Relationships between group size, feeding time, and agonistic behavior of mountain goats

KENNETH L. RISENHOOVER[1] AND JAMES A. BAILEY
Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO, U.S.A. 80523

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Relationships between group size, intragroup spacing, movement rates, foraging behavior, and frequency of agonistic behavior of mountain goats (*Oreamnos americanus*) using alpine tundra were examined during summer. Feeding time of goats increased with group size to about 12 goats because of a reduction in time devoted to alert behavior. Rates of movement by foraging goats increased with group size, whereas rates of agonistic behavior between goats declined with increased group size. Intragroup spacing declined as group size increased. Nannies and 2-year-old goats were more aggressive than were other sex- or age-classes. Two-year-old goats, yearlings, and billies received more threatening displays than did other classes. In Colorado, nannies with kids form large nursery bands on alpine tundra. This behavior can reduce the risk of predation to individuals while allowing nannies with kids to exploit forage away from precipitous terrain. Average group size may be a useful index to forage abundance and continuity on summer goat range.

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Les relations entre le nombre d'animaux dans un groupe, l'espacement entre les animaux au sein du groupe, les taux de déplacements, le comportement de recherche de nourriture et la fréquence des comportements agonistiques ont fait l'objet d'une étude chez des chèvres de montagne (*Oreamnos americanus*) d'une toundra alpine, pendant l'été. Le temps consacré à l'alimentation augmente en fonction du nombre d'animaux dans un groupe (jusqu'à 12 chèvres) car le temps consacré aux comportements d'alerte se trouve alors à diminuer. La fréquence des déplacements des chèvres à la recherche de nourriture augmente en fonction de la taille du groupe, alors que la fréquence des comportements agonistiques entre les chèvres diminue lorsque la taille du groupe augmente. L'espacement entre les chèvres diminue lorsque leur nombre augmente. Les chèvres nourricières et les chèvres de 2 ans sont plus agressives que les chèvres des autres classes d'âge et de sexe. Les chèvres de 2 ans, les chèvres de 1 an et les boucs sont l'objet de nombreux comportements menaçants, plus que toutes les autres classes d'animaux. Au Colorado, les femelles nourricières avec leurs petits forment de grands troupeaux dans la toundra alpine. Ce comportement a pour effet de réduire les risques de prédation sur les individus, tout en permettant aux femelles nourricières avec des petits d'exploiter des territoires autres que les zones très escarpées. Le nombre moyen d'animaux dans un groupe peut constituer un bon indice de l'abondance de la nourriture et de la continuité du broutage sur les territoires de chèvres de montagne au cours de l'été.

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Introduction

Although various aspects of mountain goat (*Oreamnos americanus*) behavior have been described (Geist 1965, 1978; DeBock 1970; Rideout 1974; Chadwick 1977; Dane 1977; Singer 1977), the adaptive behavioral strategies that enable goats to exploit their physical environment are not well understood. Quantitative descriptions of mountain goat social dynamics and foraging behavior are lacking.

On native ranges, goats are intimately associated with cliff outcrops and fell-fields in mountain habitats (Brandborg 1955; Chadwick 1977). Goats possess dangerous weapons and have been considered more aggressive and socially unstable in groups larger than five (Chadwick 1977). However, during summer, goats in Colorado often congregate in large groups on alpine tundra far from precipitous terrain (Adams 1981; Risenhoover and Bailey 1982). The larger group sizes observed in Colorado suggest that different social and environmental conditions are shaping mountain goat social and foraging behavior.

In this study, we examined the effects of group size on the foraging and agonistic behavior of mountain goats using alpine tundra on Mount Evans, Colorado. The following questions were addressed. (*i*) Do individuals in larger groups forage more continuously than do goats in smaller groups? (*ii*) Are individuals in larger groups less vigilant than are goats in smaller groups? (*iii*) Do goats become more aggressive when foraging in larger groups? (*iv*) Is intragroup spacing determined by group size? and, (*v*) Are movement rates of foraging goats affected by group size?

Study area and methods

Mount Evans (4346 m) is located east of the Continental Divide about 45 km west of Denver, Colorado. The vegetation on Mount Evans is typical of the region and has been described by Marr (1967). The Mount Evans goat herd originated from a release of 15 goats from Idaho and South Dakota in 1961 (Denney 1977). The herd grew rapidly and was estimated at 150 goats in 1981 (B. Goforth, Colorado Division of Wildlife, personal communication).

During summer, much of the herd can be observed on alpine tundra and is accessible via a paved road. Despite being a hunted population, goats on Mount Evans have habituated to the abundance of people on or near the Mount Evans road each summer. This relative tameness provided an unusual opportunity to observe goats closely, often at less than 15 m. From such distances, goats were accurately classified into seven sex- and age-classes using horn characteristics, urination postures, external genitalia, and nanny–kid associations (Smith 1976; Chadwick 1977). The social dynamics of goats on Mount Evans have been described briefly in a preliminary report (Risenhoover and Bailey 1982).

During 20 July to 19 August 1981, groups of foraging goats were observed in alpine tundra habitats. A variety of group sizes was selected. While observing a group, nearest-neighbor distances were recorded for each member at 10-min intervals. Kids were excluded

[1]Present address: Department of Biological Sciences, Michigan Technological University, Houghton, MI, U.S.A. 49931.

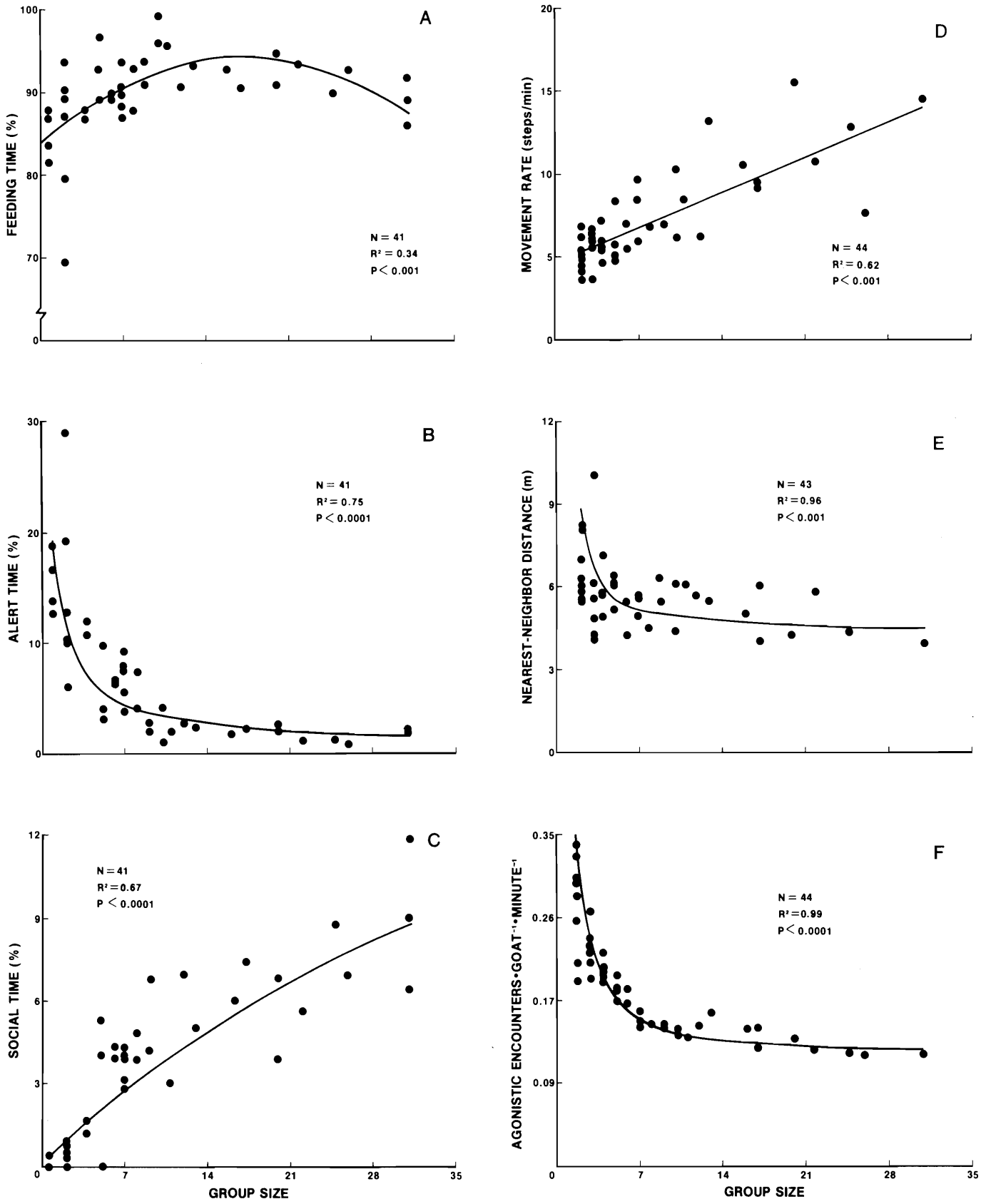

FIG. 1. Behavior of foraging mountain goats in relation to group size on Mount Evans, Colorado, during late July – August 1981. Relations of group size to (A) feeding time: $Y = 83.8 + 1.2X - 0.033X^2$; (B) alert time: $Y = 19.41X^{-0.758}$; (C) social time: $Y = 14.62(1 + e^{-0.0296X})$; (D) movement rate: $Y = 4.65 + 0.30X$; (E) goat spacing: $Y = 4.39X/(-1.02 + X)$; and (F) rate of agonism: $Y = 0.12X/(-1.63 + X)$.

TABLE 1. Classification of mountain goat behavior observed during foraging periods (adapted from Risenhoover and Bailey 1980)

Type	Description and characteristics
Feeding	Ingesting forage; looking at forage; moving toward forage. Head is oriented toward the ground
Alert	Head is upright; surveying surroundings for potential danger. May lead to the alarm posture
Social	Interactions among goats; play; aggression; display; looking at other goats, moving toward other goats

from these measurements because of their close associations with nannies. Focal animals were observed for 5–10 min unless observations were terminated by animals moving out of good view. Behavior of focal animals was described into a tape recorder and later transcribed using a stopwatch to determine rates and averaged for each group member (excluding kids). Data for group members were then averaged for each group. Throughout the study, some goats were likely to have been reobserved in different groups on subsequent days.

Agonistic encounters expressed and received by focal animals were transcribed as encounters per goat per minute. With each encounter, the sex and age of the expressor and recipient were recorded. In addition, agonistic encounters were classified as "low intensity" (e.g., present threats, orientation threats) or "high intensity" (e.g., rush threats, weapons threats) using descriptions given by Geist (1965) and Chadwick (1977). Low intensity displays included any agonistic display oriented toward conspecifics and eliciting a response. High intensity displays involved sudden movements toward conspecifics and often resulted in physical contact.

Activities of goats during foraging periods were classified as either alert, social, or feeding behaviors (Table 1). During these observations of focal animals, each step (movement by only one of the front legs) was recorded to determine the number of steps per minute of feeding activity as an index to forage continuity. This index has been correlated with habitat preferences of other ungulates (Owen-Smith 1979; Risenhoover 1981; Dunham 1982). Alertness of goats was measured as the percent of foraging periods spent in alert behavior. Feeding time was defined as the percent of foraging periods spent in feeding behavior.

Feeding time, alertness, the percent of foraging periods spent in social behavior, frequency of agonistic encounters, intragroup spacing, and movement rates were tested for relationships with group size using regression analyses (Sokal and Rohlf 1969).

Results

Foraging behavior

Foraging behavior was observed for 64 groups ranging from 2 to 31 goats. Feeding rate of mountain goats increased with increasing group size to approximately 12 animals (Fig. 1A). This increase was due to a decline in the time devoted to alert behavior as group size increased (Fig. 1B). Goats assembled in larger groups spent less time surveying their surroundings and therefore had more time to devote to forage acquisition. Feeding time declined slightly as group size exceeded 12 animals. This decline was attributed to an increase in social behavior. The time share devoted to social behavior during foraging periods increased significantly with group size ($P < 0.0001$, Fig. 1C).

The rate of movement (steps per minute) of foraging goats increased with group size (Fig. 1D). Intragroup spacing declined with increasing group size to approximately 10 animals (Fig. 1E).

Agonistic behavior

The rate of agonistic encounters for groups (calculated from the average number of encounters per goat per minute × group size) increased linearly with increasing group size. However, the rate of agonistic encounters per goat declined with increasing group size (Fig. 1F), suggesting that goats in larger groups were less agonistic than were goats in smaller groups. The rate of agonistic behavior per goat was negatively related to the rate of movement by foraging goats (Fig. 2).

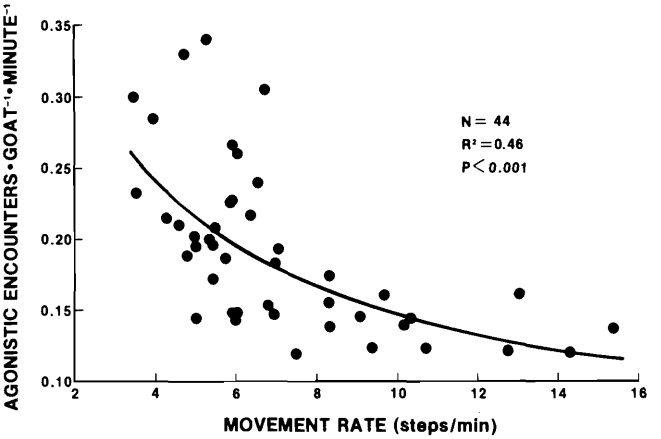

FIG. 2. Movement rate of foraging mountain goats in relation to rate of agonistic behavior, Mount Evans, Colorado: $Y = 0.52X^{0.5533}$.

Observations of agonistic behavior among goat sex- and age-classes (Table 2) were not analyzed by inferential statistics for two reasons. First, likely reobservation of some individuals on subsequent days violated the required assumption of independence. Second, the expected number of agonistic interactions for each sex- and age-class would have to be calculated to test the null hypothesis. Expected numbers would be a function of (*i*) the proportion of focal-animal time observed for each sex- and age-class, and (*ii*) the percent frequency of each class in each observed group. These values could not be retrieved from the original data. However, the data are described for comparison with studies that have used similar procedures.

High-intensity displays were slightly more frequent (55%) than were low intensity displays (45%, Table 2). Judging the frequency of agonistic encounters for each sex- and age-class against the sex–age composition of the study population (Table 2), it is suggested that (*i*) nannies and 2-year-old males used high-intensity displays more than did other sex- and age-classes; (*ii*) yearlings and 2-year-olds of both sexes received more high-intensity displays than did other classes; (*iii*) nannies and kids received few high-intensity displays; (*iv*) 2-year-olds used low-intensity displays most frequently; and (*v*) compared with other classes, billies and 2-year-olds received more low-intensity displays (Fig. 3).

When all agonistic interactions are considered (Table 2), 2-year-old males were especially aggressive, followed by 2-year-old females, nannies, and perhaps yearlings. However, 2-year-olds were especially frequent recipients of aggression, followed by yearlings and billies. Billies rarely directed threats toward nannies and were never observed to express agonistic displays towards nannies with kids (Fig. 3). However, 2-year-old males often displayed to both barren nannies and to nannies with kids. Chadwick (1977) also noted high rates of agonistic behavior directed at nannies by 2-year-old males and reported that 2-year-old males dominated 2-year-old females and all other subadult age-classes. Although we could not demonstrate any dominance by 2-year-old males over 2-year-old females,

TABLE 2. Frequency analysis of agonistic encounters expressed and received by different sex- and age-classes of mountain goats on Mount Evans, Colorado

Class	% of study population[a]	Expressor			Recipient			Total interactions
		Low intensity	High intensity	Total	Low intensity	High intensity	Total	
Nannies	31.0	47 (32.9)[b]	89 (50.0)	136 (42.4)	32 (22.4)	13 (7.4)	45 (14.0)	181 (28.2)
Billies	10.1	13 (9.1)	17 (9.6)	30 (9.4)	26 (18.2)	23 (12.9)	49 (15.3)	79 (12.3)
2-year-old ♂	4.2	24 (16.8)	22 (12.4)	46 (14.3)	21 (14.7)	19 (10.7)	40 (12.5)	86 (13.4)
2-year-old ♀	7.0	21 (14.7)	18 (10.0)	39 (12.1)	24 (16.8)	42 (23.6)	66 (20.6)	105 (15.4)
Yearlings	16.9	38 (26.5)	32 (18.0)	70 (21.8)	36 (25.2)	71 (39.9)	107 (33.3)	177 (27.6)
Kids	31.0	0 (0.0)	0 (0.0)	0 (0.0)	4 (2.8)	10 (5.6)	14 (4.3)	14 (2.2)
Totals		143 (44.5)	178 (55.5)	321	143 (44.5)	178 (55.5)	321	641

[a]Data from Risenhoover and Bailey (1982).
[b]Numbers in parentheses are percentages of the column total.

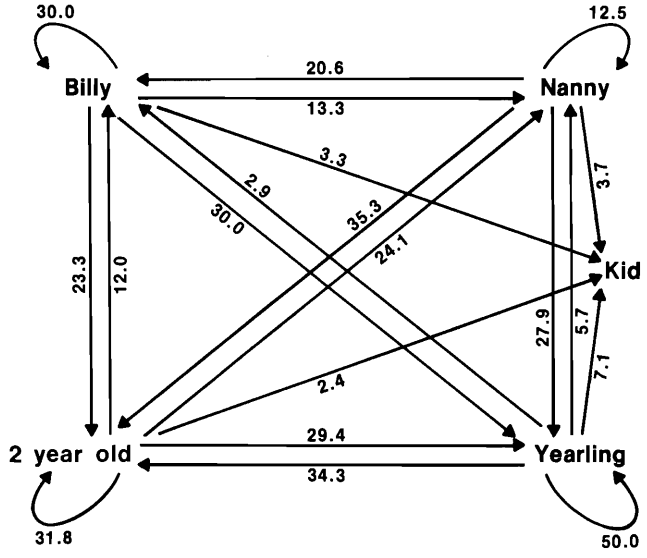

FIG. 3. Agonistic encounters expressed and received by mountain goat sex- and age-classes on Mount Evans, Colorado. Arrows indicate expression of agonistic behavior towards sex- and age-classes. Numbers are the percent of total observed interactions expressed towards each sex- and age-class.

there was a tendency for yearlings to interact more with 2-year-old females and to avoid interactions with 2-year-old males. Yearlings rarely directed threatening displays at billies or nannies, and 84% of all observed yearling interactions were with other yearlings or with 2-year-olds. Kids frequently engaged in "play behavior" with other kids, but these encounters were not included in this analysis. Kids were sheltered from many interactions by their nannies. They were threatened by yearlings and nannies more than by other sex- and age-classes.

Discussion

The advantages of group size to predator detection and avoidance have been documented (reviews by Wilson 1975 and Bertram 1978) and similar relationships have been demonstrated for ungulates occupying open habitats (Underwood 1976; Berger 1978; Lipetz and Bekoff 1982; Risenhoover and Bailey 1985). Forage quality should be critically important to nannies during lactation, as energetic costs of milk production can result in a rapid decline of a female's body reserves (Moen 1973, 1978; Armann et al. 1974; Pond 1977). Clutton-Brock et al. (1982) demonstrated that milk yield by red deer (*Cervus elaphus*) hinds was a major factor determining growth rates of calves, and thus, their winter survival. We anticipate that a similar relationship exists for mountain goats.

Therefore, when goats are especially vulnerable to predation (e.g., nannies with kids) and require large intakes of quality forage for lactation, it can be adaptive to form large nursery groups and to feed in areas of abundant forage, even far from steep escape terrain. On Mount Evans, goats in such nursery bands foraged more constantly as group size increased up to 12 (Fig. 1). Presumably, these goats also shared the risk of predation and benefitted from mutual alertness.

It can be in the interest of billies to avoid competing for forage with nannies they have bred. The few billies observed in groups containing nannies with kids were obliged to keep their distances by frequent agonistic encounters with nannies. As a result, billies generally remained on the peripheries of foraging groups containing nannies and kids, or they abandoned these groups entirely. Billies were most often observed solitary or in small bachelor groups (Risenhoover and Bailey 1982). In addition we observed two instances of 2-year-old males being expelled from groups of 10–12 goats by nannies with kids. Chadwick (1977) and Geist (1978) also reported billies being expelled from groups by nannies with kids. Sexual segregation is relatively common among northern ungulates (Peek and Lovaas 1968; Watson and Staines 1948; Geist 1971; Geist and Petocz 1977, Clutton-Brock et al. 1982) and several studies (Geist 1965, 1974; Rideout 1974; Risenhoover and Bailey 1982) have indicated differential habitat use between male and female goats, with males occupying more marginal habitats.

Nannies might also be expected to expel subadults from groups to reduce forage competition and to prevent injury to kids. Subadults were frequently engaged in agonistic behavior while attempting to gain positions in close proximity to dominant nannies with kids. However, if these subadults are close kin they may be tolerated providing they do not greatly reduce foraging efficiency (Clutton-Brock et al. 1982).

We found goats in larger groups to be less aggressive toward other group members than were goats in smaller groups (Fig. 1). These findings are not in agreement with Chadwick (1977) who studied goats on native range. He reported increasing rates of agonistic behavior as group size increased. Perhaps different social or environmental factors were operating in our study of introduced goats.

During summer, alpine tundra forage is spatially heterogeneous. Goats competing for this forage in small groups on Mount

Evans emphasized agonistic threats and defense of feeding sites (inferred from their relatively slow movement rates and spacing behavior, Fig. 1). As group size increased, goats apparently switched from feeding-site defense and frequent agonistic behavior to a "scramble" competition characterized by increased movement rates, reduced antagonism, and closer intragroup spacing (Fig. 1). Reasons for this switch are not clear. We suggest that, with increasing group size, it became less profitable to defend and thoroughly utilize a feeding site.

Perhaps, in a large group, a goat surrounded by competitors is unable to defend all the best forage in its vicinity. Confrontation with one competitor would allow still another goat to utilize the best nearby forage. Consequently, rapid movement among the very best feeding sites would be the more profitable strategy in large groups.

However, it is still not certain why antagonism and less movement were more common, and presumably more profitable, when group sizes were small. Perhaps small groups occurred mostly where forage was less abundant and more patchy, emphasizing the value of patch defense (Geist 1978; Davies 1978; Mitani and Rodman 1979). This would have occurred if large groups were unstable and separated into small groups in such environments, whereas large groups would not separate when using environments having abundant and continuous forage. Evidence from several ungulate species suggests that variation in the size of female groups is closely related to the distribution of food (Jarman 1974; Estes 1974; Owen-Smith 1977; Clutton-Brock et al. 1982). If this hypothesis can be tested and supported, group size could be a useful index to forage conditions. Also, differences in forage conditions between native mountain goat ranges and ranges where goats have been recently introduced may explain the large group sizes observed among Colorado mountain goats (Adams et al. 1982) and the discrepancy between our data and those of Chadwick (1977) regarding rates of agonistic behavior versus group size.

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