem group and oestrus group. We also recorded if we were observing a milk hind, yeld hind or a female yearling. Milk hinds were defined as hinds that had been observed nursing a calf or that were closely followed by a calf. Yeld hinds were those that had not given birth this year or had lost their calf. We defined them using two characteristics. Either they had not been observed nursing a calf for at least three hours or they were in a group with no calf that had not already been assigned to a hind. Hinds that could not be defined were recorded as unknown. During focal watches, we continuously recorded the exact time of every behavioural transition and the subsequent behaviour if it lasted longer than five seconds. We defined the following behaviours; grazing, standing, walking, lying, ruminating, nursing a calf and self-grooming. These data on the overall activity budgets were collected for a different study (Rieser, in prep.) and are not analysed in detail here. For my study, the time and type (Table 2) of every aggressive interaction were recorded and if the focal hind was the aggressor or the receiver. In addition, changes in group size or harem size of the focal hind were continuously recorded. The hinds were observed for 422 hours in total. The total number of focal watches was 213. The focal watches lasted as long as the focal hind could be seen, which was between 10 and 422 minutes (mean = 120.13 ± 7.86).

Table 2: Ethogram of female and male aggression types (Clutton-Brock et al. 1982; McElligott et al. 1998)

Female aggression types	
Mild threats:	
- Nose threat:	One hind pokes her head towards another, mostly at the neck, shoulder or rump
- Ear threat:	One hind lays back her ears while moving towards another
- Displacement:	One hind walks steadily towards another until the other one retreats
Severe threats:	
- Kick:	Kicks are usually performed with a single foreleg but sometimes with both
- Bite:	Bites are usually directed at the head, neck or shoulder of the opponent
- Chase:	Chases frequently follow bites and kicks
Male aggression types	
Interactions without antler contact:	
- Displacement:	Low-intensity interaction characterized by a clearly evident approach and threat, followed by a retreat of the opponent.
- Parallel walk:	A ritualized display in which 2 males walk in parallel, with a stiff-legged gait and with antlers held high. It is a high-intensity interaction since it often occurs during, and as a prelude to, fighting sequences.
Interactions with antler contact:	
- Sparring:	Low-intensity interaction because the opponents usually engage antlers slowly and push gently, if at all.
- Fighting	High-intensity interaction. The two stags lock their antlers and push to and fro, occasionally disengaging, until one individual is driven rapidly backwards.

2.3.2 Male identity and dominance relationships

The stags finished growing their antlers by mid July. We then sketched the antlers of all mature males to allow individual identification (Appendix 4). At the beginning of the breeding season we had sketched and named 60 stags. During the breeding season we continued sketching unknown mature stags holding a harem or those involved in agonistic interactions. By the end of the breeding season we had sketched 90 stags, which we recognised individually. We carried out all-event recordings of agonistic interactions. We recorded the type (Table 2) and duration of the aggressive interaction and the outcome (winner or loser).

2.3.3 Harems

During the breeding season all harems seen in the valley were noted twice per day. Once at the beginning of the daily observation period and once at the end. We recorded the harem-holding stag, the total number of hinds, the number of hinds in oestrus and the location of each harem.

2.3.4 Hind movements between harems

In the study population there were five individually recognisable females. These had collars around their necks with a transmitter and a number on each. Every day during the breeding season, we recorded if they were seen in a harem and if yes, the harem-holding stag and the location.

2.4 Data analysis and statistics

All data were organised 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 $P \leq 0.05$. Means are given with standard errors.

2.4.1 Female aggression types in the different social contexts

A χ^2 test was carried out to check for a difference in the proportions of the six different aggression types between foraging groups, harem groups and oestrus groups.

2.4.2 Female aggression rate

I calculated aggression rates as the number of aggressive interactions per hour. For all the statistical analyses, if not specially indicated, the overall aggression rate was used. This includes the aggressive interactions both when the focal hind was the receiver and when it was the aggressor.

2.4.3 Female aggression rate and percentage time a focal hind was inactive

As aggressive interactions occur mostly when an animal is active, I first checked if a significant difference existed in the percentage time inactive between hinds in foraging groups, hinds in harem groups and hinds in oestrus groups. This was carried out with a random sample (n = 24; n = 8 from each social context) out of the whole dataset. First, I used the Levene's test to examine the homogeneity of variances. I then carried out a univariate general linear model (GLM). If this GLM showed a significant difference, then only the percentage time a focal hind was active could have been used for the calculation of aggression rates. This was to avoid obtaining a difference in aggression rate between the three social contexts only because the percentage time a hind is inactive is different in each.

2.4.4 Female aggression rate and group size

Group sizes were generally much bigger 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, I first divided the 213 focal watches into several periods with different group sizes. This resulted in 320 periods for which aggression rates were calculated. I then removed periods in which the aggression rate was zero (n=202) and four extreme values to improve the distribution of the residuals. In addition, both the aggression rates and the group sizes were log transformed. I examined the relationship between group size and aggression rate using Pearson correlation. The Pearson correlation was carried out once for the whole dataset and once for each social context separately.

2.4.5 Female aggression rates in the different social contexts

I tested for significant differences in aggression rates between hinds in foraging groups, in harem groups and in oestrus groups. I 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 χ^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 aggressions 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 aggressions per minute, i.e. 30% more aggressions per additional hour. Within this GLM the three categories of the independent variable (foraging groups, harem groups, oestrus groups) were contrasted against each other to check for a significant difference.

2.4.6 Female aggression rates of milk hinds, yeld hinds and yearlings

I carried out a Kruskal-Wallis test to examine significant differences in aggression rates between milk hinds, yeld hinds and yearlings. Once this test was used for the total aggression rate and once for the active aggression rate, i.e. when the focal hind was the aggressor.

2.4.7 Aggression rates of the tagged females in realtion to the different social contexts and group sizes

Finally, I carried out a repeated measures GLM for the data from the five tagged females to check again for a significant difference in aggression rate between foraging groups and harem groups. The aggression rates for hinds in oestrus groups were not included in the analysis because only one of the tagged females was observed in oestrus. The two categories (foraging groups and harem groups) of the independent variable were further divided to check simultaneously for a significant difference in aggression rate between the different group sizes. Thus the following four categories were obtained: foraging groups with group size 1 – 10, foraging groups with group size 11 – 20, harem groups with size 1 – 10 and harem groups with size 11 – 20. The design therefore has two repeated measures factors (group size and social context). I used the mean aggression rates for each tagged hind and for each category.

2.4.8 Male dominance rank

We observed 67 stags involved in at least one agonistic interaction with one other known stag. For the calculation of the dominance ranks, I only considered stags that were observed in at least two agonistic interactions. Therefore the dominance ranks of 38 stags were calculated using 67 agonistic interactions. The Clutton-Brock Index (Clutton-Brock et al. 1979) and the David's Score (David 1987; Gammell et al. 2003) are the two most appropriate methods for calculating dominance ranks. Both of these can be used to calculate ranks for individuals in a group, based on the outcomes of their agonistic interactions with other group members, while taking the relative strengths of their opponents into account. The main disadvantage of the Clutton-Brock Index is that it does not include the total number of interactions recorded between different dyad members. For example, if one individual had interacted 10 times with another, winning on nine occasions and losing once, the formula of the Clutton-Brock Index would treat this as if each individual had beaten the other once

(Gammell et al. 2003). Because the ranks were calculated using a low number of interactions, I carried out both methods. I then applied Spearman rank correlation to test if the ranks of those two methods were correlated. The David's score was then used for any additional calculations.

2.4.9 Harems

I used an indirect method of estimating the mating success for each harem-holding stag. Because only a few matings (n = 6) were actually observed, the measure of each individual's mating success was the total number of days he held hinds multiplied by the mean number of hinds held on each day. This gave a total number of hind/days held for each individual (Clutton-Brock et al. 1979). Then, I first used the Levene's test to check for homogeneity of variances. Next, I carried out a univariate GLM with hind/days as the dependent variable. The independent variables were dominance rank and antler size (number of tines). One stag (Elrond) was not included in this model. Elrond had the second highest mating success but also had a very low dominance rank. The rutting ground for this male was in the forest and so we did not see any of his agonistic interactions except one towards the end of the rut, which he lost.

2.4.10 Hind movements between harems

I first tested for a relationship between the number of days each tagged hind was seen and the number of males visited by each one of these hinds. Therefore I carried out Pearson correlation to determine if the higher amount of males visited by certain females was not just because these females were seen on more days. I then carried out a Spearman rank correlation for each tagged female between the total number of days spent in the harem of a certain stag and the mating success of this stag. Otherwise, I analysed the hind movements between the harem-holding stags on a qualitative basis.

3. Results

3.1 Female aggression types in the different social contexts

Displacement was the aggression type that occurred most frequently in all three social contexts (Table 6). Nose threats also occurred very frequently and often appeared simultaneously to 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 hinds in foraging groups, harem groups and oestrus groups (χ^2=14.05, P=0.25).

Table 6: Number of aggressive interactions for each aggression type and for each social context

Aggression type	Foraging group	Harem group	Oestrus group	**Total**
Ear	21	4	0	**25**
Nose	147	36	19	**202**
Displacement	199	46	24	**269**
Kicking	79	14	11	**104**
Biting	40	15	0	**55**
Chasing	5	0	0	**5**
Total	**491**	**115**	**54**	**660**

3.2 Female aggression rate

It was possible to observe the hinds for longer periods in their foraging groups than in the harem and oestrus groups (Figure 4). During the breeding season, the hinds often stayed in the forest, and therefore they could only be observed when they moved into open patches and avalanche aisles. The number of focal watches and the summary statistics of the observation duration for each social context are given in Table 3. The total overall aggression rate ranged from 0 to 22.5 aggressive interactions per hour (median = 0). The total number of focal watches in which the aggression rate was zero was 111. If each social context considered separately, the number of focal watches in which the aggression rate was zero was 18 for the foraging groups, 86 for the harem groups and 6 for the oestrus groups. The summary statistics of the group size and the overall aggression rate for each social context are given in Table 4. The group sizes were much larger in foraging groups than in harem and oestrus groups (Figure 5).

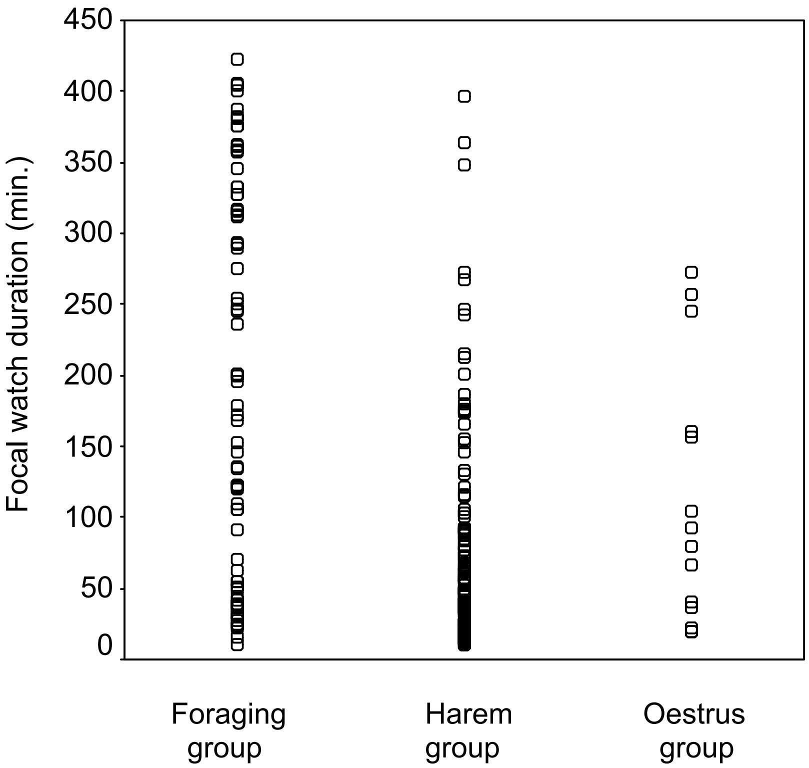


Figure 4: Focal watch durations (min.) for hinds in foraging groups (n = 73), harem groups (n = 126) and oestrus groups(n = 14).

Table 3: Number of focal watches and summary statistics of the observation duration for each social context

		Observation duration		
Social context	Focal watches	Total duration	Range (min.)	Mean ± SE (min.)
Foraging group	73	244h 56min	11-422	195.95 ± 15.45
Harem group	126	151h 1min	10-397	75.5 ± 6.72
Oestrus group	14	26h 20min	19-273	112.36 ± 24.44

Table 4: Summary statistics of the group size and the overall aggression rate for each social context

	Group size		Overall aggression rate	
Social context	Range	Mean ± SE	Range	Median
Foraging group	2-180	38.33 ± 4.57	0-22.5	0.39
Harem group	2-19	5.16 ± 0.26	0-20	0
Oestrus group	2-15	5.67 ± 0.62	0-3.75	0.82

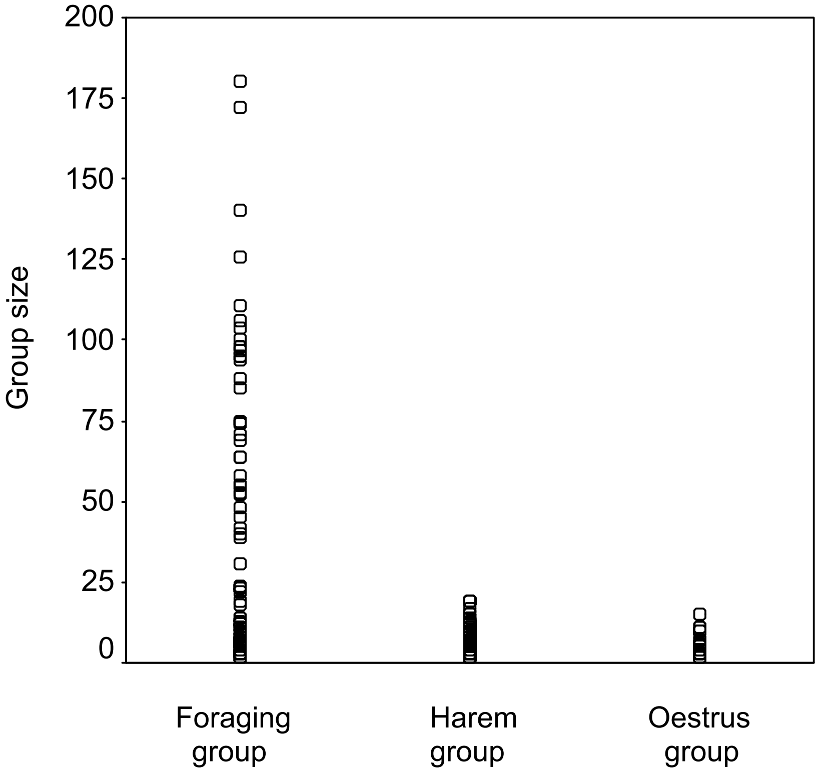


Figure 5: Group sizes of focal hinds in foraging groups (n=73), in harem groups (n=126) and in oestrus groups (n=14)

3.3 Female aggression rate and percentage time a focal hind was inactive

The percentage time that hinds were inactive in foraging groups, harem groups and oestrus groups was not significantly different, for a random sample (n = 24) out of the whole dataset (GLM: $F_{2,\ 0.87}$=1.63, P=0.22, r^2=0.14; Figure 6). This indicates that any difference in aggression rate between the three social contexts was not only because the percentage time hinds were inactive was different in each. Therefore the total observation time was used for calculating aggression rates.

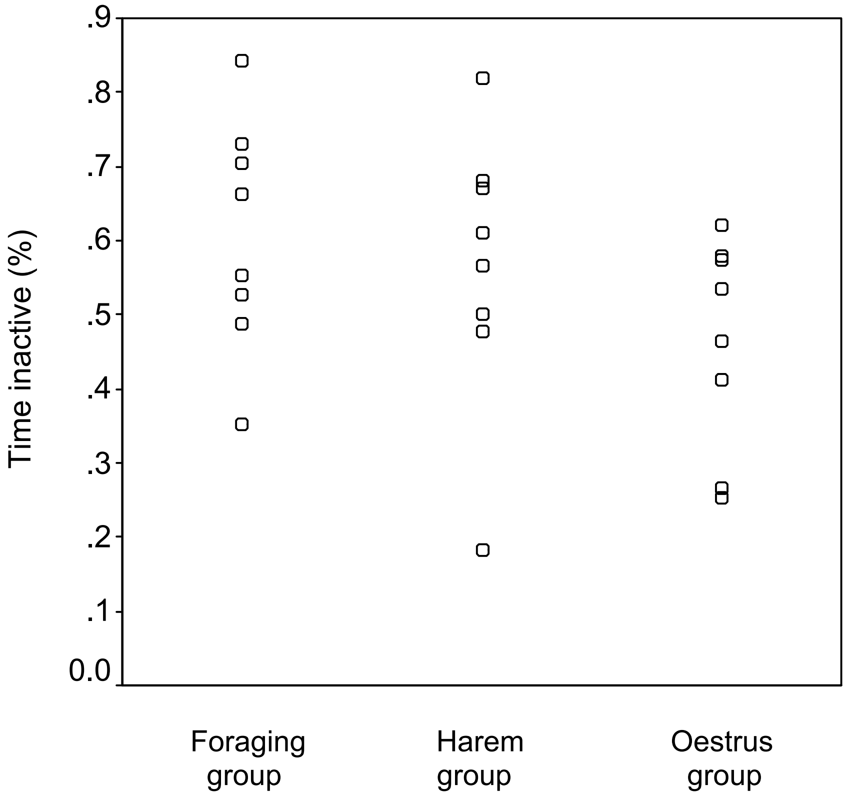


Figure 6: Percentage time inactive for focal hinds in foraging groups (n=8, mean=0.61 ± 0.06), in harems (n=8, mean=0.57 ± 0.07) and in oestrus (n=8, mean=0.46 ± 0.05)

3.4 Female aggression rate and group size

There was a significant negative relationship between overall aggression rate and group size for the whole dataset (Figure 7). However, the relationship between overall aggression rate and group size for each social context (foraging group, harem groups, oestrus groups) separately was not significant (Figure 8a-c). This suggests that the overall aggression rate is influenced by the different social contexts, rather than by the group size.

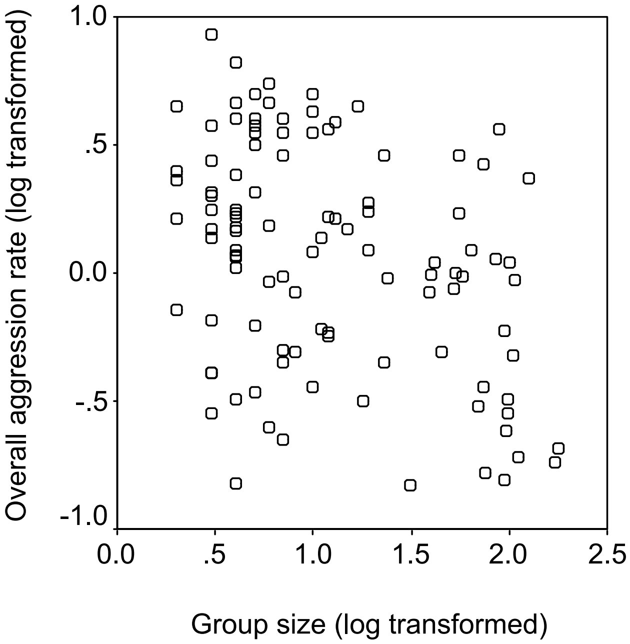


Figure 7: Relationship between group size and overall aggression rate per hour for the whole dataset (Pearson correlation: n=105, r=-0.38, P<0.001). The data in which the aggression rates are zero, and four extreme values were excluded.

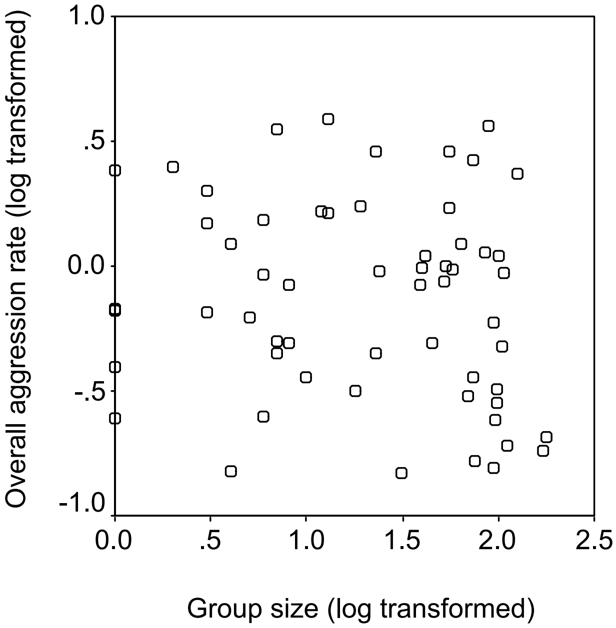


Figure 8a: Relationship between group size and overall aggression rate per hour for hinds in foraging groups (Pearson correlation: n=58, r=-0.15, P=0.27)

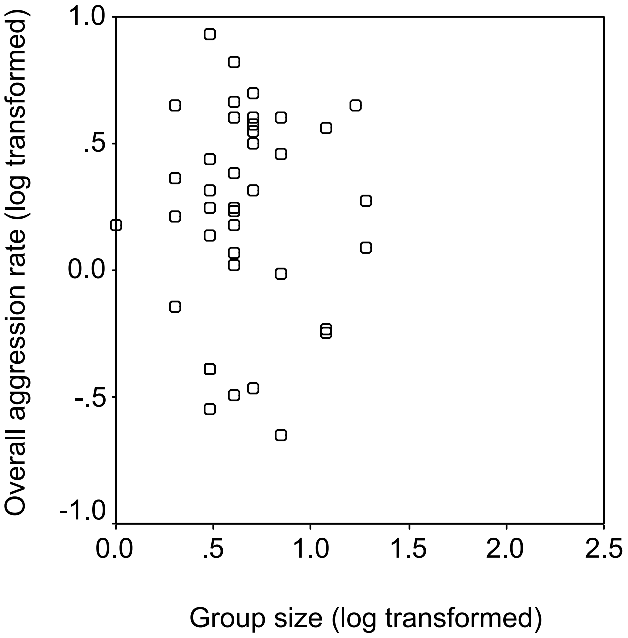


Figure 8b: Relationship between group size and overall aggression rate per hour for hinds in harem groups (Pearson correlation: n=40, r=0.01, P=0.97)

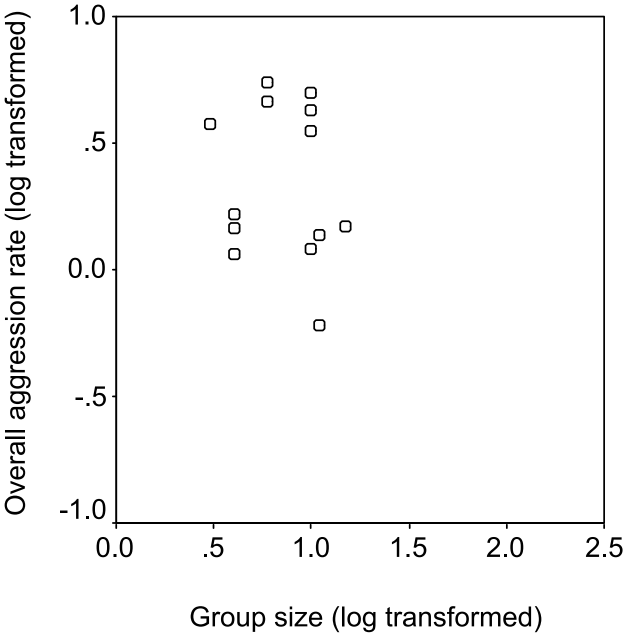


Figure 8c: Relationship between group size and overall aggression rate per hour for hinds in oestrus groups (Pearson correlation: n=13, r=-0.13, P=0.67)

Figure 8: Relationship between group size and overall aggression rate per hour for each social context separately. The data in which the aggression rates are zero, and four extreme values were excluded.

3.5 Female aggression rates in the different social contexts

There were significant differences in the overall aggression rates between the three social contexts (Table 5, Figure 9). Focal hinds in harem groups had significantly lower aggression rates than focal hinds in foraging groups. In addition, they had significantly lower aggression rates than focal hinds in oestrus groups. There was no significant difference between focal hinds in foraging groups and in oestrus groups.

Table 5: GLM analysis with overall aggression rate as a function of the three different 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 – Oestrus group	25.16	<0.001
Foraging group – Oestrus group	0.08	0.78

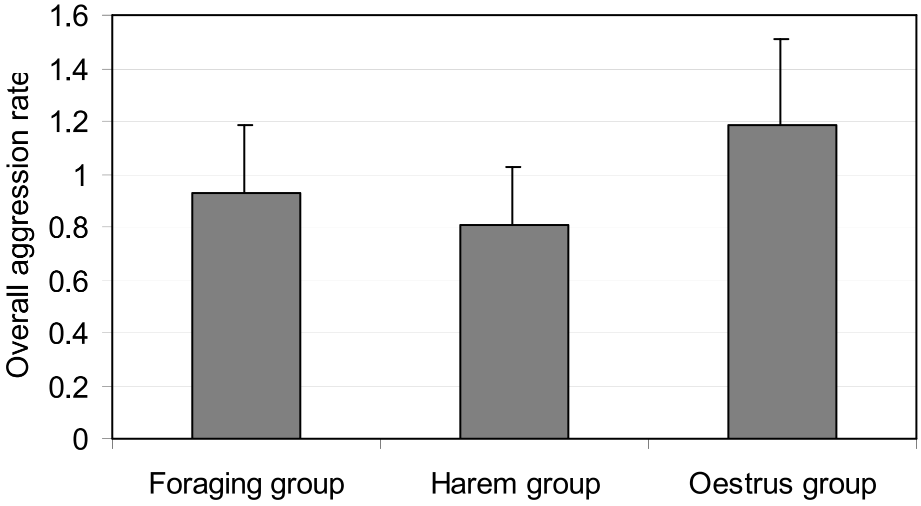


Figure 9: Mean + SE of the overall aggression rate per hour for the focal hinds in foraging groups (n = 92), in harem groups (n = 198) and in oestrus groups (n = 30)

3.6 Female aggression rates of milk hinds, yeld hinds and yearlings

In total, we observed 51 milk hinds and 17 yeld hinds. Out of these, there were three milk hinds and one yeld hind that were tagged. The calf of one of the tagged hinds died on August 14. In addition, we observed 12 female yearlings and 72 hinds which we recorded as unknown. There was no significant difference in the overall aggression rate between milk hinds, yeld hinds and female yearlings (Kruskal-Wallis Test: n=223, χ^2=0.15, P=0.93; Figure 10). However, the difference was marginally significant for the active aggression rate, i.e. when the focal hind was the aggressor (Kruskal-Wallis Test: n=223, χ^2=5.53, P=0.06). Female yearlings never started an aggression towards another hind (Figure 11). Therefore, there was a significant difference in the active aggression rate between milk hinds and female yearlings (Mann-Whitney U-test: n=136, z=-2.35, P=0.02) and between yeld hinds and female yearlings (Mann-Whitney U-test: n=100, z=-2.25, P=0.03). The difference in active aggression rate between milk and yeld hinds was, however, not significant (Mann-Whitney U-test: n=210, z=-0.3, P=0.76).

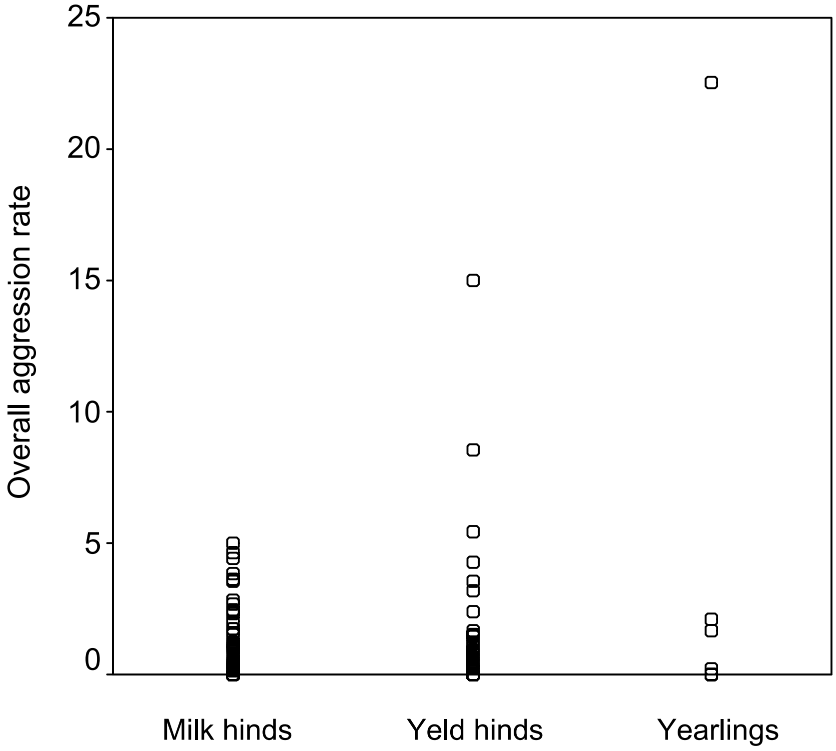


Figure 10: Overall aggression rates per hour for milk hinds (n=84, mean=0.61 ± 0.11), yeld hinds (n=45, mean=0.38 ± 0.07) and female yearlings (n=12, mean=2.21 ± 1.86)

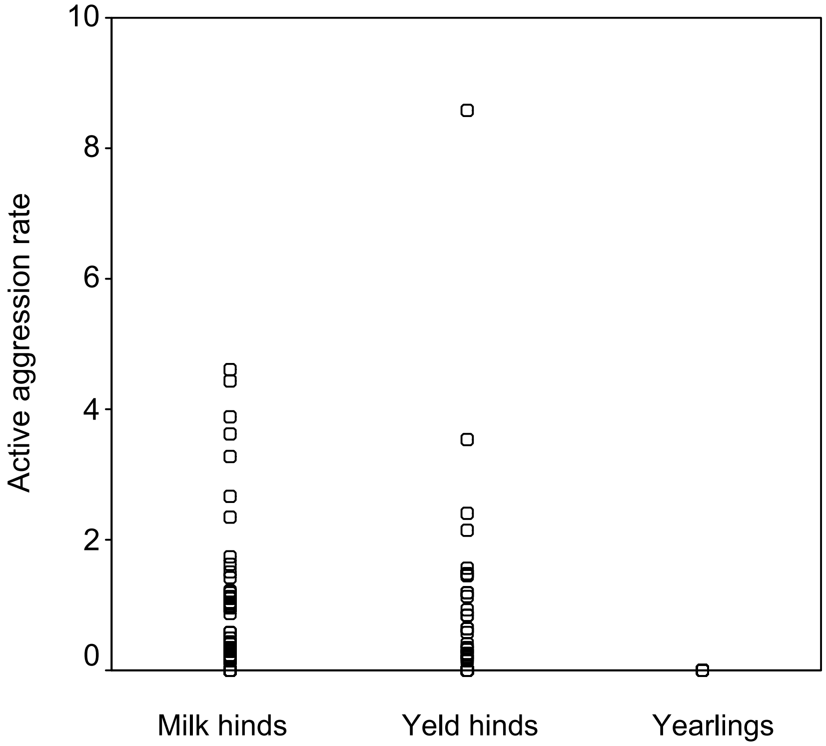


Figure 11: Active aggression rates per hour for milk hinds (n=84, mean=0.44 ± 0.10), yeld hinds (n=45, mean=0.27 ± 0.06) and female yearlings (n=12, mean=0)

3.7 Aggression rates of the tagged females in relation to the different social contexts and group sizes

The mean aggression rates for each tagged hind and for each category are shown in Table 7. The effects of the two social contexts (foraging group and harem group) and the two group sizes (n=1-10 and n=11-20) on the mean aggression rate were not significant for the five tagged females (Table 8). Only one of the five tagged hinds had been observed in oestrus, and therefore this social context was ommitted.

Table 7: Mean aggression rates for the five tagged females for each category (g=foraging group, h=harem group, group sizes 1-10 and 11-20)

	g 1-10	n	h 1-10	n	o 1-10	n	g 11-20	n	h 11-20	n	o 11-20	n
Heidi	0.48	5	0.2	11	2.74	4	0	1	0	1	1.49	1
Oekovreni	0	2	1.03	23					0.57	1		
Principessa	0	3	0	12					0.29	2		
Bohnatrulla	0.22	2	0	6			1.12	3	0	3		
Wilhelmina			0	2			0.32	1	0	1		

Table 8: Repeated measures GLM with overall aggression rate as a function of group size and social context for the 5 tagged females. There are 2 categories for each explanatory variable: Group size: 1-10 and 11-20, Social context: foraging group and harem group

Source	*df*	Mean Square	F	P
Group size	1	0.01	0.02	0.92
Error (Group Size)	1	0.31		
Social context	1	0.33	2.31	0.37
Error (Social context)	1	0.14		
Group Size x Social context	1	0.05	0.28	0.69
Error (Group Size x Social context)	1	0.17		

3.8 Male dominance rank

The dominance ranks calculated with the David's Score and with the Clutton-Brock Index are shown in Appendix 1. There was a significant relationship between the ranks of the two methods (Figure 12). Therefore the David's Score ranks were used for further calculations.

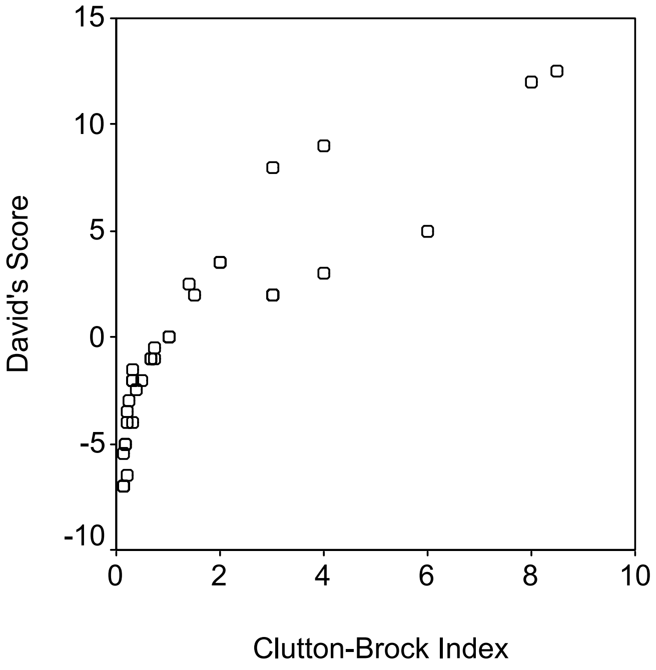


Figure 12: Relationship between David's Score and Clutton-Brock Index of dominance (Spearman rank correlation: n=38, r_s=0.97, P<0.001)

3.9 Harems

A summary of the estimated mating success (hind/days) and the behavioural and morphological data of the stags used in the analyses are given in Table 9. The data for all stags used in the analyses are shown in Appendix 2. Neither the effect of the dominance rank nor the effect of the antler size on the mating success was significant (Table 10 and Figure 13a+b). The relationship between the dominance rank and the antler size was also not significant (Pearson correlation: n=38, r=0.28, P=0.09).

Table 9: Summary statistics of the estimated mating success (hind/days), of the dominance ranks (David's score) and of the antler size (no. of tines)

	Mean ± SE	Median	Range	n
Mating success (hind/days)	14.75 ± 4.36	4	0 - 188.83	52
Dominance rank (DS)	0 ± 0.79	-0.75	-7 - 12.5	38
Antler size (no. of tines)	10.83 ± 0.23	10.5	8 - 15	52

Table 10: Univariate GLM analysis with hind/days as a function of dominance rank (David's score) and antler size (no. of tines).

Source	*df*	Mean Square	F	P
Dominance Rank	1	1573	1.24	0.27
Antler Size	1	2354	1.86	0.18

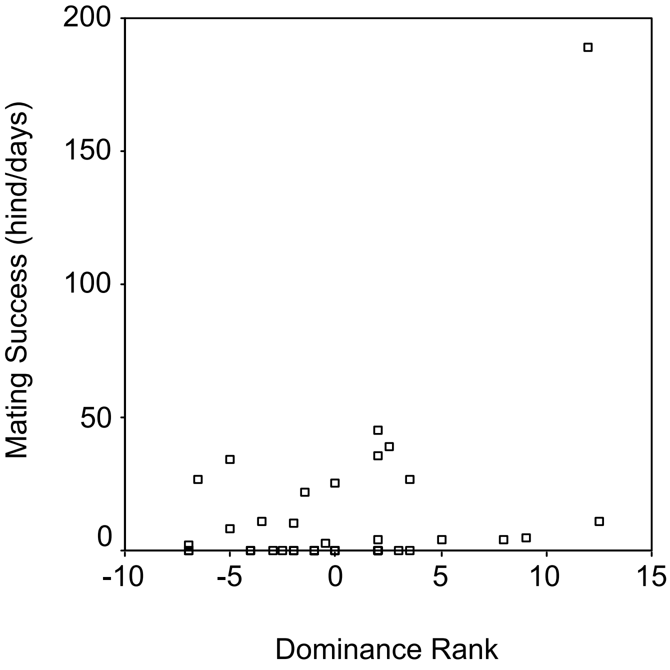


Figure 13a: Relationship between the estimated mating success and the dominance rank (David's score); n=38, r=0.4, P=0.27

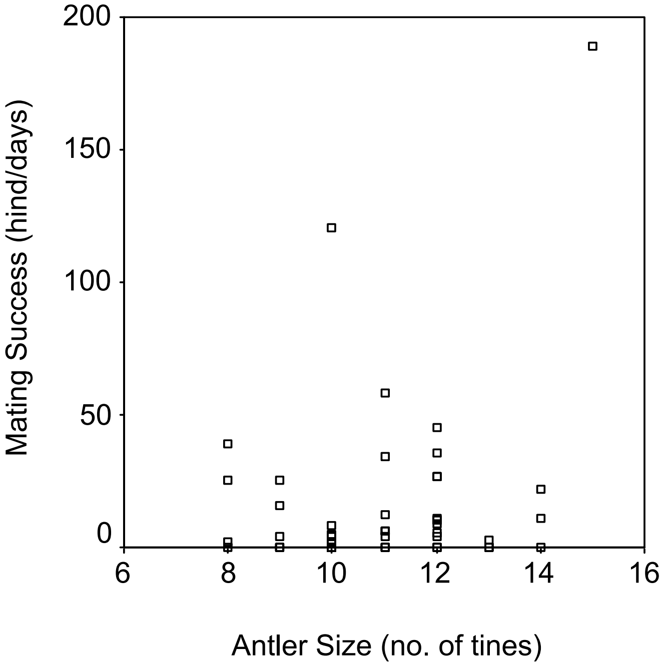


Figure 13b: Relationship between the estimated mating success and the antler size; n=52, r=0.27, P=0.18

Figure 13: Relationships between the estimated mating success (hind/days) and a: dominance rank (David's score) and b: antler size (no. of tines).

3.10 Hind movements between harems

The five tagged females visited between 3 and 12 males (mean= 6.4 ± 1.57) during the breeding season (Figure 14). Each tagged female was seen between 9 and 24 days (mean= 16.2 ± 2.62) during the breeding season.The relationship for the tagged females between the number of days seen and the number of males visited was not significant (Pearson correlation; n=5, r=0.45, P=0.45). Therefore a higher amount of males visited was not just because these females were seen on more days. Furthermore, the total number of days spent in the harem of a certain stag was positively correlated with the estimated mating success of this stag for each tagged female (Figure 15a-e). However, the relationship between the total number of days spent in the harem of a certain stag and the antler size of this stag was not significant for all tagged females (Spearman rank correlation; n=52, r_s=0.2, P=0.15). The relationship between the total number of days spent in the harem of a certain stag and the dominance rank of this stag was also not significant for all tagged females (Spearman rank correlation; n=38, r_s=0.07, P=0.68). The detailed movements between harems for each tagged female are given in Appendix 3.

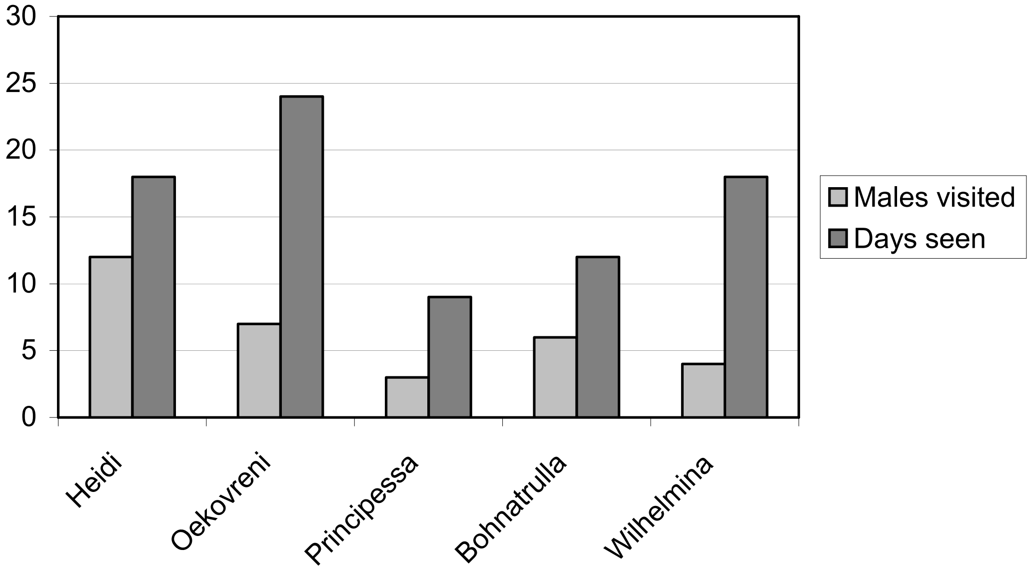


Figure 14: Mean number of males visited and mean number of days seen for each tagged female

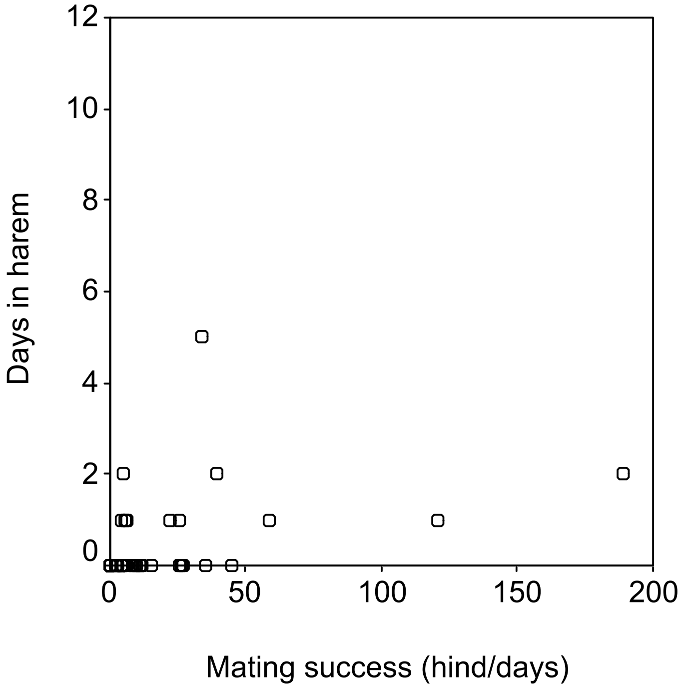


Figure 15a: Relationship between the total number of days spent in the harem of a certain stag by Heidi and the estimated mating success (hind/days) of this stag (Spearman rank correlation; n=52, r_s=0.44, P<0.001)

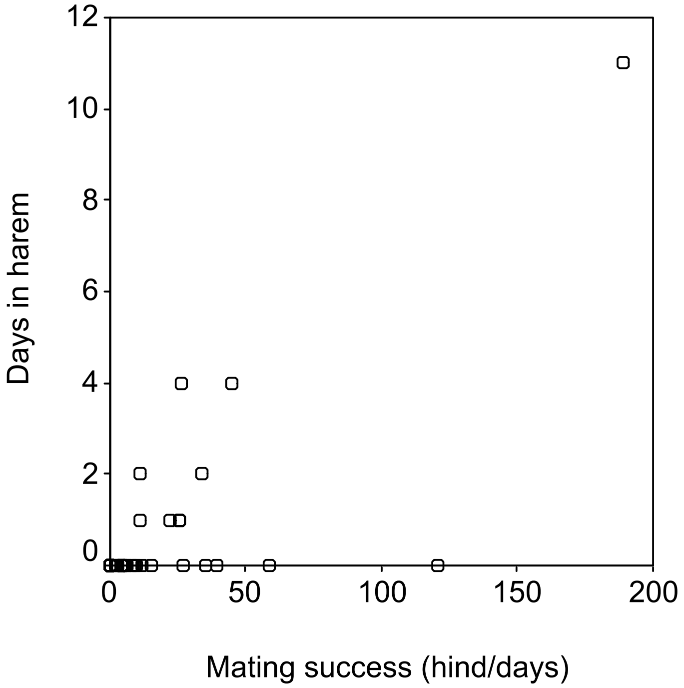


Figure 15b: Relationship between the total number of days spent in the harem of a certain stag by Oekovreni and the estimated mating success (hind/days) of this stag (Spearman rank correlation; n=52, r_s=0.76, P<0.001)

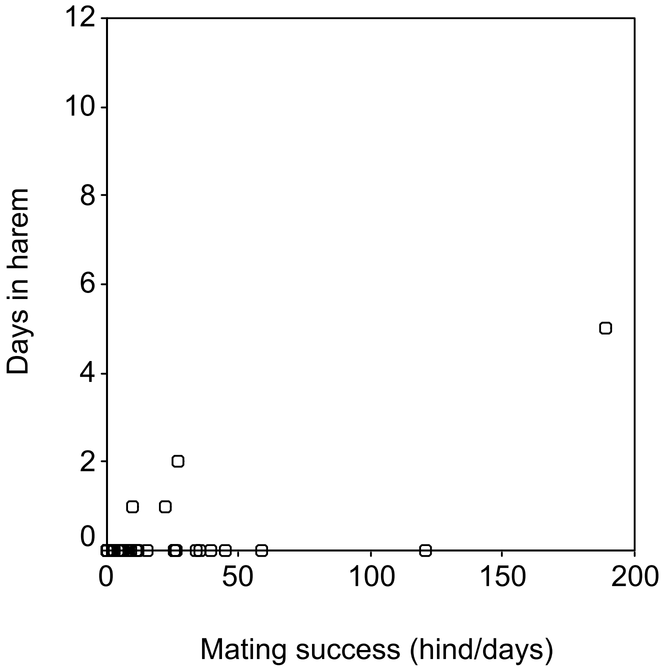


Figure 15c: Relationship between the total number of days spent in the harem of a certain stag by Principessa and the estimated mating success (hind/days) of this stag (Spearman rank correlation; n=52, r_s=0.72, P=0.01)

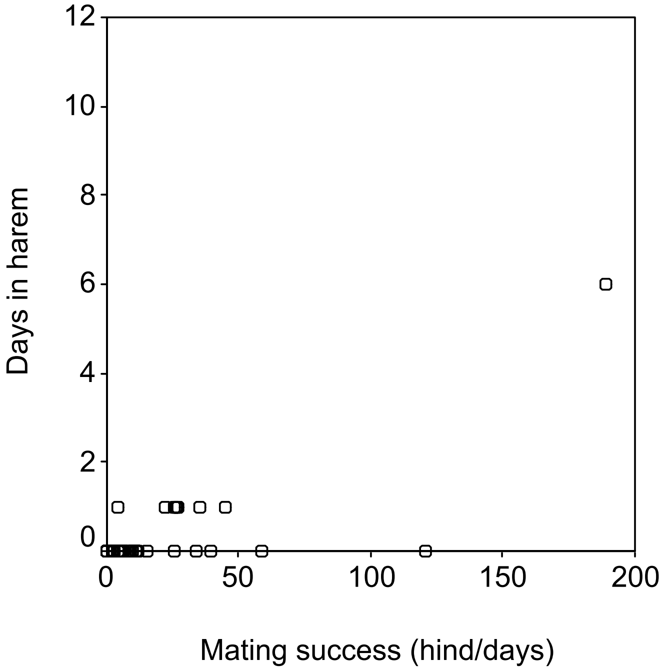


Figure 15d: Relationship between the total number of days spent in the harem of a certain stag by Bohnatrulla and the estimated mating success (hind/days) of this stag (Spearman rank correlation; n=52, r_s=0.78, P<0.001)

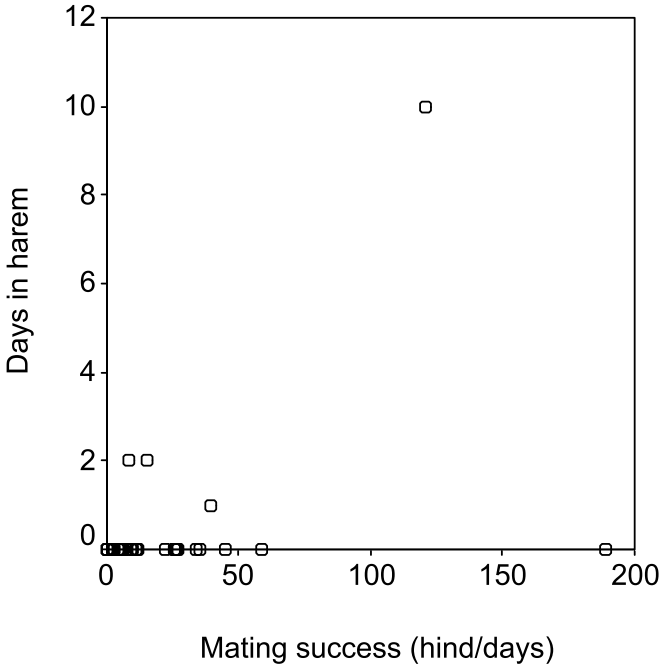


Figure 15e: Relationship between the total number of days spent in the harem of a certain stag by Wilhelmina and the estimated mating success (hind/days) of this stag (Spearman rank correlation; n=52, r_s=0.46, P=0.02)

Figure 15: Relationship for each tagged female (a-e) between the total number of days spent in the harem of a certain stag and the estimated mating success (hind/days) of this stag.

4. Discussion

Aggressive interactions among female red deer were clearly evident in the study population. I divided these interactions into six different aggression types. Between the three social contexts I found no difference in the proportion of the different aggression types. The overall female aggression rate was influenced by the different social contexts; it was significantly higher in foraging groups and in oestrus groups than in harem groups. The five tagged hinds visited between three and twelve males during the breeding season, but it is not clear if these movements were mate-sampling actions. The total number of days spent in the harem of a stag was positively correlated with the estimated mating success of this stag for each tagged female. However, there was no relationship between the total number of days spent in the harem of a stag and the antler size and dominance rank of this stag for all tagged females. For the stags, neither the effect of the dominance rank nor the effect of the antler size on the mating success was significant. The relationship between the dominance rank and the antler size was also not significant.

4.1 Female aggression types

Displacements and nose threats were the most common forms of aggressive interactions among hinds in all three social contexts. The occurrence of ear threats and chases was very low in all three social contexts. These results are consistent with the findings of one other study (Clutton-Brock et al. 1982, 1986), except that ear threats were much more common in that study than in our study population. This difference could be due to a measurement error during our observations. Because the animals were mostly at least 200 metres away from our observation sites, these subtle ear movements were hardly visible. The difference in the proportion of the six different aggression types between the three social contexts was not significant. This suggests that the hinds would use the same aggression types for competition over food and other resources than for competition over mates.

4.2 Female-female competition

The mean aggression rate among hinds in foraging groups was 0.93 interactions per hour in our study population. In another study, this rate was lower; approximately 0.5 interactions per hour (Clutton-Brock et al. 1982, 1986). The mean aggression rate among hinds in harem and oestrus groups in our study population was 0.81 and 1.19 respectively, but no other data on female aggression rates in harems are available in the literature for comparison. Most aggressive interactions occurred while females were competing over particular feeding and resting sites. A dominance rank can normally be assigned to each hind, with older hinds being generally dominant to younger ones (Bützler 1986; Clutton-Brock et al. 1982). Dominant hinds have on average a higher mating success than subordinate hinds (Clutton-Brock et al. 1986). For topi antelopes, in which the females actively disrupted the matings of others, subordinate females suffered interference from other females during 15% of mating bouts whereas dominant females were disrupted during only 2% of bouts (Bro-Jørgensen 2002). Therefore it can be expected that if female-female competition over mates does occur in red deer, then it would be mainly the dominant hinds that show aggressive behaviour towards the subordinates. However, I could not check this hypothesis in my study as it was not possible to individually recognise the females, except the five tagged hinds.

The overall aggression rate for hinds in foraging groups was significantly higher than for hinds in harem groups. A possible reason is that the group size in foraging groups was bigger than in harem groups, because the nearest neighbor distances decline as group size increases (Clutton-Brock et al. 1982). However, my results do not show any relationship between the group size and the overall aggression rate for each social context separately. For all three social contexts together, there was a negative relationship between overall aggression rate and group size, which means that the smaller the group size, the more aggressive interactions occur. Firstly, these results are contradictory with the theory that aggression rate increases as group size increases. One other study on Roosevelt elk (*Cervus elaphus roosevelti)* also showed that the number of aggressive interactions does not correlate with group size (Weckerly 1999). Secondly, my results suggest that the overall aggression rate is influenced by the different social contexts, rather than by the group size. One other explanation why the aggression rate in foraging groups is higher than in harem groups is that related hinds tend to be found in the same harems (Clutton-Brock et al. 1982) and the degree of competition will be reduced if rivals are related to one another, due to kin selection (Rosenqvist & Berglund 1992; König 1990). This is probably the most likely explanation for the higher aggression rate in foraging groups than in harem groups.

The overall aggression rate among hinds was significantly higher in oestrus groups than in harem groups. The active aggression rate among hinds, i.e. when the focal hind is the aggressor, was also significantly higher in oestrus groups than in harem groups. An oestrus female is aggressive towards other females to ensure her access to a high quality male and her fertilization (Petrie 1983; Preston et al. 2001). For example, one study showed that large Soay rams (*Ovis aries)* copulating up to 13 times per day become increasingly depleted of sperm as the mating season progresses (Preston et al. 2001). Therefore it is possible that the oestrus females compete with other females to ensure their fertilization before the high-quality males become depleted of sperm. In addition, other females could be aggressive towards the oestrus female to prevent her from mating with a high-quality male (Foster 1983; Berglund et al. 1993). Due to these reasons, female-female competition over mates is a likely explanation for the higher active and overall aggression rate when the focal hind was in oestrus.

Even though I found a significantly higher aggression rate in oestrus groups, the number of focal hinds in oestrus and the amount of aggressive interactions was nevertheless low. The main reason is probably that the summer 2003 was extraordinarily hot and dry. Therefore a substantial part of the population already left the study site at an early stage of the breeding season and moved to lower valleys, where the food resources were still more abundant. Due to this decrease in population size, we observed only three times that there was more than one female in oestrus on a particular day in a particular harem. Therefore, female-female competition over mates was less likely to occur under these circumstances. Although I did not find strong evidence that female-female competition over mates occurs in our study population, it may occur under different conditions. An important prerequisite for female-female competition over mates to occur, is a female biased operational sex ratio. In the critically endangered saiga antelope (*Saiga tatarica tatarica*), a catastrophic drop in the number of adult males due to selective poaching for their horns, led to a strongly female biased operational sex ratio. Normally, an adult male defends a harem of 12 to 30 females. However, after the drop in the number of males, single males were surrounded by large numbers of females, and dominant females were seen to be aggressively excluding subordinate females from the males (Milner-Gulland et al. 2003). This study shows that the female behaviour can be highly flexible. Therefore, if it would be possible to reduce the number of mature males in our study population, female-female competition over mates is likely to increase in this red deer population.

Female competition over mates can also sometimes take subtle and indirect forms that do not involve overt aggressive interactions (Jennions & Petrie 1997). Mate guarding by females is one of these. Prolonging the mount sequence durations is for example a method for females to guard a male. However, this form of female-female competition could not be shown in fallow deer (Farrell 2001) and is also not likely to occur in red deer.

Between milk and yeld hinds, the active and the overall aggression rate did not differ significantly. This is consistent with Clutton-Brock et al. (1982) who found that a hind’s rank did not vary with reproductive status. However, there was a significant difference in the active aggression rate between female yearlings and milk hinds and between female yearlings and yeld hinds. Female yearlings never initiated an aggressive interaction towards another hind.

This result supports the theory that female dominance rank in red deer is correlated with age (Clutton-Brock et al. 1982).

4.3 Hind movements between harems

The five individually recognisable hinds visited between 3 and 12 males during the breeding season. This indicates that the hinds can move freely between the harems. The order in which they visited the different harems was not related to mating success, dominance rank or antler size of the harem-holding stags (see Appendix 3).

The reasons why hinds change harems can be diverse. Hinds sometimes leave a harem to feed elsewhere. When family groups are split up, individuals often leave the harem they are in to rejoin their relatives in another harem. In cases in which the harem-holding stag persistently threatens a hind's calf or yearling, the mother often leaves the harem (Clutton-Brock et al. 1982). And finally, harem changes can be explained as mate-sampling actions. In pronghorns (*Antilocapra americana*), it was found that females change harem in two circumstances. Firstly, they always leave when the harem-holding male abandons or fails to defend his harem, or when his defense perimeter shrinks to the extent that activity budgets suffer. These changes account for 29% of all moves between harems. The remaining 71% of moves are referred to as mate-sampling actions of females. Females often returned to and mated with a male that they had previously visited (Byers 1997). In my study, we have seen the mating of only one of the five tagged hinds, and this hind stayed with the same stag while she was in oestrus. Therefore it is not possible to tell if the observed movements were mate-sampling actions and if yes, what mate-sampling tactic they use.

One experimental study on fallow deer suggests that females joining leks are attracted to groups of females rather than to males and copy each other's movements (Clutton-Brock & McComb 1993). Oestrus females showed a clear preference for males already with females over males without females, but this preference proved to be absent in anoestrus females.

The most likely functional explanation is that oestrus females gain immediate benefits from joining pre-existing harems which arise from reduced harassment by non-territorial males (McComb & Clutton-Brock 1994). However, the reliabilty of this so called “harassment avoidance” model and of the “preference” models remains controversial (Carbone & Taborsky 1995; Clutton-Brock et al. 1995). These “preference” models assume that females have the ability to select particular males. One other experimental study on fallow deer showed that female movements between harems seem to be governed by the distribution of females already on the lek, but the tendency for females to return to the same males when the lek is temporarily cleared indicates that other factors, like female preferences for particular male characteristics must also be important (Clutton-Brock et al. 1989). My results can not provide evidence for the “preference” model, as we have seen only one mating of the five tagged hinds. However, they neither support the “harassment avoidance” model, because the hinds did not only change from smaller to bigger harems but also vice versa.

4.4 Female mating preferences and male mating success

Dominance rank is usually one of the most important factors in affecting male mating success in ungulates. Mature fallow deer males that attain high dominance rank also achieve the majority of matings (McElligott et al. 1998, 2001). A study on red deer showed that dominance was more important than rut duration and rut area in affecting male mating success (Gibson 1987). In territorial rutting red deer in Spain, the mating success of a male largely depends on the forage quality of his territory. The hinds are attracted by the area rather than by the male and the most competitive males get those territories preferred by females (Carranza 1995). In other studies on red deer, they found no firm evidence that hinds actively selected particular breeding partners (Gibson 1978; Gibson & Guinness 1980; Clutton-Brock et al. 1982). These findings therefore suggest male-male competition to be the main component of sexual selection in red deer, rather than female mate choice. However, in my study I found no relationship between the number of days a tagged hind spent in the harem of a stag and the dominance rank of this stag. In addition, male mating success in my study population was not related to dominance rank. The most probable reason for these unexpected results is that the dominance ranks of the males were calculated using relatively few interactions. We only saw 94 aggressive interactions because the males were very spread out in the study site. Of these interactions I only used 67 to calculate the dominance ranks, because I only calculated them for those males I've seen in at least two interactions. Therefore the calculated dominance ranks probably do not accurately represent the real dominance ranks. In addition, the mating success could only be estimated indirectly because only six matings were observed.

I found no relationship between the number of days a tagged hind spent in the harem of a stag and the antler size of this stag. The male mating success was also not related to the antler size. This suggests that hinds do not prefer stags with bigger antlers and is consistent with an experimental study, in which they showed that the fallow deer females are not more attracted to antlered than to deantlered males (McComb & Clutton-Brock 1994). On the other hand, it is contradictory with Lincoln's (1992) experimental study, in which he showed that antlers could function in attracting red deer hinds. However, determining the factors on which mating preferences are based is complex. Studies of mate choice commonly ignore variation in preferences and assume that all individuals should favor the highest-quality mate available. But individuals may differ in their mate preferences according to their own age, experience, size or genotype. In addition, Fawcett & Johnstone (2003) showed that if there is costly competition for mates, the poorest competitors might be better off avoiding the highest-quality partners and instead targeting low-quality partners, so that they minimize the costs they incur. Their findings offer a new explanation for adaptive variation in mating preferences based on differing abilities to cope with the costs of mate choice.

5. Conclusion

Aggressive interactions among red deer hinds were common in our study population and the frequency of their occurrence was independent of group size. Higher aggression rates of oestrus hinds suggest that female-female competition over mates plays a role in the mating behaviour of red deer. However, we observed relatively few hinds in oestrus (n=14), because a substantial part of the study population had left the park at an early stage of the breeding season. Therefore, the significance of this finding is uncertain. In addition, my results showed that hinds can move freely between the harems. The five individually recognisable hinds visited between 3 and 12 different males during the breeding season, but it is not clear if these movements were mate-sampling actions. Therefore, my results can not provide evidence for the “preference” model, but they are contradictory with the “harassment avoidance” model. Furthermore, my findings suggest that hinds do not base mating preferences on the antler size of the stags. However, determining the factors on which mating preferences are based is complex. Experiments would be required to determine the mating preferences of female red deer. On the whole, this study indicates that female behaviour plays a more important role in red deer matings than previously assumed.

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8. Appendix

Appendix I: The proportion of wins and losses (w:l), the David's score ranking (DS) and the Clutton-Brock Index (CBI) for each of the 38 stags involved in at least two agonistic interactions

	w:l
Dumbledore	8:1
Gandalf	8:1
David	7:1
Ross	5:1
Bill	3:0
Rex	3:0
Pukeko	3:1
Dario	3:1
Valentin	2:0
Walter	2:0
Florentin	2:0
Goofy Anan	2:0
Neo	1:0
Bonaparte	2:1
Sansibar	4:3
Pippo	2:2
Sindbad	1:1
Arthur	1:1
Günsel	1:1
Nepomuk	1:1
Bart	1:2
Käpt'n Blauhirsch	1:2
Ron	1:3
Quert	1:4
Aragorn	1:5
Harry	1:5
Gustav	0:2
Boris	0:2
Robin	0:2
Pino	0:2
Chris	0:2
Philipp	0:2
Quaki	0:2
Elrond	0:2
Ouwa	0:3
Papageno	0:3
Homer	0:4
Rufus	0:4

	DS
Dumbledore	12.5
Gandalf	12
David	9
Ross	8
Bill	5
Bonaparte	3.5
Pukeko	3.5
Florentin	3
Sansibar	2.5
Walter	2
Ron	2
Valentin	2
Goofy Anan	2
Rex	2
Neo	2
Arthur	0
Pippo	0
Sindbad	0
Harry	-0.5
Dario	-1
Käpt'n Blauhirsch	-1
Günsel	-1
Ouwa	-1.5
Nepomuk	-2
Robin	-2
Chris	-2
Bart	-2.5
Pino	-3
Quaki	-3.5
Quert	-4
Gustav	-4
Homer	-5
Boris	-5
Elrond	-5.5
Aragorn	-6.5
Papageno	-7
Rufus	-7
Philipp	-7

	CBI
Dumbledore	8.50
Gandalf	8.00
Bill	6.00
David	4.00
Florentin	4.00
Walter	3.00
Ross	3.00
Valentin	3.00
Goofy Anan	3.00
Rex	3.00
Neo	3.00
Bonaparte	2.00
Pukeko	2.00
Ron	1.50
Sansibar	1.40
Pippo	1.00
Sindbad	1.00
Arthur	1.00
Dario	0.75
Harry	0.75
Käpt'n Blauhirsch	0.67
Günsel	0.67
Nepomuk	0.50
Bart	0.40
Quert	0.33
Robin	0.33
Chris	0.33
Ouwa	0.33
Pino	0.25
Aragorn	0.22
Gustav	0.20
Quaki	0.20
Homer	0.17
Boris	0.17
Elrond	0.14
Papageno	0.13
Rufus	0.13
Philip	0.13

Appendix II: Estimated mating success (hind/days=total no. of days each stag helds hinds × mean no. of hinds held on each day), David's score dominance rank (DS) and antler size (no. of tines) for each stag used in the analysis.

Stags	Hind/days	DS	No. of tines
Gandalf	188.83	12	15
Elrond	120.5	-5.5	10
Knoffel	58.5		11
Neo	45	2	12
Sansibar	39	2.5	8
Valentin	35.5	2	12
Homer	34	-5	11
Aragorn	27	-6.5	12
Pukeko	26.5	3.5	12
Sindbad	25.5	0	8
Rodriguez	25.5		9
Ouwa	22	-1.5	14
Abdul	15.5		9
Mickey	12		11
Dumbledore	11	12.5	14
Quaki	11	-3.5	12
Chris	10	-2	12
Dagobert	9		12
Boris	8.25	-5	10
Elia	6.5		11
Bappo natale	6		11
Beno	5.5		12
David	5	9	10
Fangorn	5		10
Ross	4	8	11
Bill	4	5	10
Walter	4	2	12
Vegas	4		9
Björn	4		10
Harry	3	-0.5	13
Rufus	2	-7	8
Zidane	2		10
Romulus	2		10
Bonaparte	0	3.5	10
Florentin	0	3	10
Goofy Anan	0	2	13
Ron	0	2	11
Rex	0	2	10
Arthur	0	0	10
Pippo	0	0	10
Käpt'n Blauhirsch	0	-1	12
Dario	0	-1	14
Günsel	0	-1	10
Nepomuk	0	-2	8
Robin	0	-2	10
Bart	0	-2.5	9
Pino	0	-3	12
Quert	0	-4	9
Papageno	0	-7	13
Philipp	0	-7	10
Plotz	0		11
Kaligula	0		10

Appendix III: The movements between harems for each tagged female; a: Heidi, b: Principessa, c: Oekovreni, d: Bohnatrulla, e: Wilhelmina. Days when the hind was not seen are not listed.

Appendix 3a:

Date	Harem
29.08.2003	Elrond
31.08.2003	none
01.09.2003	Beno
02.09.2003	unknown stag with 8 tines
07.09.2003	Ouwa
08.09.2003	probably Ross
09.09.2003	Sansibar
10.09.2003	Sansibar
12.09.2003	Knoffel
12.09.2003	Rodriguez
19.09.2003	Gandalf
20.09.2003	Gandalf
20.09.2003	Gandalf
22.09.2003	Homer
25.09.2003	Homer
27.09.2003	Homer
29.09.2003	Homer
29.09.2003	Bappo natale
30.09.2003	Fangorn
01.10.2003	Fangorn
04.10.2003	unknown stag (chased away by Homer)
04.10.2003	Homer

Appendix 3b:

Date	Harem
03.09.2003	none
10.09.2003	Gandalf
11.09.2003	Gandalf
11.09.2003	Gandalf
16.09.2003	Aragorn
17.09.2003	Aragorn
18.09.2003	first Ouwa, then Gandalf
19.09.2003	Gandalf
20.09.2003	Gandalf
21.09.2003	Chris

Appendix 3c:

Date	Harem
03.09.2003	none
04.09.2003	Gandalf
05.09.2003	Gandalf
07.09.2003	Gandalf
09.09.2003	Gandalf
10.09.2003	Gandalf
11.09.2003	Gandalf
11.09.2003	Gandalf
14.09.2003	Pukeko
15.09.2003	Pukeko
16.09.2003	Pukeko
16.09.2003	Gandalf
17.09.2003	Gandalf
18.09.2003	first Ouwa, then Gandalf and last Pukeko
19.09.2003	Gandalf
19.09.2003	Gandalf
19.09.2003	Rodriguez
20.09.2003	Gandalf
21.09.2003	Sindbad
22.09.2003	Neo
22.09.2003	Neo
22.09.2003	Neo
23.09.2003	probably Quaki
24.09.2003	Bappo natale (later she takes refuge with Homer)
24.09.2003	Homer
25.09.2003	Neo
26.09.2003	Homer
27.09.2003	Neo
28.09.2003	Neo
30.09.2003	probably Quaki
04.10.2003	Dumbledore

Appendix 3d:

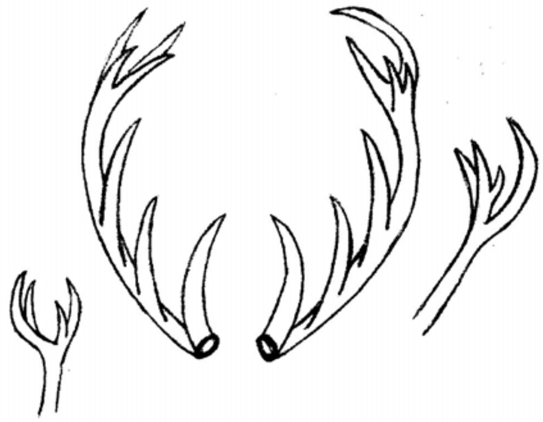
Date	Harem
04.09.2003	none
05.09.2003	Gandalf
09.09.2003	Gandalf
10.09.2003	Gandalf
14.09.2003	Valentin
17.09.2003	probably Aragorn
18.09.2003	first Ouwa, then Gandalf and last Pukeko
19.09.2003	Gandalf
20.09.2003	Sindbad
22.09.2003	Neo
22.09.2003	Neo
28.09.2003	Gandalf
29.09.2003	Walter

Appendix 3e:

Date	Harem
28.08.2003	Elrond
29.08.2003	Elrond
30.08.2003	Elrond
31.08.2003	unseen stag in the forest
01.09.2003	Elrond
04.09.2003	unseen stag in the forest
06.09.2003	Elrond
06.09.2003	foraging group without a stag
07.09.2003	Elrond
08.09.2003	Elrond
11.09.2003	Elrond
12.09.2003	foraging group without a stag
12.09.2003	small ♀ group, but Elrond’s harem close by
13.09.2003	small ♀ group, but Elrond’s harem close by
15.09.2003	foraging group without a stag
15.09.2003	Sansibar
18.09.2003	foraging group without a stag
21.09.2003	Abdul
21.09.2003	Abdul
29.09.2003	Boris
30.09.2003	Abdul
01.10.2003	Boris

Appendix IV: Examples of our antler sketches which allowed individual identification of the males

Dumbledore



Gandalf

Valentin