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SOCIAL DOMINANCE AND ITS INFLUENCE ON THE FORAGING EFFICIENCY OF THE MOUNTAIN GOAT: A PRELIMINARY REPORT.

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Abstract: The social behavior of mountain goats (Oreamnos americanus) was studied as part of a study of reproductive success and population dynamics in an unhunted population in west-central Alberta, Canada. Social dominance relationships were examined, in a nursery herd, to assess the possibility that dominance influenced the foraging efficiency of adult nannies. Foraging efficiency was measured as the proportion of time spent feeding during the time the goats were active. It was hypothesized that dominant animals would forage more efficiently than subordinate goats. There was no significant difference between these 2 classes. Dominance hierarchies have been suggested for this species, but detailed quantitative measures are lacking. This study reveals a non-linear dominance hierarchy that is weakly age-related.

During the evolution and radiation of ungulates in the northern hemisphere, animals immigrated into unoccupied suitable habitats following glacial retreat (Geist 1971). This led solitary forest-dwelling animals to venture into open areas where the security of vegetative cover was absent. Mammals evolved social systems to benefit from group living (Wilson 1975), and since living in an open environment involved an increased predation pressure, ungulates benefited from groups in the form of anti-predator behaviors (Hamilton 1971).

There are disadvantages as well as benefits in sociality. Animals living in groups must compete with other group members for resources such as food or mates and individual space sometimes must be defended. Defense of resources produces intraspecific aggression and mechanisms to cope with competition. One such mechanism is social dominance.

Social dominance is defined as the relationship between 2 individuals, where one (the subordinate) yields to the second (the dominant) during aggressive interactions (Kaufmann 1983). Rowell (1974) suggested that when a group establishes a social dominance hierarchy, the outcome of subsequent aggressive interactions are predictable according to previous encounters. Dominance may serve 2 major functions. First, it may allow priority access to a limited resource which enhances the fitness of the

individual (Kaufmann 1983). Second, it may reduce the level of aggression in a group (Rowell 1974, Bernstein 1981).

The benefits of dominance are the same for males and females, but the currency may be different. For most polygynous sexually dimorphic mammals, a dominant status is necessary for males in order to obtain access to estrous females during reproduction (Emlen and Oring 1977).

For females, on the other hand, dominance usually ensures priority access to a food resource. If dominance status does guarantee priority access to food, this advantage could translate into better growth and therefore may influence reproductive success. Such priority, and its benefits, have been described for other female ungulates such as red deer (Cervus elaphus, Clutton-Brock et al. 1982), woodland caribou (Rangifer tarandus, Barrette and Vandal 1986) and bison (Bison bison, Rutberg 1986).

The influence of dominance on feeding behavior may be evaluated by measuring foraging efficiency, defined as the amount of time that an individual spends foraging during its active time (Owen-Smith 1979). Individuals should benefit from increased foraging efficiency.

The mountain goat social system is based on dominance-subordination relationships. This system should favor a more predictable social environment, thus reducing the risk of injury and also lowering energy expenditures through diminished fighting. Reduction in aggression would be very profitable since these animals possess weapons than can inflict severe wounds to conspecifics (Geist 1964). If this social system does in fact provide a predictable environment, rates of aggression should be low. On the other hand, one may expect the rates of aggression to increase with group size since the distance between individuals may be reduced.

The objectives of this study were to characterize social dominance relationships between adult nannies, to determine whether social dominance affects the foraging efficiency of mountain goats, and to test if rates of aggression are a function of group size. Mountain goats are a good model for examining the possible advantages of social dominance because goats have a social system based on aggression, and they have a higher level of aggression compared to other gregarious female ungulates (Fig.1).

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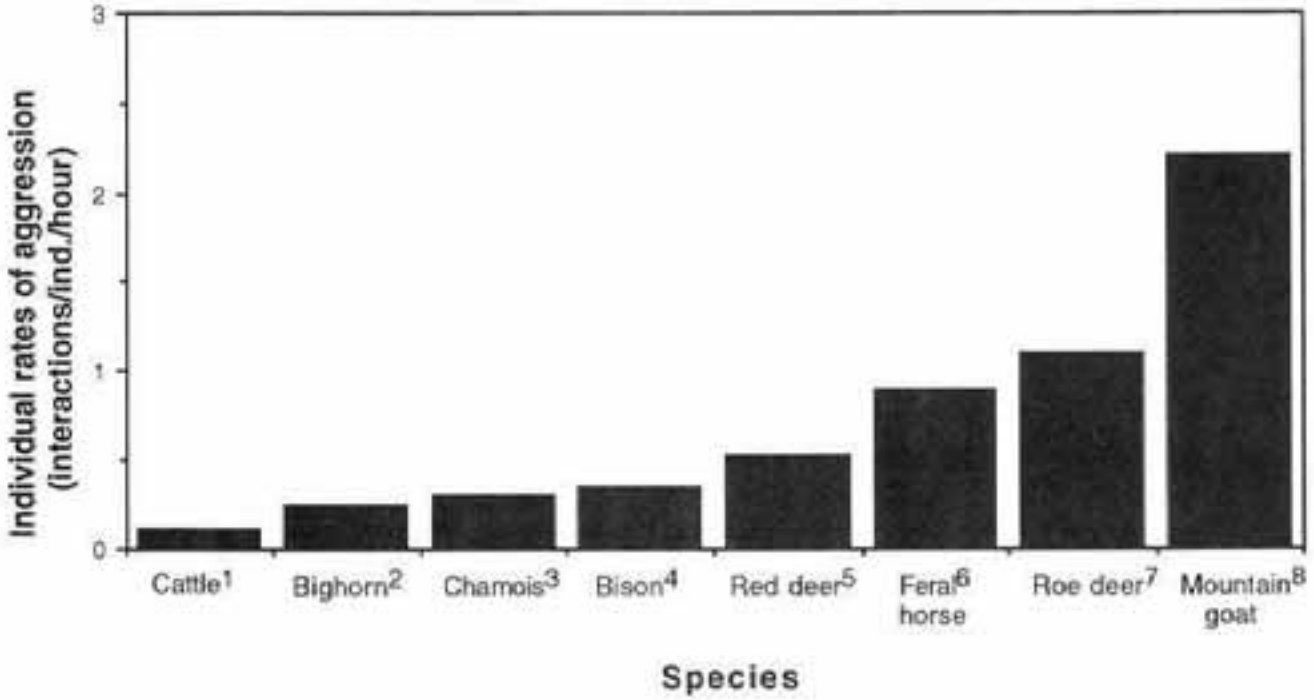

Fig. 1. Rates of aggression among female ungulates (1: Clutton-Brock et al. 1976, 2: Hass 1986, 3: Locati and Lovari 1990, 4: Rutberg 1986, 5: Thouless 1990, 6: Rutberg and Greenberg 1990, 7: Espmark 1974, 8: Caw Ridge, this study).

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METHODS

Study Area and Population

This study was conducted at Caw Ridge (54°N, 119°W), located approximately 30 km northwest of Grande Cache, Alberta. This site harbors the largest native population of mountain goats, in Alberta, outside of the National Parks. The area used by mountain goats (approximately 21 km^2) is a typical alpine habitat, characterized by forbs and grasses, between 1750-2150 m in elevation. The study area is a front range of the eastern slopes of the Rocky Mountains, and is separated from the main mountain range by 10-30 km of coniferous forest. Goat hunting on this site has been prohibited since 1969.

Goats were trapped with 2 remote-controlled Stevenson's box traps and 4 self-releasing clover traps. All traps were baited with salt blocks. Goats were drugged via intramuscular (IM) injection of xylazine and, once the handling of the animals was completed, the effects of the drug were reversed by IM injection of idazoxan (Jorgenson et al. 1990). Kids and most yearlings were not drugged. Captured goats were measured and weighed, then fitted with either plastic ear tags or canvas collars to permit easy identification. As of November 1991, about 62% of the 82 goats were individually marked and recognizable, including 23 adults fitted with radiocollars.

Goats were located visually and/or by radio telemetry on a daily basis between May and September 1991. Once located, the animals in the group were classified. Animals were separated into age-sex classes as follows: kids (male, female), yearlings (male, female), 2 year-olds (male, female) and adults (male, female). Nannies were also classified as with or without a kid.

Data Collection

Behaviors were observed with a 15x-45x spotting scope or 15X60 binoculars. Observations were centered on the nursery herd. Focal animal sampling (Altmann 1974) was used to measure time budgets and aggressive interactions. During aggressive interactions the following information was noted: initiator, receiver, winner, and approximate distance between the 2 goats at the start of the aggression. All aggressive interactions seen were noted using all-occurence sampling (Altmann 1974). Aggressive interactions were used to establish dominance relationships among adult nannies. Foraging efficiency was

defined as the proportion of time that a goat spent feeding during its active time (Owen-Smith 1979). The remaining behaviors included in the time budget were alert, bedded, social and other.

Additionally, in order to evaluate the assumption that mountain goats defend a personal space (Chadwick 1977), I designated an arbitrary area of approximately 4 m around each focal animal. Whenever another goat entered this area it was noted as a possibility of aggression and the outcome of this meeting was noted. Ensuing aggression was noted, and lack of aggression was noted as no defense.

Dominance Relationships

Dominance ranks were determined by assembling a win-loss matrix (Schein and Fohrman 1955) based on outcomes of aggressive interactions between adult nannies (≥ 3 years old). Individuals were ordered according to the ratio of wins versus losses, the highest ratios indicating superior ranks.

Since age was presumed to be a major determinant of dominance, a dominance index, which removes the effects of age, was calculated for each individual nanny. The index used was a modification of the one used by Clutton-Brock et al. (1986) which can be found in Festa-Bianchet (1991). First, the following ratio was calculated

$$OSD+OU+1/YSD+YU+1,$$

where OSD is the number of nannies of the same age or older dominated by the subject, OU is the number of older nannies with whom the subject interacted with no clear outcome, YSD is the number of nannies of the same age or younger that dominated the subject, YU is the number of younger nannies with whom the subject interacted with no clear outcome. The ratio was used to rank animals in each cohort, then the ranks were divided by the number of nannies in the cohort, resulting in dominance indices ranging from 0.25 to 1, in which higher indices represent higher ranks within the cohorts.

The linearity of the hierarchy was measured by Kendall's coefficient, K (Appleby 1983), using the win-loss matrix. Values of Kendall's coefficient range from 0 (complete absence of linearity) to 1 (complete linearity). For this study, a hierarchy is considered linear if $K \geq 0.9$. Arranging win-loss matrices into a specific order may create linear relationships were no such relationships exist, so the structure of the hierarchy was tested using the $\underline{x}^2$-test presented in Appleby (1983). This test measures the probability of the hierarchy occuring by chance.

RESULTS

In this population, rates of aggression of adult nannies were not a function of group size (r^2 = 0.008, P = 0.5, Fig. 2). Rates ranged in values from 0.01 to 13.5 interactions/individual/hour with an average of 2.18. The average group size sampled was larger than those examined in other studies ($\bar{x}$ = 58.9, SD = 8.59, n = 50, range = 34-68).

Regarding the defense of a personal space, the relationship between the possibility of interaction and the resulting number of aggressive interactions was significant but weak (r^2 = 0.283, P < 0.001, Fig. 3). Removing the outermost datum produced a weaker correlation (r^2 = 0.217, P = 0.0008). Possibilities of interacting with another goat averaged 9.1 per hour of observation, and the actual number of resulting interactions was 2.02 (n = 50).

Dominance Hierarchy

A sample of 123 aggressive interactions between marked adult nannies was used to calculate the dominance hierarchy. Results of the win-loss matrix (Table 1) revealed a hierarchy among adult nannies that was not linear, but significantly non-random (K = 0.57, χ^2 = 105.9, P < 0.001). Forty percent of possible dyads (nanny-nanny pair) were observed to interact.

The correlation between dominance rank and age was tested since 86% of the interactions were won by the older animal. The relationship between dominance and age for adult nannies was significant but weak (r^2 = 0.443, P < 0.001). Rank appears to increase with age until the animal reaches the age of 7, and then it may drop (Fig. 4).

In 50 hours of focal animal sampling the time budget of nannies did not vary significantly according to their dominance indices (Kruskall-Wallis ANOVA, P > 0.05). More specifically, there was no correlation between dominance index and the percent of time spent foraging (r^2 = 0.004, P = 0.80, Fig. 5), or the percent of time spent alert (r^2 = 0.057, P = 0.32, Fig. 6).

DISCUSSION

Previous studies of the effects of group size on the rates of aggression of mountain goats provide conflicting results. Chadwick (1977) found that rates of aggression increased with group size, whereas

Table 1. Win-loss matrix for adult female mountain goats, Caw Ridge, Alberta, 1991. Read across the table for number of interactions won by an individual; down for number of losses. Percentage of dyads observed interacting = 40. Number of interactions = 123.

Age	Individual	16	57	42	41	15	7	71	34	60	68	63	31	50	86	8	73	59	49	54	46	84
7	16			•	• •	• • •	• •		• • •	•			•	• •	•		• •			•		•
7	57	•						•	• •	•			•			•		•	• •	•	•	
9	42									• • •			• •			•	•	•			•	•
9	41							•		•						• •			• • • •	•		
8	15				• •				• •							•					•	
8	7								•							•		•	•			
6	71											•			•			•		•	•	•
9	34									•	•	•		• •		• •		•				
7	60										•	• •				•	• •		•	•	•	•
3	68												• •									•
5	63		•							•	•		•				•	•				
4	31							•											•			• • • •
4	50							•											• •			•
5	86																	•				
7	8																• •		• •		•	• •
6	73													•				•				•
5	59											• •							•			
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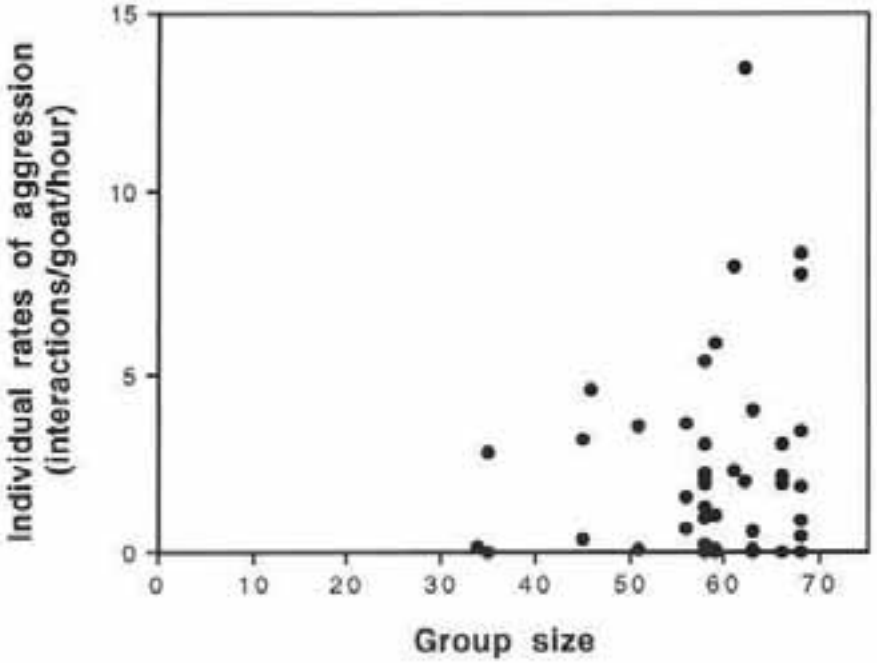

Fig. 2. Relationship between individual rates of aggression by adult female mountain goats and group size (r^2 = 0.008, P = 0.6, n = 50).

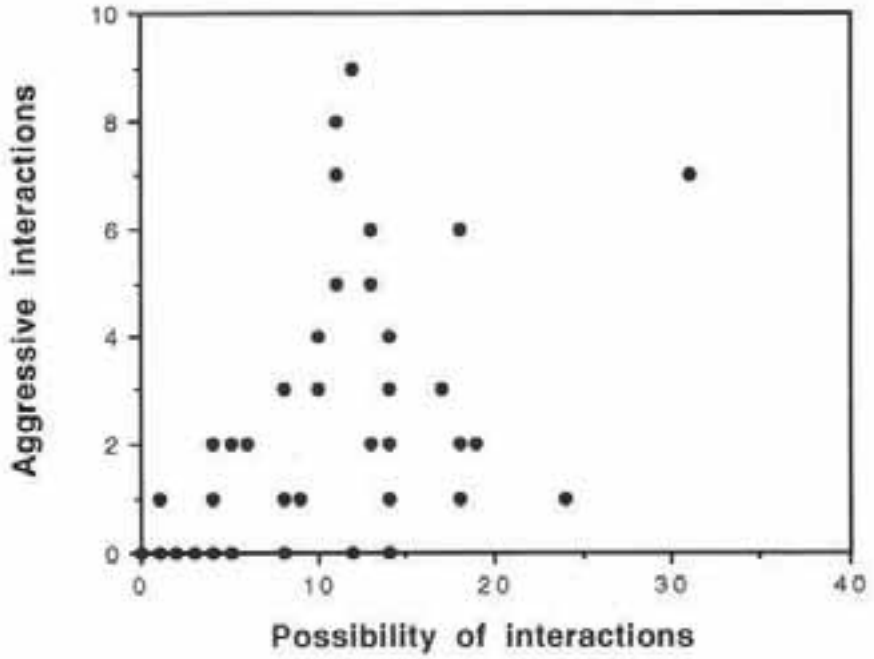

Fig. 3. Relationship between the possibility of interactions (goats within 4m) and the number of interactions according to 1-hour focal samples of mountain goat adult females (r^2 = 0.283, P = 0.0001, n = 50).

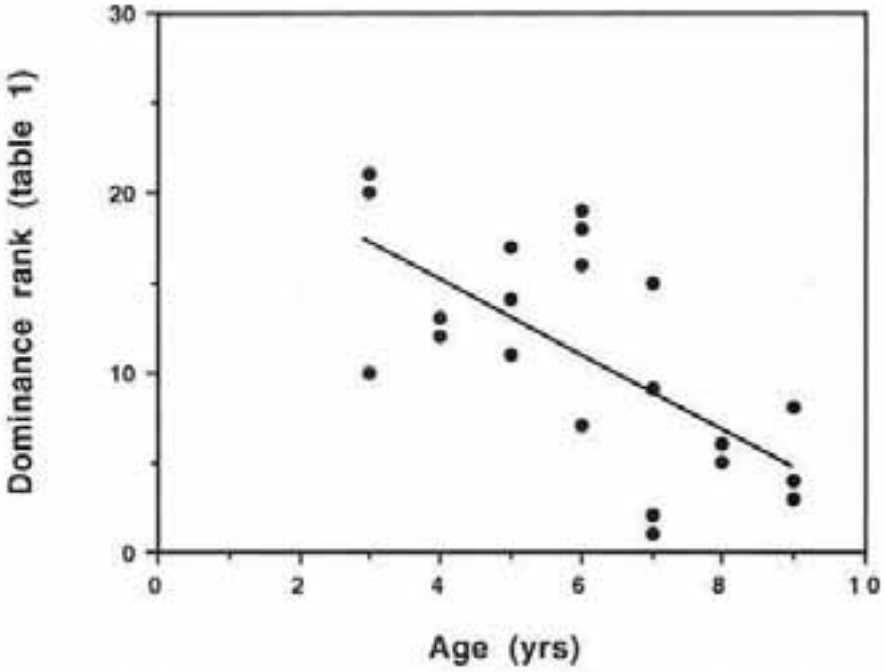

Fig. 4. Relationship between age and dominance rank of adult female mountain goats, Caw Ridge, Alberta, summer 1991 (r^2 = 0.44, P = 0.001, n = 21).

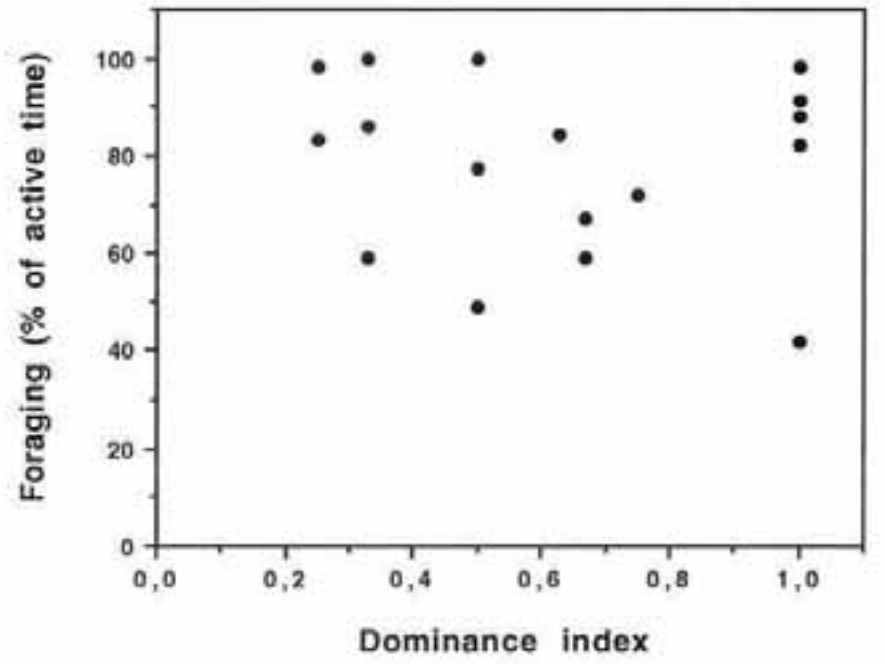

Fig. 5. Relationship between dominance index and the percent of active time spent foraging by adult female mountain goats, Caw Ridge, Alberta, summer 1991 (r^2 = 0.004, P = 0.80, n = 19).

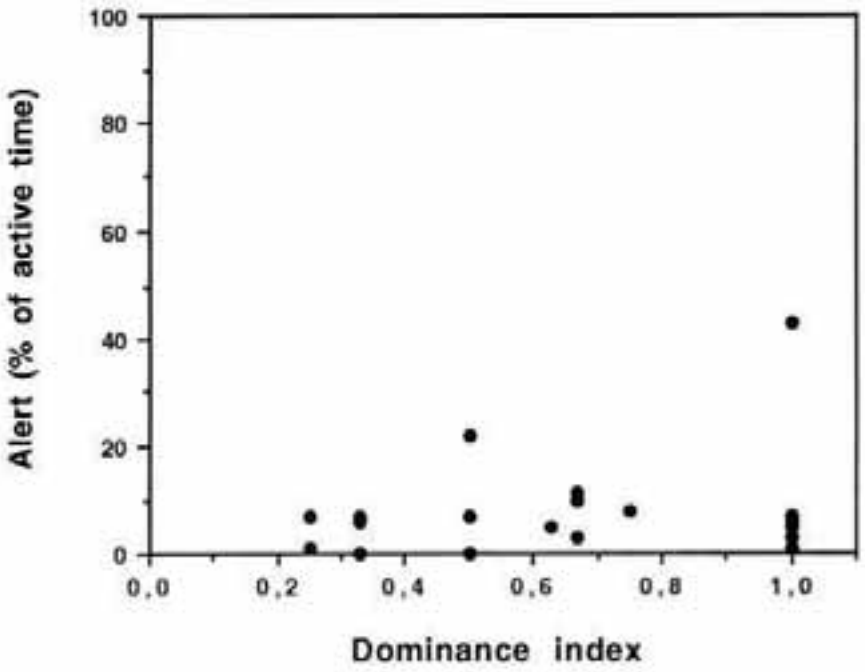

Fig. 6. Relationship between dominance index and the percent of active time spent in alert behavior by adult female mountain goats, Caw Ridge, Alberta, summer 1991 (r^2 = 0.057, P = 0.32, n = 19).

Risenhoover and Bailey (1985) reported that rates of aggression declined as group size increased to about ten animals. Their results differed from those of Chadwick because goats they observed in Colorado were introduced and their social structure might differ from native herds. Average group sizes recorded by Chadwick in Montana were small (2-3 goats), making it difficult to measure effects of group size. Furthermore, the goats used different habitats. In Montana (Chadwick 1977), the goats were on cliff outcrops where food was spatially limited, while Colorado's animals were in alpine tundra where food was more available (Risenhoover and Bailey, 1985). Although Caw Ridge might have offered me a chance to test the predictions that group sizes affect rates of aggression, it was found, however, that rates of aggression were not correlated with group size. In my study, the average group size was larger than those previously reported making a comparison with small groups difficult.

Chadwick (1977) suggested that the social organization of mountain goats was based on defense of a mobile personal space. A preliminary test of this assumption suggests that the goats do not always defend a personal space. The occurence of 2 adult females did not always result in an

aggressive interaction. These results must be interpreted cautiously since they are preliminary, and this question will be addressed more thoroughly in the second summer of research.

Although the social organization of mountain goats has been classified as a dominance hierarchy (Chadwick 1977, Masteller and Bailey 1988), a detailed study of this organization is lacking. The goats have a dominance hierarchy, but this hierarchy is non-linear, indicating many reversals of rank. These conclusions have been drawn from studies on wild bighorn ewes (Hass 1991), captive ewes (Eccles and Shackleton 1986), bison (Rutberg 1986), and feral cattle (Hall 1986). Hass and Jenni (1991) found that for bighorn rams, the dominance hierarchy was linear and stable over many years. This suggests that a linear hierarchy is possible mainly when a contested resource (estrous females) may be defended. It is not clear if female mountain goats can defend a non-patchy food resource, and this might account for the lack of linearity in their hierarchy.

Dominance is correlated with age in bison (Rutberg 1986), red deer (Clutton-Brock et al. 1984, Thouless and Guinness 1986), white-tailed deer (Odocoileus virginianus, Townsend and Bailey 1981), bighorn sheep (Ovis canadensis, Festa-Bianchet 1991) and addax (Addax nasomaculatus, Reason and Laird 1988). Weight and age determined dominance in chamois (Rupicapra pyrenaica, Locati and Lovari 1991), whereas weight (Hirotani 1990) but not antler size (Barrette and Vandal 1986) correlated with dominance in caribou. Although most interactions were won by the older goat in each dyad (86%), dominance rank was only weakly corrrelated with age. This suggests a better clue for dominance in this population of goats may be weight or horn size; but available data are insufficient to permit me to explore these possibilities.

Other studies have shown that dominants differ in their time budget in comparison with subordinates (Appleby 1980, Deutsch and Lee 1991). Dominant animals had a priority to food resources in captive rhesus monkeys (Macaca mulatta, Deutsch and Lee 1991), in red deer stags (Appleby 1980), woodland caribou (Barrette and Vandal 1986) and wintering mountain goats at a localized bait (Masteller and Bailey 1988). Although I expected similar feeding competition in this population, no differential access to food, or foraging efficiency, was found. Thouless (1990) suggested that, for red deer hinds, feeding competition is a passive process whereby subordinates avoid conflict with a dominant by moving away from them during feeding bouts. He also found that dominant hinds had a better feeding efficiency than did subordinates (Thouless 1990). The data from Caw Ridge do not support this hypothesis for mountain goats. Lovari and Rosto (1985) found that, in a group of Apennine chamois, dominance affected foraging efficiency. Dominant females had a greater number of bites per minute and significantly fewer head-lifts per minute,

a measure of alertness, than did subordinate females. These authors suggested that the stress encountered by subordinates was not from predation pressure but rather from the presence of potentially aggressive conspecifics (Lovari and Rosto 1985). This conclusion may be also valuable for mountain goats, but further work needs to be done in order to test this assumption.

According to Hamilton (1971) subordinate goats should be found more often on the periphery of the group and should therefore spend more time in alert behavior. These results were found for pronghorns (Antilocapra americana, Lipetz and Bekoff 1982). Although predation was a major mortality factor in this population (Smith et al. 1992), the goats often fed a fair distance away (> 400 m) from what appeared to be escape terrain and I found no difference between dominant and subordinate goats in the amount of time they were alert.

Although mountain goats demonstrate a high level of aggression, the reasons behind their aggression are poorly understood. This behavior must serve a purpose since valuable energy is spent on aggression. Further investigations into this aspect of mountain goat social behavior may enable us to better understand these animals.

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