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SOCIAL STATUS AND NANNY-KID SEPARATION IN ROCKY MOUNTAIN GOATS.

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Abstract: The social structure of Rocky Mountain goats (*Oreamnos americanus*) in the Gore Range of central Colorado was studied using a cardinal ranking system. On average, nannies with kids were most dominant, followed by billies, adult females without kids, male 2-year-olds, female 2-year-olds, female yearlings, and male yearlings. Nannies with kids ranked 1 through 3 had larger spacing between cardinal values than mountain goats ranked 3 and below indicating that the relationship between dominant nannies was relatively well established. Nannies with kids interacted 2 to 10 times more among themselves than with non-nanny goats but, the overall average level of aggressive interactions for nannies was lower than for non-nanny goats (Kruskal-Wallis $p<0.05$). It was hypothesized, and demonstrated (Kruskal-Wallis $p<0.01$), that lower ranking nannies at the salt lick would be separated from their kids more frequently than high ranking nannies.

Early studies on dominance in social animals usually were descriptive accounts of social organization. Gradually, ordinal ranks, based on dyadic matrices replaced the descriptive accounts with more quantitative studies (Thouless and Guinness 1986, Holekamp and Smale 1992). However, the use of ordinal ranks for structuring animal societies suffers from several problems: 1)difficulty in assessing the magnitude of difference in dominance among individuals; 2) difficulty in comparing dominance matrices based on different herd sizes and observation periods; and 3) difficulty in employing statistical techniques to relate dominance rank to other qualities of interest (Boyd and Silk 1983). To overcome these draw-backs, cardinal ranking systems have evolved.

Cardinal ranking methods incorporate information about interactions that end in wins, losses, and ties to generate an index of dominance rank. This paper describes the social organization of Rocky Mountain goats using a cardinal ranking system from data of 14 herds observed congregating at mineral licks during the summer months of 1992 and 1993.

Observations that led to the investigation of social structure included: 1) aggressive interactions between cohorts for access to salt lick holes; 2) a tendency for nannies to aggressively interact specifically with other nannies; and 3) separations of kids from nannies who lost in aggressive interactions. Frequency of nanny-kid separations (Hopkins et al. 1992), maintenance of proximity (DeBock 1970, Hutchins 1984), and distances between nanny and kid (Chadwick 1983) have been evaluated.

We hypothesized that nannies who were chased or displaced from the salt lick by other nannies were of low ranking status. Furthermore, we hypothesized that low ranking nannies were becoming separated from their kids more often than high ranking nannies.

METHODS

Population

The mountain goats studied were members of a population of approximately 125 animals in the Gore-Eagle's Nest Wilderness Area of the north central Colorado Rocky Mountains west of the Continental Divide. Observations were restricted to Elliott Ridge, a long narrow alpine ridge with numerous salt licks (Hopkins et al. 1992). Mountain goats entering the salt lick area together during any one observation period were considered a herd sample. All nannies were identified as individuals by tags, collars, pelage patterns, scars, or broken horns. Two-year-olds were classified visually as animals ranging in height and horn size between the majority of all adults and yearlings at the salt

lick. Gender was determined by urination postures and during opportunities to observe genitalia. Mother -offspring relations were established on the basis of nursing and close association. Agonistic and separation data were collected for individuals in 14 herds ranging in size from 10 to 45 animals, with a mean herd size of 21. A total of 93 hours was spent in behavioral observation.

Analysis

Dominance hierarchy structure was assessed by scoring win- loss outcomes in competition between individuals (Chase 1974). In this study, dominance is defined as an individual's ability to acquire access to a salt lick hole and defend it from competitors. A win was tallied when an individual chased another away with a rush, horn, or present threat (Chadwick 1983) or if by moving towards a salt lick hole it displaced an individual that was there originally. These events are marked by the approach of a challenger, the encounter, and the resulting win or loss. The wins and losses were tallied in dyadic matrices.

Ordinal Ranking with Dyadic Matrices

Analysis involved three steps. First, mountain goats were ranked ordinally through placement along a dyadic matrix. Ordinal ranks were the arrangement of mountain goats based on win/loss outcomes, where losers had the lowest placement relative to others in a dyadic (sociometric) matrix. Each dyadic matrix used the common convention of listing losers along the top and winners along the left column respectively. The matrix was sorted to maximize the total of entries listed in the upper triangular portion of the matrix. This procedure placed animals in ordinal positions of dominance from most dominant on the top of the left column to least dominant on the bottom. The most dominant animal is placed at ordinal number 1 and less dominants take higher numbers relative to their positions lower down in the hierarchy. Nannies and their kids are listed together as one individual in the dyadic matrix. Lone kid interactions are ignored because these do not constitute a determination of rank within the herd. Such interactions include play behaviors with other kids and rejection of lost kids by nannies to whom the kid does not belong.

Cardinal Ranks Obtained from the Estimator of Probable Dominance

Secondly, cardinal ranks were derived from the ordinal ranks (Equation 1) . Cardinal ranks were values derived from the total number of wins per total number of contests. Unlike ordinal ranks, they help to normalize the rank values for all mountain goats found in different size herds and observation periods.

$$R_j = R_i + 2\left[\frac{A_{ij}}{A_{ij} + A_{ji}}\right] \quad (1)$$

The alpha goat is given an ordinal rank of i = 1 and a cardinal rank, R1 = 1.00 . To calculate each subsequent rank we let j = i + 1 . This means that the cardinal rank, Rj, of each goat was calculated from the next higher up, Ri, in ordinal rank. This allowed subordinate ranks to be determined relative to each ordinally higher ranking goat. Aij is the number of wins by ordinal j against ordinal i. Aji is the number of wins by ordinal i against ordinal j.(Aij + Aji) equals the total contests between i and j. The expression Aij/(Aij + Aji) is the ratio of wins by the higher ordinal rank to the total number of contests fought; it has a range of [0,1]. It is also the estimator of probable dominance of j over i.

If i and j win equal numbers of contests against one another then the estimated probability of dominance is 0.5, which means that i is not shown to be dominant to j. The cardinal rank, Rj, provided by Equation 1 will be equal to Ri when the data fails to support dominance. This is achieved by subtracting 0.5 from the estimator of probable dominance to obtain a range of [-0.5,0.5]. This expression is then multiplied by 2 to make it consistent and comparable to the whole number ordinal ranking system by giving the rank difference a range of [-1,1]. If i wins all contests against j then Rj = Ri + 1 making the cardinal ranking system comparable to the ordinal ranking system.

Dominance is increasingly well established as series rank differences get closer to one. The series ranking given by Equation 1 is particularly useful in quantifying how well various ages or sexes of animals are placed in a hierarchy. We define the rank difference, (Rj = Rj - Ri . These rank differences can be averaged for age and sex groupings.

Equation 1 is undefined where (Aij + Aji) = 0. The dyadic matrices were fairly sparse. Arbitrary selection of any two goats will usually give the undefined result, but in such cases Equation 1 is not applicable. The equation depends on first properly ranking the goats ordinally in a dyadic matrix and calculating the cardinal ranks starting with the alpha goat. Most of the contests were

fought between goats of close ordinal rank. If contests had been fought randomly, independent of ordinal rank, then Equation 1 would not be a useful estimator of cardinal rank. There were a few cases where (Aij + Aji) = 0 between adjacent ordinal ranks because there were no contests. We adopted a convention that assumed such cardinal ranks to be equal. The main reason for this assumption is that some of the nannies were the first to take possession of one of the several salt lick holes and remained unchallenged during the entire period of observation. Randomness in nanny-kid separations based on ranks was evaluated with a Kruskal-Wallis (K-W) test (Devore 1991).

Herd Sample Normalization of Cardinal Ranks to a Scale of Ten

One problem with Equation 1 is that the cardinal ranks of the lower ranking animals have a high dependency on herd size. The maximum possible cardinal rank number is equal to the number of animals in the herd, but could only occur if all dominants won all contests against their subordinates. Nevertheless, larger herds will force the subordinate ranks downward relative to smaller herds. An improvement to the method would minimize any herd size dependency in dominance ranking.

After herd sample has been ranked using Equation 1, a conversion factor is calculated that allows the ranks to be adjusted to a scale of ten. This means that for every herd sample the maximum rank number is 10 with all other ranks multiplied by the same conversion factor. The conversion factor, c, is calculated by Equation 2:

$$c = \frac{10}{R_{MAX}} \qquad (2)$$

R_{MAX} is the maximum rank number obtained from the herd sample using Equation 1. After Equation 2 has been applied, cardinal ranks are confined to a scale of 10. Any number could be substituted for 10 in Equation 2. If it is equal to the herd size, the cardinal ranks will be closest to the ordinal ranks. The value, 10, itself is not important. Its importance lies in the fact that the conversion factor reduces the effect of herd size on cardinal rank and allows valid comparisons to be made from one herd sample to the next regardless of size.

Definitions, Terminology, and Notation

The following terms are used: a nanny is an adult female with a kid. Female goats without kids are designated simply as 'females'. Kids are designated lower ranking or higher ranking according to the ranking of their mothers. Billies are adult males (3 years or older), younger males are subadults. Each goat in each herd is designated by an uppercase letter starting with "A" for the most dominant. These designations are valid only within the context of a given herd. Lowercase "k" indicates a kid, for example "Ak" is a nanny with kid. Lowercase "b" indicates a billy, "m" indicates a male subadult, and "f" indicates an adult female without a kid. An accompanying number indicates age in years. For example "Fm1" is a sixth ordinal ranking male yearling, "Eb" is a fifth ranking billy. Cohort refers to any nearest ranking goat relative to another. Peer groups are mountain goats with the same or similar cardinal rank values, meaning that peer group mountain goats may be similar in rank with only fractional difference in values. When a nanny and kid lose sight of one another and either animal exhibits searching behavior, or bleats, the event is called separation.

Definitions for cardinal rank statistics include rank average (R_{AVG}), standard deviation of ranks (SD_R), rank minimum (R_{MIN}), rank maximum (R_{MAX}), and average difference between ranks ($\triangle R_{AVG}$). The average difference in rank was used to evaluate the linearity of the hierarchy for various sex-age groups. Highly linear sex-age groups have higher average rank differences ($\triangle R_{AVG}$). Less linear sex-age groups, or peer groups, have lower average rank differences.

RESULTS

Rankings

Nannies occupied the three most dominant positions in 12 of 14 herd samples. In herd H a billy held the third most dominant position and in herd A there were only two nannies. Nannies had the highest average rank difference, suggesting their dominance relationships to one another were well established (Table 1). The remaining sex-age groups had average rank differences near 0.5 except for male yearlings who were considerably lower than the rest.

Average rank differences were calculated using the herd ranks obtained only from Equations 1. The series ranks obtained from Equation 1 alone emphasized contest results between adjacent peers. Equation 2 was applied to emphasize herd placement and reduce the dependency, especially of the lower ranks, on herd size (Table 2). The

Table 1. Cardinal Rank Statistics. Series ranks using only Equation 1.

	Nanny	Female	Female 2-yr-old	Female yearling	Billy	Male 2-yr-old	Male yearling
R_{AVG}*	3.12	6.58	7.60	8.56	6.31	7.68	8.42
SD_R	2.12	1.94	3.08	2.82	2.44	2.96	2.90
R_{MIN}	1.00	4.00	3.44	3.83	2.44	3.67	3.60
R_{MAX}	9.64	10.00	13.33	13.33	9.64	13.33	13.33
ΔR_{AVG}	0.73	0.72	0.48	0.52	0.59	0.46	0.29

* Definitions provided in text.

Table 2. Cardinal Rank Statistics. Herd normalized cardinal ranks using Equations 1 and 2.

	Nanny	Female	Female 2-yr-old	Female yearling	Billy	Male 2-yr-old	Male yearling
R_{AVG}*	3.24	6.42	7.64	9.02	6.27	7.57	8.83
SD_R	1.72	1.60	1.58	1.35	1.93	1.54	1.36
R_{MIN}	0.75	3.75	4.52	4.91	2.93	4.70	5.44
R_{MAX}	7.48	10.00	10.00	10.00	10.00	10.00	10.00

* Definitions provided in text.

Table 3. Sex-age Group Distribution (%) in Normalized Herd Ranks using Equations 1 and 2.

Rank	Nanny	Female	Female 2-yr-old	Female yearling	Billy	Male 2-yr-old	Male yearling
0-2	31.5	0	0	0	0	0	0
2-4	37.0	8.3	0	0	22.2	0	0
4-6	24.7	33.3	19.2	8.0	27.8	25.0	7.1
6-8	6.9	50.0	38.5	16.0	38.9	32.1	14.3
8-10	0	8.3	42.3	76.0	11.1	42.7	78.6

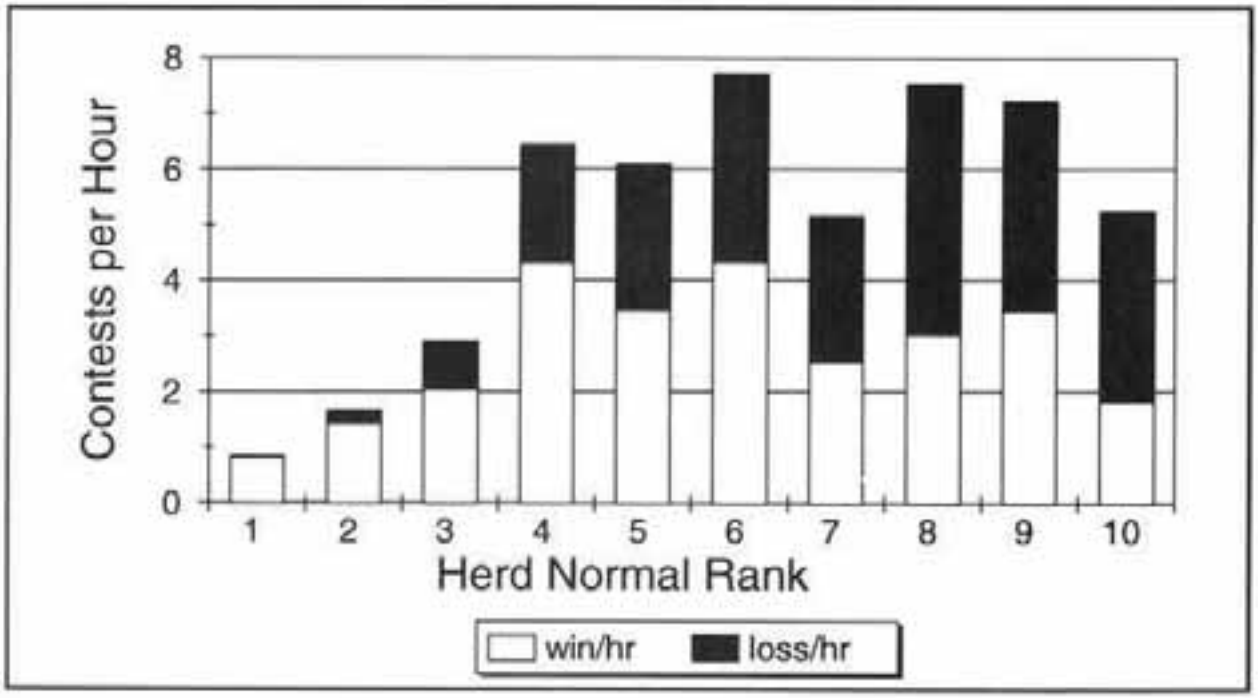

Figure 1. Mean number of agonistic encounters observed per hour versus cardinal rank for all 14 herds of Rocky Mountain goats on Elliott Ridge.

standard deviations of cardinal ranks are higher when only Equation 1 is used (see Table 1). This higher standard deviation results from variance in the herd sizes from which samples were taken. The standard deviation using herd normalized ranks is low for male yearlings. This coincides with the low average rank difference for this sex-age group.

The percentage of mountain goats distributed at various herd normalized ranks was calculated (Table 3). Kidless females showed a significant ($P<0.05$) difference from nannies. Male and female yearlings and 2-yr-olds are similar, respectively, in rank distribution despite male yearlings' much lower average rank difference.

Aggression in Herd Normalized Ranks

Mountain goats with herd normalized ranks of 4 through 10 had more agonistic encounters per hour than goats ranked 1-3 (Fig. 1). Dominant mountain goats (rank 1-3) had more wins relative to losses but this relationship reversed for subordinate goats. In small herds, we observed the top-most nanny being challenged a few times by the next highest ranking nannies, but almost never by lower ranking goats. However, in large herds the top-most nanny was challenged by, but usually defeated, goats who were not nannies with kids.

Contests with Top Ranking Nannies in Large Herds

Behavior of one female yearling (Ff1) in herd J indicates how females may move towards dominance positions within a herd. The yearling had over four times as many agonistic encounters with high ranking nannies as her cohorts. She won 9 of 29 contests with Dk and 11 of 28 with Ek (Table 4). She was chased by Ak 22 times with no wins. Lower ranking nannies in large groups were also seen to compete with higher ranking nannies more frequently than cohorts (Table 5). Herds J and L were used to evaluate which sex-age groups were more likely to compete with top ranking nannies. These herds were selected because observation times were 17 hours over 3 days for J and 14 hours over 2 days for L. These times were well in excess of those for the other large herds and provided the only opportunities to make significant observations of subordinate goat behavior toward dominant

Table 4: Dominance matrix of mountain goat herd J (22 animals) on Elliot Ridge, 1993 after 17 observation hours.

Winners		Losers														
		Ak	Bk	Ck	Dk	Ek	Ff1	Gm2	Jm2	Hk	If	Kf2	Lm2	Mf2	Nm1	Of1	Pb
1.0	Ak[b]	-	7[c]	1			22	1									
2.0	Bk		-	14		3		1									
3.0	Ck			-		12				2	1						
3.0	Dk				-	14	20	11		4	2						
3.1	Ek			1	12	-	17	8		5	1						
3.3	Ff1				9	11	-	5									
4.3	Gm2							-		11	1						
4.3	Jm2								-	2	1						
5.3	Hk			1	1	4				-	4					5	1
6.3	If										-	9	12	13			2
6.3	Kf2								10		1	-	17	13		2	1
7.0	Lm2								9			3	-	2			
7.3	Mf2								4		1	12	1	-	1		
7.3	Nm1														-	5	2
7.4	Of1														4	-	5
8.1	Pb														3	1	-

[a] Series rank.
[b] See text for letter definitions.
[c] Wins by goat listed on row against goat listed in column.

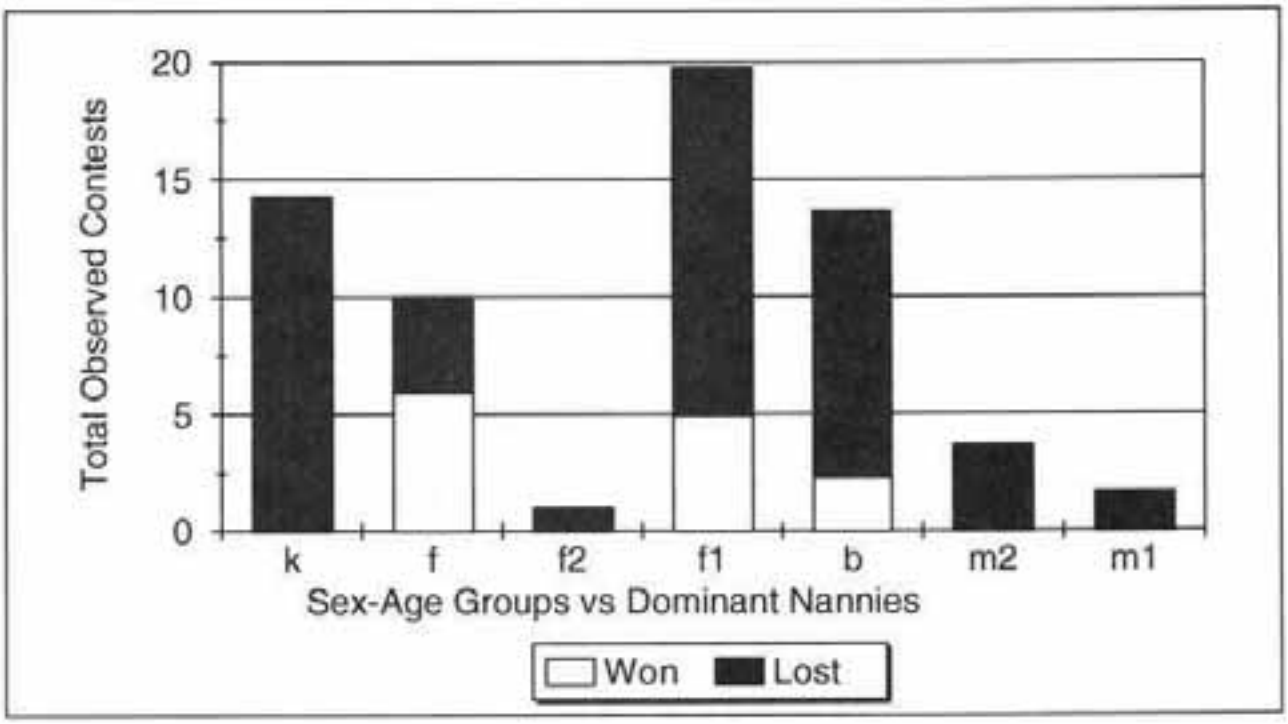

Figure 2: Agonistic encounters between subordinate goats and dominant nannies in herds J and L averaged for individuals in listed sex-age groups. k = nanny with kid, f = female without kid, f2 = female 2-year-old, f1 = female yearling, b = billy, m2 = male 2-year-old, m1 = male yearling.

nannies. The top five ranking nannies in herds J and L were designated dominant. Nannies ranked below these were also ranked below other sex-age group goats. Unlike some of their more dominant cohorts, these nannies tended to infringe upon the dominant nannies and be chased away (Fig. 2). The high average for female yearlings in both groups is solely attributable to Ff1 of herd J. Dominant billies also were observed to infringe upon dominant nannies, but totally avoided encounters with the top three nannies.

Nanny-kid Separation

During the course of the study, 73 cases of kids being separated from their nannies were observed. Separation times ranged from 2 minutes to 3 hours. The tendency for lower ranking nannies to interact agonistically with higher ranking nannies suggests an explanation for this high incidence of nanny-kid separation. Such interactions occurred when lower ranking nannies infringed on nannies of higher rank or were chased from a lick. After being displaced, the low ranking nanny moved around the salt lick searching for a lick hole which could more easily be acquired. During this search, a kid often became "lost" due to the kid's inattentiveness, sleeping, playing, or too many mountain goats blocking the view, or because the nanny moved out of the salt lick area. When the kid "discovered" loss of visual contact (i.e. when it awoke or finished play activities) it was considered separated when it could not immediately find its nanny and then initiated "abandoned kid" behavior. Behavior of abandoned kids included searching for the nanny, bleating, and the occasional trailing after a juvenile playmate and its nanny only to be rejected by the playmate's nanny. With one exception each lost kid was eventually found by its nanny. In the one event where I did not observe the kid reuniting with its nanny, the nanny had left the salt lick area alone and vocalized twice. The kid had moved down the mountain side and was apparently out of hearing range. Two hours after the separation, the remaining herd (n=21) left the salt lick together. The kid remained with this group and repeatedly vocalized while moving out of observation range. Reunions typically were marked by nose to nose contact with the nanny smelling her kid along the length of its body.

Separations per hour increased with increasing lower rank among nannies (Fig. 3 and 4). The relationship between lower normalized herd rank and average nanny-kid separations per hour are correlated and significant(K-W $P<0.01$).

The second cause of separation is walk-aways (Fig. 5 and 6). Walk-aways occur when lower ranking nannies searched for a lick hole, or departed from the salt lick area without being chased by another nanny. The parting of the nanny-kid pair under these circumstances is not as sudden as those of the chase. The walk-away separation relationship also was correlated and suggested that, at the salt lick, separations between nannies and kids occurred more frequently among lower ranking nannies(K-W $P<0.01$).

Lower ranks appeared to have a steady increase in average separations as the ranks decreased. The average separation result at the lowest ranks appeared to be nearly linear with the trend that began at the highest ranks. The exceptions in the middle may have been due to the sparseness of the data relative to the higher ranks (See Fig. 4 and 6). High ranking nannies were abundantly observed, being present in all herds. Only the largest herds provided opportunities to observe nannies of middle and low herd normalized ranks.

DISCUSSION

The level of aggression for nannies was lower than the average for all other goats in the herd (Fig. 1). The conditioning induced by repeated wins would tend to place the more experienced and dominant nannies into an increasingly linear hierarchy and reduce aggression (Jackson 1987). This would allow energy otherwise spent in intraspecific competition to be spent on rearing young.

Subordinate aggression may have been increased by crowding which reduced access to salt lick holes and encouraged lower ranking goats to approach the high ranking nannies more frequently. Male yearlings appeared to form peer groups.

It is possible that Ff1 of herd J may be the offspring of one of the dominant nannies. Chadwick (1983) reported that yearlings and newborn siblings often accompany their mothers onto the salt lick area. As such, the yearling may still be afforded some protection by her mother. The yearling Ff1 may also have been conditioned to winning by the protection of her dominant mother (Ginsburg and Allee 1942). Likewise, lower ranking nannies that frequently challenged higher ranking nannies at the salt licks may be offspring of higher ranking nannies.

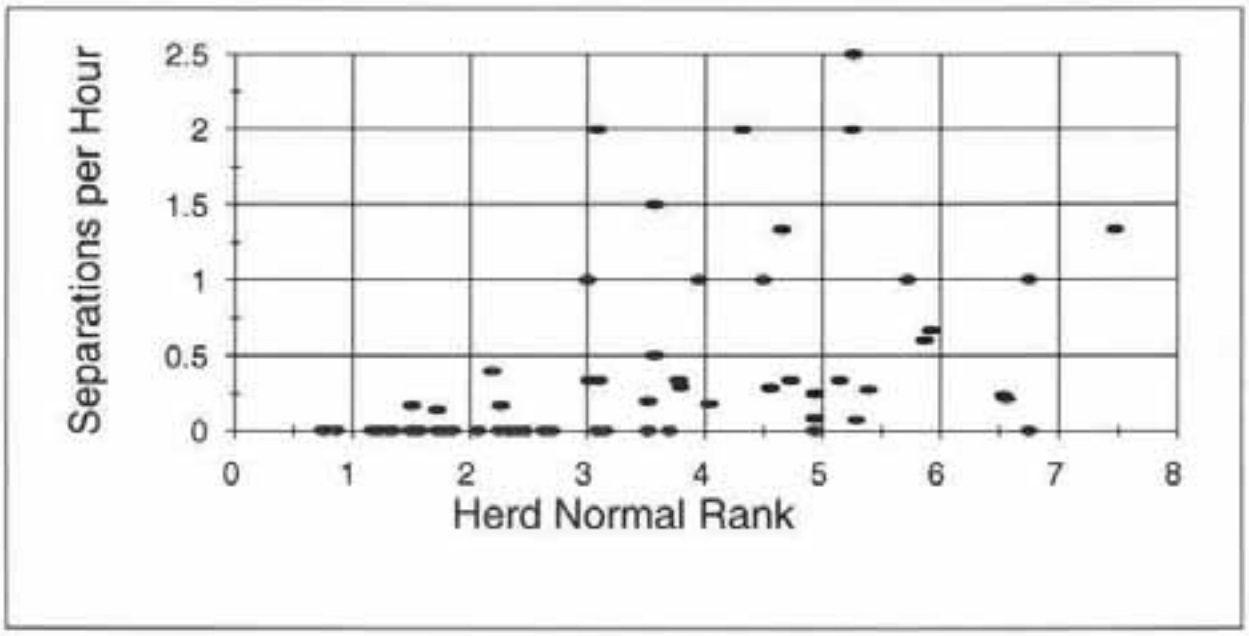

Figure 3. Nanny-kid separations per hour caused by the nanny being chased, in relation to herd normalized rank.

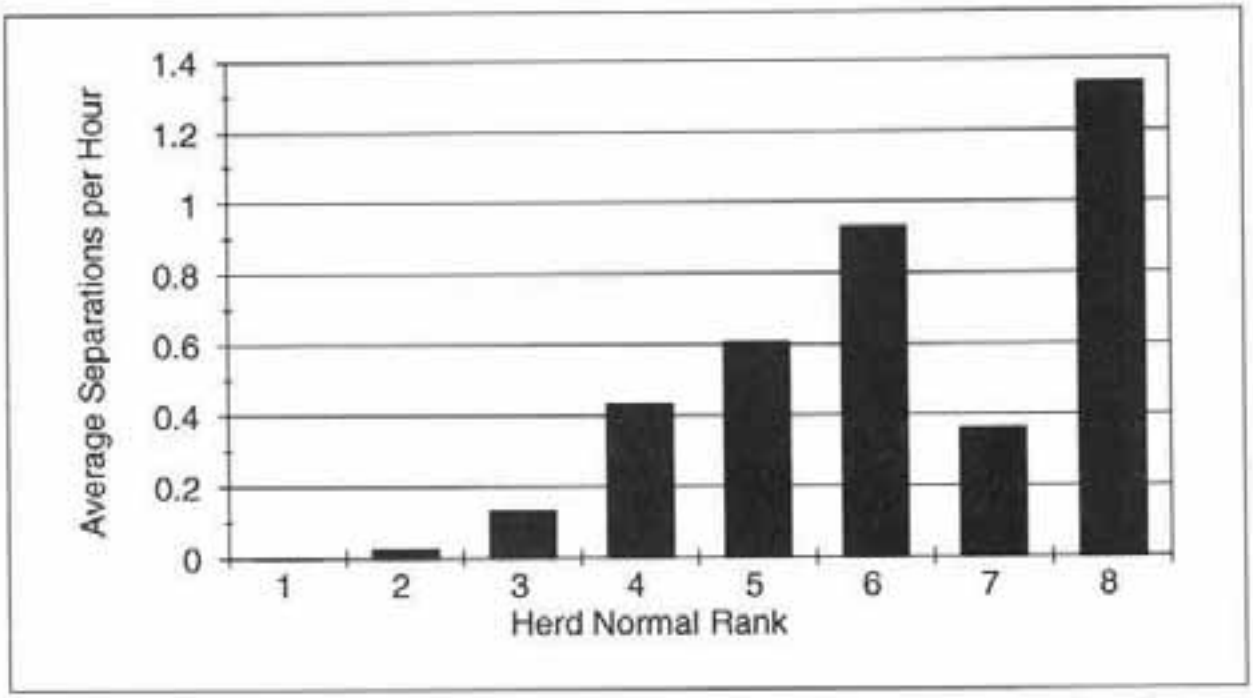

Figure 4. Average nanny-kid separations per hour caused by chases, in relation to herd normalized rank.

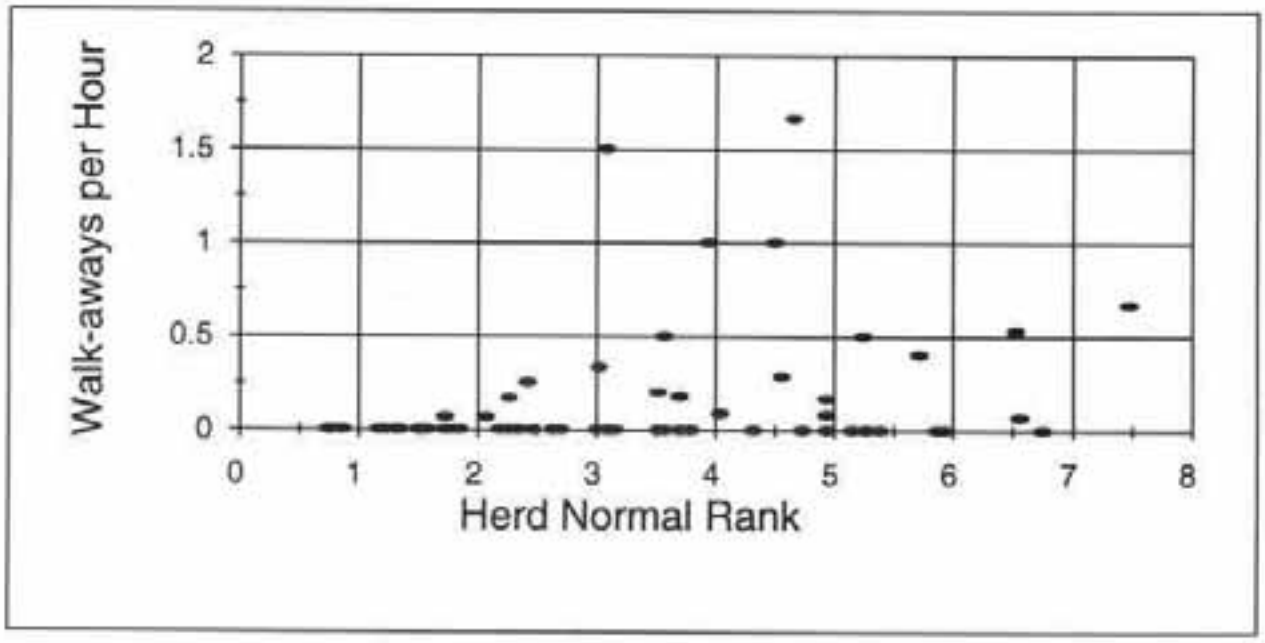

Figure 5. Nanny-kid separations per hour caused by walk-aways, in relation to herd normalized rank.

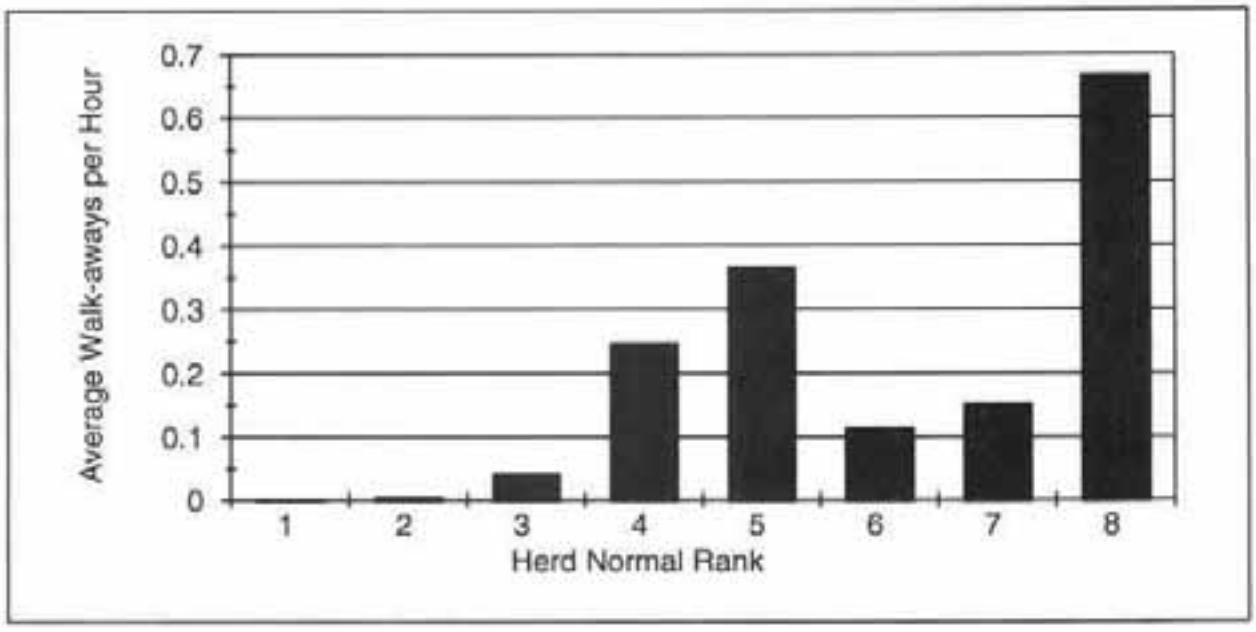

Figure 6. Average nanny-kid separations per hour caused by walk-aways, in relation to herd normalized rank.

Low ranking nannies generally failed to avoid encounters with high ranking nannies. Subadults minimized encounters with high ranking mountain goats by positioning themselves along the outer periphery of the salt lick area. Lower ranking nannies had from two to ten times more encounters with higher ranking nannies than did their non-nanny cohorts. This suggested several possibilities: 1) higher ranking nannies singled out lower ranking nannies and preferentially chased them; 2) some lower ranking nannies were very competitive against the higher ranking nannies; 3) lower ranking nannies had not learned to stay outside the individual space of dominant nannies. The nanny Hk, along with the female yearling Ff1, in Herd J was observed to have more agonistic encounters with higher ranking nannies and actually won several of them. In Herd L, nanny Hk encroached, competed, and won in contests against higher ranking nannies. Let us consider the relative ranking of Hk to higher ranking nannies Ck-Ek using Equation 1. If we remove goats Fk and Gb, then Hk will have a considerable increase in cardinal rank value. The results from Hk against Ck, Dk, and Ek, places Hk as a dominant of rank 3 to 3.6 rather than the 5.29 that results from Hk's losses to the intervening mountain goats. The point is that Hk competed intensively with these higher ranking nannies.

Although other lower ranking nannies did not win against higher ranking nannies, they sometimes encroached upon them only to be repelled. Encroachment by lower ranking nannies and preferential attack of lower ranking by higher ranking nannies are not mutually exclusive possibilities. Both situations arose during the herds' occupation of the salt lick.

Nannies with an ordinal rank of 1 were never separated from their kids either by being chased or by walking away. Rank 1 nanny dominance over the rest of the herd may allow her to remain in one place for long periods, reducing chance separations. Nannies with kids were the highest ranking mountain goats in the Gore-Range Rocky Mountain herd. Nannies with kids interacted two to ten times more among themselves than they did with other non-nanny mountain goats. It is likely that nannies without kids were younger. If so, much of the social hierarchy could be explained by age and might also be correlated with experience in rearing young. When separated, kids may be exposed to greater risk of predation, increased frequency of aggressive encounters with older mountain goats, and longer periods of time without access to milk.

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