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Dominance relationships and competition for resources among chamois *Rupicapra rupicapra rupicapra* in female social groups

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Abstract

Studied in a region in the Bernese Oberland (Switzerland) which animals in social groups of female chamois *Rupicapra rupicapra rupicapra* are able to assert themselves in competition for resources (licks, resting and feeding sites), and how losers behave after an interaction. The older animals regularly asserted themselves against younger individuals. Within the class of adult females (with or without kids) certain animals regularly asserted themselves against others. The most striking behaviour on the part of the loser, after having been forced to give up a resource to which it had previous access, was urination directly following the interaction, as a result of the latter and as a possible sign of stress.

Introduction

Outside the rutting season, which occurs in November/December, chamois live separately with regard to sex. The female chamois form social groups consisting of adult and subadult females, yearlings (including males) and kids (KRÄMER 1969; KNAUS and SCHRÖDER 1983). Even in nonhunted, local populations (e.g. in game reserves) the number of animals remains fairly constant over a longer period of time, migration occurring only very rarely (KRÄMER 1969; KNAUS and SCHRÖDER 1983).

These findings aroused the suspicion that social processes could play an important role in limiting population density (KRÄMER 1969). Later on, some indications supported this suspicion (BERDUCOU and BOUSSES 1985; LOVARI and ROSTO 1985). LOVARI and ROSTO (1985) showed, that younger female chamois had a lower bite rate in the presence of older (dominant) females, suggesting, that in the long run that could be a reduced food intake of young females, influencing e.g. winter survival and reproductive processes.

The aim of the present study was to investigate one aspect of this problem, in particular: 1. whether certain individuals assert themselves in the competition among licks, resting and grazing sites; 2. how the behaviour of losers is influenced by the winners of an interaction.

Study area and animals

The study was carried out in the Swiss Federal Game Reserve Augstmatthorn in the Bernese Oberland (Switzerland) in summer 1987. The study area lies on the north-west slope of the Augstmatthorn at a height between 1500–2100 m altitude. It covers a surface area of approximately 3 km².

It was possible to observe a maximum of 126 predominantly female chamois; approximately 61 adult and 26 subadult females and yearlings as well as 39 kids. Animals were allocated according to age classes, using as criterion the length of their horns in relation to ear length (LOVARI 1985; PATTERSON 1988). Males (except for male yearlings) were seldomly observed in this area.

Every day many animals visited the apparently very attractive licks including 3 optimal licks, the remainder being less attractive (MARBACHER 1989), which were spread over a small area. The fact that, as a rule, there were considerably more animals than licks led to very strong competition at these sites.

Methods

The chamois were observed from May to October at a total of 90 days. Observations were made each day from morning to evening using the "behaviour sampling" method (ALTMANN 1974).

Aggressive interactions (e.g. advancing with lowered horns towards conspecifics) in connection with competition for resources, occurred at the few available licks, at resting sites and during grazing. In order to classify which individuals were able to assert themselves, the numbers of animals remaining compared to those leaving were recorded, during situations when an older animal approached a younger one within three body lengths or vice versa at the licks, at resting and grazing sites. The Fisher exact test was used for statistical analyses for a total of 250 events.

It was possible on two occasions to observe two groups of four adults with kids (individually identifiable by morphological features such as colour of coat) at the licks during a period of several hours and to determine which animal drove the other away.

The winner of an interaction took over the resource or continued to use it and the loser retreated a few meters, stopped and often began to urinate. In order to determine whether urination was indeed a result of having been driven away, we then proceeded as follows:

We recorded the time until any urination occurred over a period of 5 minutes, a. after an animal had been forced to leave a site, b. after an animal had left a corresponding site on its own accord. The comparison was made with the Mann/Whitney U-Test.

Results

Winner and loser in the competition for resources

At licks: In all combinations of the 4 age-groups there were significant differences in the number of animals leaving to those staying at the approach of an other animal (Table 1). Almost without exception the younger animals retreated when an older one approached, while in the opposite case the older ones stayed. Among the individually recognizable adult females with kids, the same animals always asserted themselves in the course of a series of interactions (except in the case of animals E and F; Fig. 1), i.e. the subdominant animals had to "involuntarily" leave the lick together with their kids (Fig. 1).

At resting sites and when grazing: In the combinations studied the result was the same as at the licks. In all combinations studied, younger animals retreated at the approach by older individuals but not vice versa (Table 1). In some cases certain adult females with their kids retreated from other adult females.

Urination by the loser as a consequence of the interaction with a dominant animal

The most striking behaviour of an animal that had been driven away was urination after it had retreated a few meters. Animals driven away from licks and when grazing urinated in about 95 % of the cases, those driven away from resting places in slightly less than 90 %. Those not driven away, if they had left the corresponding place "voluntarily", urinated in 79 %, 52 % and 56 % of the cases. The difference between animals driven away and those not driven away when grazing and at resting sites was significant (Table 2). The lack of a difference at licks was clearly due to the fact that animals that had been licking for some time as a rule urinate upon leaving the lick. In all three situations, however, urination occurred significantly earlier in cases where animals had been driven away than in voluntary departures, i.e. within a few seconds (Fig. 2).

Discussion

Competition does not only occur at the few attractive licks, but also at resting sites and during grazing. Older animals in general tend to assert themselves in certain situations against younger ones, as has already been mentioned elsewhere (KRÄMER 1969; LOVARI

Table 1. Frequency of animals (belonging to different age classes) winning or losing in competition for licks, resting and feeding sites

OF = old female; YF = young female; YA = Yearling; sK = strange kid; K = kid; a = animal at the site; b = animal approaching; ns = not significant (Fisher exact test)

a	b	animal at the site remains retreats		p
at licks				
OF	YF	12	4	< 0.001
YF	OF	0	16	
OF	YA	12	0	< 0.001
YA	OF	0	25	
OF	sK	19	0	< 0.001
sK	OF	0	27	
YF	YA	8	0	< 0.001
YA	YF	0	7	
YF	K	2	0	< 0.05
K	YF	0	8	
YA	K	10	0	< 0.001
K	YA	0	12	
at resting sites				
OF	YF	3	0	ns
YF	OF	0	2	
OF	YA	6	0	< 0.001
YA	OF	0	7	
OF	sK	7	0	< 0.001
sK	OF	0	7	
at feeding sites				
OF	YF	1	0	ns
YF	OF	0	2	
OF	YA	6	0	< 0.001
YA	OF	0	13	
OF	sK	7	0	< 0.001
sK	OF	0	13	
YF	YA	2	0	ns
YA	YF	0	3	
YA	K	4	0	< 0.01
K	YA	0	5	

and ROSTO 1985). However the same evidently also occurs among older females, and in particular among animals whose age difference cannot be readily determined (on the basis of the length of their horns). The kids of the respective mothers shared the advantage or disadvantage. For example, kids of dominant mothers could use a lick unhindered during the period that their mother used the resource and conversely kids of subdominant mothers were forced to leave a lick together with their mother.

Older animals and those dominant within their class of adults were thus privileged in the utilization of resources. At licks: The best licks (with respect to humidity, access, see

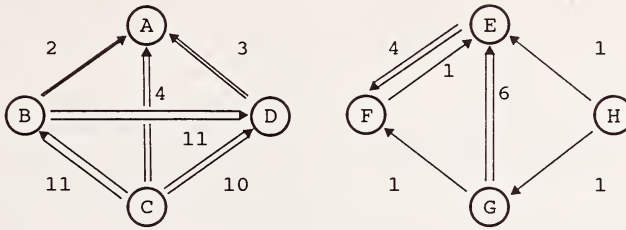


Fig. 1. Sociograms showing the number of successful approaches of adult females to other adult females staying at licks. A-H: Individually identifiable females with kids

Table 2. Number of animals urinating after leaving a lick, a resting or a feeding site after (a): it had been driven away or (b): it had left the site on its own accord; (+) = urination occurred; (-) = urination did not occur; ns = not significant

	at licks		at resting sites		at feeding sites	
	(+)	(-)	(+)	(-)	(+)	(-)
(a)	30	2	26	3	20	1
(b)	26	7	14	11	12	11
Chi-square	3.05		10.26		7.92	
p	ns		< 0.01		< 0.01	

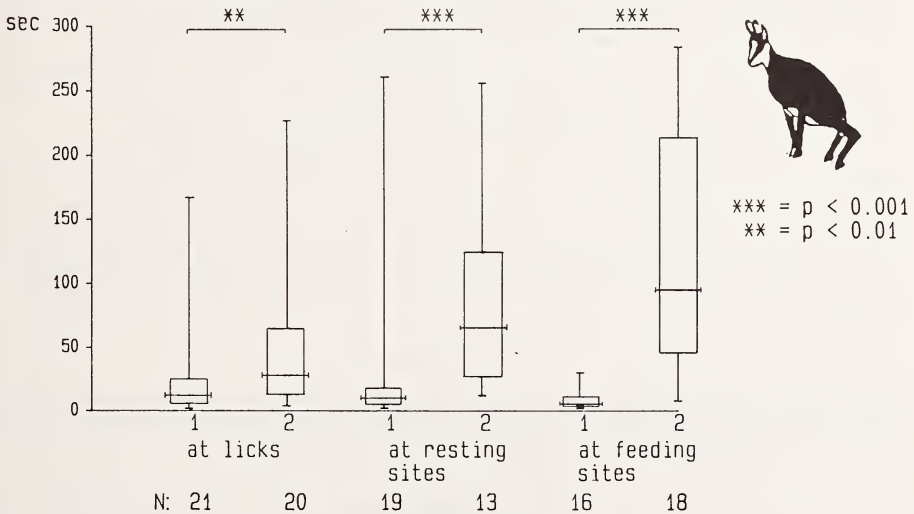


Fig. 2. Time until urination after an animal had been driven away or after it had left on its own accord at the licks, resting and feeding sites. Median, first and third quartil, minimum and maximum; 1 = driven away, 2 = left on its own accord (Mann/Whitney U-Test)

MARBACHER 1989) were mainly occupied by adult females with kids and as far as could be determined also by certain adult individuals without kids. At resting sites: Dominant animals occupy and retain desirable resting sites (e.g. shady sites during summer or at the very limited areas remaining snow in late spring), in contrast to subdominant animals. When grazing: Chamois eat selectively and have a particular preference for certain plants (KNAUS and SCHRÖDER 1983; FERRARI and ROSSI 1985; LEONI 1985). The fact that animals, after having driven away another one, continued eating at exactly the same place suggests that they fed on plants discovered by the previous animal. In individual cases this could be clearly ascertained. The distances between the chamois were small (a few body lengths on average; MARBACHER 1989) so that it can be assumed that they could see what kind of food their neighbour had been eating. It may be a question of special tactics on the part of the dominant animal, i.e. to keep an eye on what subdominant animals have found and to appropriate this at the expense of the others, as is said to be the case with Brent geese (DRENT, pers. comm.). It is quite possible that when grazing, subdominant animals are at a disadvantage, particularly when large areas are covered with snow or when snow remains for a long time.

It is striking that at the licks but also in a herd of grazing animals, short agonistic interactions occurred almost continuously. In such cases mostly younger, but also certain adult animals in the social group gave up resources, some of which they had discovered themselves and others that were well known resources (licks). Therefore they were probably almost always under a certain stress. The regularly occurring urination of an animal driven from a resource could be, in our opinion, the sign of such stress (some farm animals show enhanced defecation and/or urination under the influence of certain stressors, e.g. WOOD-GUSH et al. 1975). In any case it could be of importance as an indication of inferiority, as described in mountain sheep (GEIST 1971). Nevertheless, in the latter species it is thought to be a kind of submissive behaviour which prevents attacks from dominant animals. We have no indication for this theory in the present study. The dominant animal seems to be fixed on the resource, and pays apparently very little attention to the subdominant animal that has been driven away. There were virtually no observations of behaviour towards the urinating animal or to the urine itself (e.g. sniffing) within the herd of largely female animals studied (the only males were yearlings in this group).

More or less strongly pronounced stress leads to physiological responses which may change the function of the immune system, increasing susceptibility to disease (explored in some laboratory and farm animals, e.g. FRASER and BROOM 1990). Within social groups of female chamois it appeared that the social processes of competition for resources could have such an effect, especially under the circumstances of high population density. In order to examine this supposition, long-term studies on individually marked animals would be necessary.

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Zusammenfassung

*Dominanzbeziehungen und Konkurrenz um Ressourcen in Gruppen von weiblichen Gamsen (*Rupicapra rupicapra rupicapra*)*

In einem Gebiet im Berner Oberland, Schweiz, wurde im Sommer 1987 untersucht, welche Individuen in Gruppen von vorwiegend weiblichen Gamsen (*Rupicapra rup. rup.*) sich in der Konkurrenz um Ressourcen (Leckstellen, Liegeplätze, Nahrungsorte) durchzusetzen vermögen, und wie sich die Verlierer im Anschluß an eine Auseinandersetzung verhalten.

Generell setzten sich ältere Tiere gegenüber jüngeren Tieren durch und innerhalb der Klasse der adulten Geissen mit Kitzen regelmäßig bestimmte Tiere gegenüber andern.

Auffälligstes Verhalten der Verlierer, welche eine durch sie gehaltene Ressource aufgeben mußten, war Harnen unmittelbar nach der Auseinandersetzung als Folge davon und als möglicher Ausdruck von Streß.

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