Determining Social Rank in Ungulates: A Comparison of Aggressive Interactions Recorded at a Bait Site and under Natural Conditions

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Abstract

Researchers often assume that dyadic interactions at bait sites have similar outcomes to those occurring under natural conditions, but this assumption has seldom been tested. I used aggressive interactions recorded during 1994–97 among marked mountain goats (Oreamnos americanus) to compare dyadic relationships near an artificial salt lick with those observed under natural conditions. I also examined how observations recorded at the lick affected the structure of dominance matrices. The probability of winning an encounter was strongly and positively related to age, both under natural conditions and at the salt lick. The proportion of interactions that adult females lost to 2-yr-olds and the proportion won by the youngest individual among adult females, however, more than doubled at the salt lick compared to natural conditions. Two-year-old females were 22 times more likely to win interactions against 2-yr-old males at the lick than under natural conditions. A decrease in the directional consistency index revealed that the outcomes of repeated encounters of the same dyad were more inconsistent at the salt lick than elsewhere. When interactions recorded at the lick were added to female dominance matrices, the number of inconsistencies more than doubled and the strength of the inconsistencies increased 2–8 times compared to matrices restricted to interactions recorded under natural conditions. Interactions seen at the salt lick caused substantial changes in the hierarchical rank of individual goats. Because interaction rates were high and animals were very concentrated at the trap site, individual recognition may have been difficult, explaining the differences observed in dyadic relationships at the lick compared to natural conditions.

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Introduction

The study of dominance relationships among animals has interested ethologists since the early 1920s (Bernstein 1981; Drews 1993). Because the observation of aggressive behavior is difficult under natural conditions, much research, especially on ungulates, has relied on observations of animals in captivity or at baiting sites (Clutton-Brock et al. 1976; Townsend & Bailey 1981; Hall 1983, 1986; Masteller & Bailey 1988; Alados & Escós 1992; Cassinello 1995). Under natural conditions, animals have often been observed near small, defensible resources: waterholes (Berger 1977; Rutberg & Greenberg 1990; Möller et al. 1996), natural salt licks (Chadwick 1977; Singer 1977), or supplemental feeding sites (Ozoga 1972; Espmark 1974; Grenier et al. 1999). Behavioral observations of ungulates have been conducted at artificial feeding sites or artificial salt licks, often on the assumption that dyadic interactions seen at bait sites should have outcomes similar to those occurring under natural conditions (Ozoga 1972; Clutton-Brock et al. 1976; Masteller & Bailey 1988; Hall 1986). This assumption is important to studies assessing the role of social rank in social organization, but it has seldom been tested (but see Clutton-Brock et al. 1976).

Among those ungulates for which the agonistic interaction rate of adult females has been documented, mountain goats (Oreamnos americanus) are the most aggressive (Fournier & Festa-Bianchet 1995). Females are organized in highly linear and stable dominance hierarchies that are strongly correlated with age (Côté 1999). Dominance appears to be important in the social organization of mountain goats, because kid production increases with maternal rank (Côté 1999).

I compared behavioral observations collected at an artificial salt lick and under natural conditions to test whether dyadic relationships in mountain goats were consistent in the two situations. Because age strongly affects social rank, I compared age and dominance at the salt lick and under natural conditions. Finally, I determined how the addition of the data recorded at the lick, to the observations conducted under natural conditions affected the proportion of interactions won by the same animal within dyads, and the social rank of individuals in the dominance hierarchy.

Materials and Methods

I studied the Caw Ridge (54°N, 119°W) mountain goat population in west-central Alberta (Canada) in the front range of the Rocky Mountains. Goats used about 28 km² of alpine tundra and open subalpine forest at about 2000 m of altitude. During the study, the population of mountain goats at Caw Ridge ranged from 76 to 86 individuals, ≥ 1 yr old, of which 81–97% were marked.

From 1988 to 1997, 207 mountain goats were marked and measured. Goats were captured in four remotely controlled wooden box traps and five self-tripping Clover traps (Clover 1956) baited with salt. Adults were drugged with xylazine hydrochloride; drugging was reversed by injection of idazoxan (Haviernick et al. 1998). Côté et al. (1998) provide further details on capture procedures. Animals
were marked with canvas collars and Allflex plastic ear tags. All females \( \geq 3 \) yr old were marked during the study. Unmarked juvenile goats (1 and 2 yrs olds) were sexed and aged according to body size and horn characteristics (Smith 1988). The exact age was known for all goats born after 1987. For goats first caught as adults, age was determined by the number of horn annuli (Smith 1988).

My five assistants and I recorded goat agonistic encounters from late May to mid-Sep. for each year from 1994 through 1997, using ad libitum and focal sampling (Altmann 1974). We used spotting scopes (15–45X) to sample goat behavior at distances of 200–700 m during > 1700 h of observation. I trained all field assistants and checked the accuracy of their observations before they started sampling on their own. I recorded most interactions myself and each assistant saw 1–4% of the total number of interactions. I personally recorded interactions at the traps (artificial salt lick) from a blind at approximately 80 m distance. Goats often licked salt that had leached onto the ground around the traps and interacted at trap entrances and around the traps. Dominant females had priority access to salt blocks and to patches of ground with leached salt (Côté 1999). Individuals came to the trap site in groups of between 13 and 75 individuals (mean of 31, \( n = 31 \)), congregating on approximately 70 m\(^2\). We observed 5779 interactions between goats \( \geq 1 \) yr old under natural conditions during 255 d, and 905 interactions at the traps in 24 d of trapping. The interactions observed were distributed among all goats in the population, each marked individual contributing an average of 0.97% (SE = 0.06) of the total interactions observed. The maximum contribution was 2.3% from an adult female observed during the 4 yr of the study. Sampling at the traps was most intense in 1995 and 1997 and a total of 96 individual goats \( \geq 1 \) yr old were observed interacting at the traps. The initiator, winner, and loser were noted for each interaction (Hand 1986). The outcomes of agonistic encounters were evident in > 99% of cases. I defined an interaction as resolved when one of the opponents withdrew, i.e. moved > 1 goat length (about 1.5 m) while showing submissive behavior (Locati & Lovari 1991; Drews 1993). Aggressive behaviors included present threat (broadside orientation during which apparent size is enhanced through arching of the back), horn threat (display or use of the horns), rush threat (quick movement toward an opponent), and orientation threat (a low-intensity form of rush threat involving walking; see Chadwick 1977 for more details). Submissive behaviors included orientation avoidance (slowly avoiding the opponent by walking or staring) and rush avoidance (quickly moving away from the antagonist; Chadwick 1977).

**Statistical Analyses**

I calculated the linearity of dominance hierarchies with the linearity index \( h' \) developed by de Vries (1995). The \( h' \) index is based on Landau’s index \( h \) (Landau 1951) but takes into account unknown relationships to test linearity. To determine the statistical significance of \( h' \) for each annual dominance hierarchy, a two-step randomization process using 10 000 randomizations was performed (de Vries 1995). Because dominance hierarchies were strongly linear in all years (Côté 1999),
I ranked individuals in annual hierarchies that were most consistent with a linear hierarchy according to the method of de Vries (1998) (Fig. 1). This ranking method is more reliable than the win/loss ratio technique used by Fournier & Festa-Bianchet (1995), as discussed in Côté (1999). The dominance hierarchy was reorganized by an iterative procedure (1000 randomizations) that ranks the individuals by minimizing the number and strength of inconsistencies in the matrix. An inconsistency occurs when individual j dominates i, and j’s rank is lower than i’s (de Vries 1998). The rank difference between two individuals involved in an inconsistency is the strength of that inconsistency (de Vries 1998).

For each matrix, I calculated the directional consistency index (DC; van Hooff & Wensing 1987). Directional consistency index is calculated across all dyads as the total number of interactions whose outcome is in the most frequent direction within each dyad (H), minus the number of interactions occurring in the less frequent direction (L), divided by the total number of interactions performed by all individuals:

\[
DC = \frac{H - L}{H + L}
\]

The directional consistency index ranges from 0 (equal exchange) to 1 (complete unidirectionality). All calculations were performed with Matman 1.0 for Windows (Noldus Information Technology 1998).

I used goodness of fit G-tests to assess the effects of sex–age class on the probability of winning an encounter. Expected frequencies were calculated assuming that each class would win an equal proportion of interactions.

**Results**

Adult females (≥ 3 yr old) won all interactions with yearlings (n = 934), independently of the site, and most interactions (80–99%) against 2-yr-olds. Adult females, however, lost against 2-yr-old males more than twice as often (9–20%) at the salt lick compared to natural conditions ($G_1 = 9.8$, \(p = 0.001\), Fig. 2). Adult females lost 1% of interactions against 2-yr-old females under natural conditions and 9.1% at the salt lick ($G_1 = 23.8$, \(p < 0.0001\), Fig. 2). Finally, 2-yr-old females won 31.0% of encounters with 2-yr-old males at the salt lick compared to only 1.4% under natural conditions ($G_1 = 18.0$, \(p < 0.0001\), \(n = 102\)).

Among adult females, the proportion of dyadic interactions won by the younger goat more than doubled (6–13%) at the salt lick compared to natural conditions ($G_1 = 22.7$, \(p < 0.0001\), Fig. 3). In addition, in cases when the younger female won, the opponent was significantly older at the salt lick than under natural conditions (salt lick: 2.09 ± 0.22 yr older, \(n = 55\); elsewhere: 1.45 ± 0.06 yr older, \(n = 157\); \(Z = -1.8\), \(p = 0.03\)).

The number of interactions recorded at the salt lick was insufficient to construct dominance matrices. Therefore, I added interactions seen at the salt lick to dominance matrices based on interactions recorded under natural conditions, using the 2 yr with adequate sample size, 1995 and 1997. Interactions recorded at
**Fig. 1:** Dominance matrix of adult female mountain goats at Caw Ridge, Alberta, in 1997. Individuals are ranked according to de Vries (1998), wins are listed across rows, and losses down columns. The first row and column show individual goat numbers (ID) and the second column indicates ranks when interactions recorded at the trap site (marked with +) were included in the matrix of interactions recorded under natural conditions.
the salt lick decreased the directional consistency index from 0.951 to 0.924 in 1995, and from 1.000 to 0.976 in 1997, and the number of inconsistencies more than doubled (Table 1). More importantly, the strength of these inconsistencies doubled in 1995 and increased by a factor of eight in 1997 (Table 1). When interac-

\[Fig. 2: \text{Proportion of interactions lost by adult (}\geq 3\text{ yr old)}\text{ female mountain goats against 2-yr-olds at Caw Ridge, Alberta 1994-97. Sample sizes are shown on top of each bar. Black bars represent interactions observed at the artificial salt lick; white bars represent interactions recorded under natural conditions.}\]

\[Fig. 3: \text{Proportion of interactions among adult (}\geq 3\text{ yr old)}\text{ female mountain goats won by the older (white) and the younger (black) female according to observation site. Sample sizes are shown on top of each bar.}\]

tions recorded at the salt lick were included in matrices, many goats (37.5% in 1995, 51.1% in 1997) changed rank, creating differences of up to five ranks (Fig. 1).

Discussion

It is generally expected that aggressive behavior should be more frequent at bait sites where resources are more concentrated than under natural conditions (Clutton-Brock et al. 1976; Hall 1983; Barrette & Vandal 1986; Masteller & Bailey 1988; Grenier et al. 1999). The direction of dyadic relationships, however, is thought to be similar in various environments (Clutton-Brock et al. 1976). Hall (1983) found that social ranks were almost identical in captive red deer (Cervus elaphus) hinds observed in a large enclosure and at feeding troughs. Similarly, the provision of food had little effect on the social ranks of highland ponies and cows, although three of the younger cows moved several ranks up the hierarchy when food was provided (Clutton-Brock et al. 1976). Masteller & Bailey (1988) reported that the dominance order among sex–age classes of mountain goats at a bait site was similar to that reported at small mineral licks, except that two 2-yr-old males dominated adult females at the bait site and not at licks. One could argue, however, that in both cases goats were observed in confined situations. I found that aggressive interactions at the salt lick had markedly different outcomes compared to interactions seen under natural conditions. Most importantly, all measures used to describe dominance relationships changed significantly when interactions recorded at the salt lick were included.

Two-year-old females almost never won against 2-yr-old males under natural conditions (see also Chadwick 1977), but won > 30% of encounters with 2-yr-old males at the salt lick. Similarly, for interactions among adult females, there was a substantial increase in the proportion won by the younger female at the salt lick. Interactions at the salt lick significantly modified age-related dominance relation-

<table>
<thead>
<tr>
<th>Year</th>
<th>Natural conditions only</th>
<th>With interactions recorded at the trap site</th>
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<tbody>
<tr>
<td></td>
<td>Inconsistencies*</td>
<td></td>
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<tr>
<td>1995</td>
<td>4</td>
<td>7</td>
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<tr>
<td>1997</td>
<td>3</td>
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<td>Strength of inconsistencies*</td>
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<tr>
<td>1995</td>
<td>20</td>
<td>39</td>
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<tr>
<td>1997</td>
<td>9</td>
<td>74</td>
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*see text for definitions (de Vries 1998).
ships. When those interactions were excluded, age was very strongly correlated with social rank \( (r^2 > 0.9) \), and the older female won 94% of the interactions (Côté 1999), a finding similar to those for other ungulates (Thouless & Guinness 1986; Festa-Bianchet 1991).

The directional consistency index decreased when I included interactions recorded at the salt lick, indicating that encounters within the same dyad were less consistent there than under natural conditions (van Hooff & Wensing 1987). Furthermore, adding interactions recorded at the salt lick modified individual dominance ranks and may consequently affect the analyses of potential effects of social ranks on adult female fitness. For example, analyses of the effects of maternal social rank on offspring production or differential investment in the two sexes could lead to spurious results if ranks were wrongly assigned in the first place. The effects of social rank on reproductive success could therefore be underestimated or at least biased.

I suggest that the discrepancy observed in the outcomes of aggressive interactions is due to the concentration of animals near the traps. Because there was much activity at the trap site, individual recognition may have been difficult (Lamprecht 1986; Kendrick et al. 1995). Interaction rates at salt licks or other patchily distributed resources are much higher than elsewhere, and potential threats can come from many directions (Berger 1977; Chadwick 1977; Grenier et al. 1999). Animals likely use visual cues to recognize each other (Kendrick et al. 1995) and may not correctly identify opponents in crowded situations. At the trap site, individuals appeared to retreat from all threats where they could not identify the initiator. When approached from behind, a goat, licking salt, often initiated a submissive avoidance behavior. Although the same behaviors were observed under natural conditions and at the trap site, the rate of aggressive interactions was lower and the average distance between animals was likely greater under natural conditions than at the trap site. Thus, individuals were probably rarely surprised by another goat approaching from behind under natural conditions. When the initiator (and eventual winner) of the interaction was normally subordinate to the receiver, inconsistencies in dyadic dominance relationships were created (de Vries 1998). Dominant goats often retaliated (initiated a second interaction) immediately after losing an encounter at the salt lick, but unfortunately I did not systematically record the order of interactions in a sequence. Immediate retaliation would be expected if goats first reacted submissively when they could not identify their opponent, but then retaliated if the initiator was a subordinate.

Alternatively, goats could be more aggressive at the trap site because salt is a defensible resource (Clutton-Brock et al. 1976; Appleby 1980; Schoener 1983), unlike most of the vegetation eaten by goats (Geist 1974; Thouless 1990). If goats were willing to take more risks to lick salt than to eat grass, inconsistencies would appear in dyadic relationships. Subordinates that won interactions at the salt lick, however, did not normally try to use the patch where the dominant goat was licking, and when they did they usually experienced immediate retaliation. Future studies of dominance relationships in confined situations should pay particular
attention to retaliatory interactions, to determine how often a normally subordinate winner will actually obtain access to a resource.

Although results may differ for other species, my observations suggest caution in the interpretation of aggressive encounters recorded in confined situations such as baiting or supplemental feeding sites. In the abundant primate literature for instance, several studies were based on observations conducted in captivity or at supplemental feeding sites (Silk et al. 1981; Fedigan et al. 1986; Meikle & Vessey 1988; Hiraiwa-Hasegawa 1993 and references therein; Pusey et al. 1997). Comparisons with natural conditions are needed to address the reliability of social ranks established in confined situations because ranks based on these interactions may not be representative of natural conditions and may bias the assessment of dyadic relationships. More than 50% of the adult females, for example, changed rank in 1997 when I included interactions recorded at the salt lick. So many individuals incorrectly ranked could bias conclusions about the role of dominance in the social organization of a species, or about the potential effects of dominance on fitness traits. Researchers should be aware of this phenomenon and interpret published studies and their own results accordingly.

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**Literature Cited**


Hall, M. J. 1983: Social organization in an enclosed group of red deer Cervus elaphus L. on Rhum. I. The dominance hierarchy of females and their offspring. Z. Tierpsychol. 61, 250—262.


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