THE INFLUENCE OF MOUNTAIN GOAT SOCIAL RELATIONSHIPS ON POPULATION SIZE AND DISTRIBUTION

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Abstract: Sexual, agonistic and leadership relationships of the mountain goat (Oreamnos americanus) were studied from 1971 through 1976 in native Montana populations. Adult females were socially dominant over all other classes outside the rut. Females with young organized most group activities, mainly through strong following tendencies which they elicited from other females and subadults. Maturing males experienced difficulty interacting successfully within female-subadult groups and subsequently began utilizing ranges peripheral to or separate from them. Yearlings (not distinguished by sex) were solitary 3 percent of the time; two-year-old males 36 percent, and adult males 50 percent; revealing increased isolation of the male population segment with age, which further reduced range competition with breeding females. Social instability, measured as rates of agonistic encounters/goat/hour, increased in groups of increasing size. This proved to be an important factor in the dispersion of herds into groups of small average size. In resultant groups, competition mediated by the social hierarchy magnified resource shortages for subordinate animals. Juvenile mortality, characteristically high, was found to vary markedly with winter conditions while the proportion of adult females in the population remained fairly constant. Social mechanisms, particularly in a species such as the mountain goat with strong home range traditions, thus appear to play a critical role in population stability and distribution within habitats.

Populations of mountain goats are intimately associated with early stages of high elevation geologic succession - cliff outcropping and fellfield structures. Within its narrow, topographically defined niche, the species has evolved unique morphological characteristics, climbing abilities and food habits. Complex social relationships have also evolved. Adaptive aspects of mountain goat social behavior were investigated from 1971 through 1976 as part of a study of mountain goat ecology. Because factors which control mountain goat numbers are poorly understood at present, special attention was paid to the possible role of social mechanisms in regulating population size and distribution within ranges.

STUDY AREA AND METHODS

Investigations from 1971 through 1973 focused on a single herd of approximately 30 animals. The herd occupied a limited and well-defined year-round range of 25km^2 near Bunker Creek in the Swan Mountains of northwestern Montana. From 1974 through 1976, investigations concerned a population of about 360 goats inhabiting a 310km^2 central portion of Glacier National Park, Montana, 125km north of the Swan Mountains study area. The Glacier Park study population was composed of herds from 10 separate wintering areas including ranges east and west of the continental divide. Glacier Park goats generally occupied higher and more extensive cliff terrain than those in the Swan Mountains. Descriptions of physiographic features and plant communities for Bunker Creek and Glacier Park may be found in Chadwick (1974) and Habeck (1970), respectively. Both study areas contain indigenous goat populations. Those in the Swan Mountains are subject to hunting; those in Glacier Park are not.

Studies of movements, grouping patterns, and behavioral development were aided by the presence of individually recognizable animals. The Bunker Creek herd included five animals with radio collars, five wearing braided nylon collars, and two marked with dye. Additional goats could be identified by natural markings such as scars or horn deformities. Since the herd was observed daily for up to 18 continuous months, other goats could be distinguished for various periods of time through familiarity. In Glacier Park, recognition of naturally marked animals was supplemented by dye-marking 12 individuals. Certain park herds could be approached to within 10m, permitting detailed identification and behavioral study.

Observed goats were separated into kid, yearling, two-year-old female, two-year-old male, adult female, and adult male classes. Kids and yearlings are collectively referred to as juveniles. Kids, yearlings, and two-year-olds are collectively termed subadults. Data recorded for each sighting include pertinent structural and biotic habitat information, geographic location relative to a Universal Transverse Mercator (UTM) 100m grid, and location relative to other goats, predators,

and competitors.

Alertness was measured in different social classes by recording amount of time (in seconds) spent surveying surroundings in an alert posture during five-minute intervals. Aggressive rates were examined in groups of different size and composition by recording number of agonistic interactions observed between group members over a given period of time. In the Swan Mountains, intervals were variable and corresponded to complete feeding or bedding period durations in most instances. All group members were not always simultaneously visible, so number of encounters observed was less than actually occurred. In Glacier Park, 15-minute intervals when all group members were simultaneously visible were selected and include all encounters, yielding absolute aggressive rates rather than relative rates as in the Swan Mountains.

Efforts were made to measure relative frequency of potentially harmful climbing events. Subjective assessments of climbing 'danger' were related to events causing goats to yield overall balance and position relative to the substrate.

Percentage figures in tables may not total exactly 100 due to rounding.

RESULTS

Alertness - Mountain goats raised their head to survey their surroundings at frequent but irregular intervals. Unquantified observations indicated that lone animals were more wary than group members and less likely to perform uninterrupted maintenance activities such as foraging or resting.

Measurements of alertness were carried out which confirmed these impressions (Table 1). Mountain goats with at least one companion (other than a kid) were substantially less alert than solitary animals. Individual alertness continued to decrease with increasing group size to a point where goats in groups larger than five spent only a fraction of the surveying time that solitary animals did. However, the combined surveying time of individuals in groups increased with increasing group size and nearly always exceeded alertness of solitary animals. Group alertness was further increased in holistic fashion by the tendency of members to feed and bed facing different directions. Bedded goats often rose, surveyed their surroundings, then rebedded facing the opposite direction. Rebedding activity of this type was more common in large groups than in solitary animals or small groups, partly as a consequence of more frequent social interaction.

Table 1. Relationship of alertness to group size in foraging mountain goat classes. ( ) denotes small sample size.

		Ave. Surveying Time (No. Seconds/5 Minutes)										
		Group Size										
Class	Sample Size	Solitary 1	2	3	4	5	6	7	8	9	10	≥10
AM	29	38	16	25	(5)	(5)		(2)		(6)	(6)	
AF without K	193	50	15	20	(19)	61	5	(0)	(11)	(2)		10
AF with K	62	40	*	30	22	23	5	(17)	(20)		(0)	6
2M	23	32	(14)	(8)	(16)	(18)	(12)	(11)				(5)
2F	45	35	21	16	(26)	(9)	(5)	(6)	(21)	(2)	(0)	(0)
Y	47	25	(32)	14	29	(0)	8	(6)	(2)	(0)	(8)	(2)
Mean	399	37	20	19	20	19	7	7	14	2	4	5
Mean x Group Size = Total Group Surveying Time		37	40	57	80	95	42	49	112	18	40	

*Nanny-kid pairs in the absence of other goats were classified as solitary.

Alertness develops with age (Table 1). Kids surveyed their surroundings so infrequently that they were not included in Table 1. Yearlings were less alert than two-year-olds as solitary animals,

and adult classes were more alert than two-year-olds. Two-year-old and adult females were somewhat more alert than males of equivalent age. Contrary to expectations, adult females with kids spent less time surveying than adult females without kids.

Leadership - Mountain goat neonates are followers rather than hiders. They undergo precocial locomotor development and frequent reinforcement of maternal-infant bonds following parturition (Chadwick 1974). Kids typically followed within 2-20m of their nanny until 10-11 months of age, at which time maternal care terminated. Mountain goat females were extremely attentive and protective toward their young during this entire 10-11 month period, even though documentation of nursing durations indicate that weaning is effectively accomplished by 6-8 weeks of age (Brandborg 1955, Chadwick 1974).

Subadults older than kids strove to maintain contact with older females. Adult females retained strong following tendencies in relation to other, usually older, adult females. Adult females with kids at heel elicited stronger following tendencies than adult females without kids. This was also noted by Singer (1975) in a separate study of mountain goats in Glacier Park. I found this relationship to hold regardless of relative dominance. It was not unusual to observe an adult female without kid following an adult female with kid to which the former was clearly dominant during agonistic encounters. Darling (1939) observed that leaders of red deer (Cervus elaphus) hind groups were usually older females and that "a female which ceases to be a regular breeder soon ceases to be a leader." A lack of correlation between leadership and dominance in the domestic goat (Capra hircus) was found by Stewart and Scott (1948).

Adult mountain goats showed little interest in the behavior of subadults, particularly juveniles, even when juveniles were escaping predators. Followers were highly attentive to older leaders. As Gilbert (1974) found in fallow deer (Dama dama), older females waited longer in assessing situations, acted with more deliberate and decisive movements, and were less reliant upon the behavior of companions than were other classes.

Leaders determined the type, tempo, and direction of nearly all activities among female and subadult mountain goats. Followers were reluctant to initiate activities when in the presence of a leader. The role of leadership was further emphasized by observations of subadult groups, particularly those composed solely of juveniles. These groups commonly exhibited undirected movements and appeared to spend considerable time searching for other goats.

Maturing males showed increasing independence of activity within female-subadult groups. Within male groups, adult males tended to follow older males, but no positive correlation between leadership and dominance, such as Geist (1971) found in bighorn sheep (Ovis canadensis) ram bands, could be clearly established.

Group Structure - Groups composed solely of subadults were rare (Table 2), again emphasizing the role of adult leadership. Two-year-old females were nearly as likely to occur in mixed groups as were yearlings. Two-year-old males, by contrast, began to exhibit a tendency toward the solitary habits of adult males. Whereas yearlings (not distinguished by sex) were solitary only 5 percent of the time, 36 percent of all two-year-old males and 50 percent of all adult males observed from May through September were alone (Table 3). Males began limited association with exclusively male groups at two years of age (Table 2). As adults, most male associations were with other males. Males were most gregarious with other males during May at the same time that all other classes were most solitary due to separation of parous females from herds and disruption of leadership patterns.

Group Size - Mountain goat groups were considered separate if further apart the 50m and not oriented toward one another or engaged in related activity. Mean monthly group size varied between 1.9 and 3.3 in Glacier Park, with an overall average of 2.5; and between 2.1 and 4.6 in the Swan Mountains, with an overall average of 3.2 (Chadwick 1976). This is in agreement with data from Brandborg (1955), Lentfer (1955), Kuck (1970), and Smith (1976).

Close to 50 percent of all mountain goat groups sighted in Glacier Park were solitary animals and an additional 25 percent were pairs (group size 2). In terms of number of goats sighted, 20 percent of the population occurred alone and an additional 15 percent occurred in pairs from May through September (Table 3). The most common pair group was an adult female with a kid, a group behaviorally equivalent to a solitary animal in many respects. Thus the mountain goat assumes the status of a semi-gregarious species rather than a true herd animal. However, since groups tended to occupy the same general portion of available range at any given time, they retained certain herd qualities.

Table 2. Occurrence of mountain goat social classes in groups of different structure in Glacier Park from May through September.

Month	Class	Sample Size	Percent Occurrence: Solitary	With Subadults Only	With Males Only	In Mixed Group
May	AM	237	30	2	51	17
	AF*	308	47			53
	2M	33	61		3	36
	2F	36	25	4	2	70
	Y	114	12	12		77
	Ave.	748	35	3	11	51
June	AM	137	55		27	18
	AF	199	34			66
	2M	18	22			78
	2F	19	10	5		84
	Y	43	7	5		88
	Ave.	416	26	2	5	67
July	AM	76	64		12	24
	AF	209	25			75
	2M	21	14		5	81
	2F	20	10	10		80
	Y	65	5	3		92
	Ave.	391	24	3	3	70
August	AM	125	28		43	29
	AF	290	20			80
	2M	21	28	5		67
	2F	37		3		97
	Y	52	4			96
	Ave.	525	16	2	8	74
September	AM	118	46		48	6
	AF	374	21			79
	2M	34	20	3	9	68
	2F	47	13	2		85
	Y	96	4			96
	Ave.	669	21	1	11	67

*Nanny-kid pairs in the absence of other goats were classified with solitary adult females.

The kid class is not analysed since, with the exception of orphans, they were alwasy associated with adult females.

Table 3. Occurrence of mountain goat social classes in groups of different size in the Glacier Park study area from May through September, 1975.

Class	Sample Size	Group Size*										
		1	2	3	4	5	6	7	8	9	10	>10
AM	362	50	18	8	8	2	3	3	1	1		6
AF	592	18	18	9	10	7	5	5	4	5	2	18
2M	60	36	7	2	1	3	8	2	11	12		18
2F	83	12	12	8	8	3	8	7	24	1		17
Y	136	5	9	19	12	15	5	2	12	1	2	18
K	284	1	27	12	14	8	6	2	5	2	2	21
Ave. all Classes	1517	20	15	10	9	6	6	3	10	4	1	16

*Expressed as percent occurrence.

Description of Agonistic and Sexual Behavior Patterns - Most postures associated with behavior patterns of the mountain goat have been described by Geist (1964), DeBock (1970), Petocz (1973), and Rideout (1974). These will be redefined in terms of a scale from high intensity threat to high intensity avoidance for agonistic behavior, and from initiation of courtship to completion for sexual behavior, respectively.

A Present Threat (PT) is a broadside orientation toward an antagonist during which apparent size is enhanced through arching of the back and further erection of prominent dorsal ridge pelage. It is accompanied by tense, exaggerated movements, extreme tucking of the tail between the legs, and often a high, humming vocalization. High intensity PT involves conspicuous arching of the back and drawing in the head and neck toward the sternum. Moderate to low intensity PT incorporates less arching and some aversion and extension of the head and neck. The PT is associated with protracted agonistic interactions during which antagonists circle one another in antiparallel position.

A Weapon Threat (WT) involves display or actual use of the sharp, potentially injurious horns. Horns are displayed and aimed by lowering or cocking the head, and thrusts may be delivered through quick upward or lateral swipes.

A separate form of behavior involving the horns was recognized. Jousting (WTJ), so called because it involves a head-on orientation toward the opponent rather than head-to-tail, is distinguished from typical WT by its rapid, shorter, and repeated horn swipes. It is more a nodding or shaking of the head than preparation or delivery of a powerful thrust. WTJ was accordingly considered a less intense form of threat than WT.

The Rush Threat (RT) involves leaping, galloping, or trotting toward an antagonist. Like WT and WTJ, it may be accompanied by grunting and snorting vocalizations.

An Orientation Threat (OT) is simply a lower intensity form of RT effected by walking, turning, or staring fixedly toward an antagonist.

The Head-Elevated Orientation Threat (OTE) is the least intense form of threat. It is an approach or orientation toward an antagonist in which the head and neck are extended and slightly upraised.

Orientation Avoidance (OA) is essentially the converse of OT; that is walking, turning, or staring fixedly away from an antagonist. It is the least intense form of escape behavior. OA, like OT, grades into normal spacing-maintenance behavior of non-interacting group members. Therefore low level behavior of this type was recorded only when it caused other goats to abruptly modify ongoing activities and spatial relationships.

Rush Avoidance (RA) is the converse of RT; that is, leaping, galloping, or trotting away from antagonistic.

Most intense expressions of avoidance are specifically related to removal of target areas, particularly the rump and flank, from the horns of an aggressor. Collectively termed Weapon

Avoidance (WA), these postures involve crouching and, in extreme cases, squatting. Squatting, sometimes accompanied by urination, was observed mainly in instances where a subordinate animal was prevented from escaping an aggressor because of steep terrain or the presence of other dominant animals. Squatting appeared to inhibit further attack and sometimes stimulated similar behavior in the aggressor(s).

Most avoidance behavior, especially when performed at high intensities, incorporates certain common elements such as flattening of the ears and tail erection. Subordinate behavior is known to consist of postures and movements that are the antithesis of threat displays (Darwin 1872) or mimic either juvenile features (Wickler 1972) or female features (Geist 1971). Examples in the goat would be use of tail erection, a signal also displayed by neonates and developing juveniles to solicit nursing or other maternal care, and bleating vocalizations also used by kids to solicit maternal care.

During agonistic encounters behavioral sequences are often interrupted by vigorous performance of apparently unrelated bedding or comfort-related activities such as shaking, scratching, and dustbathing. Such activities were recorded as Non-Specific Displays (ND). ND also includes overt agonistic behavior not directed toward an opponent, such as horn-swiping inanimate objects and whirling. Whirling is a combination of rearing on the hind legs and random horn-tossing and has been described in detail by Dane (see these proceedings). Normally associated with exuberant play in juveniles, whirling may occur with intermittent running and leaping. It was observed in solitary animals as well as those in groups.

This paper is primarily concerned with social relationships outside of the rutting period. However, mountain goats exhibited sexual behavior throughout the year and used the same basic postures both during and outside of the rut.

The Low Stretch (LS) is the basic male courtship approach posture. The male moves directly toward the female in a crouch with the neck highly extended and lowered and the ears directed forward. The tail is usually elevated to a horizontal position. When performed at high intensity, the LS may include tongue-flickering, lateral jerking of the head, and a muted, buzzing vocalization. As Geist (1964) pointed out, the LS is the antithesis of the broadside PT. Threat elements are minimized to facilitate entry of the male within critical personal space defended by the female. When directed toward females and most subadults, the PT of fully mature males usually contains sexual elements from the LS. Described by Geist as a distinct 'conflict posture', the male PT amounts to a broadside display with some arching of the back and stiff movement, in which the neck is fully extended and lowered. Because an effective WT cannot be delivered when neck musculature is extended, threat potential of the pale PT, or conflict posture, is less than that of a typical PT as expressed by females and immature males, or by males toward other males.

Additional male sexual postures, described in the sequence in which they are usually expressed following positioning at the rear of the female, include Sniffing and nudging the anogenital area (SN), often followed by a lip curl (flehmen); delivery of a foreleg kick (K) to the female side or inguinal region; placing the Chin (CH) on her rump or back; placing one or both Forelegs (FL) over her rump or back and rising to Mount (M); then firmly Clasping (CL) her hindquarters and performing rapid, rhythmic pelvic Thrusts (TH). Other courtship behavior includes grooming activities similar to those seen in maternal-infant relationships. Males rub their muzzle along the back and flant of the female and, less often, the face. They may also lick these areas.

No unique female sexual postures other than standing for the male (lordosis) were observed.

Analysis of Agonistic and Sexual Interactions - Behavioral postures exhibited by mountain goat social classes outside of the rutting season were summarized. Results of kid-kid interactions are not included due to association of agonistic and sexual postures with play behavior in this class. The PT category includes male conflict postures.

Overall use of PT rose slightly from juvenile to adult classes. Adult males, expressing the PT as a conflict posture, utilized this more frequently than any other agonistic posture (Table 4). The proportion of PT was greatest in the behavior of each class toward members of the same or adjacent age classes and lowest toward disparate age classes. Adult females, two-year-old males, and yearlings expressed PT toward members of their own class most frequently (Table 5, 6 and 7, respectively). Two-year-old females displayed PT toward two-year-old males slightly more often than toward other two-year-old females (Table 8). The few instances of PT observed in kids, apart from interactions with other kids, were directed to yearlings (Table 9).

As with PT, proportion of WT use in overall behavior did not vary greatly between yearlings, both two-year-old, and adult female classes. Kids and adult males were least likely to employ WT during interactions. Yearlings, two-year-old females, and adult females all showed increased use of WT toward age classes younger than their own, most of it directed toward the kid class.

Table 4. Behavior of the mountain goat kid class during social interaction outside of the rutting period.

		Relative Frequency of Expression (Each class total = 100%)						
		Class Interacted With						
Behavior Pattern (N = 395)		AM	AF	2M	2F	Y	K	% of All Patterns
Agonistic: Intense Avoidance	WA							
	RA		82	18	52	54		62
	OA		11	63	23	13		20
	DB			2	2	5		2
	OTE		2		2	.9		2
	OT		3	14	13	4		6
	RT					2		.5
Agonistic: Intense Threat	WTJ		2		8	17		7
	WT			3		4		1
	PT					2		.5
Courtship: Initiate	LS							
	SN							
	K							
	CH							
Courtship: Complete	FL							
	M							
	CL							
	T							
% of All Patterns*			45	13	13	29		100

*Kid-kid interactions not included due to association with play behavior.

Table 5. Behavior of the mountain goat yearling class during social interaction outside of the rutting period.

		Relative Frequency of Expression (Each class total = 100%)						
		Class Interacted With						
Behavior Pattern (N = 1218)		AM	AF	2M	2F	Y	K	% of All Patterns
Agonistic: Intense Avoidance	WA		.8					.2
	RA	20	64	30	42	17	.8	36
	OA	30	19	26	17	9		15
	DB		3	5	7	9	7	6
	OTE	20	2		1	.6		1
	OT	30	3	8	7	15	21	10
	RT		1	3	2	9	18	5
Agonistic: Intense Threat	WTJ		3	9	7	9	12	7
	WT		2	12	6	16	36	11
	PT		2	5	7	11	4	6
Courtship: Initiate	LS				3	.3		.7
	SN				.4			.1
	K					.3		.1
Courtship: Complete	CH				.4	2		.6
	FL					.6		.2
	M					1		.3
	CL					.3		.1
	T							
% of All Patterns		.8	30	11	19	29	10	100

Table 6. Behavior of the mountain goat two-year-old female class during social interaction outside of the rutting period.

		Relative Frequency of Expression (Each class total = 100%)						
		Class Interacted With						
Behavior Pattern (N = 734)		AM	AF	2M	2F	Y	K	% of All Patterns
Agonistic: Intense Avoidance	WA			1		.8		.4
	RA		60	27	19	.4		27
	OA	10	16	20	5	10		13
	DB	10	5	4	10	9	6	7
	OTE		3	4	2	.4		2
	OT	80	4	13	21	26	29	17
	RT		8	1	11	22	22	13
	WTJ		1	5	6	7	10	5
	WT		2	9	15	18	33	12
Intense Threat	PT		1	17	11	6		6
Courtship: Initiate	LS		.4					.1
	SN							
	K							
	CH							
	FL							
	M							
	CL							
Complete	T							
% of All Patterns		1	36	14	8	33	7	100

Table 7. Behavior of the mountain goat two-year-old male class during social interaction outside of the rutting period.

		Relative Frequency of Expression (Each class total = 100%)						
		Class Interacted With						
Behavior Pattern (N = 570)		AM	AF	2M	2F	Y	K	% of All Patterns
Agonistic: Intense Avoidance	WA		.9					.4
	RA	10	26		.9	.8		11
	OA	3	16	11	4	4		9
	DB	10	7		10	12	10	9
	OTE	3						.2
	OT	35	18		17	27	40	22
	RT	23	2	6	10	19	5	9
	WTJ		5	22	4	4		4
	WT	10	3	33	10	8	17	8
Intense Threat	PT	3	5	28	18	10	3	9
Courtship: Initiate	LS	3	3			.8		1
	SN		9		6	4		5
	K					.8		.2
	CH				9	3	14	4
	FL		3		.9	2		2
	M		3		10	4	10	5
	CL							
Complete	T							
% of All Patterns		5	39	3	20	22	10	100

Table 8. Behavior of the mountain goat adult female class during social interaction outside of the rutting period.

		Relative Frequency of Expression (Each class total = 100%)						
		Class Interacted With						
Behavior Pattern (N = 2369)		AM	AF	2M	2F	Y	K	% of All Patterns
Agonistic — Intense Avoidance	WA		.6	.5				.3
	RA	13	18	6	.8		.5	11
	OA	18	14	24	1	.3	1	11
	DB	7	6	2	2	1	2	4
	OTE	6	1	1				.8
	OT	33	28	34	45	42	24	33
	RT	9	12	18	31	43	38	21
	WTJ	1	.4	2	.8	.3	1	.6
Intense Threat	WT	9	6	5	8	9	33	9
	PT	5	14	8	10	3		9
Courtship — Initiate	LS					.3	1	.1
	SN							
	K							
	CH							
	FL							
	M							
Complete	CL							
	T							
% of All Patterns		4	53	9	11	15	9	100

Table 9. Behavior of the mountain goat adult male class during social interaction outside of the rutting period.

		Relative Frequency of Expression (Each class total = 100%)						
		Class Interacted With						
Behavior Pattern (N = 237)		AM	AF	2M	2F	Y	K	% of All Patterns
Agonistic — Intense Avoidance	WA							
	RA	9	3					3
	OA	18	21	30	47	8		23
	DB	4	6	17	6			7
	OTE	4						.8
	OT	31	15	10		17	100	16
	RT	7		5		17		3
	WTJ		2					.8
Intense Threat	WT	4	.8					1
	PT	18	27	34	41	42		28
Courtship — Initiate	LS	4	17	5	6	17		12
	SN		2					1
	K		.8					.4
	CH		5					3
	FL		.8					.4
	M							
Complete	CL							
	T							
% of All Patterns		19	51	17	7	5	.4	100

WTJ was less frequent than WT in the behavioral repertoire of all classes except the kid class. Adult classes rarely employed WTJ, while two-year-olds used it slightly less often than juveniles. Two-year-old females, yearlings, and kids directed most WTJ toward juveniles.

Table 10 is a summary of actual horn contact resulting from all observed use of WT and WTJ outside of the rutting period, and it includes social interactions not analysed in Tables 4 - 9. It is evident from Table 10 that only a small proportion of weapon-related threat behavior resulted in actual contact. Table 10 data illustrate further the gradual shift from WTJ to WT with age. Kids and yearlings exchanged most of the horn contacts to the anterior body area; older animals oriented contact more toward the rump and flank. Thus with increasing age and ability to inflict serious injury, weapon use orientation changes from the poorly protected cephalic region toward posterior dermal shields described by Geist (1967).

Table 10. Summary of horn contact resulting from weapon threat behavior of mountain goats outside of the rutting period.

Body Area Receiving Horn Contact	Class Receiving Horn Contact						
	AM	AF	2M	2F	Y	K	Total
Head		2			10	17	29
Side	1	1	1	2	1		6
Flank		2		4	7	2	15
Rump		3	3	6	80	56	148
Total	1	8	4	12	98	75	198
Class Effecting Horn Contact							
AM					2		2
AF		8	3	5	15	26	57
2M			1	7	4	4	16
2F					32	1	33
Y	1				43	44	88
K					2	*	2
Total	1	8	4	12	98	75	198

*Kid-kid interactions excluded due to association with play behavior.

Kids effected only 1 percent of all horn contact while receiving 38 percent, mostly from yearlings. Yearlings effected 44 percent and received 49 percent, again mostly from yearlings. Adult females delivered 29 percent of all horn contact but received only 4 percent, despite better numerical representation in the population than any other class. Behavioral changes in maturing males are suggested by the fact that two-year-old males regularly employed WT and WTJ (Table 6) and delivered 16 horn contacts while adult males, at least three times as numerous as two-year-old males in typical population structures, rarely exhibited either WT or WTJ (Table 4) and effected horn contact only twice. Geist (1971) documented waning overt aggression and increasing display within mountain sheep ram bands.

RT was employed by adult females more often than by other classes; 21 percent of all behavior patterns as compared to 13 percent for two-year-old females, the class expressing RT next most frequently. This is significant because use of RT by an individual indicates that the animal 'expects' to dominate the individual toward which it directs the behavior. Adult females exhibited RT toward adult males but received none from them. The opposite situation was evident among two-year-olds, with males directing RT toward females but receiving RT from them rarely.

OT was exhibited more commonly by all classes than RT. With the exception of kids and adult males, goats utilized OT as the most common threat posture. OT was directed toward all classes by adult females. Other classes employed it most often in interactions with classes younger than their own. Percent of OT shown adult females by adult males was about half that shown adult males by adult females; 15 percent and 33 percent, respectively. Among two-year-olds, the situation was again reversed, as with RT. OT comprised 17 percent of male behavior toward females and 13 percent of female behavior toward males in the two-year-old class. Two-year-old males used OT toward adult females 18 percent of the time; two-year-old females used OT toward adult females 4 percent of the time.

OTE was not common in the behavior of any class. Since it was employed by each class primarily toward goats of the same age class or older, it might best be termed a subordinate threat form.

As expected, use of OA was highest in juvenile classes and lowest in adult classes. A similar relationship was evident in RA. Subadults used RA more frequently than OA. Adults used OA more than the higher intensity RA. Adult males were the least likely to express avoidance behavior more intense than OA. Among two-year-olds, female OA and RA toward males were 20 percent and 27 percent, respectively; male OA and RA toward females, 4 and 0.9 percent respectively. Two-year-old female OA and RA toward adult females were 16 percent and 26 percent, respectively. Two-year-old males are therefore seen to show the same amount of low intensity avoidance toward adult females as do two-year-old females, but less than half as much higher intensity RA. Adult females showed 24 percent OA and 6 percent RA toward two-year-old males, but only 1 percent OA and 0.8 percent RA toward two-year-old females.

No obvious pattern emerges from analysis of ND between classes. ND was generally most likely to occur in conjunction with high intensity behavior patterns and in approach-withdrawal situations.

Data from Tables 4 - 10 suggest that higher social status or dominance may be correlated with increasing age in mountain goats. Using data from Tables 4 - 9, relative dominance in mountain goat social classes is described in Table 11 as percentage threat behavior in the total agonistic behavior recorded for each class. The ability of older classes to dominate younger ones is clearly evident in Table 11. Increasing age in this species is in turn related to increasing size, strength, and horn development. Measurements by Brandborg (1955), Rideout (1974), and Moorhead (pers. comm.) show substantial differences in these parameters between successive age classes. Among goats known to be of the same age and sex, my observations consistently showed that individuals of greater size/strength/horn development were able to dominate smaller goats.

Table 11. Relative dominance of mountain goat social classes outside of the rutting period.

	No. Threat Behavior Patterns/ Total No. Agonistic Behavior Patterns[1]					
	Class Expressing Behavior					
Recipient Class	AM	AF	2M	2F	Y	K
AM	.70	.67	.85	.88	.50	-
AF	.67	.65	.44	.20	.13	.07
2M	.62	.69	.89	.30	.39	.17
2F	.47	.98	.92	.73	.34	.23
Y	.91	1.00	.93	.88	.64	.32
K	1.00	.98	1.00	1.00	.98	

[1]Using data from Tables 4-9. DB is excluded from total number of agonistic behavior patterns.

Relationships between sexes were more complex. Where marking or close-up observation permitted sexing of juveniles, males were found to be somewhat thicker-horned, larger, more exploratory, and more aggressive than females of the same age. Sexual postures appeared very early in the development of neonates (Chadwick 1974) and were more common than agonistic postures in play up to four to six months of age.

Kid-kid, kid-yearling, and yearling-kid sexual behavior was not analysed due to its inclusion in the context of play. Kids were not seen to direct sexual postures toward any goats older than yearlings (Table 9). Yearlings used courtship postures during interactions with other yearlings and two-year-old females. Yearlings used the LS, a posture not observed during juvenile sexual play, more often in courtship of two-year-old females than in interactions with other yearlings (Table 7). Although older males directed some courtship toward unresponsive yearling females during the rut, no active participation in breeding by either sex of yearling was noted. Yearling breeding has not been reported by other investigators, even under conditions stimulating unusually high productivity (Lantfer 1955).

Developing two-year-old males begin to approach adult females in size, weight, and horn development by the end of August. Two-year-old males clearly dominated two-year-old females (Tables 6, 8 and 11). They were also considerably more agressive toward adult females than any other subadult class was. Between July and October, two-year-old males began to utilize the male conflict posture to the exclusion of typical PT during interactions with females and with adult females in particular. At the same time, two-year-old males began to direct courtship toward older females and 25.9 percent of postures used in interaction with two-year-old females were sexual. Sexual interactions with adult females involved use of LS while interactions with two-year-old females did not.

Relative dominance of adult males and adult females toward one another was quantitatively identical in terms of agonistic behavior (Table 11). Qualitative comparison of Tables 4 and 5 reveals that males exhibited a high percentage of PT toward other classes while adult females did not. Aside from PT, which, it should be remembered, is expressed by the male toward females and subadults as a unique conflict posture, containing subordinate sexual elements, adult males directed little threat behavior toward females and subadults. Adult females, on the other hand, showed high percentages of typical threat behavior toward all other classes, including adult males. Excluding PT, 17.8 percent of adult male agonistic behavior toward adult females involved threat postures compared to 58 percent of adult female behavior toward adult males. An additional 21.1 percent of adult male behavior toward adult females involved sexual postures. The highly subordinate LS was used by adult males toward all other classes except kids. Additional courtship postures were shown only toward adult females outside the rut.

Total adult male behavior patterns, N, is 237 (Table 4), compared to 2,367 adult female patterns (Table 5) during the same time period. In the Bunker Creek herd, in which three-year-old males could consistently be distinguished from older adult males, 85 percent of adult male interactions with other classes were performed by three-year-old males. Most adult males in Glacier Park mixed groups outside the rutting season appeared to be no more than three or possibly four years of age. Thus, males older than two years of age are not only less likely to direct threat behavior toward other goats than are the immature males; they are less likely to have any social interaction with females and subadults. Most interactions which do take place between adult males and the female-subadult herd component involve young adult males. Table 4 should be interpreted accordingly to be more representative of young adult males than of older adult males. Older adult males very rarely threatened females or subadults. During interactions with these classes, older adult males typically assumed a rigid PT conflict posture and withdrew. Older males were observed to retreat in this fashion from yearlings and even from kids in the Swan Mountains (these interactions were not included in Table 4).

Agonistic Rates - Frequency of agonistic encounter/goat/hour increased with increasing group size during foraging, bedding, and salt licking activities (Table 12). As expected, rates were lowest in bedded groups and highest at salt licks where activity was related to a spatially limited resource. Number of encounters/group/hour (that is, the number of encounters/goat/hour x group size) is shown for foraging mountain goats in Galcier Park to illustrate magnitude of social interaction in large groups compared to small groups. Agonistic rates were found to be markedly higher in mixed groups than in a small sample of male-only groups. Observation of marked animals indicated that both frequency and intensity of agonistic interaction were lowest between individuals which regularly associated and highest between individual which appeared unfamiliar with one another.

Agonistic encounters were evident in all activities and in all habitats, including precipitous cliff terrain. Data from 4,400 goat-hours (number of goats in a group x number of hours that group was observed) of observation in the Swan Mountains is presented in Table 13. During that time, 291 out of a total of 3,435 agonistic encounters occurred in what was judged to be a dangerously steep climbing situation from the perspective of the animals. Thirty-nine of these encounters resulted in a potentially harmful climbing event. Data from Tables 13 and 10 are similar in that most of these encounters in dangerously steep terrain involved WT and primarily affected juveniles. Kids sustained 44 percent and yearlings 36 percent of 39 aggression-related climbing events. Aggression-related climbing incidents occurred with greater frequency than normal climbing mishaps; .89 per 100 goat-hours, compared to .66 per 100 goat-hours.

Table 12. Relationship of mountain goat group size and structure to frequency of agonistic behavior (modified from Chadwick 1976).

A = All Groups M = Male Only E = Excluding Male Groups

	No. Agonistic Encounters/Goat/Hour						No. Agonistic Encounters/ Group/Hour
	Swan Mountains			Glacier Park			Glacier Park
Group Size	Bedded A	Feeding A	Licking A	Feeding A	Feeding M	Feeding E	Feeding A
2*	.06	.26	1.47	1.08	0	1.08	2.16
3	.06	.63	3.04	.94	.44	1.16	2.84
4	.39	.83	4.17	2.75	.66	2.78	11.00
5	.22	.82	3.69	1.83	.80	1.65	9.16
6	.52	.89		2.47		2.48	14.80
7	.47	.65		4.64		4.64	32.48
8	.80	1.30	6.06	5.20		5.32	41.60
9	1.25	1.50		3.01		3.28	27.09
10	.44	1.82		1.12		1.12	11.20
>10	.54	1.87		4.24		3.04	46.16
Sample Size	549	1055	43	95	14	109	95

Data from the Swan Mountains and Glacier Park are not quantitatively comparable due to different sampling techniques.

*Nanny-kid pairs are not included in group size 2.

Table 13. Potentially harmful climbing events recorded during 4,400 goat-hours (number goats in group x number hours group observed) of observation of mountain goats in the Swan Mountains.

		Number Events in:								No. Events/ Goat-Hour
	Type of Event	AM	AF	2M	2F	Y	K	Unid.	Total	
	Climbing misstep		9	3		5	5	7	29	.0066
Events from 291 agonistic encounters in dangerously steep climbing situations	Knocked, pushed, or prodded over edge		1	1		9	7		18	.0041
	Forced to leap over edge to avoid goat		2	1		5	10		18	.0041
	Knocked or forced to leap over edge as result of another encounter (innocent bystander)		1		1				2	.0005
	Aggressor loses footing during pursuit		1						1	.0002
	Total aggression-related events		5	2	1	14	17		39	.0089
Total All Events		0	14	5	1	19	22	7	68	.0155

DISCUSSION

Benefits of Aggregation - The fundamental unit of mountain goat society is the prolonged mother-infant association. Lent (1974) states that a major function of maternal behavior if facilitation of learning processes in the infant through provision of potimum levels of stimulation and a relatively stable social environment. Stabilization of the social environment relative to young of the year is particularly important in the mountain goat. All other classes are aggressive toward the kid class and, as pointed out by Geist (1964, 1974), all older classes possess potentially injurious horn weaponry. The present study revealed that even with maternal protection, the kid class sustained 38 percent of all horn contact and 44 percent of agonistic behavior leading to potentially harmful climbing events. Weapon threats and other aggressive behavior exhibited toward kids probably reinforced the prolonged close following tendencies of the kid class.

That kids experienced relatively less social interaction with other classes than any other class except adult males did is a measure of the extent to which aggressive maternal protection stablilized the social environment of kids. If agonistic behavior were adjusted according to percent representation of classes in total population figures, it would be evident that the yearling class, without benefit of maternal protection, received proportionately more horn contact and agonistic behavior leading to potentially dangerous climbing events than did the more numerous kid class. Yearlings also received a far greater actual number of threat postures than did any other subadult class.

In addition to buffering a rigorous social environment, maternal care mitigates the demands of the harsh physical environment of the mountain goat niche. For several weeks subsequent to partuition, adult females positioned themselves between their unstable offspring and the outer edge of available footing to prevent accidental falls by the neonate. Parous females also assisted neonates in negotiating precipitous terrain by trial and error selection of the least difficult routes. Kids experienced considerable difficulty obtaining forage beneath deep snow and icy crusts. They obtained a substantial portion of their forage during the critical winter-early spring period within feeding craters pawed by their mother and not yet utilized by classes dominant to the kid dur to continued presence of the mother nearby. The small (12 - 20kg) kids were further able to conserve relatively limited energy reserves by following the mother's path through deep snows and by bedding in sheltered sites defended by her against other classes. Kids generally bedded on the leeward side of the nanny in contact with her body during winter (Chadwick 1974). Without maternal protection from dominant animals, kids would be relegated to the least desirable forage and shelter situations.

Following tendencies of older goats appear to be extensions of the durable mother-kid relationship. After kids, yearlings, the two-year-old females were the most gregarious class. Altmann (1963) states that post-weaining bonds function by affording guidance in choice of feeding site, shelter, and decisions regarding safety and flight. Within the relatively small, traditional home ranges occupied by mountain goats, knowledge of key winter feeding areas, protected bedsites, escape terrain, and efficient daily travel routes may confer important survival advantages. Such advantages would accrue to yearlings of both sexes, two-year-olds of both sexes to a slightly lesser degree, and thereafter primarily to females since they are more likely to inherit ranges than males. Information about salt licks and migration routes must be transmitted to all classes.

A primary stimulus to aggregation is the selective advantage enjoyed by individuals in groups when predators are present. It was demonstrated that goats in groups were more collectively alert to potential danger than solitary animals while expending less individual time and energy surveying their surroundings. Group members would therefore have more time available for maintenance activities. Greater foraging time permits animals to be increasingly selective for forage of the highest digestibility. Estes (1974) suggests that in African bovids, isolated individuals and small groups spend a greater proportion of time watching and listening for danger than do members of larger herds. Walther (1969) states that individual Thompson's gazelles (Gazella thompsoni) may be unalert for periods extending up to 15 minutes, but because they inhabit large herds, there is a high probability of one animal always having its head raised. Because alertness increases with age in mountain goats, subadult group members are able to share the advantages of greater alertness in older animals.

In a similar sense all group members benefit from the abilities of those animals with the most acute senses (shared genetic traits) or experience (shared learned behavior). Bergerud (1974) points out that herding reinforces escape behavior since naive animals can learn without having to experience attacks directly. During actual predator attack, group members benefit from group defensive abilities and predator difficulties in isolating targets. An excellent general discussion of the values of grouping in animal societies is available in Wilson (1975).

Factors Limiting Group Size - Ewer (1968:99) states "Large societies are only able to exist in situations where members can easily keep in contact ... and only in adequate food can be found for all within the normal feeding period ... Terrain and type of food are thus the two external factors which have the most influence on the evolution of social relations." Habitat utilization data demonstrate that precipitous terrain is favored throughout the year by mountain goats (Brandborg

1955, Geist 1971, Feck 1972, Chadwick 1976, Smith 1976). That large goat groups experience difficulty coordinating activities on steep cliff faces and narrow ledges may be confirmed by direct observation and by data from Chadwick (1976) showing that large groups were more often observed on moderate slopes than on steep slopes. Large groups size can also lead to crowding which in turn restricts maneuverability on cliffs. All group members are then forced to share to some degree the genetic and experienceable limitations of the poorest mountaineers. Seton (1927) relates an incident in which goats crowding onto a thin ledge were unable to turn past one another and eventually fell to their death.

Another factor, also topographic, which may select against aggregation in the mountain goat is catastrophic downslope movement of rocks, ice, and snow. Holroyd (1967) commented that because goats generally occur in small groups, avalanches are not likely to affect more than a small part of a herd at any one time. Such evidence as is available (Brandbor 1955, Chadwick 1976) points to avalanches as a major source of mortality and therefore an important selective agent in evolution of mountain goat social characteristics.

Severe winter storms, deep snows, and icy crusts can remove potential forage in some habitats and reduce its availability throughout wintering areas independent of the condition of range forage per se. Duration of winter conditions becomes critically important during March and April as available forage is reduced. Deep snow also restricts movement between available forage sources. Goats were observed to remain in areas no more than 100m in diameter for over a week on occasion under severe snow regimes (Chadwick 1974).

The ability of native goat populations to exploit a wide variety of food items has been documented by Casebeer (1948(, Brandborg (1955), Saunders (1955), Hibbs (1967), Hjeljord (1973) and others and has been related to compensation for narrow habitat preferences (Geist 1971). It follows that small groups and individuals would be capable of obtaining sufficient forage in microhabitat refugia under severe winter conditions by utilizing all available edible plant species from lichen to conifer. Larger groups, however, would be more likely to exhaust the limited resources of a small area during confinement, thereby causing all group members to suffer shortages. Similarly, sheltered sites such as overhanging ledges and caves or crevices are also a limited and highly localized resource most efficiently and equitably utilized by individuals and small groups.

Houston (1974) points out that conditions of deep snows and scattered forage set an evolutionary premium on small group size in the moose (Alces alces) since single moose or small groups would be more successful at finding and utilizing forage than larger groups. Small group size in the mountain goat also minimizes general animal impact such as trampling and heavy grazing within fragile alpine and subalpine plant communities.

The value of groups as anti-predator devices has been discussed briefly. However, mountain goats as a species are insulated by the exclusive nature of the terrain which they favor from most predators. The advantages of grouping are thus somewhat diminished, particularly for mature animals whose defensive abilities in relation to medium-sized predators such as lynx (Lynx canadensis), coyote (Canis latrans), and wolverine (Gulo gulo) were observed to be formidable.

Optimum group size in any species represents an appropriate balance between beneficial aspects of aggregation and disadvantages of intraspecific competition for limited resources relative to individual survival. Though ultimately determined by the nature of the terrain and food supply, grouping characteristics in the mountain goat appear to be directly mediated by social mechanisms involving agonistic, sexual, and leadership behavior. Analysis of behavior patterns suggests that aggression is the primary device through which social tendencies are limited and defined.

Since exploitation of montane habitats involves both horizontal and vertical movement between seasonal ranges, a social hierarchy based upon defense of a mobile personal space rather than fixed territory characterizes mountain goat society. Personal space is maintained at all times under normal conditions including resting periods. Agonistic interactions are essentially contests over personal space which ultimately determine the right to occupy a particular site, and the resources contained therein, at any given time.

Trespass of personal space was common in large groups as a result of temporary crowding which inevitably occurred during the course of group movements. It was noted that high intensity agonistic threat behavior was most common between goats of similar rank. Larger groups were generally more likely to include goats of similar status than were small groups. Furthermore, status rivalry appeared to lower aggressive thresholds in onlooking goats, predisposing them to agonistic behavior. Group members were also subject to frequent redirected aggression from one or both contestants following encounters. The consequence of these different factors was a notable increase in social instability, measured as rates of agonistic interaction, with increasing group size. Large groups were characterized by numerous social interactions and disruption of maintenance activities. Larger groups usually separated into smaller, more durable, and more efficient social units. Average size of these typical, more highly ordered units was between one and five. Stable groups of females and subadults were more structured along a linear rank order than larger groups.

Stable female-subadult groups therefore assumed a family-like appearance, containing, for example, an adult female, two-year-old, yearling, and kid. Observations of marked animals suggested that such associations were merely stable aggregations and, except for the nanny-kid pair, not necessarily composed of related individuals.

With sexual maturation, males underwent a transition from agonistic to largely sexual modes of interaction with females. Thus an increasing ability to successfully contest relative rank, seen in two-year-old males, was countered by developing use of sexual behavior which emphasizes submissive signals and minimizes threat content. Overall use of threat postures by males became less common after two years of age. At the same time, however, maturing males showed no increase in avoidance behavior and rarely exhibited high intensity avoidance postures or signs of fear during withdrawal. That males remain capable of effectively intimidating smaller classes when sufficiently motivated is implied by observations of male dominance at salt licks in Glacier Park (Singer 1975, Bansner 1976) and elsewhere (Rideout 1974, Moorhead pers. comm.).

Neither clearly dominant nor obviously subordinate under normal conditions, yound adult males were unable to establish stable rank relationships within mixed groups. It is hypothesized that unsatisfactory social interactions and stress generated by conflicting sexual and agonistic drives, exemplified in the unique male FT, caused maturing males to develop grouping and movement patterns independent from those of females and subadults. Beginning at two years of age and established as a general pattern by three years of age, males tended to occupy ranges peripheral to or separate from those of females and subadults. Those adult males which were observed in mixed groups remained in them for shorter durations and exhibited greater independence of activity than other classes. Most adult males occurred alone, being more solitary than any other class, or in small bachelor bands. Bachelor bands were often stable over a period of several days or more, compared to daily changes of composition in typical mixed groups. This greater stability of male groups may be correlated with lower rates of agonistic interaction which in turn suggests that resource competition between adult males outside the rut may be less significant than within mixed groups.

Consequences of the male social relationships described are twofold. First, the potential for injury to other classes by the large, powerful billies is reduced. Secondly, resource competition between adult males and the female-young population component is minimized. Foss (1962), DeBock (1970), Geist (1974, 1975), Rideout (1974), and Smith (1976) have suggested that males occupy more marginal range than females and subadults. In both Glacier Park and the Swan Mountains, males were observed in more rugged terrain at higher average elevations with greater snow depths than females and subadults. Adult male:adult female ratios typically vary between 70:100 and 90:100 in native goat populations (Hibbs 1966), indicating slightly lower survival of adult males relative to adult females. Similar figures were recorded in present studies (Chadwick 1974, 1976). Higher than average male:female ratios have been recorded wher production of young was also above average (Anderson 1940, Hanson 1950). Rideout (1974) found adult male:adult female ratios to be lowest following a heavy winter. All male:female ratios are likely to contain some bias toward adult females since the more solitary and dispersed habits of males and the more rugged terrain favored by them can lower survey success for this class.

Females and subadults occupied optimum habitats within available range. Within typical female-subadult groups such as were observed dispersed throughout winter ranges, the highly aggressive, socially dominant adult female class enjoyed prior access to resources. Agonistic relationships within the social hierarchy, based upon threat behavior ultimately involving the horn weapons, promoted dispersion of herds into relatively small, ordered groups. Within these groups, intra-specific competition was minimized, again to the advantage of adult females. Under chronic conditions of resource scarcity, therefore, the resource base available to adult females, the breeding segment of the population, should remain relatively constant while subordinate animals suffer socially magnified resource shortages.

First year mortality varies between 30 and 80 percent in studies of mountain goats summarized by Hibbs (1966) and Vaughan (1975). First year mortality was found to be variable in Glacier Park (Bansner 1974, Singer 1975, Chadwick 1976). By distinguishing two-year-old classes, it was discovered that mortality in the yearling class may also be high; close to 50 percent in certain Glacier Park herds east of the continental divide (Chadwick in prep.). Gains in size and energy reserves from the previous year are apparently offset to some extent by loss of maternal protection in the yearling class. Juvenile mortality has been shown to vary with winter conditions in Glacier Park (Chadwick 1976) and elsewhere (Rideout 1974, Smith 1976).

Within optimum goat habitat, it is expected that adult male and juvenile mortality will vary while the proportion of adult females in the population remains more or less constant under different winter regimes. Productivity of three-year-old females is expected to be somewhat lower than that of older, more dominant females, but overall production of young should not vary greatly between winters. In marginal range situations, adult male and juvenile mortality should show fluctuations of greater magnitude under different winter regimes. Production of young should be more dependent upon winter conditions, particularly in young adult females. Alternate year production of young may occur.

In summary, mountain goats are characterized by occupation of a narrow, topographically defined niche; utilization of stable alpine and subalpine post-Pleistocene habitats; slow maturation; and retention of juveniles on traditional home ranges. Social mechanisms have evolved to facilitate transmission of learned home range behavior and, in the absence of significant predation of competition from other species, to maintain population size (N) within the carrying capacity of the environment (K). Reduced sexual dimorphism and the aggressiveness of adult females in this species have been attributed directly to the evolution of sharp horns by Geist (1974). It is hypothesized that a rigorous social environmnet influences mountain goat distribution both within and between ranges and acts to regulate population size through differential vulnerability of social classes to the physical environment.

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