Mountain Goat Sodium Dynamics in the Eagle Nest Wilderness, Colorado

Richard W. Thompson

quantities (Lehr 1941, Black 1968, Brownell and Crossland 1972). Low availability may reduce what little Na is accumulated by plants. Regions far removed from the influence of marine aerosols generally have low Na content in soil and rainwater (Eriksson 1952, Jordon et al. 1973), and alpine soils may be severely dificient of Na because of leaching by melting snow (Denton 1965).

Na is an essential mammalian macronutrient comprising approximately 92 percent of all extracellular fluid cations (Guyton 1976). Its primary functions include the regulation of osmotic pressure, maintenance of acid-base balance and conduction of nerve impulses (Mills 1969, Guyton 1976, Lloyd et al. 1978). The importance of Na is accentuated in ruminants because of the large, alkaline salivary secretions buffering the acidic products of microbial fermentation in the rumen (Denton 1956, 1957, Kay 1960, Church 1976). Ungulates in Na-deficient regions may be limited, at least seasonally, by an inability to maintain a positive Na balance (Jordan et al. 1973, Botkin et al. 1973). However, it can be assumed that wild ungulates balance their annual Na budget since death from Na deficiency rarely occurs, although wild animals apparently incur severe Na deficiency during spring and summer (Blair-West et al. 1968). Seasonal utilization of natural licks, mineral springs, and/or plants which accumulate this ion, recurrently combats Na deficiencies induced by forage depauperate in Na and ecological conditions e.g., (succulent spring forage) which accelerate the depletion of body Na (Blair-West et al. 1968).

Mountain goats were transplanted into the Gore Range between 1968 and 1972. During the initial transplants, three NaCl blocks were placed on Dora Mountain to hold the goats in the area. Mountain goat utilization has formed licks at these sites. In recent years, additional salt blocks deposited for goats by local ranchers and localized areas around camps where recreationists and hunters persistently urinated have caused a proliferation of new licks on the mountain. The purpose of the following study was to investigate the role of artificial salt licks in mountain goat ecology by documenting patterns of lick use and environmental Na availability.

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STUDY AREA

The Eagles Nest Wilderness is located in north-central Colorado, northwest of Dillon (Figure 1). The study area is defined by the boundaries of the ENW, which contains the high peaks of the Gore Range. The area encompasses 542 km^2, 54 percent above timberline (U.S. Forest Service 1979).

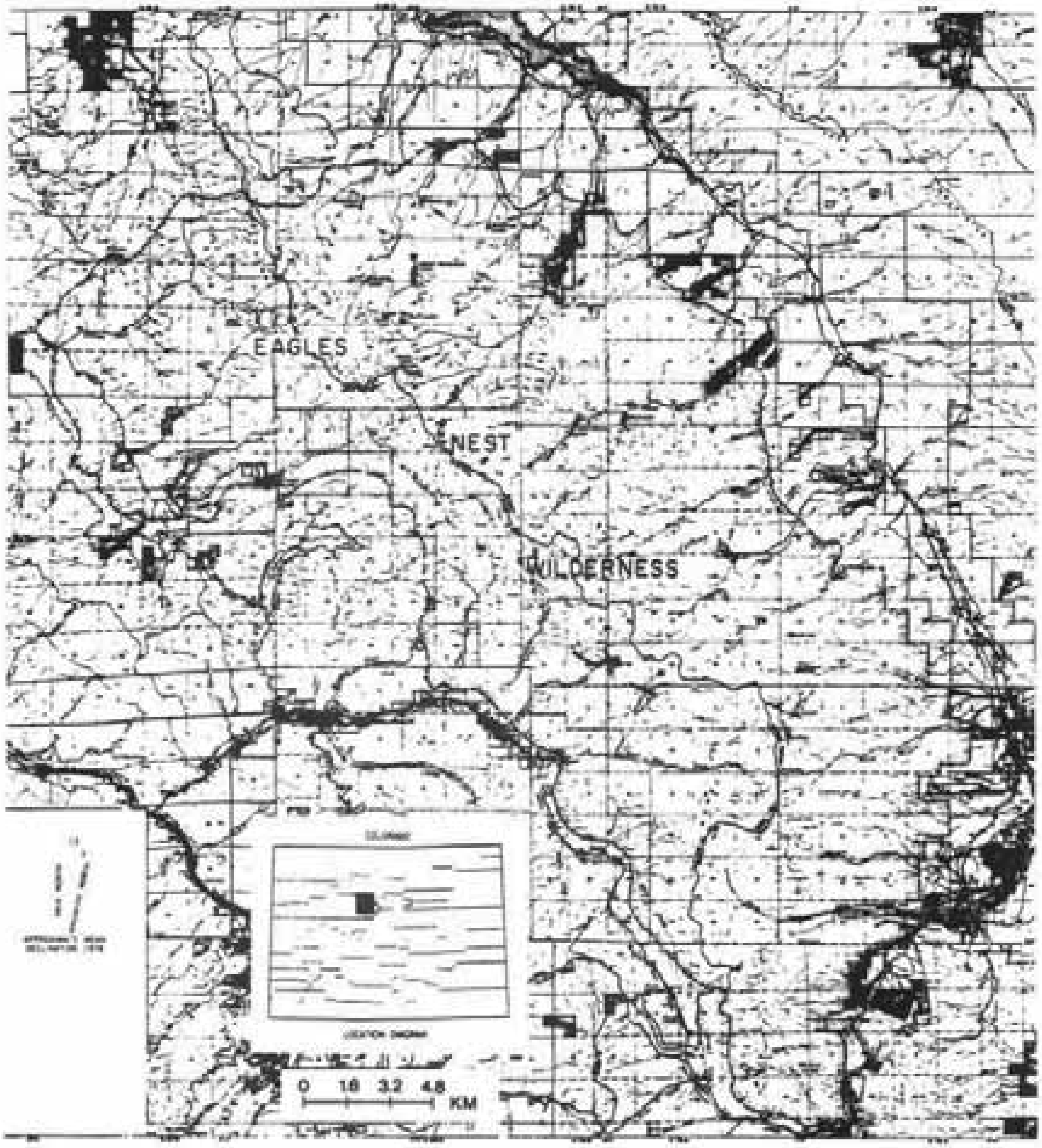

Figure 1. Eagles Nest Wilderness study area in north-central Colorado.

Intensive research was conducted on Dora Mountain in the northern half of the study area, due to the distribution of mountain goats and the salt licks located on Dora Mountain.

Dora Mountain is a large, horseshoe-shaped, mesa-like peak gently sloping to the northeast from Eagles Nest Mountain (4,084 m) and the main divide (Figure 2). The summit ranges from 3,658 m - 3,780 m and is a remnant of a preglacial erosion surface (Tweto et al. 1970).

Summer typically have cool, short growing seasons while winters are long and cold. Annual precipitation varies from 51 cm to over 102 cm at higher elevations, falling primarily as snow (U.S. Forest Service 1977). Severe thunderstorms are common in July and August. Permanent snowfields are common on north and east headwalls, and snowpack from normal winters often persist into fall.

Flora of the study area varies according to exposure and elevation. Lodgepole pine (Pinus contorta), aspen (Populus tremuloides), and Douglas fir (Pseudotsuga menziesii) occur in the montane zone. Dense stands of Engelmann spruce (Picea engelmannii) and subalpine fir (Abies lasiocarpa) dominate the subalpine zone. Timberline occurs between 3,413 m and 3,504 m. Above treeline, the spruce-fir become dwarfed and give rise to alpine vegetation such as carices (Carex spp.), sheep fescue (Festuca ovina), spike wood-rush (Luzula spicata), and forbs such as alpine avens (Geumturbinatum [= G. rossii]), clover (Trifolium spp.), blueleaf cinquefoil (Potentilla diversifolia), and marsh marigold (Caltha leptosepala). Willows (Salix spp.) myrtle whortleberry (Vaccinium myrtilus), and Rocky Mountain sage (Artemisia scopulorum) are the most significant shrubs in the alpine.

Approximately 14 artificial salt licks were located on the flat summit of Dora Mountain between 3,701 m and 3,734 m (Figure 2). Mountain goats used these licks extensively. Licks were named by their location on the mountain. The main licks, Northeast Lick #3 (NEL3), Southwest Lick (SWL) and Northwest Lick #1 (NWL1), originiated from three salt blciks placed by Division of Wildlife personnel shortly after the initial transplants to hold the mountain goats in the area (Denny 1977). None of the original salt was present aside from that which had leached into the soil. However, attempting to recover what little salt remained, the goats dug into the mineral soil. The Northeast Lick #1 (NEL1), Northeast Lick #2 (NEL2), and smaller associated Northeast Licks resulted from a local rancher dropping salt blocks for the goats from a fixed-wing plane in 1976. The Northeast Lake Licks (NELL 1&2) resulted from mountain goats ingesting the urine-soaked soil from the camp of a 1978 hunting party. The recent origins of the remaining licks are uncertain.

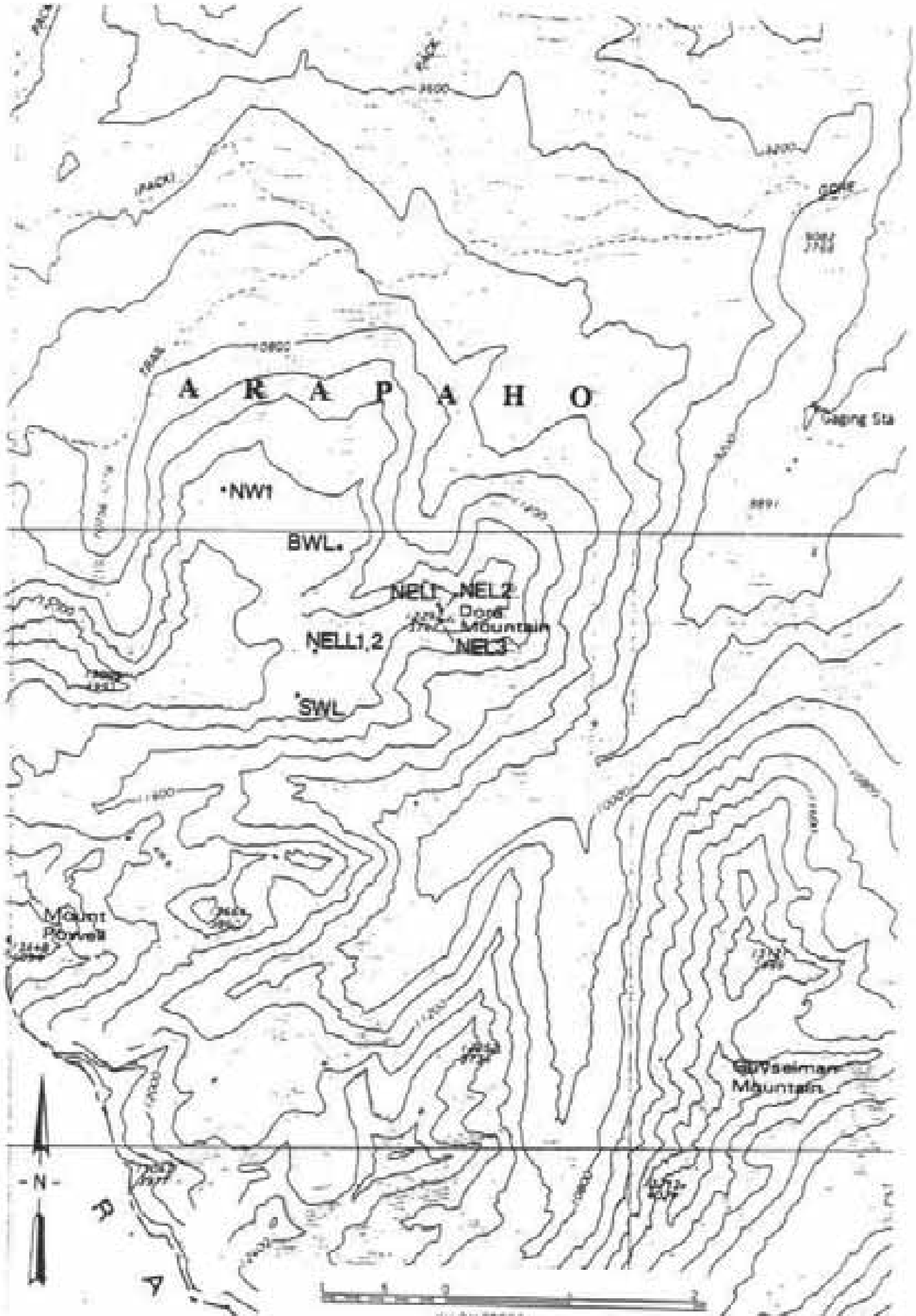

Figure 2. Detail of Dora Mountain in Eagles Nest Wilderness showing locations of major artificial salt licks.

METHODS

Mountain goats were observed in the study area from 8 June 1977 to 8 September 1979, primarily during the summer months. Direct observations were aided by the use of 7 x 35 binoculars and a 20x spotting scope.

Animals were classified into eight sex and age classes based on external genitalia, nanny-kid (NwK) or nanny-yearling (NwY) associations, urinating posture, horn morphology, tooth succession rostral width/length, and discerning the vulva (Brandborg 1955, Hibbs 1967, Thompson 1981). A combination of these criteria was used whenever possible because of inconsistencies of individual characters.

The role of Na, K, and salt licks in mountain goat ecology was investigated by field observation and laboratory analyses. Behavioral patterns of lick use were determined from field data. Recognizable goats were identified by characteristic shedding patterns, unique horns, group associations, telemetry collars, facial scars, and behavior. Laboratory methods determined the Na and K content of the animals, vegetation, water, and lick soils.

Samples of mountain goat serum, urine, milk, hair, and organic and inorganic feces (feces composed largely or entirely of lick soil) were obtained from five goats, one hunter-killed on 8 September, and four captured with rope nooses at the SWL on 25 and 28 July and 1 August. Additional fresh fecal samples were collected. Blood samples were extracted via jugular veinipuncture using nonheparinized 5-milliliter Vacutainers and 18-gauge needles. Serum, urine, and milk samples were immediately cooled in Dora Lake, packed in snow during transport out of the field, and later frozen. Blood serum was separated on a portable centrifuge. Feces and hair were air dried and stored in plastic bags. All samples were frozen until required for analysis.

In July (1979), 46 forage species were collected from Dora Mountain, taking special precautions to avoid contamination, particularly from our hands. An array of phenological growth stages was collected for each species. Chemical composition of plants, therefore, reflected average values. Collecting consisted of clipping a minimum of 20 individual plants just above the base, simulating the lower extent of a bite. Chemical content of specific plant parts (Dailey 1981) was not investigated. Browse samples were limited to the current year's growth of leaves and stems. Clipped plants were air dried and stored in paper bags until needed for chemical analysis.

Composite lick samples and soil from high use licking sites were collected from 14 licks on Dora Mountain. Only surface soils were taken at each site, representing what goats were actually ingesting. Samples were air dried and stored in plastic bags.

Samples were collected from areas where backpackers, campers, and hunters had urinated. At these specific sites, mountain goats were consuming the urine-soaked vegetation and soil. The vegetation-soil samples collected were not separated into their vegetative and soil components. Analysis results, therefore, reflected the ionic composition of the complex ingested. Control samples containing a similar vegetative and edaphic composition were collected for comparison. Samples were frozen in plastic bags.

Analyses for Na and K were modified from Isaac and Kerber (1971) and Walsh (1971). Random subsamples of all vegetation, feces, hair, lick soils, and recreationist samples were ground and dry-ashed in a muffle furnace at 500°C for four hours. Dry weight, ash weight, and the ash weight/dry weight were calculated for all subsamples. At this point, one of two procedures was followed, depending upon whether the sample was normally ingested or excreted from a mountain goat.

Analysis of solid samples ingested by mountain goats (vegetation, lick soils, and recreationist samples) followed a 0.1 NHCL extraction procedure suggested by Keiss (1976 pers. comm.), the results of which reflect only those minerals available to animals upon ingestion, rather than an absolute chemical composition. All samples were analyzed a minimum of three times. Values reported are dry weight values ($\bar{x} \pm SE$). Na and K concentrations were measured on a Coleman model-21 flame photometer and associated Coleman Junior IIA linear absorption spectrophotometer. Ash weights of samples ranging from 0.025 g for vegetation to 1.5 g for lick soils were weighed to $\pm$ 0.1 mg. on a Sartorius 2400 digital analytical balance. The ashed sample, quantitatively transferred into a 12 x 75 mm culture tube, was dissolved in 3 milliliters of 0.1 NHCL to approximate the pH of a ruminant's large and small intestine, the primary sites of Na absorption (Mills 1969). The solution was agitated on a mixer, covered with Parafilm, and refrigerated for two hours. After centrifugation at 7000 rpm for 20 minutes to remove any suspended particles, 50 microliters of the clear, supernatant fluid were transferred to a beaker containing 5 milliliters of micropore distilled water. An additional 5 milliliters of micropore distilled water were subsequently added and the solution placed into the flame photometer for analysis. Standard NaCl and KCl solutions were used to calibrate the spectrophotometer. Ion concentrations were calculated from the curvilinear regression equation representing the standard curve. Mountain goat serum, urine, and milk were analyzed as shown using a 50-microliter aliquot directly from the sample.

Solid samples shed or excreted from mountain goats (hair, organic feces, and inorganic feces) followed a 2NHCL extraction procedure to reflect the absolute chemical composition of nutrients lost. The procedure follows the 0.1 NHCL extraction as described above.

Orchard Leaves (Standard Reference Material 1571, National Bureau of Standards) were used as a reference to evaluate the efficiencies of the total extraction (2 NHCL) and in vitro simulation (0.1 NHCL) techniques.

Based on known Na and K quantities in the reference materials (Na, 82 ± 6 ug/g; K, 1.47 ± 0.03 percent dry weight), 100 percent of the Na (84.6 ppm) and 95.1 percent of the K (1.37 percent dry weight) were recovered using the 2 NHCL extraction. The low recovery of K was probably due to an inadequate sample of reference material rather than intrinsic inefficiency of the method. Critical values for Orchard Leaves were based on a minimum sample of 250 mg. A sample of only 56.8 mg was used in the assay. Using the in vitro simulation in comparison with results of the total extraction, a goat's digestive tract extracts approximately 96.2 percent and 91.7 percent of the total Na and K content of the ingested material, respectively. If the K value obtained from the total extraction technique is equated to 100 percent for reasons described above, the comparative in vitro simulation efficiency for K would be 96.4 percent. In vitro Na extraction efficiency results march well with Mills (1969) who stated that essentially all Na in ingesta is available to ruminants through digestion.

RESULTS AND DISCUSSION

LICK USE

Inception of mountain goat lick use on Dora Mountain varied annually with the onset of the growing season and, specifically, with the ingestion of new, succulent spring forage. A similar temporal onset has been noted for mule deer (Odocoileus hemionus) (Black 1955), white-tailed deer (O. virginianus) (Chapman 1939, Weeks and Kirkpatrick 1976), elk (Cervus elaphus) (Dalke et al. 1965, Knight and Mudge 1967), and mountain goats (Hebert and Cowan 1971) across North America, suggesting some common environmental perturbation effecting a Na deficiency and, therefore, a salt drive (Weeks and Kirkpatrick 1976). Weeks and Kirkpatrick (1976) postulated that the temporary negative Na balance results from a high obligatory intake of K and water in the new spring forage. Increased water flux and high K levels in the glomerular filtrate of the proximal tubule reduce intestinal and nephridic Na resorbtion resulting in excessive Na loss through fecal and urinary routes (Frens 1958, Hebert and Cowan 1971, Weeks and Kirkpatrick 1976). This excessive loss appears to initiate Na drive, hence lick use. Na drive declines during summer with increasing plant maturity and simultaneous declines in forage moisture content and K/Na ratios (Weeks and Kirkpatrick 1976). At this time and in early fall conservatory mechanisms are thought to be at peak efficiency (Weeks and Kirkpatrick 1976).

Lick use on Dora Mountain was confined to the spring and summer months beginning between 7 and 14 June, peaking between 1 and 7 July and terminating around 1 August, though goats infrequently visited the licks into September. Additionally, while the onset and cessation of lick use varied annually, the annual duration of lick use was essentially constant. There was no evidence indicating licks on Dora Mountain are used outside this period. Singer (1975) reported goats using the Walton Goat Lick in Glacier National Park from 15 April to 15 September 1975 with peak use in late June and early July. A natural lick in the Sapphire Mountains, Montana, was utilized by goats from June through December, although post-August visits to the lick averaged only three per month compared to a peak of 191 visits during July (Rideout 1974). Hebert (1967) observed lick use by goats in British Columbia from late April to early September with use of high elevation licks beginning and ending later. Variability in the onset of lick use between these areas probably reflects different local climatic and phenological influences.

All sex and age classes 1-year-old and over utilized the salt licks. This concurs with data from Hebert and Cowan (1971). Although kids were observed ingesting lick soil on five occasions, they consumed little. Each observation consisted of only a few bites or licks of soil. They appeared to be emulating their nannies who were always nearby. All kids observed ingesting lick soils either appeared to have been bored from lying outside the lick waiting for their nannies to finish licking or were forced into the lick (next to their nannies) because of a large number of aggressive goats around the lick. Based on this and Na data presented below, kids would receive little Na from lick soil relative to their nannies' milk.

Lick use differed temporally between the sexes; billies utilized licks approximately two weeks earlier than female groups. Peak use occurred around 1 and 14 July for adult males and females, respectively. Differential lick use has been observed in other studies (Brandborg 1955, Hebert 1967, DeBock 1970, Rideout 1974, Singer 1978) and has been attributed to the selection of isolated terrain by nannies until after parturition (Hebert and Cowan 1971). My data support this contention, however, even after parturition when nannies and their neonates are no longer in seclusion, nannies hesitate to bring their kids into or near the large groups found at licks until after a week or two. In general, kids accompanied their nannies to licks for the first time when they were no less than two weeks old. For the kid, this delay is probably adaptive because it allows for more advanced physical development before involvement is highly aggressive lick situations. Duration of lick use was similar between male and female groups. Peak use for male and female groups is offset one week earlier and later than peak use for all groups, respectively (Thompson 1981).

Licks were not used with consistent frequency or intensity throughout the summers, nor were areas within individual licks. At least some goats visited licks throughout the lick season and all licks were visited at least during portions of each summer, although utilization of individual licks varied. This may have been due to the moisture content of the lick and the surrounding vegetation. Licks receiving the highest use changed from NEL3 in June to the SWL in early July. During July, the SWL had a greater moisture content than the NEL3, a trend paralleling the forage moisture content-grazing trend from these same respective areas (Thompson 1981). Singer (1975) found water seeping into licks was a major factor determining late summer use.

Specific areas within each lick were "perfered" over others. In group situations, these sites were contested and first utilized by the most dominant animals, then by goats in order of decreasing hierarchial status. The "prime" areas were sites of recent goat urine deposition and their locations continually changed within the lick. Prime areas were moister than other lick sites and had a greater mean Na content (discussed below).

Small depressions within licks collected and temporarily held water from thunderstorms. Such areas also received more frequent use than drier areas, lending support to the theory that late summer lick use is a function of moisture content.

Three small new licks were formed in 1979 and four in 1980 as a result of human urine from 1978 and 1979 hunting camps. Although at least two of these licks (NELL1 and NELL2) had a high mean Na content (see discussion below), their use in early summer and midsummer was predominantly by NwK and small nursery and female groups who may have sought to avoid the agressive behavior and large groups at the SWL.

NA INTAKE

Mean vegetative Na concentrations of 46 alpine species was 48.69 ± 36.0 ppm (Table 1). Na values ranged from 7 - 142 ppm. Hebert and Cowan (1971) reported a similar mean Na value of 49 ppm for 13 alpine spring species on British Columbia goat range. Mean values from the present study are also similar to spring and summer forage values from Indiana deer range (Weeks and Kirkpatrick 1976). Since plants do not require Na, it is not surprising that the Na values are extremely low.

Seven plant species (Antennaria alpina, Oreoxis alpina, Trifolium dasyphyllum, Besseya alpina, Primula angustifolia, Oxyria dignea.and Salix arctica) contained Na concentrations over twice the mean value. With the exception of Antenaria and Primula, all species were eaten by mountain goats, although only Trifolium was consumed in significant quantities (Thompson 1981).

Vegetative K concentrations averaged 1.41 ± 1.05 percent dry weight and ranged from 0.23 - 5.54 percent (Table 1). This mean concentration mediates values reported for Indiana forage (Weeks and Kirkpatrick 1976) and alpine vegetation from British Columbia (Hebert and Cowan 1971). Four species, Oxeoxis alpina, Vaccinium myrtilus, Lloydia serotina, and Castilleja occidentalis, had K concentrations exceeding twice the mean value. These species were utilized to a low degree by goats, although Lloydia was ranked sixth in importance (Thompson 1981).

The mean forage Na/K ratio was 0.0082 ± 0.0074. Trifolium dasyphylum, Abies lasiocarpa, and Juniperus scopulorum had the highest Na/K values (Table 1). Trifolium are the most important forage species of goats on Dora Mountain; no utilization was recorded on Abies or Juniperus (Thompson 1981). Lowest Na/K ratios occurred in Geum, Lloydia, Potentilla, Castilleja, and Vaccinium whose Na concentrations were low (Geum and Potentilla) or whose K levels were elevated well above mean values.

Chemical content of 1977 composite soil samples from the NEL3 and SWL are presented in Table 2. Magnesium (Mg), iron (Fe), calcium (Ca), K, Na, and phosphorus concentrations are within the range of values reported from licks across North America (Cowan and Brink 1949, Stockstad et al. 1953, Dalke et al. 1965, Knight and Mudge 1967, Hebert and Cowan 1971, Weeks and

Table 1. Mean Ash, Na, K and Na/K values from vegetation collected 11 and 12 July 1979 on Dora Mountain, Gore Range, Colorado. Extraction employed 0.1 NHCL. Values reflect only those nutrients available to animal through digestion.

Species	Ash % Dry Wt.	Na ppm[a](meq/l)[b]	K % Dry Wt. (meq/l)[b]	Na/K meq/l/meq/l
Antennaria alpina	7.92	142(6.17)	1.56(400.00)	0.0154
Oreoxis alpina	19.94	127(5.52)	5.54(1,420.51)	0.0039
Trifolium dasphyllum	8.15	124(5.39)	0.52(133.33)	0.0404
Besseya alpina	18.60	123(5.35)	1.78(456.41)	0.0117
Primula anugustifolia	8.49	113(4.91)	1.18(302.56)	0.0162
Oxyria dignea	9.67	105(4.57)	1.50(384.62)	0.0119
Salix arctica	16.86	103(4.48)	1.52(389.74)	0.0115
Vaccinium myrtilus	2.85	72(3.13)	5.14(1,317.95)	0.0024
Trisetum spicatum	5.68	71(3.09)	1.02(261.54)	0.0118
Hymenoxys grandiflora	17.00	69(3.00)	2.02(517.95)	0.0058
Erigeron simplex	7.65	63(2.74)	2.33(597.44)	0.0046
Saxifraga rhomboidea	6.55	57(2.48)	1.25(320.51)	0.0077
Artemisia scopulorum	11.15	53(2.30)	1.97(505.13)	0.0046
Pedicularis parri	7.38	53(2.30)	1.04(266.67)	0.0086
Poa epilis	5.62	53(2.30)	1.04(266.67)	0.0086
Carex capitata - C. rupestris	4.89	53(2.30)	0.90(230.77)	0.0100
Pentaphylloides floribunda	3.92	51(2.22)	0.77(197.44)	0.0112
Gentianoides algida	3.67	48(2.09)	0.92(235.90)	0.0088
Erigeron pinnatisectos	15.39	47(2.04)	2.13(546.15)	0.0037
Eritrichium aretoides	8.00	47(2.04)	0.75(192.31)	0.0106

a Dry weight basis rounded to nearest ppm.
b meq/l Na = ppm/23; meq/l K = (% Dry Wt.) · 10,000/39.

Table 1 (continued). Mean Ash, Na, K, and Na/K values from vegetation collected 11 and 12 July 1979 on Dora Mountain, Gore Range, Colorado.

Species	Ash % Dry Wt.	Na ppm[a](meq/1)[b]	K % Dry Wt. (meq/1)[b]	Na/K meq/1/meq/1
Agropyron scribneri	6.36	46(2.00)	1.36(348.72)	0.0057
Sedum rhodanthrum	8.15	46(2.00)	1.31(335.90)	0.0060
Senecio fremonti	13.57	44(1.91)	1.70(435.90)	0.0044
Trifolium nannum	8.03	44(1.91)	0.73(187.18)	0.0102
Aquilegia caerulea	8.39	43(1.87)	1.64(420.51)	0.0044
Pedicularis groenlandica	7.71	43(1.87)	1.10(282.05)	0.0066
Juniperus scopulorum	3.33	42(1.83)	0.30(76.92)	0.0237
Castilleja occidentalis	18.73	40(1.74)	2.84(728.21)	0.0024
Zygadenus elegans	8.96	40(1.74)	1.98(507.69)	0.0034
Abies lasiocarpa	3.54	40(1.74)	0.23(58.97)	0.0295
Trifolium parryi	6.91	32(1.39)	0.63(161.54)	0.0086
Lloydia serotina	9.92	31(1.35)	3.02(774.36)	0.0017
Trollius laxus	10.93	31(1.35)	1.36(348.72)	0.0039
Picea englemannii	3.22	28(1.22)	0.36(92.31)	0.0132
Polemonium viscosum	7.94	26(1.13)	1.18(302.56)	0.0037
Luzula spicata	6.83	23(1.00)	1.05(269.23)	0.0037
Thlaspi alpestre	8.22	22(0.96)	1.10(282.05)	0.0034
Cirsium scopulorum	13.44	21(0.91)	1.05(269.23)	0.0034
Potentilla diversifolia	8.35	19(0.83)	1.46(374.36)	0.0022
Salix brachycarpa	3.56	17(0.74)	0.40(102.56)	0.0072
Dryas octapetala	5.41	17(0.74)	0.38(97.44)	0.0076
Polygonum bistortoides	8.71	15(0.65)	0.62(158.97)	0.0041
Festuca ovina	5.73	15(0.65)	0.48(123.08)	0.0053
Carex albonigra	7.69	12(0.52)	0.92(235.90)	0.0022
Geum turbinatum	7.48	11(0.48)	1.33(341.03)	0.0014
Mertensia viridis	10.70	7(0.30)	1.43(366.67)	0.0008

Table 1 (continued). Mean Ash, Na, K, and Na/K values from vegetation collected 11 and 12 July 1979 on Dora Mountain, Gore Range, Colorado.

Species	Ash	Na	K	Na/K
	% Dry Wt.	ppm[a](meq/1)[b]	% Dry Wt. (meq/1)[b]	meq/1/meq/1
Orchard Leaves[c]				
0.1 NHCL extraction[d]	16.86	81.42(3.54)	1.32(338.46)	0.0082
2 NHCL extraction[e]	16.86	84.6 (3.68)	1.37(351.28)	0.0074
Mean ± SE (46)[f]	8.72 ± 4.33	48.69 ± 36.00 (2.12 ± 1.57)	1.41 ± 1.05 (361.54 ± 269.23)	0.0082 ± 0.0074
Graminoids (7)[f]		39.1 ± 22.54 (1.70 ± 0.98)	0.97 ± 0.26 (247.99 ± 67.30)	0.0068 ± 0.0035
Forbs (30)[f]		54.51 ± 37.72 (2.37 ± 1.64)	1.57 ± 0.97 (401.71 ± 247.86)	0.0073 ± 0.0074
Woody Plants (9)[f]		46.92 ± 27.6 (2.04 ± 1.20)	1.23 ± 1.59 (315.38 ± 407.09)	0.0123 ± 0.0089

c Standard Reference Material 1571, National Bureau of Standards. Certified values are: Na = 82 ± 6 ppm; K = 1.47 ± 0.03%. Orchard leaves results not included in mean values.

d *In vitro* simulation based on Keiss (1976, pers. comm.). Results reflect only those minerals available to animal through digestion.

e Results reflect total chemical composition of sample.

f Number of species.

Kirkpatrick 1976, Weeks 1978, Fraser et al. 1980). Furthermore, since manganese (Mn), copper (Cu), and zinc (Zn) are thought to be in approximately normal concentrations (Keiss, pers. comm.), Na was probably the attracting element at these licks.

Composite Na and K concentrations in the SWL and NEL3 declined significantly between 1977 and 1979 (Tables 2 and 3). Considering the Na in these two licks is a product of weathering from the original salt blocks, the apparently declining Na concentrations are probably attributable to the annual consumption and continual leaching of lick soils. However, the cause of the K decrease is uncertain. Since the 1977 samples were composites, subsamples of local Na and K concentrations ("preferred" sites) may have had elevated composite values. Na and K content of prime lick sites is greater than composite values. Indeed, at prime sites in the SWL, Na is almost nine times as concentrated as mean lick values (Table 3).

Mean Na and K concentrations of all licks on Dora Mountain (Table 3) were 77.94 $\pm$ 60.02 ppm and 118.0 $\pm$ 82.0 ppm, respectively. Both values lie within the range of other North American licks, although Na values are comparatively low (Cowan and Brink 1949, Stockstad et al. 1953, Dalke et al. 1965, Knight and Mudge 1967, Hebert and Cowan 1971, Botkin et al. 1973, Vaughan 1974, Weeks and Kirkpatrick 1976, Weeks 1978, Fraser et al. 1980). Na/K values were similar to natural salt licks (Hebert and Cowan 1971) and were over 117 times greater than mean vegetation values (compare Tables 1 and 3). Mean Na concentration of composite Northeast Lick (NEL1, NEL2,

Table 2. 1977 composite chemical content of the NEL3 and SWL on Dora Mountain, Gore Range, Colorado, using 0.1 NHCL[a]. Values reflect only nutrients available to animal through digestion.

Lick	ppm								%
	Mg	Fe	Ca	Mn	Cu	K	Na	Zn	P
NEL3	1,000	450	7,500	125	50	200	450	20	0.03
SWL	575	760	1,750	40	25	400	700	10	0.01

[a] Analysis conducted by Robert Keiss, Colorado Division of Wildlife, Fort Collins.

Table 3 Na and K content of licks on Dora Mountain, Gore Range, Colorado, 1979. Extraction employed 0.1 NHCL. Values reflect only those nutrients available to animal through digestion.

Lick	Degree of Use	Sample	Na ppm[a](meq/l)[b]	K % Dry Wt. (meq/l)[b]	Na/K (meq/l/meq/l)
SWL	H[c]	Composite[d]	27(1.17)	0.007(1.79)	0.654
SWL	H	Prime[e]	238(10.35)	0.03 (7.69)	1.345
NELL1	M[c]	Composite	113(4.91)	0.012(3.08)	1.597
NELL2	M	Composite	103(4.48)	0.01 (2.56)	1.747
NW1	L[c]	Composite	93(4.04)	0.027(6.92)	0.584
NW2	L	Composite	157(6.83)	0.009(2.31)	2.958
NWML	L	Composite	33(1.43)	0.008(2.05)	0.699
NWWL	L	Composite	37(1.61)	0.009(2.31)	0.697
BWL	M	Composite	130(5.65)	0.013(3.33)	1.696
BEL	L	Composite	23(1.00)	0.006(1.54)	0.650
BSL	L	Composite	23(1.00)	0.006(1.54)	0.650
NEL3	H	Composite	50(2.17)	0.005(1.28)	1.696
NEL3	H	Prime	93(4.04)	0.026(6.67)	0.607
NEL2	L	Composite	30(1.30)	0.008(2.05)	0.636
NEL1	L	Composite	50(2.17)	0.007(1.79)	1.211
NE Control [f]		Composite	27(1.17)	0.009(2.31)	0.509
CL	L	Composite	47(2.04)	0.006(1.54)	1.328
Cabin Lick[g]	N[c]	Composite	3,705(161.09)	0.032(8.21)	19.632

[a] Dry weight basis.
[b] Dry Weight · 10,000 = ppm.
[c] H = High, M = Moderate, L = Low, N = None.
[d] Sample reflects mean composition of lick.
[e] Sample reflects specific "preferred" area of lick.
[f] Composite control sample for area of the Northeast Licks.
[g] Natural lick located outside goat range in montane zone approximately 0.4 km north of Lower Cataract Lake.

Table 3 (continued). Na and K content of licks or Dora Mountain, Gore Range, Colorado, 1979.

Lick	Degree of Use	Sample	Na ppm[a] (meq/1)[b]	K % Dry Wt. (meq/1)[b]	Na/K (meq/1/meq/1)
Mean ± SE[h] (16)[i]			77.94 ± 60.02 (3.39 ± 2.61)	0.0118 ± 0.0082 (3.03 ± 2.10)	1.172 ± 0.659
Composite [h] (14)			65.32 ± 44.62 (2.84 ± 1.94)	0.0095 ± 0.0055 (2.44 ± 1.42)	1.200 ± 0.688
Prime Sites [h] (2)			165.60 ±102.6 (7.20 ± 4.46)	0.028 ± 0.0028 (7.18 ± 0.73)	0.976 ± 0.522

[h] Results of Cabin Lick and control sample for Northeast Licks do not enter into calculations.
[i] Sample size.

NEL3) samples is 43.3 ± 11.5 ppm, only 1.6 times the mean value of a composite control sample from the area. If Na concentrations of licks continue to decline at the rate observed between 1977 and 1979 (NEL3: 450 to 55 ppm), in several years licks will have no greater Na concentrations than the surrounding soils. Indeed, the vegetation will have a greater concentration. Already two licks, BEL and BSL, have Na concentrations below the Northeast Lick control sample and four other licks, NEL2, NWML, NWWL, and SWL, have equal or slightly high Na values, although all these except the SWL receive low use (Table 3).

The NEL3 and SWL contained localized, "preferred" or "prime" sites within each lick which were areas of recent mountain goat urine deposition. Goats were observed urinating in these licks eight times throughout the study although additional deposits were suspected. As the urine-soaked soil was consumed and fresh urine deposited, a new "preferred" site was formed. The apparent intraspecific recycling of urinary Na was restricted to the NEL3 and SWL excavations. However, because of quantitative limitations this represented an insignificant Na source for the goat population. In British Columbia, goats "preferred" localized areas in mineral licks which had naturally higher Na concentrations than adjacent "less preferred" areas (Herbert and Cowan 1971).

If goats differentially consume soil from "prime" sites because of their greater Na content, this explicitly suggests goats can detect Na differences as small as 43 ppm (in the case of NEL3, Table 3). However, if this is the case, why do goats heavily utilize the NEL3 and SWL (high use licks averaging 38.5 ppm Na) when medium- and low-use licks on the average contain greater Na concentrations (115.3 and 54.8 ppm Na, respectively)? Indeed, why use the SWL at all if its composite Na content is identical to a control soil sample from the Northeast Lick area (Table 3)? I suggest the NEL3 and SWL are now traditional social centers. Kindel (1958) suggested that natural licks were an important social center for elk and that animals visit licks not because of a physiological need, but to remain in a herd. However, socialization associated with licks could only be developed after lick use was established (Knight and Mudge 1967). The NEL3 and SWL were heavily utilized for their Na content while the salt blocks were still intact. After the blocks weathered and leached into the ground, goats began excavating and consuming the soil. This behavior persists in groups of up to 41 animals; however, based upon the present Na content of the NEL3 and SWL, lick use now appears to be less related to fulfilling Na needs, although it probably ameliorates seasonal dificiencies.

The Cabin Lick, located 5.7 km outside the goat distribution about 0.4 km north of Lower Cataract Lake, was the only natural lick identified in the Gore Range. The Na concentration (3,705 ppm) and Na/K value (11.578 ppm) are extremely high. This lick is heavily utilized by deer, marmots (Marmota flaviventris), and porcupines (Erethizon dorsatum) during the spring and summer months. Although goats may travel up to 24 km, partly through forests, to visit licks (Brandborg 1955, Hebert and Cowan 1971), goats have either not found the lick yet or are avoiding the heavy recreational pressure of the surrounding area.

Seven small new licks were formed in 1979 (n = 3) and 1980 (n = 4) as a result of human urine deposits from 1978 and 1979 backpacker and hunter camps. This source of Na represents a substantial contribution to the Na supply on the mountain. At least two of these licks (NELL1 and NELL2; the four new lick located in 1980 that were formed through recreational activities were not analyzed) had Na concentrations higher than the mean licks value, though lower than "preferred" lick sites. Na and K values from the vegetation-soil complex where recreationists urinated are presented in Table 4. Mean Na concentration of the sample complex was 1,070 $\pm$ 511 ppm, 22 times the mean value of vegetation and nearly 14 times the average lick value. Furthermore, human urine (n = 1) deposited in these areas was nearly nine times as concentrated as the mean vegetation-soil complex values (Table 4). The human kidney can excrete up to 40 g of NaCl per day (Guyton 1976, Lloyd et al. 1978). K levels of the recreationist samples are also high, making the mean Na/K value an order of magnitude higher and lower than the mean vegetation and lick values, respectively.

Localized, persistent human urination gives rise to new salt licks; however, most human Na input on the mountain appear to have occurred in single, distinct urine deposits surrounding recreationists' camps. Goats readily located these sites and consumed only the urine-soaked vegetation and soil, at times within 2 hours after deposition. The first goat arriving at a recent depost, if not displaced by a more dominant individual, consumed most, if not all, of the vegetation and soil affected. No use or a highly limited use of these sites occurred after the initial animal finished, unless a new urine deposit was made. Several deposits on the same area initiated a lick.

The relationship between mountain goats, recreationists, and salt licks was not discerned until 1978. Towards the middle of the 1978 field season, small, shallow bare spots were noticed around our alpine camps. These spots appeared between the time we left camp in the morning and our evening return. On 28 July, we witnessed a 2-year-old goat consuming vegetation and soil from a site near camp where my assistant had urinated the night before. Upon investigating the area surround camp, every area where we recalled urinating had been disturbed in a similar manner. Goats apparently visited camp in our absence and consumed the vegetation and soil where we had recently urinated. This type of goat behavior is a common occurrance in Olympic and Glacier National Parks (Moorhead 1973, Bansner 1976).

In 1979, after discovering two new licks adjacent to prior hunting camps, we confirmed this unusual method of lick procreation by empirically initiating a small lick (CL) through persistent urination in a localized area for approximately 4 days. Goats abandoned this lick shortly after urine deposits were discontinued. Sampling for lick analysis occurred subsequent to the termination of use. The low Na concentration of this lick (47 ppm) was probably due to the consumption of most, if not all, of the urine-soaked soil. As such, Na content of the sample represented little more than a soil sample of the area.

Table 4. Mean Na and K values of the urine-soaked vegetation-soil complex for recreationist samples collected on Dora Mountain, Gore Range, Colorado. Extraction employed 0.1 NHCL. Values reflect only those nutrients available to animal through disgestion.

Species	Ash % Dry Wt.	Na ppm[a](meq/1)[b]	K % Dry Wt. (meq/1)[b]	Na/K meq/1/meq/1
RE2	53.26	552(24.0)	1.856(475.9)	0.0504
RC2[a]	62.89	56(2.4)	0.751(192.6)	0.0126
RE3	60.05	1,084(47.1)	1.563(400.8)	0.1176
RC3[a]	49.71	66(2.9)	0.809(207.4)	0.0138
RE4	56.9	1,573(68.4)	2.125(544.9)	0.1255
RC4[a]	61.59	123(5.3)	0.771(197.7)	0.0271
Human Urine		9,183(399.3)	2.156(552.8)	0.7222
Mean $\pm$ SE[b] (3)[c]	57.4 $\pm$ 512	1,070 $\pm$ 511 (46.52 $\pm$ 22.2)	1.848 $\pm$ 0.281 (473.85 $\pm$ 72.1)	0.0978 $\pm$ 0.0413

[a] Control sample.
[b] Excludes control and urine samples.
[c] Sample size.

There is little Na input through any water source on Dora Mountain (Table 5). Mean Na concentration of 11 water samples was 0.35 ± 0.129 meq/liter, roughly 30 percent of the Na in the Northeast Lick control sample. Two samples were not discernible from micropore distilled water. The mean K value was nearly identical to the mean content of lick samples, but was 131 percent higher than the control sample for the Northeast Licks. Na/K values were roughly similar to mean lick values.

Table 5. Mean cation concentrations of water collected on Dora Mountain, Gore Range, Colorado.

Sample	n	Na (meq/l)	K (meq/l)	Na/K (meq/l/meq/l)
Dora Lake	3	0.3	2.3	0.130
Small Lake	2	0.4	2.1	0.190
Snowfield Runoff	3	0.2	3.4	0.059
Standing Water	3	0.5	4.3	0.116
Mean ± SE		0.35 ± 0.129	3.03 ± 1.02	0.124 ± 0.054

SYSTEMIC VALUES

Serum Na values (Table 6) were within the noraml range reported for mountain goats (Hebert 1967) and similar to values reported for other ungulates (Franzmann and Thorne 1970, Anderson and Medin 1972, Seal et al. 1972 a, b, Turner 1973, Barrett and Chalmers 1977, Mautz et al. 1980). Due to the regulatory function of the kidney, serum Na levels are thought to remain essentially constant despite the Na status of the animal (Smith and Aines 1959, Beilharz et al. 1962, Hebert 1967, Hebert and Cowan 1971, Weeks and Kirkpatrick 1976). Hebert (1967) was unable to detect differences in mountain goat serum Na levels due to lick use. Serum K values were similar to plasma K values reported for desert bighorn sheep (*Ovis canadensis*) (Turner 1973).

The single saliva sample analyzed in this study was from a tame, hand-reared yearling goat used in a Division of Wildlife food habits study. This animal received mineral supplements and, therefore, probably had Na and/or K levels elevated from those of wild goats. Nevertheless, the Na and K values (Table 6) compare closely to values reported by McDougall (1948), Kay (1960), and Blair-West et al. (1964) for domestic sheep on "normal" forage. Na status of the animal has a marked effect on salivary Na and K content (Denton 1956, 1957, Kay 1960) and even under ordinary dietary conditions the salivary concentration of these two cations is widely variable (McDonald 1969). Denton (1956) demonstrated that commensurate with negative Na balance, the Na content of parotid sheep saliva decreased from 180 meq/liter to 60 meq/liter with a concomitant K increase from 10 meq/liter to 120 meq/liter.

NA OUTPUT

Urinary Na concentrations were high averaging 5.7 ± 2.4 meq/liter (Table 6). Although this elevated level was possibly an artifact of sample size, it may also be attributable (particularly in the adult male) to increased K intake inhibiting Na retention (Suttle and Field 1967, Weeks and Kirkpatrick 1976), excretion of large quantities of K resulting in concomitant Na loss (Eisenstein 1967, Weeks and Kirkpatrick 1976), a sudden intake of high Na levels on a system of adapted to conserve limited Na intake (Weeks and Kirkpatrick 1976), diuresis caused by the abrupt shift to succulent spring vegetation analagous to increased fecal Na loss (Frens 1958, Hebert and Cowan 1971, Weeks and Kirkpatrick 1976), or any combination of these factors. Weeks and Kirkpatrick (1976) found 21 percent of 78 deer urine samples were well above 4.35 meq/liter Na, yet 40 percent had Na concentrations below 0.435 meq/liter. Even under closely controlled conditions, sheep exhibit wide fluctuations in urinary Na content (Denton 1956, Suttle and Field 1967). Through similar environmental Na limitations, nephric Na retention efficiency of the mountain goat should rival or exceed that of the deer. The Na value for the tame yearling (Table 6) confirms this animal was receiving supplements.

As previously mentioned, urinary K may influence Na excretion through nephric interaction. Mean urinary K levels (Table 6) were extremely variable and significantly higher than comparable values from deer (Weeks and Kirkpatrick 1976).

Mean fecal Na concentrations for all organic samples (Table 7) were higher than those reported from mountain goats and other ungulates (Hebert and Cowan 1971, Botkin et al. 1973, Weeks and Kirkpatrick 1976); however, this was attributable to the high Na content of rectal samples which averaged almost four times the mean value of fresh organic pellets. Na content of fresh organic and inorganic feces were not significantly different ($P > 0.5$). This result differs statistically with Hebert and Turnbull (1977) who postulated that salt lick soil reduces the alimentary passage rate, thereby enhancing resorbtion of salivary, vegetative, and lick Na from the ingesta. Hebert and Cowan (1971) and Weeks and Kirkpatrick (1976) found fecal Na losses increased significantly with the abrupt spring dietary shift from dried, winter forages to new, succulent vegetation as a result of excessive water and K levels. This phenomenon probably occurs during spring in most ungulates. Mean organic and inorganic fecal K values (Table 7) are similar to values reported for white-tailed deer (Weeks and Kirkpatrick 1976).

Although quantitatively insignificant, Na and K loss through shedding was high. Na and K values averaged 260.5 ± 104.2 ppm and 1,880 ± 938.3 ppm, respectively (Table 7). Na values were low compared to moose (*Alces alces*) hair (Botkin et al. 1973, Franzmann and Arneson 1974).

Na content of milk from a 3-year-old goat was 46.5 meq/liter (Table 6). Female mountain goats probably have far greater Na demands than billies because of losses to fetal and associated tissues, amniotic fluid, and lactation. Assuming the birth weight of an average mountain goat kid is 2.96 kg (Brandborg 1955, Lentfer 1955) and based on data extrapolated from Weeks and Kirkpatrick (1976), the average nanny must supply 3.32 g Na to her fetus prepartum. Approximately 10 g Na are lost via isotonic amniotic fluid (Weeks and Kirkpatrick 1976) and during the lactational peak, nannies may lose 1.12 g Na per day via milk (Silver 1961, Cook et al. 1970, Moen 1973, Weeks and Kirkpatrick 1976).

NA BALANCE

The Na requirements of mountain goats are unknown; however, it appears that for most of the year their Na intake is far below levels recommended for comparable domestic ruminants. The general recommended Na intake for domestic sheep is 0.04 - 0.1 percent of dietary dry matter (National Research Council 1975), although this level may exceed maintenance requirements. Domestic ewes are commonly provided 7.3 - 11.3 g NaCl per day (National Research Council 1975). If a 65-kg goat consumes 1.62 kg of dried forage per day (extrapolated from Morrision 1959) at an "average" vegetative Na value of 48.69 ppm, its daily Na intake would be 78.9 mg, a level 8.2 - 20.5 times lower than the general recommended intake (0.648 - 1.62 g Na/1.62 kg dried forage) for domestic sheep.

Even through selective feeding, utilization of licks and consumption of sites soaked with recreationist urine, Na intake would fall far short of domestic requirements. Considering the five most frequently selected forage species (Thompson 1981), _Trifolium_ spp., _Carex_ spp., _Gentianoides algida_, _Geum turbinatum_, _Salix_ spp., and the mean forage value consumed in frequencies observed (33, 15, 13, 7, 7, and 25 percent, respectively), the Na intake would still only be 87.7 mg per day. Mean lick Na content is only slightly higher than mean forage values. However, exclusive intake of vegetation and soil from recretionist sites would provide 1.73 g Na per day, a value slightly exceeding the recommended 0.04 - 0.1 percent domestic level.

The Na deficit calculated above between mountain goat intake and recommended levels for equivalent domestic sheep marches well with deficits calculated for British Columbian mountain goats (Hebert and Cowan 1971) and white-tailed deer (Weeks and Kirkpatrick 1976).

Mean vegetative K intake exceeds levels required for domestic sheep. A minimum K ration of 0.5 percent of dietary dry matter is recommended by the National Research Council (1975). Mean K content of 46 forage species was 1.41 percent (Table 1), over twice the required allowance.

Table 6. Cation concentrations in Mountain goat tissue and fluid samples collected on Dora Mountain, Gore Range, Colorado

Sample	n	Na(meq/1) Mean	Na(meq/1) SD	K(meq/1) Mean	K(meq/1) SD	Na/K(meq/1/meq/1) Mean	Na/K(meq/1/meq/1) SD
Hair[a]	10	260.5[a]	104.2[a]	1,880[a]	938.3[a]	0.271	0.093
Serum	4	150.0	2.6	5.7	0.73	26.87	3.38
2M(28 July)	1	150.3		4.9		30.67	
3F(barren, 1 Aug.)[b]	1	153.3[b]		6.5		23.58	
3F(with kid, 8 Sept.)	1	147.0		6.0		24.50	
5M(25 July)	1	149.4		5.2		28.73	
Saliva[c]	1	162.7		28.0		5.81	
Urine	2[d]	5.7[d]	2.4[d]	357.5[d]	406.6[d]	0.056[d]	0.07[d]
3F(with kid, 8 Sept.)	1	4.0		645.0		0.006	
AM(19 June)	1	7.4		70.0		0.106	
YM(24 Sept.)[c]	1	132.3		169.0		0.783	
Milk (3F, 8 Sept.)	1	46.5					

[a] Values in ppm. 2NHCL used in extraction. Values represent total cation composition.
[b] Sample hemolyzed.
[c] Sample from tame, captive goat. Animal may have received mineral supplements. Saliva may be lost via drooling.
[d] Yearling male data excluded from total.

Table 7. Na and K values (mean ± SE) of mountain goat fecal material collected on Dora Mountain, Gore Range, Colorado. Extraction technique employed 2NHCL. Values reflect total composition.

Sample	n	Na ppm (meq/1)	K ppm (meq/1)	Na/K meq/1/meq/1
> 90% organic material[a]	9[b]	285.4 ± 224.8[b] (12.41 ± 9.77)	6,496 ± 1,567[b] (166.6 ± 40.2)	0.078 ± 0.0564[b]
fresh pellets	5	126.0 ± 51.2[c] (5.48 ± 2.23)	6,672 ± 1,665 (171.1 ± 42.7)	0.034 ± 0.0179
rectal samples[d]	4	484.6 ± 189.9 (21.07 ± 8.26)	6,275 ± 1,654 (160.9 ± 42.4)	0.132 ± 0.0329
tame, captive goats[e]	4	425.3 ± 20.4 (18.49 ± 0.89)	1,360 ± 314 (34.9 ± 8.1)	0.553 ± 0.1372
> 90% inorganic material[a] fresh pellets	10	110.3 ± 45.0[c] (4.8 ± 1.96)	3,085 ± 1,077 (79.1 ± 27.6)	0.149[f] ± 0.3073[f]

[a] All samples collected fit this classification.
[b] Total values of organic material exclude tame, captive goat data.
[c] Na content of fresh organic and inorganic feces is statistically identical ($t = 0.599$, $P > 0.5$).
[d] Collected on 25 and 28 July, 1 August and 8 September.
[e] Yearling study animals from Colorado Coop. Wildl. Res. Unit food habits study.
[f] Fecal pellets collected on 24 September. Animal may have received mineral supplements. Includes anomalous Na/K value of 1.022. Excluding this datum, mean ± SE is 0.0516 ± 0.0175.

During spring and summer, for reasons previously stated, mountain goats and other wild ungulates are confronted with increased Na loss and, particularly in females, increased Na demand. At that time, Na intake via plausible proportions of vegetation, water, licks, and recreationist urine is inadequate to meet even Na losses through urine, feces, shedding, and lactation. However, without lick and recreationist Na, the Na deficit would be even greater. Lick use is a highly seasonal phenomenon occurring coincident with the abrupt dietary shift to succulent, K-rich, forage and declining after dietary K and water rapidly subside to lower levels (Weeks and Kirkpatrick 1976). The shift to spring forage, with elevated K and water levels, is thought to be the environmental factor effecting the annual Na deficiency in wild ungulates. Because lick use is restricted to the spring and summer months coinciding with peak vegetative K and water values, this strongly suggests not only that ungulates utilize salt licks as supplemental Na sources to balance their Na budget, but that mountain goats, like white-tailed deer (Weeks and Kirkpatrick 1976) and probably most other wild ungulates, can maintain a positive Na balance outside the period of increased forage K and water levels on vegetative sources alone. Consequently, maintenance Na requirements of the mountain goat appear to be far below recommended levels for comparable domestic ruminants as in white-tailed deer (Weeks and Kirkpatrick 1976).

Although some form of mineral licks (mineral springs, "muck" licks or dry earth licks) are generally available to wild animals throughout most of the United States, they may be locally absent (Guest 1969, Hebert and Cowan 1977). The relative success of ungulate populations in such areas may reflect their ability to locate supplemental Na sources (bioaccumulators), conserve Na, or otherwise maintain a positive Na balance.

Several studies have related environmental Na availability to population density, distribution, and size. Aumann and Emlen (1965) noted a strong correlation between the density of microtine rodents (Microtus spp.) and the abundance of soil Na. Cyclic population fluctuations occurred independent of Na intake, but the densities at population peaks were many times higher in areas of high soil Na. They speculated that in areas replete with soil Na, enough was ingested with the forage to meet increased requirements of crowded animals, allowing continued population growth to a point where some other factor became limiting. Similarly, Jordan et al. (1973) and Botkin et al. (1973) suggested the availability of Na controlled the size of Isle Royale's moose population. In Wankie National Park, central Africa, Weir (1972) demonstrated the spatial distribution of elephants (Loxodonta africanus) was closely correlated to the Na content of the soil and water. Few elephants were observed where little Na was avialable in the soil or water, in spite of suitable forage abundance.

Since ungulates can probably maintain a positive Na balance outside the spring period of increased forage K and water levels on vegetative sources alone, only resorting to lick use for balancing periodic Na deficits, it is plausible that in areas depauperate of supplemental Na sources, ungulates simply require a longer period to balance their Na budget. The delay is probably inconsequential, but may limit potential population growth (Aumann and Emlen 1965, Jordon et al. 1973, Botkin et al. 1973) or be so costly that animals are locally absent from such areas (Weir 1972). Minor chronic Na deficiencies may only have subclinical effects on population productivity and quality. In more acute cases, managers might observe that "the population is just not doing as well as it should be." Of course, this does not imply the problems of unsuccessful, static or "unthrifty" ungulate populations are solely or in any way the result of Na limitations.

LITERATURE CITED

Anderson, A. E., and D. E. Medin. 1972. Blood serum electrolytes in a Colorado mule deer population. J. Wildl. Dis. 8:183-190.

Aumann, G. D., and J. T. Emlen. 1965. Relation of population density to sodium availability and sodium selection by microtine rodents. Nature 208:198-199.

Bansner, U. 1976. Mountain goat-human interactions in the Sperry-Gunsight Pass area, Glacier National Park. Univ. Montana, Missoula. Unpubl. Rep. 46pp.

Barrett, M. W., and G. A. Chalmers. 1977. Clinicochemical values for adult free-ranging pronghorns. Can. J. Zool. 55:1252-1260.

Beath, O. A. 1942. Biological significance of mineral licks. Pages 88-96 in R. F. Honess and N. M. Forest, eds. A Wyoming bighorn sheep study. Wyoming Game and Fish Dept. Bull. 1. 127pp.

Beilharz, S., D. A. Denton, and J. J. Sabrine. 1962. The effect of concurrent deficiency of water and sodium on the sodium appetite of sheep. J. Physiol. 163:378-390.

Black, C. A. 1968. Soil plant relationships. John Wiley, New York, NY.

Black, H. C. 1955. Salt use by mule deer in the Deschutes National Forest of central Oregon. M.S. Thesis. Oregon State Univ., Corvallis. 143pp.

Blair-West, J. R., E. Bott, G. W. Boyd, J. P. Coghlan, D. A. Denton, J. R. Goding, S. Weller, M. Wintour, and R. D. Wright. 1964. General biological aspects of salivary secretion in ruminants in R. W. Dougherty, ed., Physiology of digestion in the ruminant. Butterworths, Washington. (as cited in Hebert and Turnbull 1977).

Blair-West, J. R., J. P. Coghlan, D. A. Denton, J. F. Nelson, E. Orchard, B. A. Scoggins, and R. D. Wright. 1968. Physiological, morphological and behavioural adaptation to a sodium deficient environment by wild native Australian and introduced species of animals. Nature 217:922-928.

Botkin, D. B., P. A. Jordan, A. S. Dominski, H. S. Lowendorf, and G. E. Hutchinson. 1973. Sodium dynamics in a northern ecosystem. Proc. Nat. Acad. Sci. 70:2745-2748.

Brandborg, S. M. 1955. Life history and management of the mountain goat in Idaho. Idaho Dept. Fish and Game, Wildl. Bull. No. 2. 142pp.

Brownell, P. F., and C. J. Crossland. 1972. The requirement for sodium as a micronutrient by species having the C_4 dicarboxylic photosynthetic pathway. Plant Physiol. 49:794-797.

Chapman, F. B. 1939. The whitetail [sic] deer and its management in southeastern Ohio. Trans. N. Amer. Wildl. Nat. Resour. Conf. 4:257-267.

Church, D. C. 1976. Digestive physiology and nutrition of ruminants. Vol. 1. Digestive physiology. Metropoliton, Portland, OR.

Cook, H. W., R. A. Rausch, and B. E. Baker. 1970. Moose (Alces alces) milk. Gross composition, fatty acid, and mineral constitution. Can. J. Zool. 48:213-215.

Cowan, I. McT., and V. C. Brink. 1949. Natural game licks in the Rocky Mountain National Parks of Canada. J. Mammal. 30:379-387.

Dailey, T. V. 1981. Composition and quality of mountain goat diets in alpine tundra, Colorado. M.S. Thesis. Colorado State Univ., Fort Collins. 116pp.

Dalke, P. D., R. D. Beeman, F. J. Kindel, R. J. Robel, and T. R. Williams. 1965. Use of salt by elk in Idaho. J. Wildl. Manage. 29:333-338.

DeBock, E. A. 1970. On the behavior of the mountain goat (Oreamnos americanus) in Kootenay National Park. M.S. Thesis. Univ. Alberta, Edmonton. 173pp.

Denney, R. N. 1977. Status and management of mountain goats in Colorado. Pages 29-36 in W. Samuel and W. G. Macgregor, eds. Proceedings of the First International Mountain Goat Symposium. British Columbia Fish and Wildlife Branch, Victoria, B.C.

Denton, D. A. 1956. The effects of Na^+ depletion on the Na^+:K^+ ratio of the parotid saliva of the sheep. J. Physiol. 131:516-525.

Denton, D. A. 1957. The study of sheep with permanent unilateral fistulae. Quart. J. Exp. Physiol. 42:72-95.

Denton, D. A. 1965. Evolutionary aspects of the emergence of aldosterone secretions and salt appetite. Physiol. Rev. 45:245-295.

Eisenstein, A. B., ed. 1967. The adrenal cortex. Little, Brown and Co., Boston, MA.

Eriksson, E. 1952. Composition of atmospheric precipitation. Tellus 4:280.

Franzmann, A. W., and P. D. Arneson. 1974. Moose research center studies. Alaska Dept. Fish and Game, Juneau. 56pp. (as cited in Hebert and Turnbull 1977).

Franzmann, A. W., and E. T. Thorne. 1970. Physiologic values in wild bighorn sheep (Ovis canadensis canadensis) at capture, after handling, and after captivity. J. Amer. Vet. Med. Assoc. 157:647-650.

Fraser, D., E. Reardon, F. Dieken, and B. Loescher. 1980. Sampling problems and interpretation of chemical analysis of mineral springs used by wildlife. J. Wildl. Manage. 44:623-631.

Frens, A. M. 1958. Physiological aspects of the nutrition of grazing cattle. Cur. Assoc. Anim. Prod. Publ. 6:93-104.

Guest, J. E. 1969. Distribution and description of natural salt licks. M.S. Thesis. Univ. Wyoming, Laramie. 71pp.

Guyton, A. C. 1976. Textbook of medical physiology. Saunders, Philadelphia, PA

Hebert, D. M. 1967. Natural salt licks as a part of the ecology of the mountain goat. M.S. Thesis. Univ. British Columbia, Vancouver. 138pp.

Hebert, D. M., and I. McT. Cowan. 1971. Natural salt licks as a part of the ecology of the mountain goat. Can. J. Zool. 49:605-610.

Hebert, D. M., and W. G. Turnbull. 1977. A description of southern interior and coastal mountain goat ecotypes in British Columbia. Pages 126-146 in W. Samuel and W. G. Macgregor, eds. Proceedings of the First International Mountain Goat Symposium. British Columbia Fish and Wildlife Branch, Victoria, B.C.

Hibbs, L. D. 1967. Visual sex determination of mountain goats as related to selective hunting potential. Colorado Dept. Nat. Res., Div. Game, Fish and Parks. Game Inform. Leafl. No. 55, 2pp.

Isaac, R. A., and J. D. Kerber. 1971. Atomic absorbtion and flame photometry: Techniques and uses in soil, plant and water analysis. Pages 17-37 in L. M. Walsh, ed. Instrumental methods of analysis of soils and plant tissue. Soil Sci. Soc. Amer., Madison, WI.

Jordan, P.A., D. B. Botkin, A. S. Dolminski, H. S. Lowendorf, and G. E. Belovsky. 1973. Sodium as a critical nutrient for the moose of Isle Royale. N. Amer. Moose Conf. and Workshop. 9:13-43.

Kay, R. N. B. 1960. The rate of flow and composition of various salivary secretions in sheep and calves. J. Physiol. 150:515-537.

Keiss, R. E. 1976. Sources of trace minerals in bighorn sheep nutrition. Pages 55-56 in E. Decker, ed. Transactions of the Second North American Wild Sheep Conference. Dept. of Fish and Wildl. Biol., Colorado State Univ., Ft. Collins.

Kindel, F. J. 1958. Salt in the management of elk in the Lower Selway River Drainage, Idaho. M.S. Thesis. Univ. Idaho, Moscow. 115pp.

Knight, R. R., and M. R. Mudge. 1967. Characteristics of some natural licks in the Sun River area, Montana. J. Wildl. Manage. 31:293-299.

Lehr, J. J. 1941. The importance of sodium for plant nutrition. Soil Sci. 52:237-244.

Lentfer, J. W. 1955. A two-year study of the Rocky Mountain goat in the Crazy Mountains, Montana. J. Wildl. Manage. 19:417-429.

Lloyd, L. E., B. E. McDonald, and E. W. Crampton. 1978. Fundamentals of nutrition. Freeman, San Francisco, CA.

Mautz, W. W., U. S. Seal, and C. B. Boardman. 1980. Blood serum analyses of chemically and physically restrained white-tailed deer. J. Wildl. Manage. 44:343-351.

McDonald, I. W. 1969. Physiology of digestion, absorbtion and metabolism in ruminants. Pages 87-148 in S. D. Cuthbertson, ed. Introduction to nutrition of animals of agricultural importance. Part 1. The science of nutrition of farm livestock. Pergamon Press, New York, NY.

McDougall, E. I. 1948. Studies on ruminant saliva. I. The composition and output of sheep's saliva. Biochem. J. 43:99-109.

Mills, C. F. 1969. Mineral nutrition and metabolism. Pages 361-410 in S. D. Cuthbertson, ed. Introduction to the nutrition of animals of agricultural importance. Part 1. The science of nutrition of farm livestock. Pergamon Press, New York, NY.

Moen, A. N. 1973. Wildlife ecology. W. H. Freeman and Co., San Francisco, CA.

Moorhead, B. B. 1973. Ecology of non-native mountain goats in Olympic National Park. Ann. Rep., National Park Service, U.S. Dept. Int. 139pp.

Morrison, F. B. 1959. Feed and Feeding. Morrison, Clinton, IA.

National Research Council. Subcommittee on sheep. 1975. Nutrient requirements of sheep. 5th rev. ed. National Academy of Sciences, Washington, D.C. 71pp.

Rideout, C.B. 1974. A radio telemetry study of the ecology and behavior of the Rocky Mountain goat in western Montana. Ph.D. Thesis. Univ. Kansas, Lawrence. 146pp.

Seal, U. S., J. J. Ozoga, A. W. Erickson, and L. J. Verme. 1972a. Effects of immobilization on blood analysis of white-tailed deer. J. Wildl. Manage. 36:1034-1040.

Seal, U. S., L. J. Verme, J. J. Ozoga, and A. W. Erickson. 1972b. Nutritional effects on thyroid activity and blood of white-tailed deer. J. Wildl. Manage. 36:1041-1052.

Silver, H. 1961. Deer milk compared with substitute milk for fawns. J. Wildl. Manage. 25:66-70.

Singer, F. J. 1975. Behavior of mountain goats, elk and other wildlife in relation to U.S. Highway 2, Glacier National Park. Compl. Rep. National Park Service, West Glacier. 98pp.

Singer, F. J. 1978. Behavior of mountain goats in relation to U.S. Highway 2, Glacier National Park, Montana. J. Wildl. Manage. 42:591-597.

Smith, S. E., and P. D. Aines. 1959. Salt requirements of dairy cows. Cornell Agr. Exp. Sta. Bull. 938, Ithaca, NY, 26pp.

Stockstad, D. S., M. S. Morris, and E. C. Lory. 1953. Chemical characteristics of natural licks used by big game animals in western Montana. Trans. N. Amer. Wildl. Nat. Resour. Conf. 18:247-258.

Suttle, N. F., and A. C. Field. 1967. Studies of magnesium of ruminant nutrition. 8. Effect of increased intakes of potassium and water on the metobolism of magnesium, phosphorus, sodium, potassium and calcium in sheep. Br. J. Nutr. 21:819-831.

Thompson, R. W. 1981. Ecology of Rocky Mountain goats introduced to the Eagles Nest Wilderness, Colorado and some factors of geographic variation in the lambing season of bighorn sheep. M.S. Thesis. Univ. Wyoming, Laramie. 359pp.

Turner, J. C. 1973. Water, energy and electrolyte balance in the desert bighorn sheep, Ovis canadensis. Ph.D. Thesis. Univ. California, Riverside. 132pp.

Tweto, O., B. Bryant, and F. E. Williams. 1970. Mineral resources of the Gore Range - Eagles Nest Primitive Area and vicinity, Summit and Eagle Counties, Colorado. U. S. Geol. Surv. Bull. 1319-C, Washington, D. C. 127pp.

U.S.D.A. Forest Service. 1977. Eagles Nest Wilderness management plan and environmental analysis report. White River and Arapaho National Forests, Grand Junction, Colorado.

U.S.D.A. Forest Service. 1979. Eagles Nest Wilderness management plan. White River and Arapaho National Forests, Grand Junction, Colorado.

Vaughan, M. R. 1974. Aspects of mountain goat ecology, Wallowa Mountains, Oregon. M.S. Thesis. Oregon State Univ., Corvallis. 113pp.

Walsh, L. M., ed. 1971. Instrumental methods for analysis of soils and plant tissue. Soil Sci. Soc. Amer., Madison, WI.

Weeks, H. P. 1978. Characteristics of mineral licks and behavior of visiting white-tailed deer in southern Indiana. Amer. Midl. Nat. 100:384-395.

Weeks, H. P., and C. M. Kirkpatrick. 1976. Adaptations of white-tailed deer to naturally occurring sodium deficiencies. J. Wildl. Manage. 40:610-625.

Weir, J. S. 1972. Spatial distribution of elephants in an African National Park in relation to environmental sodium. Oikos 23-1-13. Copenhagen.