SIERRA NEVADA BIGHORN SHEEP:
HISTORY AND POPULATION ECOLOGY

by
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ABSTRACT

SIERRA NEVADA BIGHORN SHEEP: HISTORY AND POPULATION ECOLOGY

The Mount Baxter and Mount Williamson bighorn herds in the Sierra Nevada were studied from 1974 to 1979 with the objective of investigating population status and controlling factors.

Minimum herd sizes of 217 and 30 were established for the Baxter and Williamson herds, respectively, in 1978. Recruitment ratios, ram age structure, and an index of population density all indicated a substantial increase in the Baxter herd since the 1960's. Recruitment ratios for the Williamson herd suggested that it is approximately static.

Lungworm infection in the Williamson herd was 10 times that of the Baxter herd for adults and about 100 times for lambs and yearlings. Infection levels of both herds were low compared with Rocky Mountain herds, and no clinical signs of infection were apparent; lungworms were not considered an important influence on demography in the Sierra.

Human disturbance of ewe-lamb groups was investigated in summer. There was no evidence that long term spatial displacement was occurring in the Baxter herd. Also, with

its increasing population trend, it could not be argued that disturbance from humans was adversely affecting reproduction.

A small sample of interactions with the Williamson herd suggested greater wariness than the Baxter herd. Human use of Mount Williamson has increased exponentially since World War II. Coincident with this increase has been a loss of bighorn summer range. The current summer range boundaries coincide with regular routes of human use; a causal relationship may be involved.

The nutrient content of the bighorn diet was found to begin rising in early February, reaching a peak in early May, then declining until October. The timing of plant growth in spring lagged with elevation at a rate of one day per 17.8m, and elevational differences in diet quality of bighorn reflected this; forage quality was traded off for higher, safer habitat during lambing in late April and May. An elevational difference of 1100m and large differences in diet quality were found between a lambing area in the Baxter herd range and one in the Williamson herd range. However, milk consumption did not differ between the two herds. This suggests that nutrition of ewes in both herds exceeded minimum nutrient requirements of early lactation, and that lambs received maximum milk rations.

The annual pattern of diet quality closely matched that of nutrient requirements of pregnant and lactating ewes. It was predicted that lamb mortality would be low and recruitment rates would correlate well with ovulation rates, which are determined by prior nutrition. Summer nutrition in the Sierran alpine depends on snow pack, because this is the major source of water in summer. Winter nutrition appears to be influenced by the timing of winter storms. It was thus predicted that winter precipitation would influence recruitment rate two years later. It was found that 73% of the variation in recruitment of the Baxter herd was explained in a multiple regression by Nov-Dec and Jan-March precipitation two years prior.

An index of population density was entered as a third independent variable, but was not significant. It was thus concluded that population density effects are not yet important, and the Baxter herd can be expected to increase further.

Nothing is more commonly remarked by noisy, dusty trail-travelers in the Sierra than the want of animal life - no song-birds, no deer, no squirrels, no game of any kind, they say. But if such could only go away quietly into the wilderness, sauntering afoot and alone with natural deliberation, they would soon learn that these mountain mansions are not without inhabitants, many of whom, confiding and gentle, would not try to shun their acquaintance

John Muir 1894

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INTRODUCTION

Concern over the future of bighorn sheep (Ovis canadensis) in California's Sierra Nevada mountains has a long history. In 1873 they were given full protection by the California State Legislature (Trefethen 1975), a status they retain today. Although probably ineffectual at first, once enforced, protection was commonly believed to be the solution to herd losses; it was expected that remaining herds would increase and recolonize previous range (e.g. Anonymous 1926, Colby 1940). The failure of that expectation to be realized prompted an array of conjectures as to causation. Bailey (1932), Grinnell (1935), and Dixon (1936) each addressed the problem of trying to reverse the declining population trend. In 1940 the Sierra Club proposed the establishment of a sanctuary for the largest remaining herd (Blake 1940). This proposal was rejected the following year by the Fish and Game Department of California and the U. S. Forest Service on grounds that insufficient information existed by which to judge the need for such a refuge (Blake 1941b). Three decades later Inyo National Forest set aside approximately 41,000 acres as a preserve for the two remaining viable herds in the Sierra, believing that the population continued to decline due to human disturbance (Dunaway 1971a).

Hypotheses concerning Sierra bighorn have abounded over the years. Collection of solid data on this population has greatly lagged behind speculation. Consequently, hypotheses have had little foundation and have received little or no critical testing; management decisions have been based largely on guesses about population status and controlling factors. This study has been an attempt to reverse that trend. Specifically, its purpose has been to assess demographic status and to investigate pertinent parameters suspected to influence demography.

Past data on demography are scarce and, except for some age ratio data, have consisted of guesses about population sizes, as well as even the existence of some herds. At the beginning of this study, the written record supplied only two pieces of hard information on the status of bighorn herds in the Sierra -- that only two viable herds clearly existed, and that one of these, the Mount Williamson herd, was of questionable standing and probably much smaller than the other, the Mount Baxter herd. Consequently, the central study was designed to compare these two herds. Priority has been given to the collection of data on distribution, abundance, and population trends of these herds. Secondly, the investigation has considered environmental factors that possibly play a significant role in determining these parameters. The factors considered were parasitic disease, human disturbance, habitat use and availability, food habits, nutrition, and interspecific competition.

A second facet of the study was a review of historical information pertinent to the decline of bighorn in the Sierra. This investigation attempted (1) to reconstruct the pristine pattern of herd distribution, and (2) to reconstruct the temporal pattern of herd extirpation, with some consideration of causality. The results of this historical review are presented in the Appendix.

The paucity of past data on Sierra bighorn is due to logistic difficulties associated with its collection. During half the year an investigator must climb 1500-1800m elevation on foot just to enter bighorn ranges, which begin at timberline (3400m). The range of bighorn use then extends an additional 750-900m higher. Except for a few canyons with trails, most of the range can only be entered cross-country over very rugged terrain, and all equipment for survival and research must be carried by backpack. The major exception to this situation is winter, when some areas of use can be closely approached by motor vehicle. Winter range investigation rarely requires more than 600m elevation gain in a day. As would be expected, few data existed from areas outside winter ranges. Even available winter range data reflected a tendency by investigators to study only areas within easy reach of vehicular access.

Field work for this study was carried out continuously from May 1975 to October 1978. Additionally, the summer of 1974 served as a preliminary study and a small amount of field work was carried out in winter, spring, and summer of

1979. During the summer of 1976 three additional substudies were carried out under the guidance of the author, each resulting in a thesis for a master's degree. Two of these (Hicks 1977 and Elder 1977) were concerned with human interactions with the Baxter herd; the other (Garcia 1977) dealt with habitat selection and range of summer use of the Williamson herd. In addition, a management report submitted by the author to the U. S. Forest Service and National Park Service concerned the analysis of management alternatives (Wehausen 1979).

Previous Research and Hypotheses

Attempts to explain the lack of recovery and recolonization of original ranges by the Sierran bighorn populations began in the 1930's. Bailey (1932) believed that human and non-human predation exceeded the annual reproduction, thus preventing population increase. Grinnell (1935) considered Bailey's theory as "dubious" and pointed out that competition from domestic sheep was the more likely problem; elimination of domestic sheep grazing was proposed to allow recolonization along the crest. Dixon (1936) suggested that poaching of bighorn by deer hunters was the primary problem. No data were offered by any of these authors. Lack of information was clearly the stumbling block to any management action. This became apparent during a meeting on the proposed sanctuary in 1940, and an indepth study was called for (Blake 1941b). Due to World War II this did not come to pass until 1948, when Fred Jones took on the task (Blake 1949).

Jones interviewed local people, then spent five months in the summer and fall of 1948 surveying selected high country areas. His most important conclusion was that five bighorn herds remained in the Sierra Nevada totalling 390 bighorn (Table 1). Jones surveyed none of the Convict Creek herd range and little of the Langley herd range. His size estimates for these herds were thus based almost entirely on reported sightings and amount to little more than guesses. The Birch Mountain herd is the same as the Taboose Creek herd, discussed in the Appendix, that apparently disappeared in the 1920's. That this herd had reappeared is certainly not evident from the weak evidence Jones (1950a) offered (Table 1). The existence of the Baxter and Williamson herds as viable herds in 1948 seems clear; however, Jones' (1950a) population estimates for them, based on tracks and beds, are questionable.

Jones (1950a) suggested that lack of noticeable recovery of bighorn in the Sierra was due to a shortage of winter forage. He attributed this to (1) lasting changes in vegetative composition from past overgrazing by livestock, which were believed to have caused shrubs to replace grasses and forbs, and (2) competition from a high deer population. Disturbance from increasing human use of the high country was also implicated. No data were offered on any of these speculations.

Table 1. Herd size estimates made by Jones (1950a) and Dunaway (1971b).

Herd	Number of different sheep seen by Jones in 1948	Largest number of sheep seen by others as reported by Jones (1950a)*	Herd size estimates of Jones (1950a)	Herd size estimates of Dunaway (1971b)
Convict Creek	0	1948 - 15	25	0
Birch Mountain	tracks of 6	1940 - 1	15	0
Mount Baxter	22	1938 - 79	135	95
Mount Williamson	25	1940 - 23+	125	75
Mount Langley	7 (rams)	1946 - 15	90	45
			390	215

* Comparison of these figures with reported sightings listed by Jones (1949 - Appendix A) indicates that they do not represent the number of different bighorn observed, but instead are summations of all groups in a particular year.

Jones' study did not identify winter ranges. During the winters of 1963-65 Riegelhuth (1965) attempted to locate and evaluate winter ranges and assess herd status of the Langley, Williamson, Baxter, and Birch Mountain herds. The results identified some wintering areas in the Williamson and Baxter herd ranges, but no clear wintering areas for the Langley and Birch Mountain herds were located. Sightings totalled 31 bighorn in the Baxter herd and 14 in the Williamson herd.

Tule elk (*Cervus elaphus nanodes*) were introduced to Owens Valley in 1933 (McCullough 1969). Riegelhuth (1965) noted sign of elk use on some areas of the Baxter herd winter range and suggested that competition between elk and bighorn for desert needlegrass (*Stipa speciosa*) and bitterbrush (*Purshia glandulosa*) was developing with the increasing elk population. Elk were presumed to be feeding on bighorn winter ranges in summer as domestic sheep had in the past.

McCullough and Schneegas (1966) also made winter observations of the Williamson and Baxter herds in 1964-65. They further defined areas of winter use from a total of 182 bighorn sighted. Sightings of the Williamson herd were again sparse. A minimum population (maximum seen in a day) of 34 for the Baxter herd in 1965 was established by their data.

McCullough and Schneegas (1966) verified that needlegrass and bitterbrush were among the important forage species of bighorn. Their finding of overall low utilization of these two plant species refuted Riegelhuth's (1965) hypothesis concerning elk competition.

Using a simple qualitative technique to examine fecal pellets, McCullough and Schneegas (1966) found 55% of adult bighorn to be infected with lungworms of the genus Protostrongylus; none of the lamb samples showed such infection. They also found ova of an intestinal nematode of the genus Nematodirus. Their sample from the Williamson herd was only 4, thus precluding any interherd comparison of infection rates.

Between 1967 and 1973 Dunaway carried out studies of winter food habits and forage utilization (1970, 1972), population status (1970, 1971b), and human disturbance (1971a,b). Remeasurement of needlegrass and bitterbrush utilization following the severe winter of 1969 showed higher levels of utilization than reported by McCullough and Schneegas (1966). These were still below what would be considered heavy. These higher levels were attributed to a deep and prolonged snow pack that concentrated the sheep. The tule elk population in Owens Valley has continued to grow (Curtis et al. 1977) and consequently the question of competition on bighorn ranges has remained unresolved.

Dunaway (1971b) concluded that the Birch Mountain and Convict Creek herds no longer existed. The 1972 summer survey by Jorgensen and Schaub (1972) turned up no sign of the Langley herd, casting doubt on its existence. Like those of Jones (1950a), estimates of herd sizes made by Dunaway (1970,1971b)(Table 1) had no clear basis. This makes comparison of the two relatively meaningless as a measure of population change.

In an attempt to explain the loss of two and possibly three herds since Jones' study, Dunaway (1971b) turned to the consideration of human disturbance. First he noted that human use of the Baxter and Williamson herd ranges had increased substantially. Secondly, he pointed out that breaks separating the Baxter and Williamson herds and Williamson and Langley herds each coincided with corridors of heavy human use. The main shortcoming of this hypothesis is that it is based on the work of Jones (1950a). Neither Jones (1950a) nor Dunaway (1970, 1971a,b) provided convincing evidence of viable herds other than the Baxter and Williamson herds. The probability that the Langley and Convict Creek herds were already small remnants when Jones made his study is discussed in the Appendix. As such, it is unlikely that they would have survived regardless of man's activities. It is improbable that a Birch Mountain herd existed in 1948 (see Appendix).

In conclusion, the following points summarize my interpretation of past conjectures concerning Sierra bighorn: (1) The earliest concerns stressed the need for protection from hunting, but failed to recognize the adverse influence of domestic sheep grazing (see Appendix); (2) early hypotheses attempting to explain the lack of recovery of the Sierra bighorn population following protection have been based on the false premise that recolonization of historic range would occur once individual herds recovered. Geist (1971) discussed the rarity of colonization in bighorn sheep; and (3) hypotheses concerning limiting factors of existing herds have been based on few data, and consequently, tests of hypotheses have been unconvincing.

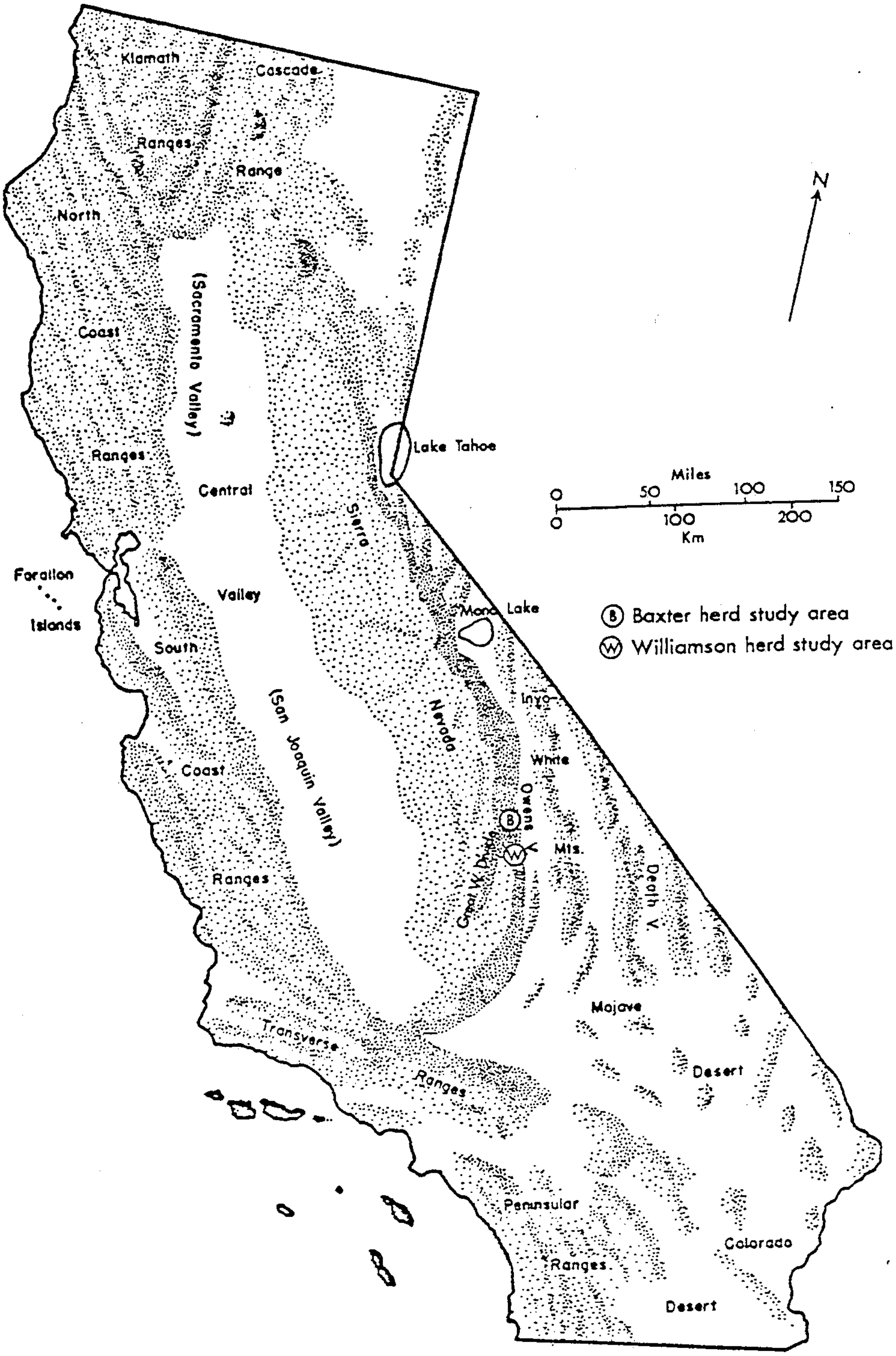
STUDY AREA

Topography and Geology

The Sierra Nevada forms the eastern backbone of California (Figure 1). Geologically it is a unified mountain range nearly 650km long and ranging from 75 to 125 km in width (Hill 1975). The two processes most influential in creating the existing topography in the Sierra are (1) a large uplifting beginning in the Pliocene, and apparently continuing today, and (2) a simultaneous severe scouring of much of the range by glaciers during the Pleistocene.

The Sierra has been uplifted as a block through faulting along its eastern base, resulting in a gently sloping west slope and a very steep east slope. The average tilt on the western side is only 2° (Hill 1975), whereas it is about 22° on the eastern side in the area of Mount Williamson and Mount Baxter, where field work has been concentrated. A distinct crest of peaks near the eastern edge of the range has resulted. These peaks rise in elevation from 1825 - 2425m in the north to over 4300m in the south adjacent to Owens Valley (Figure 1), then drop off rapidly in elevation at the south extreme of the range. The Great Western Divide in the south (Figure 1) is a substantial crest of high peaks extending somewhat west of

Figure 1. Map of California with study area locations.



the main crest; the Kern River drainage separates the two. The western slope of the range drops to near sea level in the Central Valley. The base of the eastern escarpment varied from 1525 to 1825m in Owens Valley, but rises to 2125 to 2600m in the central Sierra north of Owens Valley.

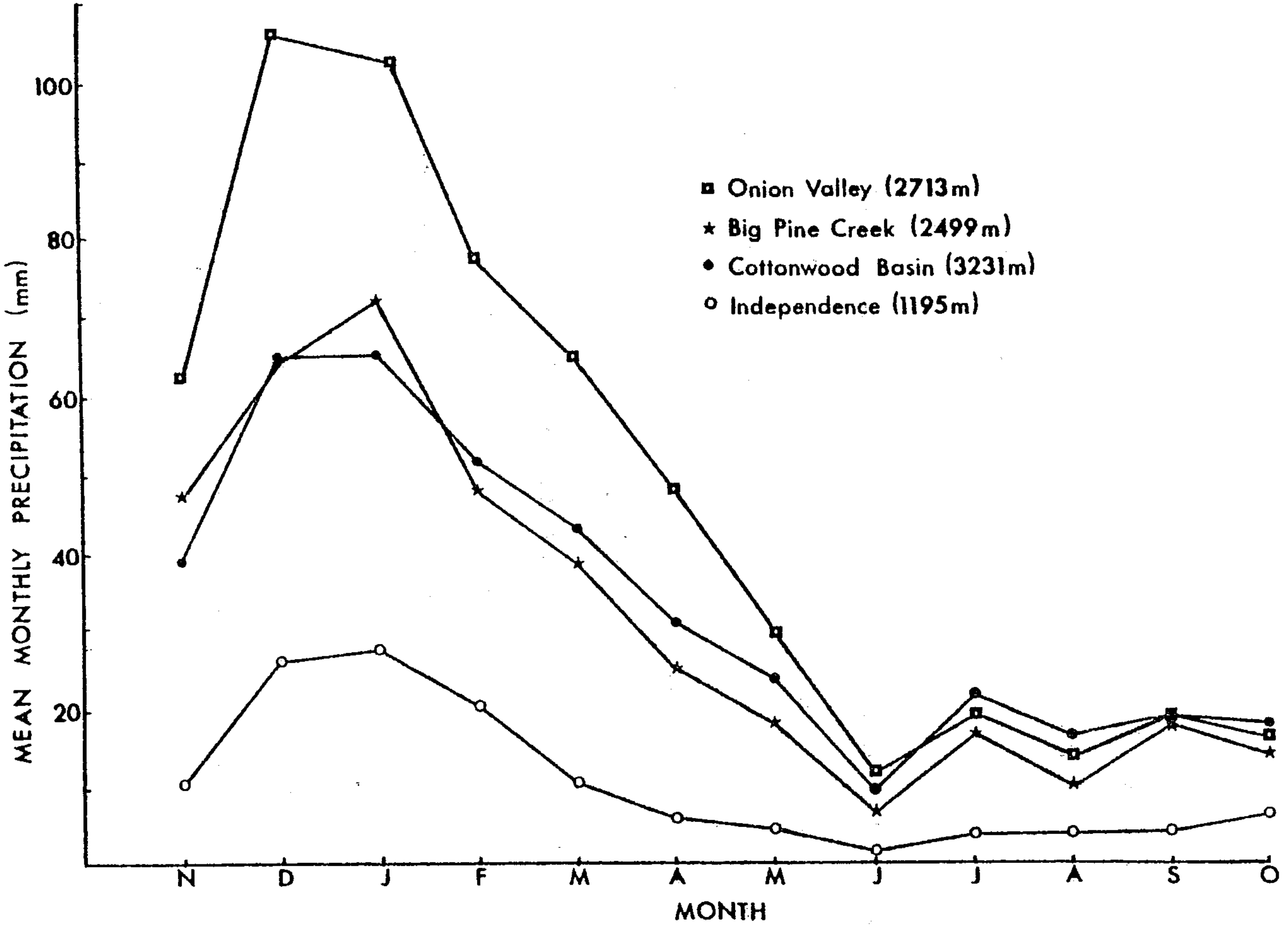
Pleistocene glaciers greatly influenced the central and southern Sierran topography, leaving U-shaped canyons with steep cirque headwalls at their upper ends and numerous lakes. Glaciation was heaviest in the central Sierra, tapering off to the north and south. It was also heavier on the west side of the range due to prevailing storm direction. On the east side of the range glaciers commonly emerged from canyon in the central Sierra, leaving morraines outside their mouths. In the southern Sierra, glaciers were mostly confined to the upper reaches of the eastern canyons; few canyons show sign of glacial activity at their mouths. Present ice fields are few and small in size, dating from the Matthes ice age that ended about 1750 A.D. (Hill 1975). Rock glaciers (ice fields covered by rocks) are currently common in high cirques of the southern Sierra.

Sierran rock is primarily granite dating from the Mesozoic (Hill 1975, Moore 1963). Older rock of sedimentary and volcanic origin that overlaid the granites have been mostly eroded away, remaining largely as high elevation pendants. Recent volcanic rocks of Quaternary origin (Moore 1963) are found in patches along the base of the eastern escarpment.

Climate

California receives most of its precipitation from northern cyclonic storms, which move south, then east. During summer months these sweep eastward north of California causing drought conditions during that season. During winter, the low pressure zone is commonly further south, placing California in the path of these storms (Major 1977); most precipitation occurs from October through April (Figure 2). How far south storms drift before sweeping east varies considerably from storm to storm. In general, precipitation decreases in quantity from north to south. The easterly direction of winter storms causes them to hit the Sierra Nevada broadside. As the air rises over the mountains precipitation increases, leaving the east side in a rain shadow that is responsible for the desert and steppe ecosystems east of the Sierra Nevada (Major 1977). Most winter precipitation in the Sierra occurs as snow, with snow line lower on the west slope of the range, but varying considerably from storm to storm. Snow line occasionally dropped as low as 1200m on the east side in Owens Valley during this study, but usually varied between 1525 and 2300m during storms. The rain shadow effect is clearly illustrated in the northern Sierra by a 2.3 times faster rate of increase in precipitation with altitude on the east slope when compared with the west slope (Major 1977). Comparison of records from Independence in Owens Valley with three nearby east side mountain stations shows the rain

Figure 2. Mean monthly precipitation for three locations on the east slope of the Sierra Nevada above Owens Valley and for Independence on the floor of Owens Valley.



shadow effect clearly (Figure 2). Differences among the three mountain stations reflect effects of topographic and north-south differences on storm patterns rather than consistent elevational relationships.

November through April accounts for 73-84% of the total yearly precipitation for the three mountain stations represented in Figure 2; summer rainfall (June - September) contributes only 14-21% for these stations. This summer rainfall consists of localized orographic thunderstorms and southern tropical storms that occasionally reach that far north. Summer rainfall varies considerably from year to year in the southern Sierra (Table 2).

Extremes in winter precipitation were observed during this study. There was a progressive drought throughout California during the first three years (1974-1977)(Table 2). Precipitation in the winter of 1977-78 was exceptionally heavy. It was also a warm winter, thus snow accumulated only on the upper portions of bighorn ranges. The winter of 1978-79 produced average precipitation, but was somewhat colder than normal.

The temperature regime in the Sierra Nevada is fairly benign compared with more continental ranges such as the Rocky Mountains. This is due to relatively warm temperatures that cause the usual "wet" (high density) snow typical of much of the Sierra Nevada. Degree of continentality is highest at the base of the eastern scarp (Major 1977) in bighorn winter ranges. Annual migratory

Table 2. Study period precipitation in the southern Sierra. Data are means from rain gauges at Big Pine Creek (2500m), Onion Valley (2700m), and Cottonwood Basin (3230m).

Year	Percent of Mean Annual Precipitation June - September	 November - April
1974(-75)	124.8*	90.0
1975(-76)	108.3	53.4
1976(-77)	410.3	42.8
1977(-78)	137.9	199.9
1978(-79)	183.8	100.1

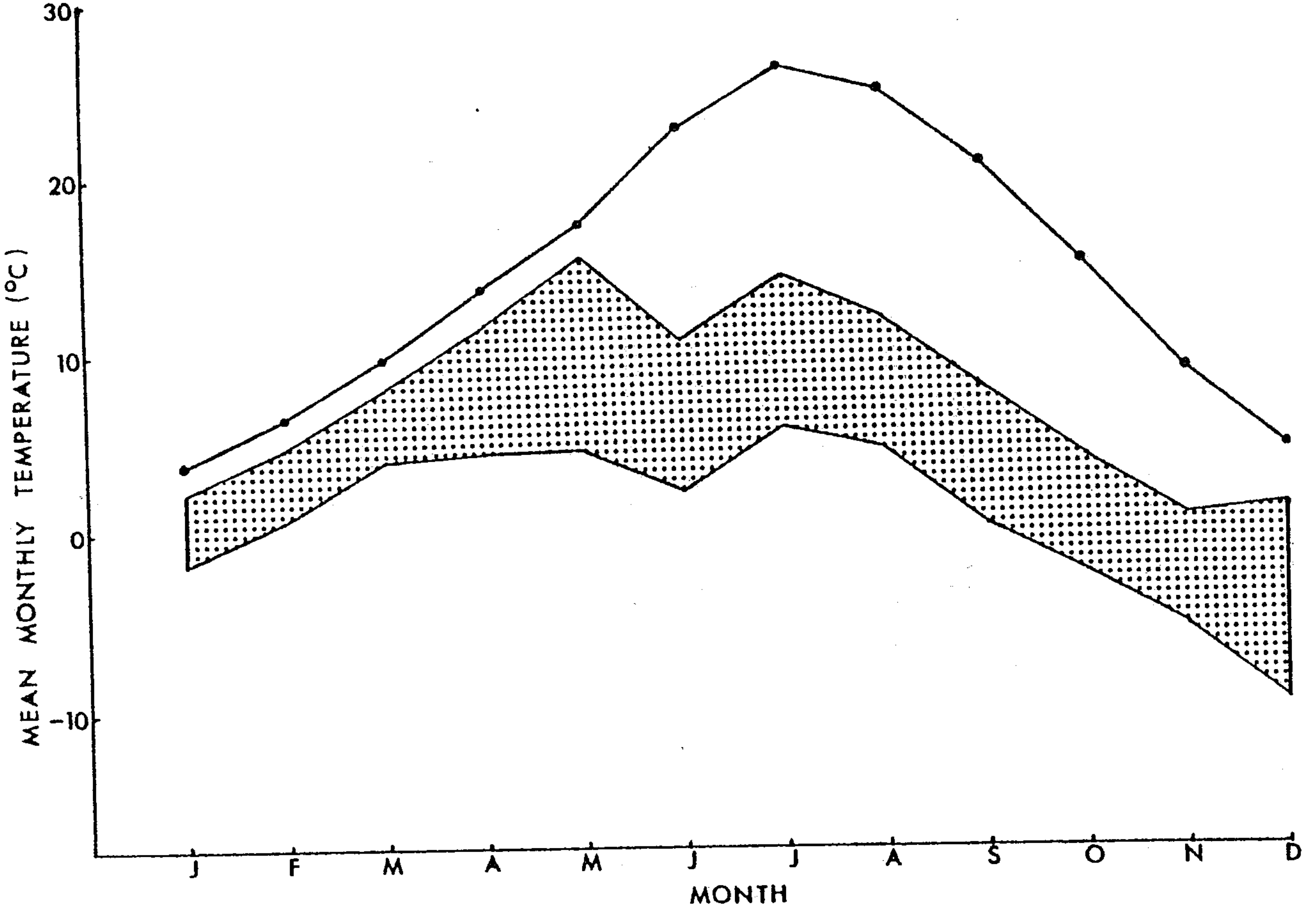
* mean of Cottonwood and Big Pine Creek (Onion Valley gauge not operative)

patterns of the bighorn place them in a more equable annual temperature regime. Figure 3 shows the approximate ranges of mean monthly temperatures experienced by bighorn in the Baxter and Williamson herds based on the mean monthly temperature in Independence, seasonal altitudinal ranges of the sheep, and temperature lapse rates for the east slope a bit north of Owens Valley (Major 1977). Monthly ranges of mean high and low temperatures would fall outside of the ranges plotted in figure 3. Bighorn remaining in winter ranges through late May experience the highest temperatures, sometimes reaching 38°C. December temperatures in the alpine, prior to descent of bighorn to winter ranges , are the lowest they encounter, but are not extreme (Figure 3). For 29 occasions in which I recorded fall (October - December) nighttime low temperatures in the high country (3050-3500m), the average has been only -2.5°C, ranging from -15.5° to 2.8°C. It is apparently unusual for Sierra bighorn to experience temperatures below -15°C. Frequent wind effectively reduces these temperatures, but warmer temperatures are usually associated with wind. Winter range low temperatures are commonly somewhat below freezing, but highs rarely remain below freezing, and may reach 10 to 20°C.

Vegetation

On a large scale, recent geologic history is of considerable influence on vegetation of southern Sierran bighorn ranges. The recent major uplifting and glaciation

Figure 3. Mean monthly temperature at Independence in Owens Valley and its approximate range (shaded) for bighorn in the Sierra Nevada.



left much of this range as steep exposed bedrock or boulder and talus fields, which support sparse vegetation if any. Time necessary for soil development limits the vegetation. Soil is found mostly on level sites such as canyon bottoms. Alpine soil is frequently little more than gravel.

Vegetation in the southern Sierra also is influenced greatly by the low and unpredictable precipitation during the growing season. However, all canyons on the east side have permanent streams and associated riparian vegetation of water birch (Betula occidentalis), willows (Salix spp.), and grasses, sedges and forbs. These frequently originate as springs in the subalpine, leaving higher areas largely devoid of surface water. Surface water from alpine springs and snow and ice field melt usually disappears rapidly into subsurface flow.

The vegetation on Sierran bighorn ranges can be broken roughly into three zones delineated by upper and lower treelines: alpine, forest, and desert scrub. Alpine ecosystems technically begin at timberline (Major and Bamberg 1967), although the ranges of many alpine plant species extend well below timberline. In southern Sierran bighorn ranges the upper limit of trees occurs at about 3400m. This upper limit appears to be determined by winter water stress and is correlated with temperature, but other factors lower timberlines locally (Major and Taylor 1977).

In the southern Sierra, the lower limit of timber occurs at about 1950m on the east side. This limit appears also to be determined by aridity, and is locally variable depending on aspect and presumably other factors influencing water availability. Scattered white firs (Abies concolor) commonly are found along streams as low as 1500m at the base of the eastern scarp, but do not constitute forest.

The forest zone thus covers an elevational range of about 1450m. However, the amount of forest on the east slope is small due to the rapid rise in elevation and locally inadequate substrate. The densest forests are found in canyon bottoms. Even these generally occur as small patches where soil has built up. Much of the forest area on the east slope consists of sparse trees on canyon sides. Subalpine forest immediately west of the crest is somewhat more extensive due to more glaciated, thus wider, canyon bottoms. The following discussion briefly treats vegetation types within the three vegetation zones.

Below the forest zone, vegetation grades from sagebrush (Artemisia tridentata) steppe into desert scrub communities. On escarpment base bighorn winter ranges (discussed later), sagebrush steppe constitutes the open vegetation, although the upper limit of blackbrush (Coleogyne ramosissima) vegetation is immediately below in the case of the Williamson herd range. Young et al. (1977) consider this sagebrush steppe as a southern Great Basin community separate from most northern sagebrush steppe, which begins north of Owens Valley; milder winters in the south are considered the important segregating factor. Species composition is nevertheless quite similar, but *Stipa speciosa*, the dominant bunchgrass, is considered indicative of the southern type (Young et al. 1977). Also, the bighorn ranges occur in the transition zone between the northern and southern forms of bitterbrush (*Purshia tridentata* and *P. glandulosa* respectively), with hybrids frequent (Nord 1965). Other important woody species in the sagebrush community on bighorn ranges are *Ephedra viridis*, *Keckiella* (*Penstemon*) *breviflorus*, *Prunus andersonii*, *Eriogonum fasciculatum*, *E. nudum*, *Haplopappus cuneatus*, *Chrysothamnus nauseosus*, *C. teretifolius*, *Ribes velutina*, *Cercocarpus ledifolius*, *Leptodactylon pungens*, and *Ceanothus greggii*.

Scrub vegetation is also an important vegetative component throughout the forest zone, extending into the lower alpine. In addition to accounting for a significant proportion of the open vegetative cover in this zone, it constitutes much of the understory of forest patches. Important woody species include *Artemisia tridentata*, *Purshia tridentata*, *Ephedra viridis*, *Cercocarpus ledifolius*, *Leptodactylon pungens*, *Penstemon bridgesii*, *Holodiscus microphyllus*, *Ribes cereum*, *Ribes montigenum*, *Ribes velutina*, *Potentilla fruticosa*, *Symphoricarpus vaccinoides*, *Ceanothus cordulatus*, *Chrysolepis* (*Castanopsis*) *sempervirons*, *Jamesia americana californica*, *Chamaebatiaria millefolium*, *Rosa woodsii*, *Acer glabrum*, *Prunus andersonii*, *Prunus emarginata*, *Arctostaphylos patula*, *Chrysothamnus viscidiflorus*, *Phyllodoce breweri*, and *Salix* spp.

The lowest forest type is pinyon (*Pinus monophylla*) woodland extending from 1950m to as high as 2900m in some canyons. Pinyon is most commonly found in pure stands; its common associate, juniper (*Juniperus* spp.) (Vasek and Thorne 1977), is largely absent from present bighorn ranges. Understory is sparse, consisting mostly of species characteristic of sagebrush steppe vegetation.

Jeffrey pine (*Pinus jeffrey*) is a mid-elevation species occurring from 2125 to 2800m elevation, occasionally mixed with pinyon. At the upper extreme of its range it also mixes occasionally with subalpine species. Jeffrey pine usually occurs in pure stands with understory varying from essentially nothing to thick manzanita (*Arctostaphylos patula*). Understory shrubs also include *Purshia tridentata*, *Cercocarpus ledifolius*, and *Artemisia tridentata*. Other mid-elevation tree species, which are common to the west slope, are absent or rare on the east slope. Within the bighorn range, red fir (*Abies magnifica*) is present only in Sawmill Canyon. White fir grows to about 2750m, but is found only immediately adjacent to streams.

Subalpine forest in bighorn ranges is comprised of four pine species: lodgepole (*Pinus contorta murrayana*), foxtail (*Pinus balfouriana*), limber (*Pinus flexilis*), and whitebark (*Pinus albicaulus*). Whitebark pine is the usual timberline species. Pure stands of all but limber pine exist, but mixed stands are more common. Foxtail and limber pine both prefer dry rocky slopes, where pure foxtail stands sometimes constitute timberline. Whitebark and especially lodgepole pine attain their greatest densities and stature on more developed soils.

Non-coniferous trees are few in the southern Sierra. Water birch lines stream banks to about 2750m elevation. Although a common element of the east slope flora north of Owens Valley, quaking aspen (*Populus tremuloides aurea*) is found in the bighorn range only in Sawmill Canyon. Oaks occur in disjunct populations along the base of the eastern scarp. In the range of the Baxter herd, black oaks (*Quercus kellogii*) are scattered between 1770 and 2600m elevation. Canyon live oak (*Quercus chrysolepis*) is scattered from about 1950 to 2300m in the range of the Williamson herd.

Meadow vegetation occurs where a shallow water table provides high year-round soil moisture (Rundel et al. 1977). In the southern Sierran alpine this condition is rarely met. Thus alpine meadows in bighorn ranges are few and mostly small in size, often consisting of short stringers below water sources that terminate quickly as surface water disappears into the rocks. The most developed alpine meadows occur as small patches in some cirque basins where topography is relatively flat. These meadows are commonly less than 10 meters in diameter. More extensive meadow systems occur in subalpine canyon bottoms west of the crest. Steepness of topography precludes much meadow development in the subalpine east of the crest.

In general, aridity and temperature decrease with elevation. High windswept alpine areas are a notable exception, since winter snowfall is blown off, leaving them essentially bare. The combination of cold dessicating wind, low yearly precipitation, and low moisture retention of poorly developed soils on these sites results in a sparse, prostrate vegetation, much of which cannot be grazed effectively due to its stature. Major and Bamberg (1967) consider the Sierran alpine as one of the most arid alpine ecosystems in the northern hemisphere. The alpine is far from uniform though, and ice and snow fields, as well as occasional springs and lakes provide a patchy source of moisture.

Land Ownership and Management

The entire ranges of the Baxter and Williamson herds fall on lands managed by Inyo National Forest and Sequoia and Kings Canyon National Parks. The dividing boundary runs along the crest with the entire east slope, which constitutes most bighorn range, being on Forest Service lands.

In 1971 Inyo National Forest designated the east slope ranges of the Baxter and Williamson herds as California Bighorn Sheep Zoological Areas. Accompanying regulations limited human use to trails and controlled numbers of backpackers by a quota system. The same year, bighorn ranges of the Baxter herd west of the crest were designated Class IV by the National Park Service. This designation prohibits the existence of man-made facilities and resulted in cessation of trail maintenance. In 1976 the Zoological Area regulations were relaxed somewhat, allowing summer off-trail use below 3050m. In 1977, the National Park Service prohibited off-trail use east of the Rae Lakes drainage in the Baxter herd summer range, and established a one night camping limit for the Baxter lakes Basin. This effectively placed summer range regulations on an approximately equal level with those on Forest Service lands east of the crest.

METHODS

Allocation of Effort

During the early stages of the study, field surveys were directed largely toward collection of data pertaining to seasonal distributions, population size, and reproduction and recruitment rates. As seasonal ranges became known and the finding of bighorn more predictable, it was possible to focus later survey work on other questions, while continuing to collect pertinent demographic information.

The first period of study was devoted almost entirely to the Baxter herd. As an understanding of the basic aspects of this herd was gained, an increasing proportion of field time was allotted to the Williamson herd until the two herds received approximately equal attention during 1978, the final full year of intensive study. Clearly, the Baxter herd received a disproportionate share of attention overall. An important aspect of early stages of the investigation concerned learning how to study these bighorn in terrain to which access was most difficult. To some degree this ameliorates the unequal time allotted the two herds in that use of abilities gained in the Baxter herd range made work in the Williamson herd range much more efficient. Nevertheless, the Baxter herd accounted for 91.3% of all bighorn groups recorded during the study. This reflects the small size of the Williamson herd (see results) and the greater difficulty of finding its members, in addition to the lesser attention given it.

Field time was also not equably allotted spatially within herds. I tended to return to areas where bighorn occurred more predictably, as well as to those of easier access. High country base camps supplied by mule train in the North Fork of Oak Creek and in Baxter Canyon in the Baxter herd range strongly influenced early distribution of research efforts. These camps were not restocked after 1976, resulting in more even spatial distribution of survey effort.

Demography

Sightings have depended heavily on the use of a spotting scope (15-60X) on a tripod due to distances involved and the exceptional camouflage of bighorn against most rocks. Slow systematic scanning of all visible terrain with a spotting scope was found very effective. In much alpine summer range bighorn can not move far without considerable accompanying movement of rocks. Repeated sounds of rock fall were frequently used to discover bighorn groups. Sightings were plotted on xeroxes of aerial photos.

Seasonal ranges were determined largely from direct sightings. Sign was used to determine some summer range boundaries, but in mid-range areas it suffers as a tool from lack of accompanying data on season of origin. Bighorn beds provided unambiguous sign and the presence of lamb pellets as evidence of ewe-lamb group use. It was not possible to survey carefully the entire summer ranges of rams; reported sightings of rams were relied on considerably to delineate approximate western boundaries of their ranges in summer.

Measures of population size consisted of direct counts. These were made on winter ranges under conditions that concentrated bighorn in the fewest places. Censuses were taken only after winter patterns of use and movement between areas were known. The first reasonably successful census was made in 1977. The most complete census results were obtained in 1978, because deep snow in upper winter range areas precluded their use by bighorn.

Bighorn were classified by sex and age whenever sighted. Classes used were lamb, yearling ram, yearling ewe, adult ewe, and adult ram. Because of the wide horn flare of Sierra rams, Geist's (1971) size classification based on curl was not found to be usable, except where direct side views occurred. Instead, rams were usually assigned precise ages based on horn annuli (Geist 1966). Rams were aged during winter censuses in attempts to obtain complete age structures of the ram population. It was possible to age most rams in winter at distances of 50-100 meters with a spotting scope. The most difficult class to distinguish was yearling females in winter. This class closely resembles adult ewes. Horn size (including annuli, the first two of which are fairly distinct on females), face length, and body proportions were used to distinguish the two classes of ewes. Variable growth rates probably introduce some error into this classification. Geist (1971) suggested that distinguishing yearling males from ewes in summer is the major problem in bighorn classification in the north. In the Sierra Nevada, yearling males were found to be easily distinguished from ewes in summer, even at long distances, on the basis of body size, presence of testicles, face length, more massive horn bases, and especially behavior.

Range Relationships

Food habits data came from three sources. A comprehensive list of plant species included in bighorn diets resulted from field observations. Direct observation of feeding bighorn provided some of this information, but most came from careful examination of plants on feeding sites shortly after departure of bighorn. On such sites, all species fed upon were recorded and sometimes given subjective importance rankings in terms of forage consumed. Other plant species present were frequently recorded. This provided considerable information on preference.

The second source of food habits information was microhistological analysis of fecal samples. Fecal samples were collected fresh from observed bighorn groups at all opportunities. These were air dried and stored in paper bags, as was a complete collection of known plant material from bighorn ranges. Fecal material and known plant material were both treated in the following way after first smashing the fecal material. Samples were simmered for half to one hour in standard clothes washing detergent, rinsed, then placed in approximately 1% sodium hypochlorite solution until white. This was followed by a second rinsing then storage in vials of standard rubbing alcohol. During the second rinsing, fecal material was washed through a 60 mesh (.0098 inch openings) soil sieve placed on top of a 150 mesh (.0041 inch openings) soil sieve, and the material on the 150 mesh was saved. Neither known plant nor fecal samples were ground before treatment. Fecal material was mounted directly from the alcohol in such a way as to minimize overlap of particles. Mounting of known plant material involved teasing pieces of cuticle from as many different leaf and stem surfaces as possible. Mounting was in glycerine with a permanent seal made with mounting medium under the edge of the cover slip and clear nail polish over the outside edge. Slides were viewed under phase contrast with a monocular Unitron microscope at 100X for winter and spring range samples and at 125X with a binocular Bausch and Lomb microscope for summer and fall range material. Sampling was systematic; the slide was moved up and down on parallel transects and all identifiable cuticle fragments were recorded. Quantification was based on frequency of identifiable fragments.

The third source of food habits information was four rumen samples from dead bighorn that were found on winter ranges; three of these were mountain lion kills. Analysis was with a point frame similar to that used by Chamrad and Box (1964). First forage item encountered by each pin was removed with forceps and later identified by eye or on the basis of microscopic cuticle characteristics where possible.

Three different nutritional parameters were investigated. A large number of forage species in varying phenology were collected for analysis of protein, phosphorus, and calcium content. In addition to known dietary items, these samples included unpalatable species with the aim of investigating bases of palatability. All samples were air dried and stored before analysis. Chemical analyses were done by Morse Laboratories, Inc. of Sacramento, California, and the Animal Nutrition Testing Laboratories of the University of Nevada, Reno.

The second nutritional parameter measured was percent fecal protein. Hebert (1973) found a close correlation between percent fecal and percent dietary protein for captive Rocky Mountain bighorn fed natural diets in Canada and suggested its use in field studies. A total of 225 fecal samples was analysed. These were collected fresh from observed bighorn groups and were air dried and stored in paper bags. Samples for analysis were selected in such a way as to make pairwise comparisons between different ranges within as short a time period as possible. Since numerous samples were usually collected from each bighorn group, replication for each sampling point was possible. Laboratory analyses were carried out by the Animal Nutrition Testing Laboratories of the University of Nevada, Reno.

The third nutritional parameter was the elucidation of nursing curves for the Baxter and Williamson herds in 1978. Both duration and frequency of suckling were recorded from time of lambing until termination of weaning, and were analysed as a function of lamb age. Concomitant with this was the determination of the lambing period. Lamb ages were estimated to the nearest week on the basis of relative lamb sizes and precise knowledge of the timing of lambing. Duration of suckles were measured to the nearest second with a wrist watch. Frequency of suckling was measured individually for the same lambs whose suckle durations were measured; period between suckles was determined to the nearest minute.

Measurements of forage utilization were made for plant species on winter ranges and in the alpine. Plant species selected for this purpose (1) were preferred forage items for bighorn, (2) showed sufficient utilization levels to be potentially in short supply, and (3) could be measured fairly unambiguously. In the case of winter range vegetation, desert needlegrass and bitterbrush were measured also because they were known to be important elk feed and would shed light on the question of elk-bighorn competition.

Quantification of needlegrass utilization has been carried out in the spring by noting whether or not clumps received grazing of the previous year's growth, and by measuring the height of the grass. In this way, the percent of plants grazed was measured as well as the percent of the biomass removed, calculated simply as:

$$\% \text{ Utilization} = \% \text{ Plants Grazed} * (\bar{X}_u - \bar{X}_g)/\bar{X}_u$$

where $\bar{X}_u$ is the average height of ungrazed clumps, and $\bar{X}_g$ is the average height of grazed clumps.

The growth pattern of bitterbrush is much simpler than needlegrass, in that it puts out new leader growth only in the spring for a period depending on moisture availability. Bitterbrush utilization was quantified following winter use by counting browsed and unbrowsed leaders on one or two randomly chosen branches per bush.

Plant cover was measured in selected areas either as point or line intercept measurements. These sample sites were chosen to illustrate the variety of vegetation on different sites within broad habitat categories. Meaningful comparison of vegetation between ranges by rigorous quantification of vegetative cover was deemed a hopeless task in most cases because of this great variation in species composition and cover within basic habitat strata.

Lists of plant species present and their phenological states were made throughout bighorn ranges during survey work. This was done as an aid in defining habitat types, making comparisons between areas, and correlating changes in forage phenology with other nutritional parameters.

Human Disturbance

Human disturbance has been investigated through consideration of (1) bighorn reaction to humans and (2) range use patterns relative to expected or historic patterns and patterns of human use. Light and Weaver (1973) used five categories to classify bighorn reactions to humans in the San Gabriel Mountains of California. These categories were used to classify reactions of bighorn to the investigator in the Sierra Nevada, but were given more precise definitions than offered by Light and Weaver (1973). These are:

(1) Unconcerned - bighorn demonstrate awareness of the investigator's presence, but do not change basic behavior patterns of feeding and bedding.

(2) Curious - bighorn stand and watch the investigator at times, but otherwise continue feeding and bedding activities.

(3) Concerned - bighorn stand and watch the investigator considerably, may feed some, but will not bed; this constitutes a delayed flight.

(4) Immediate slow flight - bighorn depart immediately at a walk.

(5) Immediate fast flight - bighorn depart immediately on the run.

Where sample sizes were small, lumping of 1 and 2, and 4 and 5 produced three categories - no flight, delayed flight, and immediate flight. Additional variables recorded were:

(1) Distance between bighorn and the investigator and between bighorn and escape cover (usually rock outcrops). These values were determined by field estimates for short distances and measurements on aerial photos for longer distances. Aerial photo scales were determined for different elevations using known distances between topographic features.

(2) Relative juxtaposition (bighorn above, below, or level with investigator.

(3) Type of bighorn group (ewe-lamb, ram, or mixed).

(4) Size of bighorn group.

(5) Season (winter, lambing through weaning, and fall).

(6) Range (winter, high country).

(7) Whether or not significant wind was present.

(8) Whether or not a substantial obstacle (e.g. ravine) lay between the bighorn and the investigator.

This analysis of bighorn reaction was undertaken where the investigator held his position as soon as bighorn were sighted until their reaction category was clear. A different situation exists when a human continuously approaches a group of bighorn. For instance, the category of delayed flight loses its meaning, since all encounters outside the conditions of immediate flight will be a delayed flight. Of more interest are the parameters that determine when this flight occurs. Data from encounters where bighorn were approached were treated separately.

Parasites

Parasite studies have consisted of standard flotation and baermannization of fecal samples. Flotation was run using a saturated sugar solution. Baermannization was done using hollow-stemmed plastic champagne glasses with fecal samples supported by a brass screen placed over the top of the stem. Dry pellet samples were weighed, broken in half, and soaked in the apparatus for 48 hours. A pipette was used to draw the concentrated larvae from the bottom of the stem. All larvae were counted on a gridded petri dish using a 20X dissecting microscope and a hand counter. Most samples consisted of 2-2.5 gms dry fecal material. The number of pellets was recorded for calculation of mean pellet weight of each sample as an index of size class of bighorn.

RESULTS AND DISCUSSION

Demography

Seasonal Ranges

The boundaries of seasonal ranges of the Baxter and Williamson herds are outlined in Figures 4-8. They include plottings of most sightings I made over the course of the study. These totalled 807 bighorn groups, including lone bighorn, comprising 8515 individuals. The range boundaries are not firm, as all boundary areas have not been thoroughly investigated; areas of substantial uncertainty are discussed below.

Williamson Herd

All sightings from the Williamson herd are plotted on Figure 4, but only the boundaries of the summer range of ewe-lamb groups and the winter range of the whole herd are drawn. These range boundaries are based on sightings as well as sign. Although no sightings were made at the mouth of Georges Creek in the winter range, it was evident in 1978 from their sign that most of the herd spent about three weeks there early in winter. Previous investigators observed bighorn in the Shepherd Creek winter range (Riegelhuth 1965; McCullough and Schneegas 1966; Dunaway,

Figure 4. Sightings and range boundaries for the Williamson herd. Dark lines outline winter range for the entire herd and summer range of ewe-lamb groups. Dashed lines are areas used in transition, or in fall in the case of upper Georges Creek.

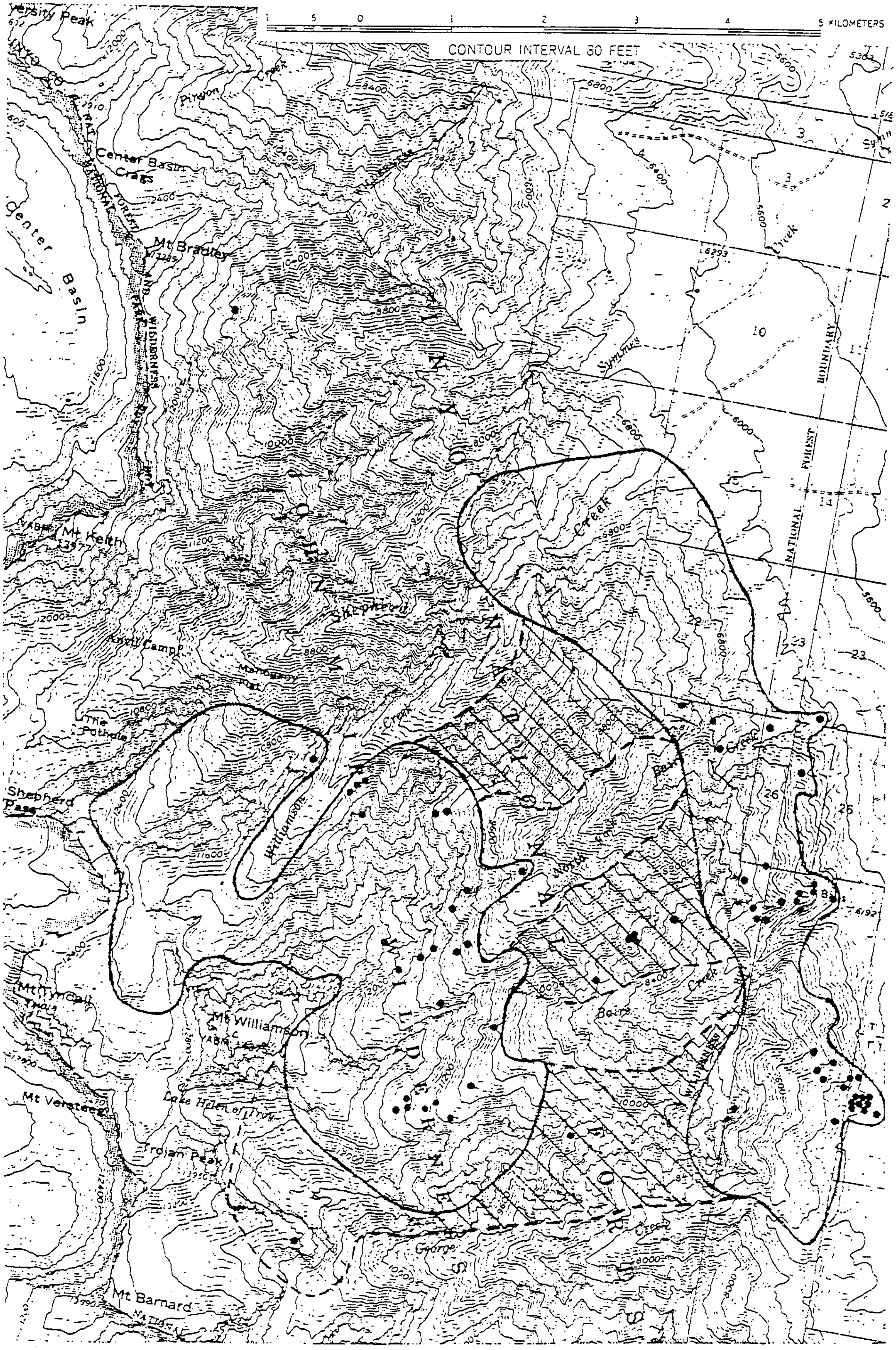

5 KILOMETERS
CONTOUR INTERVAL 30 FEET
Center Basin
Center Basin Crags
Mt Bradley
Mt Keith
Anvil Camp
Mahogany Flat
The Pothole
Shepherd Pass
Williamson
Shepherd
Creek
North Fork
Bairs
Mt Tyndall
Mt Williamson
Lake Helen of Troy
Mt Versteeg
Trojan Peak
Mt Barnard
George
Creek
Pinyon
Symmes
NATIONAL FOREST BOUNDARY
JOHN MUIR WILDERNESS

Figure 5. Summer sightings and range boundaries of rams in the Baxter herd.

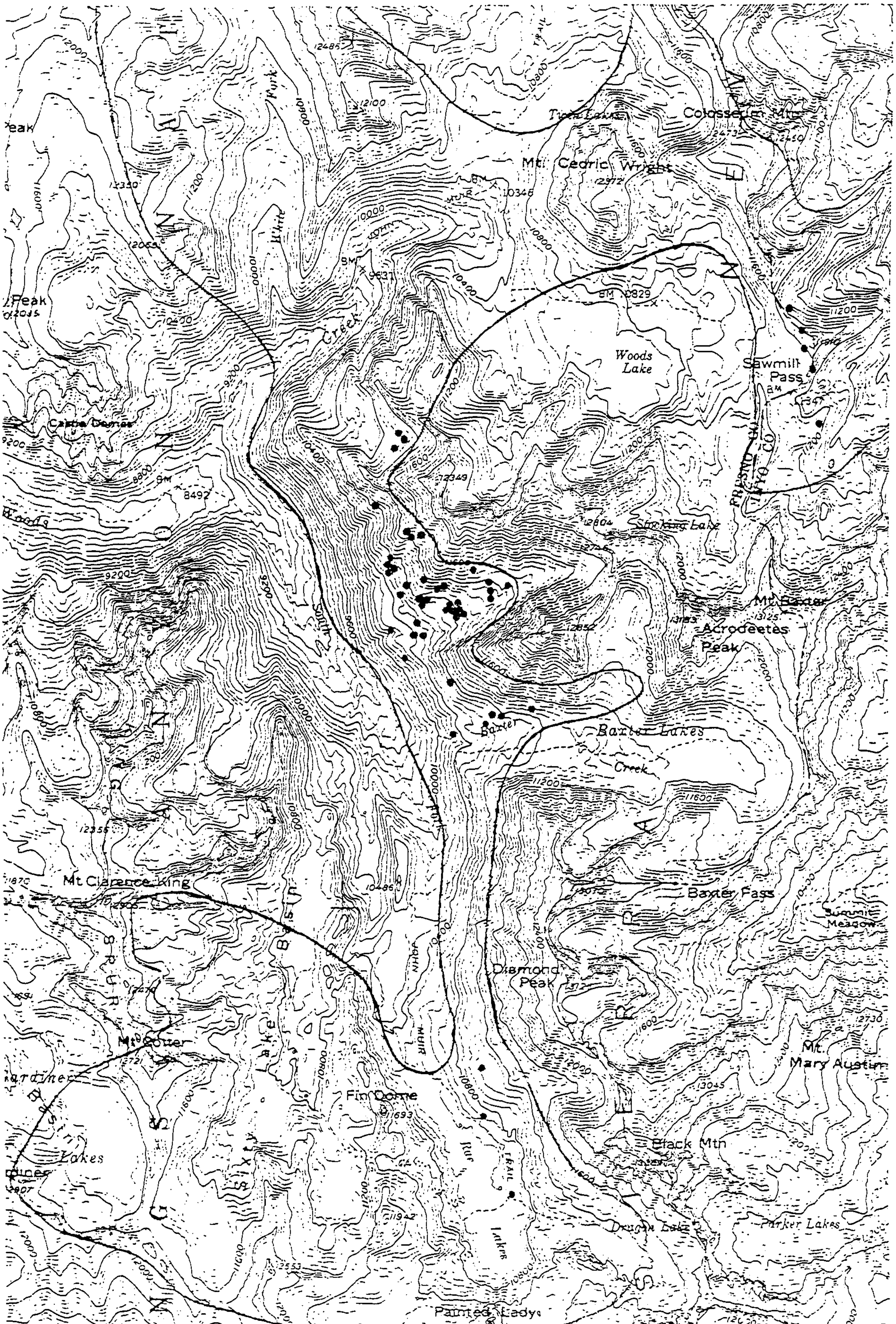

Twin Lakes
Colosseum Mtn
Mt. Cedric Wright
Woods Lake
Sawmill Pass
FRESNO CO
INYO CO
South Fork
White Creek
Castle Domes
Woods
Shocking Lake
Mt Baxter
Acrodectes Peak
Baxter Lakes
Baxter Creek
Baxter Pass
Summit Meadow
Mt Clarence King
Diamond Peak
Mt Gardiner
Mt Cotter
Mt. Mary Austin
Fin Dome
Sixty Lake Basin
Black Mtn
Gardiner Lakes
Dragon Lake
Parker Lakes
Rae Lakes
Painted Lady
JOHN MUIR TRAIL

Figure 6. Summer sightings and range boundaries of ewe-lamb groups in the Baxter herd. Sightings span the summer period up to October 10. The range boundary represents the summer period up to about mid-September.


Sawmill Meadow
Lookout P
Mule Lake
Sawmill Pass
Sawmill Lake
Woods Lake
Creek
FRESNO CO
INYO CO
Stocking Lake
Mt Baxter
Baxter Lakes
Baxter Creek
Baxter Pass
Summit Meadow
Diamond Peak
Mt. Mary Austin
Fin Dome
Black Mtn
Dragon Lake
Parker Lakes
Sardine Lake
Painted Lady
Glen Pass
Mt Rixford
Dragon Peak
Kearsarge Peak
Rex Montis Mine
Black Trout Lake
Mt Gould
Kearsarge Pass
Bullfrog Lake
Big Pothole
Onion Valley
Kearsarge Group
Phoenix Group
Rae Lakes
Basin
Woods Creek
Little Onion Valley
Sardine Canyon
North Fork
South Fork
Oak Creek

Figure 7. Sightings and range boundaries of Baxter herd bighorn in fall. Sightings span the period from October 10 until the sheep appear on the winter range. The range boundary represents the later fall period about mid-November.

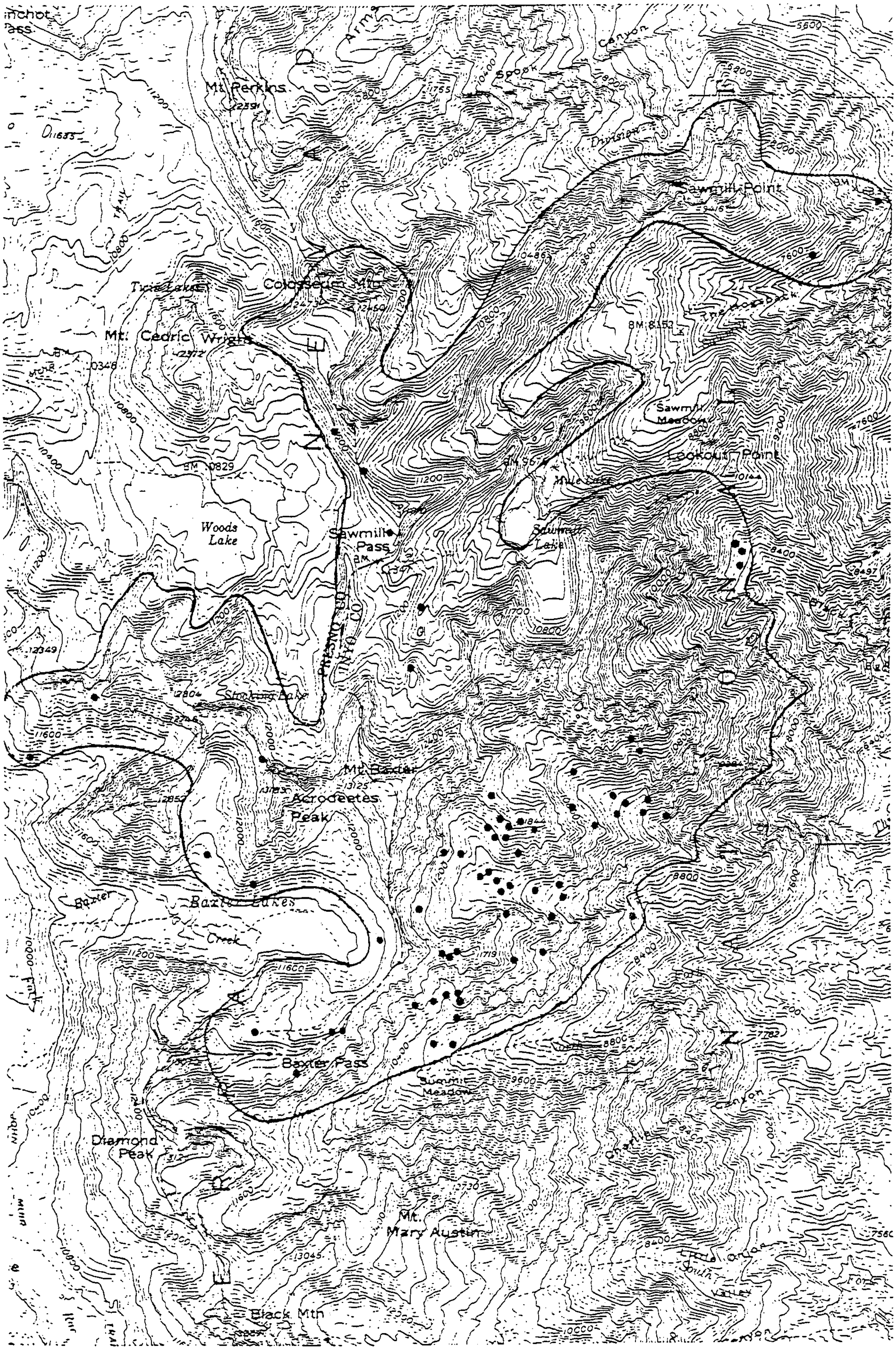
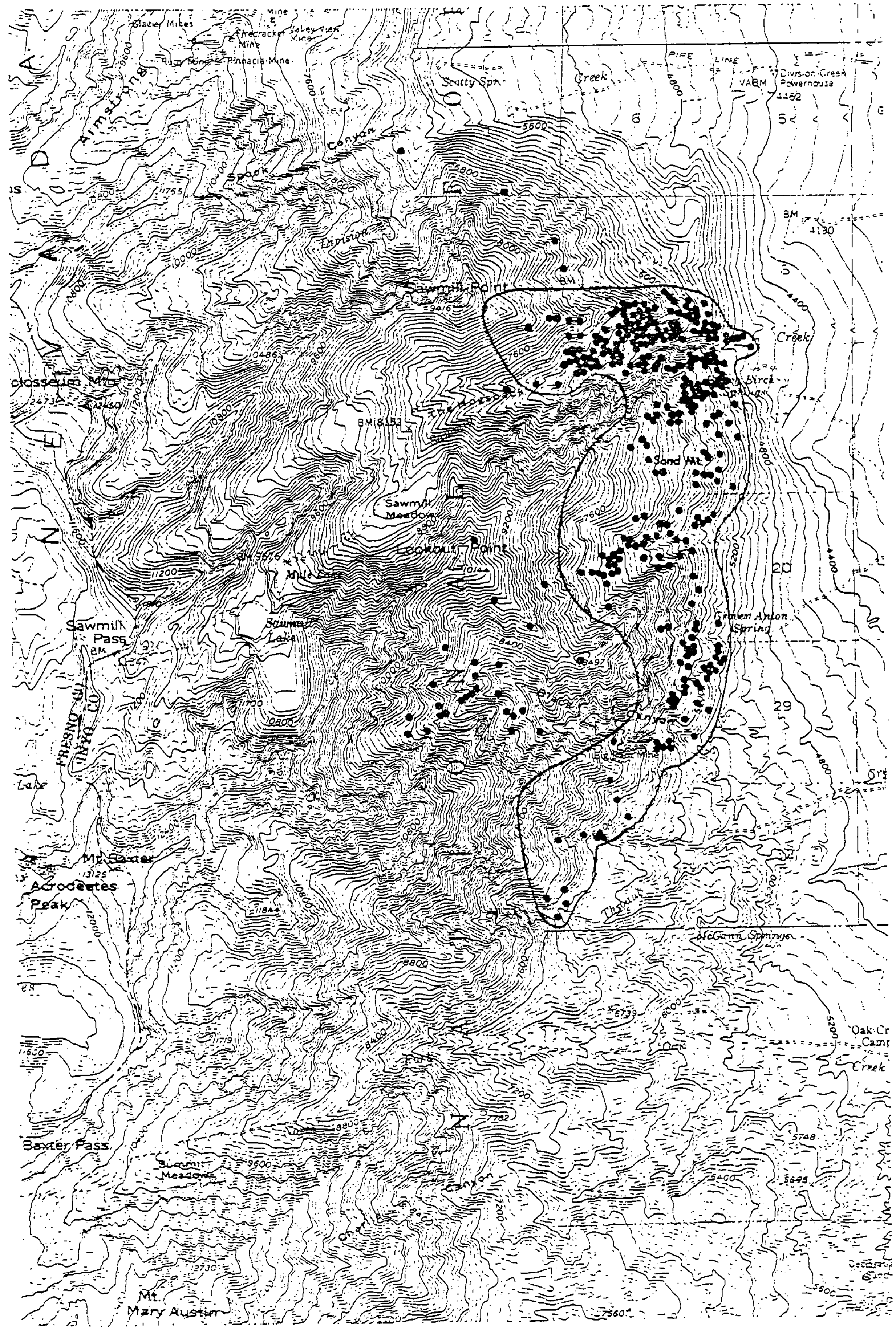

Pinchot Pass
Mt. Perkins
12591
Spook
Canyon
Division
Sawmill Point
9416
7600
The Hogsback
Colosseum Mtn
12473
12450
Twin Lakes
Mt. Cedric Wright
12372
BM 8152
Sawmill Meadow
Lookout Point
10144
Mule Lake
BM 10829
Woods Lake
Sawmill Pass
Sawmill Lake
FRESNO CO
INYO CO
12349
Stocking Lake
12804
Mt. Baxter
13125
Acrodectes Peak
13183
12852
Baxter Lakes
Baxter
Creek
11600
11200
8800
8400
Baxter Pass
Summit Meadow
9600
7782
Canyon
Diamond Peak
Mt. Mary Austin
11730
13045
Black Mtn
10000

Figure 8. Winter and spring sightings and winter range boundary of bighorn in the Baxter herd.


Glacier Mines
Firecracker Mine
Valley View Mine
Ruby Mine
Pinnacle Mine
Armstrong
Spook
Canyon
Scotty Spr.
Creek
PIPE LINE
Division Creek Powerhouse
4462
6
5
BM
4130
Division
Sawmill Point
9416
The Hogsback
BM 8152
Colosseum Mt.
12473
12460
11755
10486
Creek
Birch
Sand Mt.
Sawmill Meadow
Lookout Point
10144
Mule Lake
Sawmill Lake
Sawmill Pass
11200
11700
10800
20
Green Anton Spring
29
Black
Canyon
FRESNO CO.
INYO CO.
Lake
Mt. Baxter
13125
Acrocetes Peak
Thibaut
McGann Springs
11844
6739
Oak Cr Camp
Creek
11719
Fork
7782
5748
5695
Baxter Pass
Summit Meadow
Canyon
12730
Mt. Mary Austin
7560

Forest Service files in Bishop; Burandt, pers. comm.). I never found bighorn or their recent sign there, but in June of 1978 I encountered the carcass of a ewe that was killed by a mountain lion in late winter at the mouth of Shepherd Creek; apparently some use continues in that area.

Riegelhuth (1965) observed what he believed to be sign of winter bighorn use in the mouth of Pinyon Creek. I did not investigate this possibility, nor have there ever been any reports of bighorn there. Based on locations of high country ranges, it is unlikely that this location would receive anything but rare use by rams. In 1966 two rams were sighted by Schneegas and others 1.4 km north of Symmes Creek in winter (Forest Service files, Bishop).

The summer range of ewe-lamb use outlined on Figure 4 is based on my observations and those of Garcia (1977), who plotted areas of high country use on the basis of pellet group density. The area west of Williamson Creek is included in the ewe-lamb range on the basis of Garcia's (1977) report of ewe-lamb sign there. I found this to be poor habitat due to scant vegetation, with sparse bighorn sign that I interpreted as occasional ram use; use by ewe-lamb groups is probably infrequent. The one sighting I made on the west side of Williamson Creek (Figure 4) was a lone two-year-old ram.

The Georges Creek drainage currently appears to act as a barrier to ewe-lamb groups in summer. I checked upper Georges Creek on numerous occasions in summer without sighting any bighorn or finding evidence of recent bighorn use, despite excellent meadows adjacent to rocky terrain. Fecal pellets in these meadows always appear weathered in summer. Since the only sighting of bighorn I made in this southern area was a mixed group in November of 1975, I interpret the evidence to indicate that bighorn use there is confined to fall. Hence the dashed line in Figure 4. Garcia (1977) reached the same conclusion based on the relatively large size of lamb pellets in the upper Georges Creek meadows.

Along the crest south of the north fork of Georges Creek bighorn sign is sparse to non-existent. Garcia (1977) also noted this and pointed out that it was not always clear whether bighorn or deer were responsible for the observed sign, particularly in the large south tributary of Georges Creek where most sign was apparent. It appears that present use in this general area immediately south of Mount Williamson is infrequent. This represents a substantial decrease in the range of summer use since the 1940's. Bighorn, including ewe-lamb groups, and their sign were apparently common along the crest above Georges Creek in the 1940's (Blake 1941b,1949, Clyde 1971a,b, Jones 1949). This is no longer the case.

The Mount Tyndall area also received regular bighorn use in the past (Blake 1941b, Clyde 1971b),and the area from Mount Tyndall north to Junction Pass (see Figure 16), Mount Keith and Forrester Pass (1.2km west of Junction Pass) also previously received summer use by ewe-lamb groups (Blake 1942, 1949, Jones 1949). A sighting of a ewe-lamb group in the Wright Lakes area (see Figure 16) as recently as 1973 (Sequoia National Park files) suggests the possibility of occasional continued use in the Mount Tyndall area. This area was not surveyed by Garcia or myself. Access would be either from the upper Williamson Lakes or from upper Georges Creek, both of which receive rare bighorn use at best. Thus, the Mount Tyndall area is not likely to receive other than rare use.

There are no reported sightings to suggest that the areas north of Shepherd Pass still receive any summer use by ewe-lamb groups. Neither Garcia (1977) nor I could find sign of such use north along the crest from Mount Keith to University Peak.

Immediately south of Georges Creek in the Mount Russel-Mount Carillon area (not included in Figures 4 or 16) ram use in summer was apparently common in the 1940's and before (Clyde 1971a,b, Jones 1949, Wehausen 1979). Jones (1950a) considered this to be part of the Williamson herd. Garcia (1977) could find no evidence of recent bighorn use in this area. Ram summer range of the Williamson herd presently is located north of Shepherd Creek. Rams were found high in the Symmes Creek drainage in the summer of 1976 by Garcia (1977), and by myself in the summer of 1977. Their sign crosses Mount Bradley into the upper portions of Pinyon Creek. A sighting in 1977 by Vern Clevenger (pers. comm.) of a ram just east of Mount Genevra (7km west of Shepherd Pass) and one of an unidentified bighorn (presumably a ram) in same area in 1976 by Bob Kenan (pers. comm.) indicate that rams also use areas west of the crest in summer. These four sightings constitute the summation of all recorded summer sightings of rams from the Williamson herd in recent decades.

Dashed lines connecting high country and winter range boundaries in Figure 4 delineate areas of use between summer and winter ranges. These include lambing areas. I observed new-born lambs on south-facing slopes of South Bairs Canyon above the winter range. Pellets from very young lambs found in lower Williamson Creek indicate that it is also a lambing range. Whether or not lambing occurs in Georges Creek is unknown. Potential lambing habitat (see later discussion) exists there in the first south-facing side canyon, but only rams were found there in late May of 1978. North Bairs Canyon offers less in the way of potential lambing habitat than the other canyons due to extensive pinyon woodland. However, a ewe-lamb group was observed at the top of North Bairs Canyon as early as June 1.

Baxter Herd

The sexual segregation in summer in the Williamson herd is a lateral (north-south) separation along the east slope and crest, but some east-west separation is also apparent. Certainly rams are moving furthest from common winter ranges. This also holds for the Baxter herd rams, but the separation is largely east-west and elevational, with ewe-lamb groups in the alpine along the crest and rams in the subalpine west of the crest (Figures 6,7). Ewe-lamb groups are strictly limited to slopes with precipitous rocks close by in both herds in summer.

Rams appear to have few limitation on their movement in summer. They regularly cross wide glaciated canyons that form the western boundary of the ewe-lamb summer range (Figure 6) and are often found in forested areas. Consequently, the Baxter herd rams cover a considerable area in summer, making it necessary to base the summer range map for that sex on reported sightings to a large extent. Lone rams or small groups may occasionally stray out of the boundaries drawn in Figure 5, as evidenced by a sighting reported from Muro Blanco (Sequoia and Kings Canyon National Park files) and a skull found in 1978 at the base of Castle Domes above Woods Creek. However, one can probably expect to find at least 95% of the rams in the herd within these boundaries in summer. The summer range of rams lies west of the crest, but the range on Figure 5 is drawn to include their migration corridor over Sawmill Pass as well.

I found no sign of summer use by ewe-lamb groups of the area immediately north and east of Sawmill Pass. It nevertheless is included as part of the range drawn in Figure 6 due to a sighting of three ewes and three lambs in the north fork of Sawmill Canyon by Woody Elliott and Ernie

Garcia in May of 1976. Some uncertainty also exists regarding the exact boundary of ewe-lamb use at the north end of the ridge system lying south and west of the Woods Lake Basin. Likewise, the extent to which ewe-lamb groups cross over the east face of Dragon Peak to Mount Gould and its eastern ridges above Golden Trout Lake and Onion Valley has not been investigated. No sign could be found in the high lake basin west of Dragon Peak.

As fall progresses, the ewe-lamb range shifts north and somewhat east, placing it largely immediately west of the winter range. Rams join the ewe groups beginning in the second week of October. Bighorn use increases noticeably in the Sawmill Pass area during fall, and drops off south of the north fork of Oak Creek. Miners working at the Rex Montis Mine on Kearsarge Peak stated in 1975 (pers. comm.) that bighorn were commonly seen on the rocks above the mine during summer until the beginning of October. A sighting by Ernie DeGraff above the Rex Montis Mine at the beginning of November (Forest Service files, Bishop) indicates occasional use later in fall. Bighorn use continues west of the crest in fall, but tends to concentrate east of the crest following fall storms, spreading back as the snow from these storms melts back. The fall sightings plotted in Figure 7 begin on October 10 (except for one late September sighting low on the north side of Sawmill Creek), but the range boundary is intended to reflect the distribution a month later; the range boundaries during the fall transition period are not presented.

The Baxter herd winter range has been divided into four wintering areas. From Thibaut Creek to Black Canyon is know as the Thibaut winter range. The Black Canyon winter range lies immediately north of Black Canyon mouth for about one mile to the break in the cliffs constituting the mouth of Sand Canyon. From there to Sawmill Creek is the Sand Mountain winter range, including Sand Canyon, and north of Sawmill Creek is the Sawmill winter range (Figure 8).

The first large winter snow storm forces the bighorn down the east side of the Sierra to winter range areas. This usually takes place in the second half of December, but is known to occur as early as the second half of November. In the drought year of 1976, bighorn did not appear on the winter range until mid-February. Following the first snow storm, bighorn appear on all four winter range areas, but with initial concentrations in the Thibaut Canyon area and on the ridge north of Sawmill Creek. The Thibaut winter range is about 300 m higher and thus has deeper snow than the Black Canyon range. Most bighorn leave the Thibaut area and slowly move north to the Black Canyon range, where there is less or no snow, and better visibility. Many move further onto Sand Mountain.

Sawmill Creek is thickly vegetated with water birch and willow along its entire length in the winter range, except for one spot outside the mouth of the canyon. This, along with the Hogsback above the winter range (Figure 8), are the only locations where sheep might be expected to cross between the Sand Mountain and Sawmill wintering areas. I found no indication of them crossing at either location. It seems safe to assume there is very little if any movement across Sawmill Creek during winter (which is convenient for census purposes).

Between Sawmill Creek and Thibaut Creek the distribution of bighorn stabilizes three to four weeks after the first appearance of bighorn on the winter range. Shifts continue after that, but are mostly within each wintering area. In the drought year of 1977 about 25 bighorn continued to use the Thibaut winter range throughout winter. No use was evident in mid-winter of 1978, presumably due to heavy snowfall, and only 6 sheep could be found there in February of 1979. In the spring some reoccupation of winter range south of Black Canyon probably occurs. It is also at this time that bighorn occasionally appear near Division Creek.

The distribution of sightings plotted in Figure 8 does not necessarily represent the relative densities of bighorn in the different areas of the Baxter winter range, but rather reflects differentials in time spent investigating the different areas, as well as in average group sizes of bighorn in the different areas. In 1977 the population distribution during the most complete census (early April) was 14 percent on the Thibaut range, 17 on the Black Canyon range, 32 on the Sand Mountain range, and 36 on the Sawmill range. In February of 1978 the respective percentages were 0, 17, 55, and 29. The Sand Mountain and Sawmill winter range areas clearly support the majority of the Baxter herd in winter.

The winter range boundary outlined in Figure 8 covers the winter period through the end of March. In April, most pregnant ewes, lambs of the previous season, and yearlings leave the winter range areas south of Sawmill Creek and move to rocky areas of upper Black Canyon for lambing (see sightings plotted in Black Canyon in Figure 8). Most rams and some barren ewes, yearlings, and lambs remain in the winter range past the middle of May before moving up. Not all ewes give birth above the winter range. The Sawmill winter range is sufficiently rocky that a large percentage of the ewes remain there until their lambs are two to three weeks old. Ten lambs were born in the Sawmill winter range in 1977 and some ewes remained that year as late as June 8. In 1976 and 1978 a total of three ewes with new lambs was observed in the rugged rocks on the south side of Sawmill Creek. Thus a few of the Sand Mountain ewes also remain at low elevation to lamb. It is not known where the remaining Sawmill ewes go to lamb, or whether any lambing occurs in Thibaut Canyon.

Herd Sizes

Censuses of the Baxter herd were undertaken when all or most of the Sand Mountain wintering population appeared in large groups low on the winter range. This occurrence may be triggered by heavy snowfall as well as spring greenup, which begins at lower elevations. Such opportunities for satisfactory censuses were few. When they occurred, censuses of the entire winter range were taken immediately and provided minimum population figures. The most complete of these are found in Table 3. The apparent lack of bighorn movement across Sawmill Creek in winter has made it possible to deal separately with the ranges on either side.

Adult and yearling rams were considered separately from other sex and age classes during censuses. It has not been necessary to further stratify by sex and age classes since lambs and adult and yearling ewes are strongly associated. Rams have been commonly associated with the other sex and age classes during winter, but the common occurrence of separate groups of rams (including yearlings) has made it fruitful to treat them as separate strata.

A "probable minimum" total population figure for the Baxter herd has been derived by summing maxima of these sex and age strata for either side of Sawmill Creek (Table 3). The reason for this approach is the need of multiple attempts to achieve a satisfactory census of Sawmill Canyon. This is because much of the Sawmill wintering area is censused by slow systematic scanning from high on the south canyon wall, from where some bighorn may remain out of view behind rocks.

Table 3 lists census results for the Williamson herd

Table 3. Winter census results for the Baxter and Williamson bighorn herds in the Sierra Nevada. See text for discussion of probable minimum values.

Year & Herd	Adult ewes	Yearling ewes	Lambs	Yearling rams	Adult rams	Unidentified non-rams	Total
1977							
Baxter:							
Minimum	62	15	39	13	38	0	167
Probable minimum	62	16	39	14	42	0	173
Williamson:							
Minimum	9	1	5	3	3	0	21
1978							
Baxter:							
Minimum	78	22	35	16	50	0	201
Probable minimum	83	25	38	18	50	0	214
Williamson:							
Minimum	13	1	5	4	7	0	30
1979							
Baxter:							
Minimum	59	10	22	10	32	0	133
Probable minimum	65	11	22	12	71	5	186

for 1977 and 1978. Winter observations there were casual in 1977, but in 1978 a concerted effort was made to find every bighorn. This consisted of keeping track of known groups while searching additional areas until all suspected locations from Georges Creek to Shepherd Creek (Figure 4) had been investigated. The higher elevation of the Williamson winter range and the high snowfall in 1978 placed considerable snow on much of the winter range. This greatly aided bighorn census attempts, as presence of tracks could be used as a criterion of bighorn use, and following tracks frequently led to their source.

It is impossible to determine the total sizes of the Baxter and Williamson herds. Consequently it is not possible to derive an objective measure of the completeness of census results. However, some subjective evaluation is possible, by evaluating conditions under which the censuses took place, and by comparing subsequent counts. The major obstacle to obtaining complete counts is the occupation of forested areas by bighorn, where trees hide them. In the winter range of the Baxter herd Jeffrey pine forest on the upper portions of the Sand Mountain and Sawmill winter ranges constitute the major problem areas. In the Williamson winter range pinyon woodland predominates. The 1978 censuses of both herds are believed to be quite complete overall because deep snow concentrated the sheep on lower more open areas. Nevertheless, the 1978 Baxter herd census was somewhat incomplete, since the 1979 "probable minimum" total for adult rams exceeded the 1978 total for adult and yearling rams by 3 (Table 3). In addition, some rams must have been missed to account for any mortality between years. This would place the minimum size of the Baxter herd at about 220 in 1978.

The rams missed in 1978 were in Sawmill Canyon. An exceptionally complete ram count in 1979 resulted from fortuitous encounters with all or most of the rams there when they descended for spring greenup, as well as with a group of rams in the Jeffrey pines on Sand Mountain. Otherwise, the 1979 census was poor due to bighorn occupying higher forested areas. An increase in the number of lambs on Sand Mountain in late winter of 1979 would place the "probable minimum" herd size just over 190 if one assumes no mid-winter movement between that and the Black Canyon range. This total is nevertheless well below what would be expected based on the 1978 total and a recruitment rate of 34 lambs per 100 adult ewes.

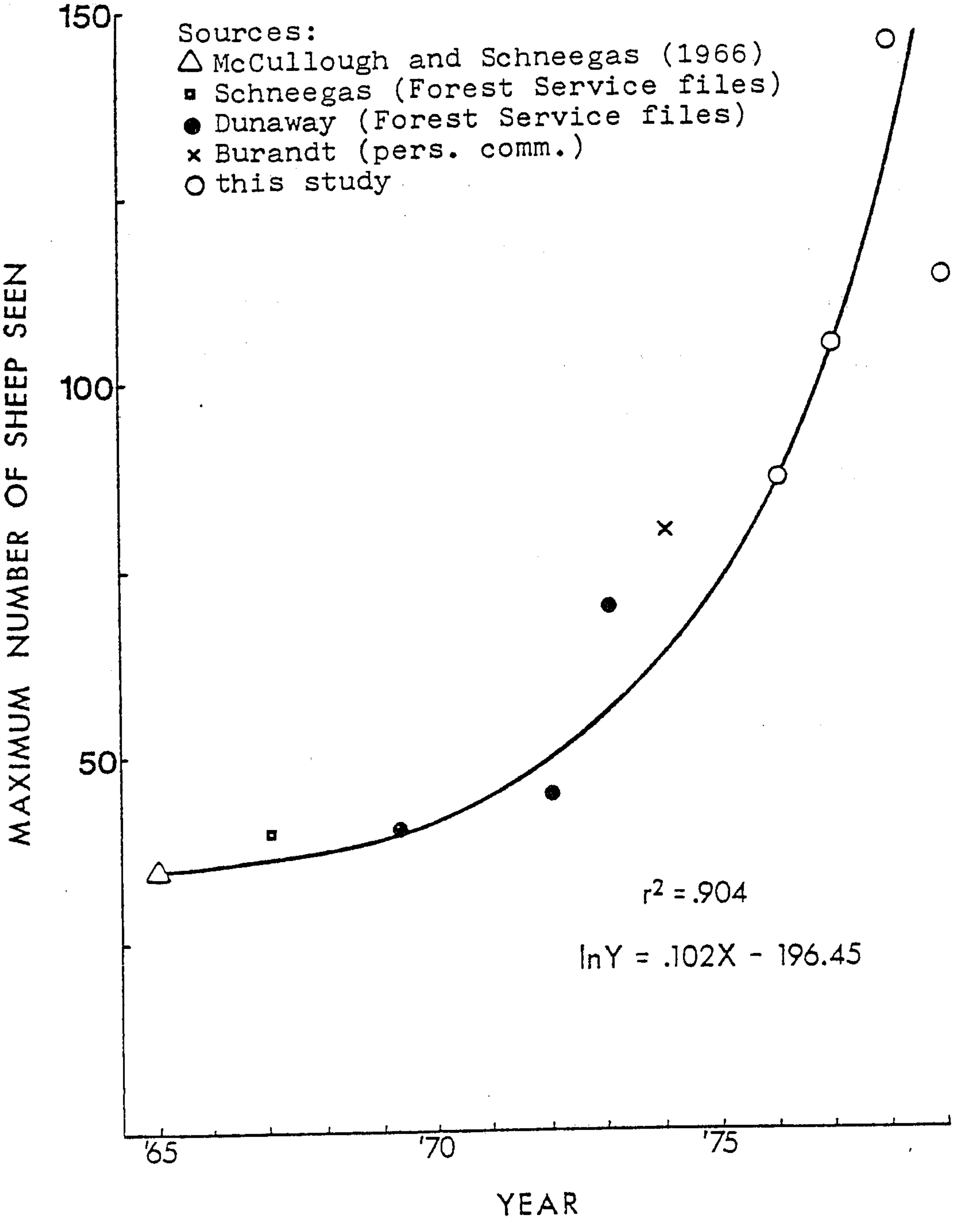
No opportunity for a winter census occurred in 1977 due to drought conditions. Instead, census results were obtained for the Baxter herd in early April, when most of the herd was feeding on new vegetation growth low on the winter range. The ram totals from 1977 appear complete when compared with those of 1978 (Table 3), but an additional 5 ewes and 4 lambs in 1977 are necessary to account for 1978 totals. This would place the 1977 population total at a minimum of 182. It was probably closer to 200 due to mortality between years.

Herd Trends

The variation in completeness of winter censuses during this study has been too great to use total counts to evaluate population changes. Of the different sex and age classes represented in Table 3, the adult ram totals represent the most complete census data and show an increasing trend. These yearly increases actually represent population increases one year prior, because recruitment of 2-year-old rather than yearling rams effect these changes. The trend of the Williamson herd cannot be investigated from census data, because only a single census was taken.

Previous investigators concerned with Sierra bighorn in the 1960's and 1970's concentrated most efforts on the Baxter herd immediately following winter storms when bighorn were most readily found. The maximum number of different bighorn observed in a single day was investigated as a possible index of population size. This measure indicates a strongly increasing trend since the 1960's (Figure 9), and fits an exponential growth curve ($\ln Y = .102X - 196.45$; $r^2 = .904$; $P < .001$). The slope in this equation is an estimate of the instantaneous growth rate r (Caughley 1967, 1977, Caughley and Birch 1971), which translates to an average finite annual increase rate of 10.7% ($\lambda = 1.107$). Caution should be exercised in accepting this figure. It is an average increase rate which assumes a linear relationship

Figure 9. Maximum numbers of bighorn seen on a single day in the Baxter herd winter range by various investigators since 1965.



between population size and maximum number of bighorn seen in a day. This latter value is likely to vary with experience of the investigators and winter conditions. Nevertheless, the relationship is strong and clearly indicates an increasing trend.

Similar analysis for the Williamson herd is impossible due to insufficient data.

Age Ratios

All data on rates of reproduction and recruitment in the Baxter and Williamson herds are listed in Tables 4 and 5. Failure of some previous investigators to distinguish yearlings has necessitated inclusion of several different ratios of varying denominators, because the denominators will vary with season of observation. Failure to distinguish yearlings in summer leads to both yearling sexes being lumped with adult ewes, while in winter it is only yearling ewes. Yearling rams commonly were lumped with other rams in winter, precluding calculation of the yearling to ewe ratio, despite the separate classification of yearling ewes in some cases.

Some of the sets of ratios obtained during this study were based on censuses where no animals were sampled more than once, and where the samples included a large percentage of the population. Such samples have little opportunity for bias from possible different spatial distributions of sex and age classes (Tables 4, 5).

Table 4. Reproduction and recruitment ratios for the Baxter herd.

Year	Season	Lambs per 100 adult ewes	Yearlings per 100 adult ewes	Lambs per 100 adult + yrlg ewes	Lambs per 100 adult ewes + all yearlings	Sample size[1]	Source[2]
1948	summer				54	26	1
1965	winter	36		32		76	2
1969	winter	66		56		79	3
1970	winter			48		25	3
1972	winter	38		32		40	4
1973	winter	40		34		143	4
1974	summer				62	29	5
1975	summer	72	52	59	46	90	5
	fall	74	24	61	60	52	5
1976	winter	55	29	46	40	246	5
	summer	75	98	52	38	111	5
	fall	77	58	60	48	95	5
1977	winter[3]	63	48	50	42	92	5
	summer	72	74	49	40	114	5
1978	winter[3]	46	52	35	30	126	5
	summer	30	36	26	22	87	5
1979	winter[3]	34	35	29	25	88	5
	summer	44	16		38	29	5

[1] Ewes plus yearlings

[2] Sources: 1 - Jones (1949); 2 - McCullough and Schneegas (1966); 3 - Dunaway (1970); 4 - Dunaway (Forest Service files, Bishop); 5 - this study

[3] Based on census in which no bighorn was sampled more than once

Table 5. Reproduction and recruitment ratios for the Williamson herd.

Year	Season	Lambs per 100 adult ewes	Yearlings per 100 adult ewes	Lambs per 100 adult + yrlg ewes	Lambs per 100 adult ewes + all yearlings	Sample size[1]	Source[2]
1948	summer				48	35	1
1971	winter[3]	30		23		13	2
1975	winter[3]			54		11	3
1976	winter	31	15		27	15	4
1977	winter	40	24	36	32	31	4
	summer[3]	54	27	50	43	14	4
1978	winter[3]	38	38	36	28	18	4
	summer	46	52	35	31	88	4

[1] Ewes plus yearlings

[2] Sources: 1 - Jones (1949); 2 - Dunaway (Forest Service files, Bishop); 3 - Burandt (California Department of Fish and Game files, Bishop); 4 - this study

[3] Based on census or other count in which no bighorn was sampled more than once

Age classifications have been advanced one year at the beginning of each lambing season. The adult ewe class thus increases at that point with the addition of yearling ewes that have just reached two years of age. One would expect the summer yearling to adult ewe ratio to be lower than the winter lamb to adult ewe ratio. The opposite occurred in 1976 and 1977 in the Baxter herd (Table 4). It is unlikely that excessive ewe mortality occurred between winter and summer to account for these ratio changes. A bias in sampling is the more probable explanation.

McQuivey (1978) suggested for bighorn in Nevada that 26 lambs per 100 ewes, including yearling ewes, represents the minimum recruitment rate for a static population. This recruitment rate would yield 11.5% yearlings among ewes, thus a recruitment rate on an adult ewe basis would be about 29 lambs per 100 ewes. Such figures are useful rules of thumb, but are not precise measures of population trend in that the ratio representing population replacement will vary depending on recent recruitment levels and adult mortality patterns. Caughley (1974) pointed out the difficulties inherent in using age ratios as measures of population change due to the double variable nature of ratios. However, extreme ratios are generally safe gauges of population trends. Recruitment ratios in the neighborhood of 40 lambs per 100 adult ewes and greater can probably be interpreted safely as population increases for bighorn. On this basis, the values in Table 4 indicate population increases of the Baxter herd during most years from 1969 to 1978. The values for 1972 and 1973 are the only possible exceptions, but may represent small population gains. During the first four years of this study (1974-1977), reproduction rates (summer values) were high, as were recruitment ratios the following winters (Table 4). These values corroborate the population increase apparent in census totals for rams and in Figure 9.

These reproductive rates are nevertheless considerably below the potentials sometimes exhibited by introduced bighorn populations (Woodgerd 1964, Kornet 1978). The percentage of ewes that were yearlings during winter should approximate the percentage of adult ewes that are two-year olds in summer. On this basis, summer reproduction rates can be expressed on the basis of ewes three years old and older. For 1976 and 1977, respectively, this yields 83 and 90 lambs per 100 mature ewes. Woodgerd (1964) recorded values for this ratio as high as 100 during the early increase phase of bighorn introduced to Wildhorse Island in Montana.

Woodgerd (1964) also noted a substantial percentage of yearlings that were pregnant. The normal age at first lambing is three years in North American wild sheep, but under favorable circumstances this is advanced one year in environments where reproduction is highly seasonal (Nichols 1978, Streeter 1970, Berger 1978) and by as much as 20 months in deserts, where the lambing season is often much longer (McCutchen 1977). Lambing at two years of age has not been evident in the Sierra Nevada during this study, but may not have been recognized due to the problem of distinguishing two-year old and older ewes. The largest yearlings are the ones most likely to breed, and are also the ones most difficult to distinguish from older ewes.

Single births are the norm for North American wild sheep, but twins have been recorded for a variety of populations (Hansen and Deming 1971, Hoefs 1978, Spalding 1966, Eccles and Shackleton 1979). The majority of the records of twins, outside of zoos, come from the subspecies *Ovis canadensis californiana*, but twins are rare overall and their appearance presumably occurs under the favorable nutritional regimes of increasing populations. At least two sets of twins were observed in the Baxter herd in 1976 and one set in 1977; this was based on observations of more lambs than ewes in summer groups. Eccles and Shackleton (1979) cautioned against such a conclusion due to the possibility of misinterpretation of what are really lamb subgroups within widely dispersed groups of adults. In the Sierra Nevada, ewe-lamb groups are small in summer, as well as distinct and almost continuously moving, thus precluding the possibility of misinterpretation on that basis. In both years, groups with twins were sighted more than once and the twins were always identical in size and color. The 1977 twins were sighted twice and each time were accompanied only by a single ewe. They were recognized by the particularly dark pelage of all three and the notably long horns on the lambs.

Reproduction in the Baxter herd dropped substantially in 1978 to approximately a herd maintenance level, but (based on small sample size) picked up somewhat in 1979 (Table 4).

Age ratio data from the Williamson herd are considerably less abundant than for the Baxter herd. The small sample sizes (Table 5) are not necessarily poor measures since the herd size itself is small. Also, a large proportion of the population was sampled with no possibility of sampling any sheep more than once in four of the samples. The values in Table 5 suggest neither poor nor good reproduction and recruitment. Recruitment rates mostly fall in the region of 30-40 lambs per 100 ewes, which is probably best interpreted as a static to slightly increasing population trend. Certainly the large population gains evident in the Baxter herd are not paralleled in the Williamson herd. However, reproduction in the Williamson herd in 1978 was notably higher than in the Baxter herd (Tables 4, 5).

Sex Ratios

Sound sex ratio data for bighorn are difficult to obtain. Divergent patterns of habitat utilization outside of the breeding season commonly make unbiased samplings of both sexes difficult. Even during the breeding season, when the sexes are mixed to a large degree, the greater mobility of rams will introduce a bias into sex ratios obtained from ground samplings. Complete or near complete herd censuses should be one of the most unbiased sources of sex ratios. Table 6 lists sex ratios for the best censuses during this study. The 1979 results are not included due to the known bias in favor of rams in the "probable minimum" total and the incompleteness of the minimum total. Both yield sex ratios deviant from the 1977 and 1978 totals for the Baxter herd.

Due to their polygynous breeding system, sexual selection should cause bighorn rams to take more risks than females in order to attain high ranking in the dominance hierarchy, because they have more to gain by it (Trivers 1972). This, along with the debilitating effects of male activities during the breeding season, should lead to greater mortality rate of males compared to females, and an adult sex ratio less than 1:1, as recorded in Table 6. If the sex ratio could be determined for each age class, it would be expected to deviate progressively further from 1:1 with increasing age. This probably explains the higher ratio when yearlings are included (Table 6). The high sex ratio for the Williamson herd when yearlings are included (Table 6) reflects an unbalanced sex ratio for the yearling class in 1978 (Table 3). The low adult sex ratio for the Williamson herd may simply be random deviation due to a small population size. Also, a single ram missed during the

Table 6. Sex ratios from winter herd censuses of the Baxter and Williamson herds. Ratios are male:female.

Year & Herd	Adults only	Including Yearlings
Baxter		
1977		
Minimum	61.3:100	66.2:100
Prob. minimum	67.7:100	71.8:100
1978		
Minimum	64.1:100	66.0:100
Prob. minimum	60.2:100	63.0:100
Williamson		
1978		
Minimum	53.8:100	78.6:100

1978 Williamson census would boost the adult sex ratio into the range of values of the Baxter herd.

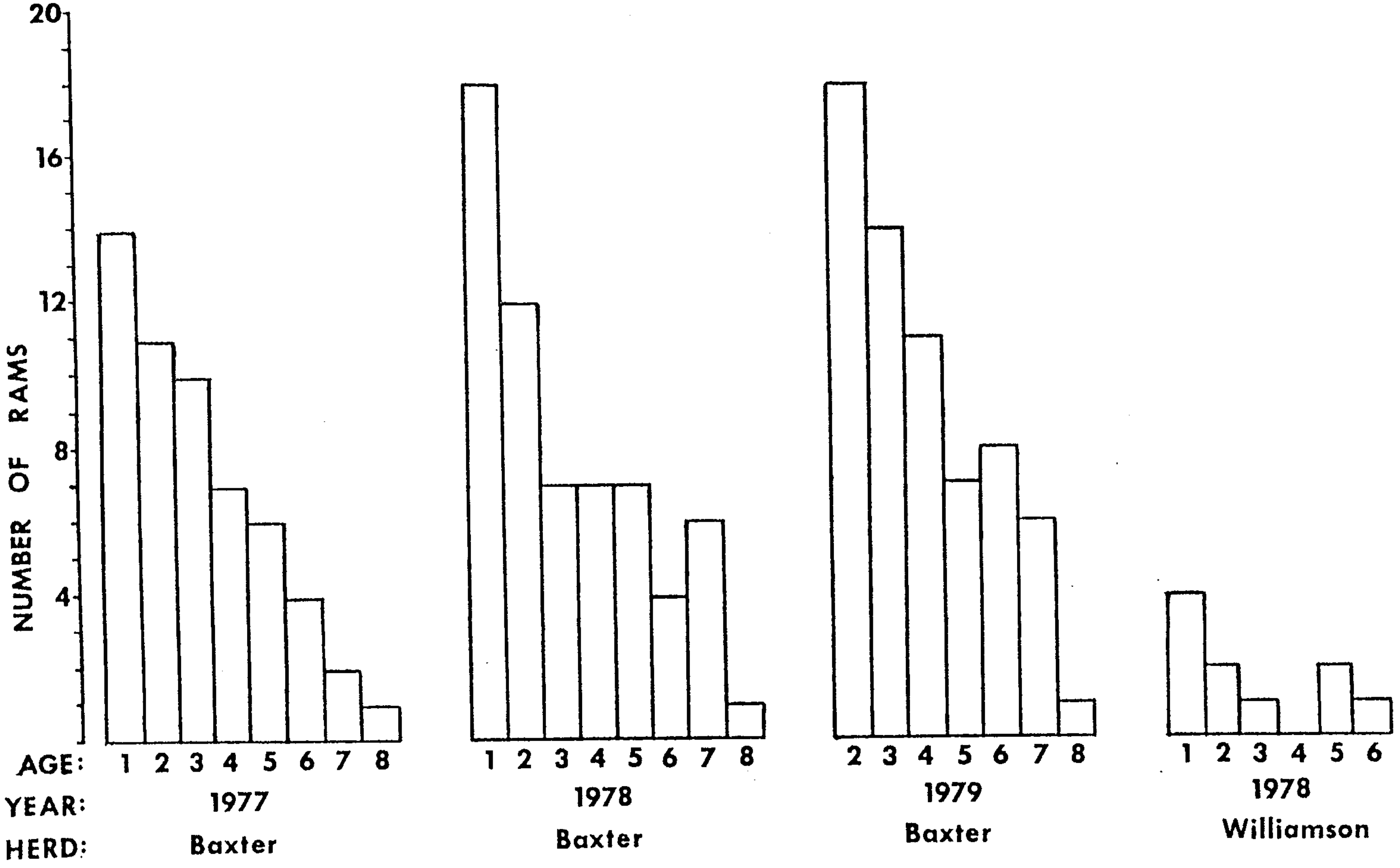
The rams known to be missed in the 1978 Baxter herd census would boost the "probable minimum" sex ratio to 65:100 or higher if added. The true adult sex ratio for the Baxter herd probably lies in the range 65-70:100. Similar bighorn sex ratios have been found elsewhere for populations where hunting is absent or insignificant relative to population size (Aldous 1957, Smith 1954, Sugden 1961, McQuivey 1978, Leslie and Douglas 1979).

Age Structure

As many rams as possible were aged on the basis of horn annuli (Geist 1966, Turner 1977) during winter censuses. The completeness of counts of yearling rams in winter depends on the completeness of both ewe counts and counts of adult rams, since yearling rams are found with both. Since the census of ewes was poor in 1979, while that of adult rams was excellent, the yearling class is omitted from the 1979 Baxter herd age structure (Figure 10).

The three age structures obtained for the Baxter herd differ in the percent of the rams accounted for in censuses for which ages were also obtained. This was highest in 1977 at 98%, second in 1979 at 92%, and lowest in 1978 at 91%. From the 1979 age structure (Figure 10), as well as the 1979 census total for rams (Table 3), it is evident that at least 9 rams were not aged in 1978, which lowers the percentage to

Figure 10. Age structures of rams in the Baxter and Williamson herds.



at least 87% for 1978. This may account for the deviation of the 1978 age structure from the linear shape exhibited the other two years.

A pyramidal age structure is evident for the Baxter herd in all three years (Figure 10). This is commonly considered an indicator of an increasing population (e.g., Krebs 1972, Smith 1974). Use of age structure shapes as measures of general population trends assumes that the population trend is influenced primarily by variation in recruitment rather than adult mortality. Caughley (1977) questioned their use on this basis, and McCullough (1978) pointed out that conventional interpretations of age structures do not hold up, since broad-based pyramidal age structures can result from rapidly declining populations in which adult mortality is high, such as with overexploitation. Given the lack of such influences on the Baxter herd and independent evidence of population increase, the Baxter herd age structures fit the conventional interpretation as evidence corroborating population increase.

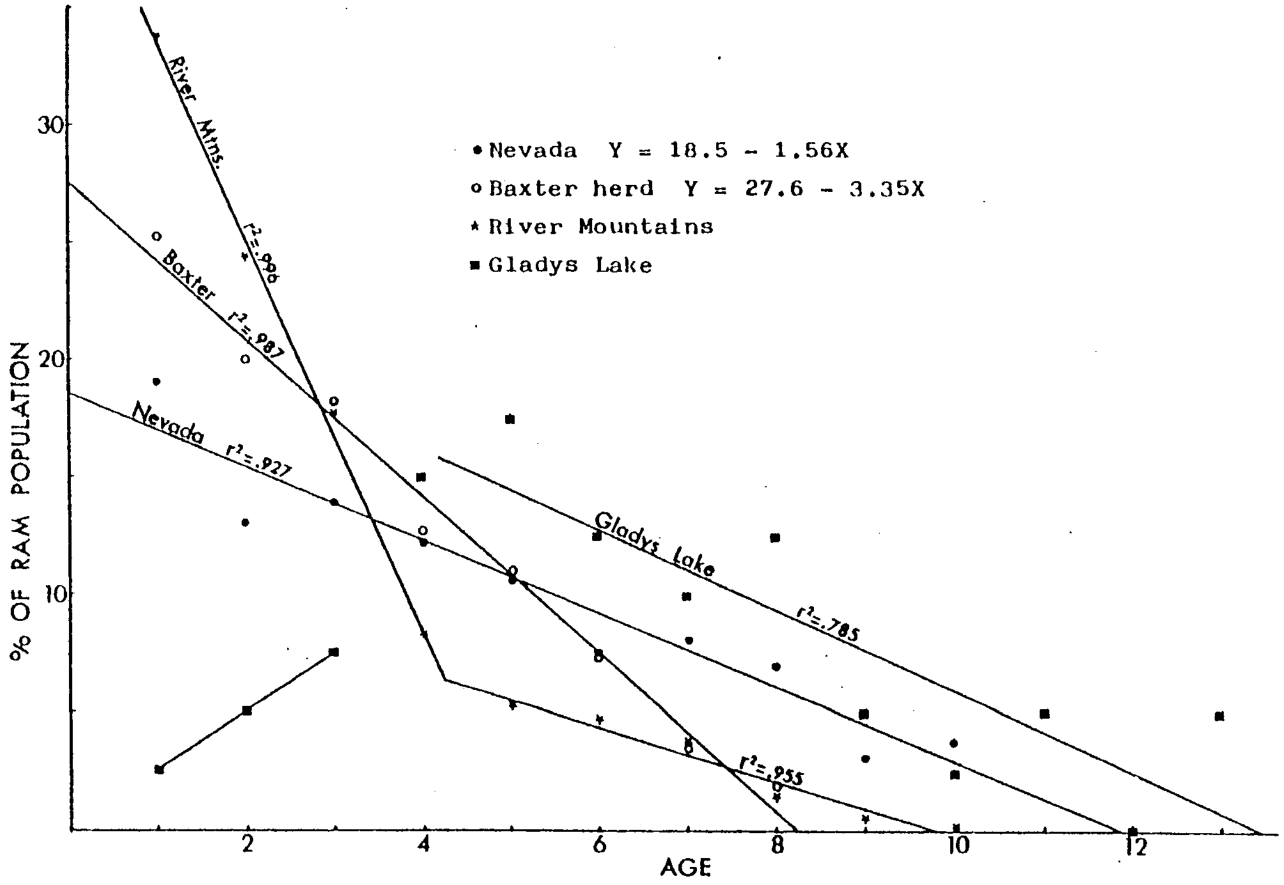
Much less can be said of the age structure obtained for the Williamson herd in 1978 (Figure 10), in which all known rams were aged. The large number of yearling rams is a function of a presumably random imbalance of the sex ratio of that age class in 1978 (Table 3). The rest of the age structure exhibits no significant pattern. Random variation in primary sex ratios of individual age classes as well as adult mortality can strongly influence the age structure of such small populations as the Williamson herd, making even conventional interpretation difficult.

Sierra bighorn rams are notably short lived. The maximum age recorded on winter ranges has been eight years (Figure 10). These few eight-year olds probably reach nine years of age, but die before reappearing on the winter range the following year. This maximum age recorded for live rams is corroborated by skulls found during this study, and by others, none of which has exceeded eight years of age.

In many North American wild sheep populations it is common for some rams to reach ages of 12-14 years (Sugden 1961, McQuivey 1978, Wells and Wells 1961, Shackleton 1973, Murie 1944) and occasionally older (Geist 1971). Geist (1971) and Shackleton (1973) presented data showing that both within and between bighorn populations, ram longevity is inversely related to individual growth rate. The explanation for this is that mortality of rams large enough to be successful at breeding is strongly influenced by the arduous activities associated with the breeding season. Those rams that grow faster and attain high dominance status sooner also die sooner from rutting activities (Geist 1971). Since rates of conception, recruitment, and body growth are all dependent on nutrition, one would expect lower longevity to be associated with increasing populations (Shackleton 1973). The Baxter herd data support this hypothesis.

Caughley (1977) suggested that the proper interpretation of age structures will be enhanced by studying their diagnostic features at the species or species group level. Figure 11 compares ram age structures recorded for one northern and three southern bighorn populations. The curve for the Baxter herd is based on the 1977 age structure and should approximate a stable age distribution. The curve for the Nevada population is based on 1,939 rams aged throughout Nevada during aerial flights spanning eight years. Corresponding recruitment rates averaged 32 lambs per 100 ewes (including yearlings) and varied relatively little spatially and temporally (McQuivey 1978). The Nevada curve should thus approximate a stationary age distribution. Comparison between it and the Baxter herd curve reveals a steeper slope for the latter, as would be expected on the basis of its increasing trend. Unexpected is the highly linear nature of both curves (Figure 11). Given a linear stationary age distribution, one curving upward at the lower ages would be expected for an increasing population, assuming unchanged adult mortality schedules. This assumption appears to be invalid for bighorn rams on the basis of changes in longevity related to nutrition and population trend discussed above. It is likely that this is the factor accounting for the linearity of both curves. Linearity may be the rule for ram stable age distributions of static or increasing populations. Data from more such populations may lead to an equation that predicts rate of population increase from the slope of the age distribution.

Figure 11. Age structures of rams in four different bighorn populations.



Stable age distributions are probably the exception rather than the rule. The 1975 age structure for the River Mountains in southern Nevada (Figure 11) is a case of a non-stable age distribution. Each segment of the curve is highly linear. The bend in the curve occurs between cohorts born in 1970 and 1971. Lamb:ewe ratios for the River Mountains show a jump at this time and the population increased from an estimated 80-100 in 1970 to 205 in 1973 to 256 estimated for the period between 1973 and 1976 (Leslie and Douglas 1979). This increase would account for the change in slope of the curve.

It is commonly incorrectly stated or implied that age structures measure survivorship (e.g., McQuivey 1978). In fact, age structure is related to survivorship through the finite increase rate λ ($=e^r$), assuming a stable age distribution; the two are equivalent only under the condition of a stationary population ($\lambda = 1$, $r = 0$)(Caughley 1966, 1977). Leslie and Douglas (1979) used the 1975 age structure from the River Mountains as a survivorship series for comparison with the classic skull-based data of Murie (1944). This use of the River Mountain data seems questionable, considering that (1) the age structure was probably not stable, and (2) the interpretation of Murie's data has been seriously questioned by Murphy and Whitten (1976).

It is common for populations at carrying capacity to exhibit considerable annual variation in recruitment as a function of density-independent factors (McCullough 1979). An age structure for a population fluctuating around carrying capacity is likely to yield a loose fit to a linear curve, as measured by its r^2 value. Geist's (1971) data for rams at Gladys Lake in 1962 seem to illustrate this case (Figure 11). The first three age classes suggest a declining population. The remaining age classes represent pre-decline cohorts and, while linear, they exhibit a much poorer fit to a line than the other data in Figure 11. The good fit of the Nevada data can be attributed to the smoothing effects of sampling many herds over numerous years.

Habitat

Bighorn, like other herbivores, are faced with the problem of maximizing their nutrient intake while concomitantly minimizing costs, such as energy expended and probability of predation. Optimization relative to nutrient intake or associated costs usually occurs at a sacrifice to the other. Natural selection can be expected to favor a behavioral program that balances the tradeoffs in such a way that maximizes reproductive success. Since the routes to reproductive success for the two sexes may differ considerably, it is likely that their behaviors will differ relative to habitat variables. Environments inhabited by bighorn differ seasonally, especially in terms of food availability and quality. One should thus expect seasonal changes in habitat exploitation.

Two habitat variables are consistently important to North American wild sheep: rockiness and openness (Geist 1971, Shannon et al. 1975). Safety from predators is sought in precipitous rocks. Openness of habitat allows optimal detection of predators; thus forests are avoided (Geist 1971). Vision is clearly the most important sense used by bighorn in this regard. Since precipitous rocks rarely support much vegetation, bighorn are frequently confronted with a tradeoff between safety and nutrient intake. The evolution of keen eyesight and choice of open areas near rocks for feeding has reduced risk by making predators detectable at sufficient distances to generally allow bighorn time to reach the safety of rocky terrain.

This section qualitatively examines seasonal use of habitats by Sierra bighorn in terms of rockiness, openness, and nutrient availability. Food habits and nutritional patterns are considered on a quantitative basis. Finally, patterns of reproduction are investigated relative to nutritional patterns.

Winter and Spring Ranges

Winter

The lowest elevations of winter ranges are set by the point at which the base of the eastern escarpment gives way to the alluvial fans constituting the western side of Owens Valley. Rock outcrops adequate for bighorn escape terrain occur in patches along the base of the escarpment, but are absent on alluvial fans. For the Baxter herd, the lowest rocks are at 1460m elevation at the mouth of Sawmill Canyon. This rises to 1580m at the mouth of Black Canyon and 1920m at the mouth of Thibaut Canyon (Figure 8). Throughout the Williamson herd range the lowest suitable rocks occur at 1950m elevation.

These elevational differences between the winter ranges of the two herds have an important effect on vegetative cover. The low elevation of the Baxter herd winter range places it largely in open steppe vegetation, below the level of forest. Only the higher Thibaut winter range has extensive pinyon forest. Pinyon forest is notably absent from the Sand Mountain and Sawmill winter ranges; thus open steppe vegetation extends to approximately 2130m where Jeffrey pines begin. Occasional sparse pinyon trees are present on the Black Canyon winter range.

The Williamson herd winter range differs markedly from the Baxter herd range in that pinyon forest is the predominant vegetation. Open steppe vegetation near rocks occurs only in scattered small patches on south-facing slopes at the mouths of the canyons of Shepherds, North Bairs, South Bairs, and Georges Creeks, and on a slope between the latter two canyons. These patches contain scattered pinyon trees, thus do not offer quite the visibility of the Baxter herd ranges. Their total area is small compared to the open habitat in the Baxter herd winter range (Table 7).

In comparison with steppe vegetation, pinyon forest suffers as bighorn habitat in three ways: (1) visibility is reduced, (2) its higher elevation means greater snow depth, and (3) understory vegetation of preferred forage species is sparse (Table 8). That pinyon forest is the less preferred of the two types is demonstrated by the common early winter movement of bighorn from the Thibaut winter range to the Black Canyon and Sand Mountain ranges. Likewise, in the Williamson winter range, bighorn show a clear affinity for the open patches of steppe vegetation (see sightings plotted on Figure 4), although pinyon forests are also used where sufficiently rocky.

The major distinction between winter ranges of the Baxter and Williamson herds lies in habitat availability as opposed to intra-habitat differences. Differences within the open habitat type are small. For instance, a comparison of favorite feeding patches in Sawmill Canyon and just north of Georges Creek show little difference in total vegetative cover or in percent cover of species preferred in the diet (Table 8). Species composition and total vegetative cover vary from location to location (Table 8), but availability of preferred forage species is consistently high on winter ranges throughout the open steppe vegetation type. *Ceanothus cordulatus* is a preferred forage species found on the Williamson winter range, but absent from the Baxter winter range due to elevation differences. Conversely, an

Table 7. Areas of seasonal ranges and population densities of the Baxter and Williamson herds.

Herd	Range	Area (km^2)	Population Density[1]
Baxter	Total winter range	10.65	20.09
	Open winter range	5.74	37.28
	Summer range[2]	52.63	3.12[2]
	Core summer range[2]	47.81	3.43[2]
	Fall range	44.81	4.78
Williamson	Total winter range	13.32	2.25
	Open winter range	1.16	25.86
	Summer range[2]	15.41	1.49[2]
	Core summer range[2]	10.85	2.12[2]
	Fall range	13.12	2.29

[1] based on 1978 census results (sheep/km^2)

[2] for ewes, lambs, and yearlings

Table 8. Vegetative cover of some winter range areas used by bighorn. Values are percent cover. Location numbers are plotted on Figure 13.

SPECIES	LOCATION:	PERCENT			COVER	
	16^1	14^1	15^1	17^2	4^1	18^3
Woody species						
*Artemisia tridentata**		1.4	1.8	5.6		
Chrysothamnus teretifolius	0.6	2.1			2.0	
Chrysothamnus nauseosus			3.1			
Chrysothamnus viscidiflorus				1.3		
*Purshia glandulosa**	1.7	2.0	2.4		0.6	
*Ephedra viridis**	1.1	2.9	3.0		3.8	
*Ephedra nevadensis**						0.1
*Prunus andersonii**			3.0		2.8	1.5
*Eriogonum fasciculatum**	11.6	5.8	1.1		13.9	2.8
Eriogonum microthecum					0.7	
Eriogonum wrightii		0.7				
*Ribes velutina**				1.5	1.6	
*Ceanothus cordulatus**	5.5					
*Keckiella breviflorus**			1.4			
Pinus monophylla seedling			0.4	0.1		
*Dalea fremontii**						2.0
Ceanothus greggii					0.01	
unidentified bush						0.2
Grasses						
*Stipa speciosa**	6.2	3.5	1.4	0.3	0.7	0.1
*Stipa coronata depauperata**				0.2		
*Bromus tectorum**						0.1
*Sitanion hystrix**	0.4					
Forbs						
Eriogonum nudum						0.5
*Convolvulus aridus**						0.8
Monardella odoratissima				0.1	0.2	
*Tauschia parishii**			0.1			
Salvia columbariae	0.01					
Opuntia erinacea	0.03					
Penstemon incertus				0.2		
*Caulanthus pilosus**				0.1		
Galium sp.					0.1	
Stephanomeria sp.					0.04	
Eriogonum sp.				0.2		
Total vegetative cover	27.1	18.4	17.7	9.7	26.4	8.1
Cover of preferred spp.	26.5	12.1	17.7	7.7	23.4	6.4
Sample size^4	183	183	244	91	183	152
Elevation (m)	1950	1975	2025	2100	1650	1450

[1] steppe vegetation typical of preferred feeding sites

[2] pinyon pine understory

[3] dry pumous slope

[4] meters of line intercept

* preferred species

herbaceous buckwheat (*Eriogonum nudum*) preferred by Baxter herd sheep is absent from the Williamson winter range. Winter range steppe vegetation offers, with few exceptions, substantially greater density of grazeable biomass than higher elevation feeding ranges.

Most of the species constituting steppe vegetation do not actively begin to grow until late winter or spring. The perennial needlegrass *Stipa speciosa* is a notable exception. New green leaves are produced at the base of dry leaves from the previous season as soon as soil moisture is sufficient. The timing of this varies considerably. Due to early fall precipitation, needlegrass in the Baxter range had considerable new growth by December of 1975 and 1976 prior to the appearance of bighorn there. In the following two winters (1977-78, 1978-79) new growth was not apparent until the first half of February.

Although winter range precipitation in fall may occur in the form of rain, early winter precipitation is largely in the form of snow. Snow on south-facing exposures melts rapidly following storms, while north slopes may remain snow covered for weeks; melting on east-facing exposures lags somewhat behind south-facing ones. It is this early snow melt that provides soil moisture for initiation or continuation of needlegrass growth. South-facing slopes should provide the earliest and most rapid needlegrass growth due to higher temperatures, thus should offer the best nutrition. Bighorn in both herds exhibit a clear preference for south-facing exposures in winter. Needlegrass growth probably plays a role in this preference, but cannot be clearly separated from preference due to the snow-free nature of these exposures. Also, for the Williamson herd, open habitat is confined largely to south exposures.

Four other winter range species, *Leptodactylon pungens*, *Eriogonum nudum*, *Bromus tectorum*, and *Sitanion hystrix* begin active growth in winter. All are of small importance in terms of density of grazeable biomass compared to needlegrass, but all are eaten by bighorn in winter.

On the basis of direct observation and inspection of feeding sites, it is evident that needlegrass is the most important dietary item in winter for both herds. Next in importance are the following browse species: *Eriogonum fasciculatum*, *Artemisia tridentata*, *Ephedra viridis*, *Keckiella breviflorus*, and *Purshia glandulosa*, *P. tridentata*, and their hybrids. *Ceanothus cordulatus* is also an important browse species for the Williamson herd. *Leptodactylon pungens*, *Chrysothamnus nauseosus*, *Eriogonum nudum*, *Sitanion hystrix*, and *Bromus tectorum* are eaten in small quantity.

Quantification of food habits by the fecal microhistological technique has verified this general order of importance (Table 9), as have analyses of rumen samples from winter (Table 10). Grass is clearly the primary dietary item in winter, constituting 42-83% of the diet.

Based on direct observation of feeding bighorn, McCullough and Schneegas (1966) and Dunaway (1972) each recognized needlegrass as an important forage species, but concluded that the winter diet of the Baxter herd was primarily browse. The discrepancy between their findings and the results in Table 9 probably lies in the variation among forage species in the amount consumed per bite. On careful examination, it is common to find bighorn taking a single browse leaf per bite, whereas a whole mouthful of grass is usually obtained with each bite of needlegrass. Browse is nevertheless an important diet component, constituting an average of 38% for the nine winter samples in Table 9.

Only minor differences in food habits between the Baxter and Williamson herds are evident for the nine winter samples in Table 9. The Williamson herd samples show a slightly higher grass content and lower *Ephedra viridis* and *Eriogonum fasciculatum* values. *Ceanothus cordulatus* is present in Williamson herd samples and absent from the Baxter herd diet. Considering the large amount of variation in diet composition apparent among samples collected the same day from a single bighorn group (e.g., 3/11 samples in Table 9), it seems unwise to assign significance to these slight dietary differences between herds.

Spring

The timing of spring greenup on winter ranges is more predictable overall than that of needlegrass. Some species

Table 9. Results of microhistological analyses of winter and spring diets in 1978. Values are percents.

	SAMPLE IDENTIFICATION																
Date:	2/2	2/4	2/4	2/4	3/11	3/11	3/11	3/14	3/14	4/16	4/16	4/20	4/20	5/12	5/12	5/18	5/18
Herd[1]:	B	W	W	W	B	B	B	W	W	B	B	W	W	B	B	W	W
Location[2]:	Sawm	Geo	Geo	Geo	Sawm	Sawm	Sawm	Geo	Geo	Sawm	Sawm	S.B	S.B	Sawm	Sawm	S.B	S.B
SPECIES																	
Grass[3]	62.9	79.0	68.5	81.3	48.8	42.7	70.4	66.4	82.6	33.6	30.0	38.6	34.5	35.0	26.0	34.1	40.3
Artemisia tridentata	17.2	5.7	9.9	7.3	8.8	9.3	13.3	10.0	3.9	1.0	1.1	5.3	11.5	5.6	.3	48.0	37.5
Eriogonum fasciculatum	6.6	1.3	1.1	1.5	25.3	15.9	5.0	1.0	1.7	11.5	7.4	3.5	7.6	22.2	16.1	.6	
Ephedra spp.	3.3	1.6	.6	2.0	5.3	11.7	.5	4.3	.2	21.4	24.2	8.5	8.8	11.1	29.1	.3	
Purshia (hybrids)	8.5	8.2	18.2	4.1	7.9	18.0	1.1	12.3	7.0	26.3	23.9	35.7	24.2	16.7	20.4	6.6	4.0
Keckiella breviflorus	.3	.3	.3	2.9	.3	2.1	.5	3.5	.7	2.3	2.1	6.6	3.0	.3	1.2	1.6	.3
Eriogonum nudum					2.8		.5			.5							
Leptodactylon pungens		1.6		.6			6.6			.3						1.3	2.8
Ceanothus cordulatus		1.9	1.4	.3				2.0	3.1			.3	.6				.6
Pellea compacta	.3	.3					.8										
Haplopappus cuneatus	.3						.8										
Cercocarpus ledifolius					.3											4.1	12.8
Lupinus excubitus									.7								
Ribes velutina										2.3	.8	.9	4.8	.6	2.8	1.3	.6
Prunus andersonii										.3	2.1	.6	.9	2.6	.6		
Tauschia parishii											8.2		3.9	5.9	3.1		.8
Chrysothamnus nauseosus																.6	
Penstemon bridgesii																1.6	.3
unknown forb or shrub										.5							
fragments sampled	302	314	352	343	315	332	359	389	414	384	376	319	330	306	323	317	352

[1] B - Baxter; W - Williamson

[2] Sawm - Sawmill Canyon; Geo - just north of Georges Creek; S.B - South Bairs Canyon

[3] primarily *Stipa speciosa*

Table 10. Results of analyses of rumen samples obtained in winter and spring. Values are percents.

TIME PERIOD:	late Jan.	Feb.-March	March-April	late April
HERD:	Baxter	Baxter	Williamson	Baxter
LOCATION:	Sand Mt.	Sawmill	Shepherd Cr.	Sand Mt.
SPECIES				
Stipa speciosa	79.3	45.5	41.7	30.0
unidentified grass[1]	.7		22.1	27.3
total grass	80.0	45.5	63.8	57.3
Artemisia tridentata	8.0	10.3	.6	
Ephedra viridis	2.0	8.3	2.4	.7
Eriogonum fasciculatum	2.0			
Purshia glandulosa		2.1		
Keckiella breviflorus		27.6		1.3
Cercocarpus ledifolius			7.4	2.7
Ceanothus greggii				6.0
Prunus andersonii				5.3
Chrysothamnus nauseosus				5.3
Leptodactylon pungens		.7	.6	
browse leaf	2.7	.7	.6	4.0
browse stem		4.8	23.9	16.0
forb				1.4
pupal case			.6	
fragments sampled	150	145	163	150

[1] including *Stipa speciosa*

are highly predictable in the timing of the appearance of new leaves, while others have been noted to vary as much as three weeks between years at the same location. The greatest variation is spatial, and depends on exposure and elevation, both of which strongly influence temperature.

Ribes velutina is the first shrub to leaf out. This occurs in the last week of February or first week of March at 1500m at the base of the Baxter winter range. Over the course of about six weeks thereafter, all other shrub species initiate new growth.

The timing of growth initiation is inversely proportional to elevation. Leaf-out of *Prunus andersonii* at 1430m elevation outside the mouth of Sawmill Canyon varied only three days (11-14 March) over three years (1977-1979). Because of this high predictability, this species was used to calculate the elevational lapse rate of greenup using data spanning four years and 1460m elevation. The resultant rate of 17.8m of elevation per day is highly predictive ($r^2=.943$; $P<.001$; $N=12$). Plant development on a favored spring feeding area at 1950m at the mouth of South Bairs Creek in the Williamson herd winter range lags about three weeks behind a similar spring feeding site at 1525m at the mouth of Sawmill Canyon.

As spring greenup proceeds, the bighorn diet expands to include fresh growth of numerous species. Table 11 is a list of species observed to be eaten during March, April, and May. A shift away from grass is apparent. Three shrub

Table 11. Forage species observed to be eaten in March, April, and May.

Species	Winter ranges Baxt.	Winter ranges Will.	Lambing ranges Blk. Can.	Lambing ranges S. Bairs
Stipa speciosa	X	X		X
Stipa coronata		X		X
Oryzopsis hymenoides	X	X	X	X
Poa sp.		X		
Sitanion hystrix		X		
Bromus tectorum	X			
Artemisia tridentata	X	X	X	X
Eriogonum fasciculatum	X			
Eriogonum nudum	X			
Eriogonum microthecum	X			
Ephedra viridis	X			
Ephedra nevadensis	X			
Keckiella breviflorus	X	X		
Purshia (hybrids)	X		X	
Lupinus excubitus	X			
Ribes velutina	X	X		
Dalea fremontii	X			
Prunus andersonii	X			
Tetradymia axillaris	X			
Leptodactylon pungens		X	X	X
Chrysothamnus nauseosus	X			
Convolvulus aridus	X			
Tauschia parishii	X			
Heuchera sp.		X		
Cryptantha sp.		X		
Caulanthus pilosus	X			
Penstemon bridgesii				X
Arctostaphylos patula (flrs)			X	
Carex rossii			X	
Angelica lineariloba			X	

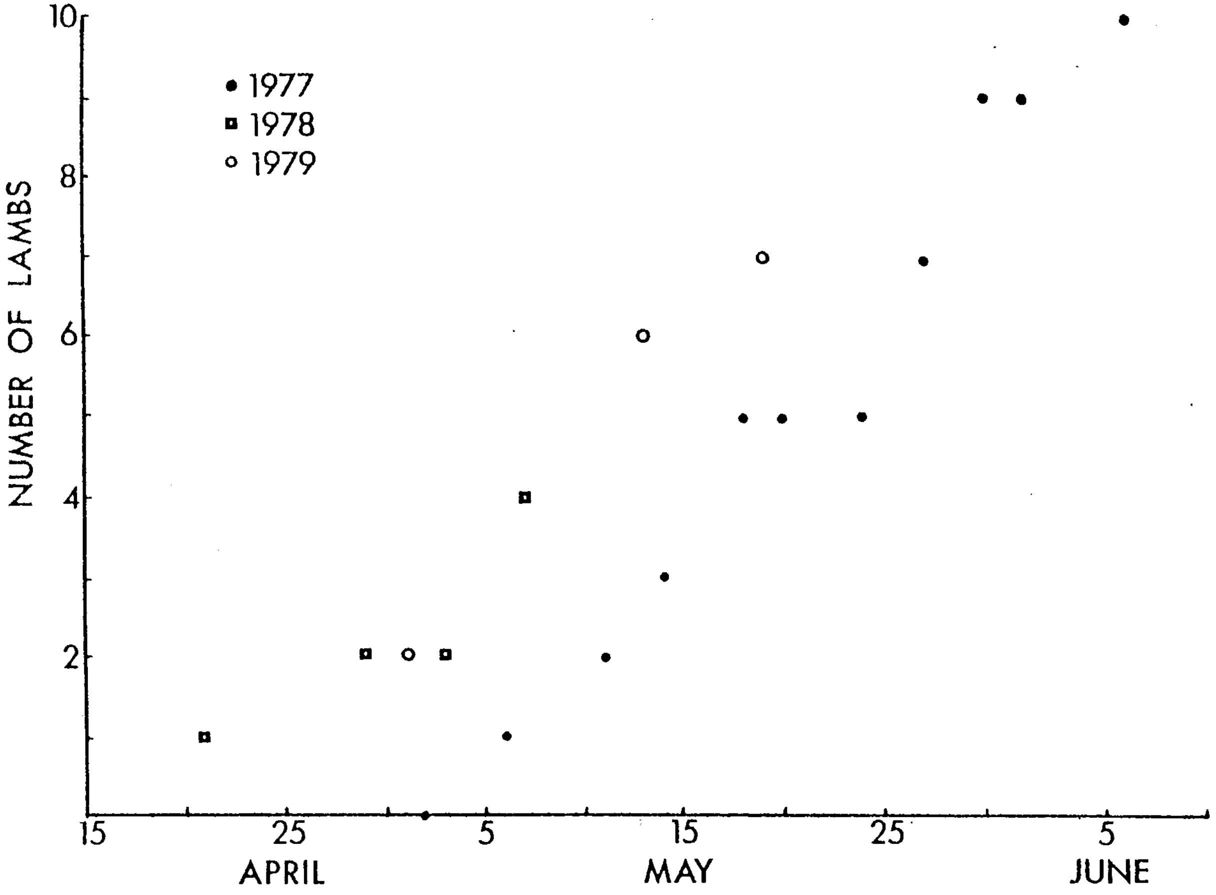
species, Ephedra viridis, Eriogonum fasciculatum, and Purshia spp. and hybrids, are frequently browsed on the Baxter herd winter range in April and May during peak vegetative growth. Fecal microhistological analysis also showed these changes in food habits (Table 9).

During early spring, while greenup is still largely confined to the lowest elevations, bighorn distribution in the Baxter herd shifts to these lower elevations. During the period from late February through the first half of April, it is common for bighorn groups to make forays out from the lowest rocks on either side of Sawmill Canyon mouth. These occasionally extend as far as 375m from rocks and allow the sheep to attain a lower elevation than the rest of the winter range.

Lambing Period

The lambing period was determined by frequent censuses of Sawmill Canyon during spring. In 1977 some ewes with older lambs left the canyon before lambing was complete, but recognition of individual lambs through size and the molting patterns of their mothers allowed a cumulative total to be obtained until all sheep had vacated the winter range in early June. Lambing was earlier in 1978 and 1979 when lamb production was relatively low (Table 4) compared with 1977 (Figure 12). For all years combined, the lambing period extended from 21 April to 6 June, but appears not to exceed one month in duration in any particular year.

Figure 12. The timing of lambing in Sawmill Canyon in 1977-1979. The 1979 data include known lambing dates of ewes transplanted from Sawmill Canyon to a new range.



Habitats used by ewes at the time of lambing are more restricted than during winter, causing many to leave most wintering areas during April and early May. This is true for South Bairs Creek in the Williamson range, and the Black Canyon and Sand Mountain areas of the Baxter range. Sawmill Canyon is the notable exception, presumably due to its open and precipitous nature. Ewes wintering on the Black Canyon and Sand Mountain ranges move into Black Canyon, except for a few Sand Mountain ewes that lamb on the south side of Sawmill Canyon. Ewes in South Bairs Canyon simply move higher in the Canyon.

Habitats in which births take place have not been recorded, but are presumably precipitous rocks away from trees. In the Sawmill Canyon winter range this occurs at 1650-1750m elevation. Judging from habitat, lambing probably takes place as low as 1950m in Black Canyon and 2600m in South Bairs Canyon. Habitats used for 2-3 weeks following births have been noted in Sawmill, Black, and South Bairs Canyons. In Sawmill Canyon the habitat is treeless winter range at 1700m elevation, composed of steep sandy vegetated slopes and chutes broken by ridges of rock outcrop. Transect 5 in Table 8 is through a feeding area in this habitat.

Black Canyon has only occasional tree patches that ewe-lamb groups easily avoid. Feeding areas include steep avalanche chutes in rock, and extensive brush slopes adjacent to rocks. The brush patches are dominated by bitterbrush (*Purshia tridentata*), sagebrush, manzanita (*Arctostaphylos patula*), and rabbitbrush (*Chrysothamnus viscidiflorus*). Additional shrubs include *Ceanothus cordulatus*, *Holodiscus microphyllus*, *Eriogonum microthecum*, *Symphoricarpus vaccinoides*, *Leptodactylon pungens*, and *Acer glabrum*. *Oryzopsis hymenoides* is the bunchgrass present. The rocks are dominated by mountain mahogany (*Cercocarpus ledifolius*). Known dietary items from this habitat are listed in Table 11. *Ceanothus cordulatus* and *Holodiscus microphyllus* are known to be preferred species elsewhere, thus are probably also included in the diet in Black Canyon.

South Bairs Canyon lacks the mid-elevation brushy feeding slopes adjacent to rocks that characterize most Black Canyon feeding sites. In mid-elevation, most of South Bairs Canyon is covered by pinyon forest, leaving open brush vegetation almost exclusively in steep avalanche chutes. These are lined with pinyon forest except at their upper extremes, where they grade into steep rock faces. It is at these upper extremes, at an elevation of about 2800m, where ewes with new lambs were observed feeding in mid-May of 1978. These sites are dominated by mountain mahogany, sagebrush, and fern bush (*Chamaebatiaria millefolium*), with occasional members of the following species: *Eriogonum microthecum*, *E. wrightii*, *Symphoricarpus vaccinoides*, *Penstemon rockrothii*, *Leptodactylon pungens*, *Acer glabrum*, *Chrysolepis sempervirens*, *Rhamnus californica*, *Prunus andersonii*, *Holodiscus microphyllus*, *Chrysothamnus* *nauseosus*, *Ribes cereum*, *R. montigenum*, *R. velutina*, *Ceanothus cordulatus*, *Penstemon bridgesii*, *Opuntia erinacea*, *Galium* sp., *Oryzopsis hymenoides*, *Stipa coronata*, *Stipa speciosa*, *Poa* sp., and *Sitanion hystrix*. Species noted to be eaten at this location by site inspection are listed in Table 11.

During the lambing period vegetation on winter ranges is at peak growth, thus should offer the best possible nutrition. This is presumably the reason why (1) many ewes remain in the Sawmill Canyon winter range during lambing, and (2) most rams and some yearlings and barren ewes remain on winter ranges until late May.

Elevation differences play a key role in the comparison of nutrition on the Sawmill Canyon, Black Canyon, and South Bairs Canyon lambing ranges. In Black Canyon, ewe-lamb groups have been observed in May in an elevational range of 2200-2650m. At the lower extreme the elevational difference from Sawmill Canyon is only 500m, which by the greenup rate of 17.8m/day would set the vegetation development back 28 days. This is equivalent to mid-April in Sawmill Canyon, when spring growth is already abundant. What is significant about the Black Canyon lambing range is that the habitat allows the sheep a large elevational range. The higher elevational records are from drought years and have not been representative of later years when snow still covered many patches which were used in May during the drought.

The South Bairs lambing range habitat does not offer the same elevational latitude because of the extensive pinyon forest. In 1978 the sheep there showed the same patterns as the Sawmill Canyon sheep of feeding low on the winter range in April, but then suddenly moved up considerable elevation for lambing. In mid-May of 1978, the elevational difference from Sawmill Canyon sheep was 1100m. By the greenup rate of 17.8m/day this should be equivalent to the Sawmill Canyon range 62 days earlier, or mid-March, when spring greenup was just beginning. This is just what was observed on the South Bairs site in May. *Leptodactylon pungens*, *Penstemon bridgesii*, and grass species were green, but other species were still in winter condition. This is reflected in the food habits data from this site (5/18 samples on Table 9), which indicate that the sheep had to fill in their diet with a large amount of sagebrush and even mountain mahogany, which is otherwise avoided. At this same time, the sheep in Sawmill Canyon were feeding largely on *Eriogonum fasciculatum*, *Ephedra viridis*, and *Purshia* spp. which were at peak growth (Table 9). The general forest and rock conditions in South Bairs Canyon is representative of the other Williamson range canyons, with the possible exception of Georges Creek Canyon, where the elevational rise to potential lambing sites appears to be less. However, no evidence of lambing could be found there in late spring of 1978. Certainly, the Williamson range offers no conditions approaching the ideal circumstances found in Sawmill Canyon.

Migration from winter to summer ranges covers a long period, beginning in mid-April, when some ewes leave winter ranges for higher lambing ranges, and ending in the first half of July when the last sheep enter the alpine. This is in strong contrast to the rapid descent that follows the first major winter snow storm. Ideally, spring ascent would be at a rate of approximately 18m per day, whereby the sheep could remain in the zone of optimum growth condition of spring vegetation. As pointed out above, other habitat requirements of ewes at the time of lambing take precedent, causing some to move up in elevation, thereby leaving the zone of optimum vegetation condition.

Rams do not exhibit the same habitat selection of ewes during the lambing period and may be found in timbered areas and away from precipitous rocks. One would expect rams to follow the elevational changes in vegetation more precisely. This appears to be the case. Most rams remain on winter ranges until mid-May, then slowly move up. They may be observed crossing Sawmill Pass and dropping down the west side from early June to mid-July.

Ewe-lamb groups were seen above timberline as early as the second week of June, but are not generally that high until late June. High peaks, such as the summit of Mount Baxter, are not used until mid-July. The greenup equation predicts that at timberline (3400m) the last week of June should be equivalent to the beginning of March at the mouth of Sawmill Canyon, when shrubs first began breaking bud.

This is a good general prediction for shrubs that are free of snow at that time, but graminoid species green up earlier, if snow-free, as was also found on winter ranges. Likewise, many alpine forb species begin growth much earlier if snow-free.

Winter Range Forage Utilization and Competition

Interspecific competition means the use by more than one species of a resource in short supply that is necessary for at least one of the species. This may occur as interference competition, where one species physically denies another access to a resource, or as exploitation competition, where access is uncontrolled. This latter type of competition has been investigated on bighorn winter ranges in the Sierra Nevada.

Ranges of mule deer and tule elk overlap the bighorn winter ranges, providing the potential for competition. Mule deer commonly migrate out of the high country in fall six to eight weeks before winter storms force the bighorn down. Many of the deer then spend the fall and early winter at intermediate elevations above the floor of Owens Valley. Sand Mountain, Sand Canyon, and the Black Canyon winter range have been found to provide such deer ranges. When snow forces bighorn down, they share their winter range with deer until about mid-February, at which time the deer move down onto alluvial fans of the valley floor. Deer spend the remainder of winter there, occasionally moving onto the lower slopes of the Sand Mountain, Sawmill, and Black Canyon bighorn winter ranges. Beginning about the first of May, deer again occupy the Sand Mountain bighorn range as they move up following spring vegetation greenup. At this time it is mostly rams that remain on the Sand Mountain range. Bighorn and deer readily mix while feeding. Thus no interference competition is apparent.

The first appearance of elk on the bighorn winter range also coincides with spring greenup. While the deer move upward as spring progresses, the elk continue to use the Sand Mountain and Black Canyon ranges. This is particularly true of the latter, due to the availability of water, which is entirely lacking in Sand Canyon and on Sand Mountain. The duration of summer elk use of these ranges has not been determined. Curtis et al. (1977) noted that, unlike the other elk herds in Owens Valley, the Goodale herd does not gather at low elevation during the rut, but remains spread out in relatively small groups. Thus, some use of the bighorn winter range by elk may continue through summer and possibly into fall. No elk have been observed on the bighorn winter ranges during winter.

On the Williamson herd winter range there is no sign of use by the Mount Whitney elk herd. Thus the only potential competition would involve deer.

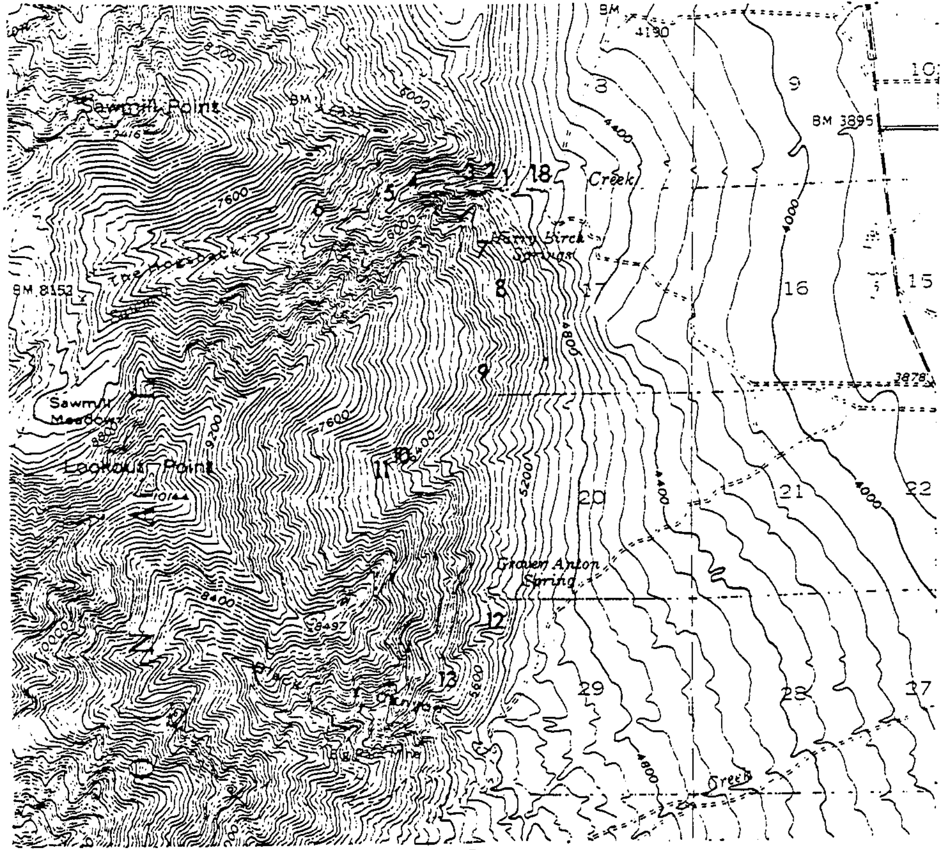
The utilization of two important forage species, desert needlegrass and bitterbrush, was quantified to determine whether either was in short supply. Elk feed on both species to a high degree (McCullough 1969, Curtis et al. 1977). Bitterbrush is an important forage species of deer on the ranges under discussion (Jones 1954, McCullough 1969), while needlegrass may receive a small amount of spring use by deer (Jones 1954).

Green growth of needlegrass dries up in late spring or early summer, depending on the occurrence of spring rains and the onset of summer heat. Initiation of new growth has been previously discussed. Competition with elk for needlegrass would involve the dry growth of the previous year, which the sheep must eat first regardless of whether new green growth exists at its base. Such competition would occur if elk were to consume a large enough quantity of needlegrass during the previous spring and summer to leave an inadequate supply to sustain the bighorn until sufficient new growth exists.

Data on utilization of needlegrass and bitterbrush are summarized in Table 12 and locations of the measurements are plotted in Figure 13. Total bitterbrush utilization has generally been quite low, and has never exceeded the 60%, which Hormay (1943) considered the maximum plants could withstand without loss of vigor. The relatively higher bitterbrush utilization recorded on Sand Mountain in 1976 (Table 12) may reflect a prolonged use of that area by deer due to the very late arrival of the first winter storms in February. It seems apparent that bitterbrush was not in short supply in the bighorn winter ranges and thus was not a

Figure 13. Locations of vegetation transects and forage utilization measurements on bighorn winter ranges in the Sierra Nevada. Map A is the Baxter herd winter range and Map B is the Williamson herd winter range.

A


Sawmill Point
BM
4130
3
9
10
BM 3895
18
Creek
Spring
16
15
BM 8152
The Hogsback
17
3878
Sawmill Meadow
Lookout Point
10144
20
21
22
Graven Anton Spring
29
28
27
Creek
1
2
5
6
7
8
9
10
11
12
13
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4400
4800
5200
5600
7600
8400
9200
10000

B

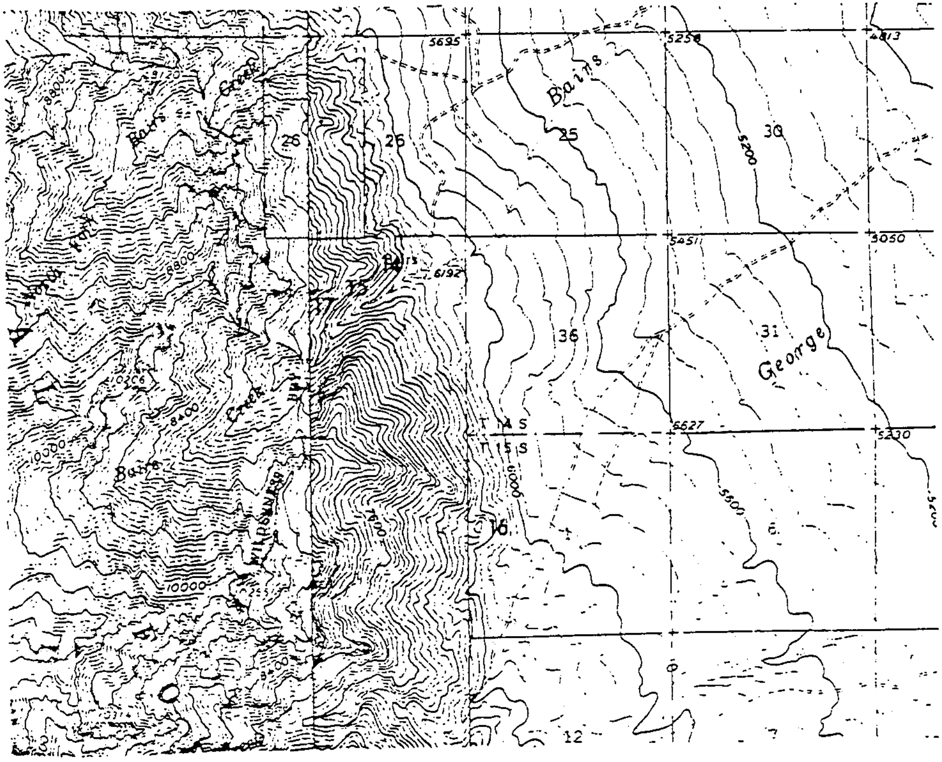

5695
5250
4813
Bairs
Creek
26
25
30
5451
3050
Bairs
6192
35
36
31
George
T 14 S
T 15 S
5627
5230
Bairs
Creek
10326
10000
6
12
7
8800
8400
5200
5600
6000

Table 12. Summary of desert needlegrass, bitterbrush, and *Keckiella breviflorus* utilization measurements on bighorn winter ranges in the Sierra Nevada. Location numbers are plotted on Figure 13.

Location & Year	Description	Forage Species	% of Plants or Leaders Grazed	Percent Utilization	Sample Size (Plants or Leaders)
		Needlegrass			
1976					
2			92		40
3			84		25
1977					
1	10 yds. from rocks		84	63	84
	20-30 yds. from rocks		28	15	54
	40-60 yds. from rocks		12	9	57
2			79	59	105
3			82	73	57
5			81	68	127
6			90	82	89
9			54	35	127
10			48	32	83
11			17	13	46
12			54	26	109
14			39	28	107
15			29	20	113
1978					
1	100 yds. from rocks		77	62	132
4			94	92	171
5			85	78	121
6			62	60	155
7			85	80	158
8			54	43	124
9			57	47	141
12			76	48	115
13			47	37	103
16			30	26	132

Table 12 (continued)

Location & Year	Description	Forage Species	% of Plants or Leaders Grazed	Percent Utilization	Sample Size (Plants or Leaders)
		Bitterbrush			
1976					
2			11		159
3			8		400
9			53		365
1977					
2			27		698
3			26		1106
5			16		976
6			10		901
9			18		1319
10			5		927
11			36		912
12			30		1108
14			6		945
15			1		922
		K. breviflorus			
1977					
2			60	36	204
3			83	42	145
9			64	28	184
10			40	18	185
12			62	27	154
14			27	8	142
15			14	8	121

resource for which competition existed during this study.

With one exception, utilization of needlegrass has been found to be heavy only on the Sawmill Canyon range, on which there is no deer or elk use during the year. The exception is the sand chute above Harry Birch Springs (location 7 in Figure 13). Higher than normal bighorn use was observed there in 1978, resulting in an overall utilization of 80% of the needlegrass (Table 12). Elk cannot be implicated in this relatively high utilization, as this site is used by elk only as they move up and down Sand Mountain, rather than as a feeding area.

Immediately prior to the appearance of bighorn on the winter range in December of 1977, the needlegrass utilization was measured at location 12 (Figure 13) on the Black Canyon range and found to be 34%, which increased only to 48% by the end of winter. Under circumstances of poor needlegrass production, these percentages will increase, and may result in a shortage where production is sufficiently low, or bighorn utilization increases due to deep snow preventing them from exploiting the Sand Mountain range. Competition is not likely to occur on Sand Mountain or in Sand Canyon since most elk use there occurs in the higher areas; these upper areas are normally snow covered for much of the winter, and thus receive little sheep use.

Other major winter forage species, i.e. _Artemisia tridentata_, _Ephedra viridis_, and _Eriogonum fasciculatum_ show only minimal signs of grazing use. _Keckiella breviflorus_ is the only species besides needlegrass that shows noticeable sign of grazing use by bighorn. Its utilization was measured in the spring of 1977 by randomly selecting branches and measuring the lengths of all leaders of the previous year's growth, while simultaneously classifying each as browsed or unbrowsed. This allowed the same calculation of % browsed and % utilization as used for needlegrass. The results (Table 12) indicate a high level of utilization. The levels for the mouth of Sawmill Canyon may approach the maximum possible utilization, because the woody structure of the plant limits access to many leaders.

Measures of plant productivity and utilization are indirect measures relative to the question of competition. If competition is of significance, its ultimate influence will involve demography of the population(s) in question. The recent population increases in the Baxter herd indicate that competition has not been of importance. Such conclusions are limited to the circumstances of investigation, since sizes of potentially competing populations as well as of the biomass of the resource(s) in question can change, as noted above. The present management of tule elk in Owens Valley calls for halting further population growth (Curtis et al. 1977). This should greatly reduce the probability of competition occurring.

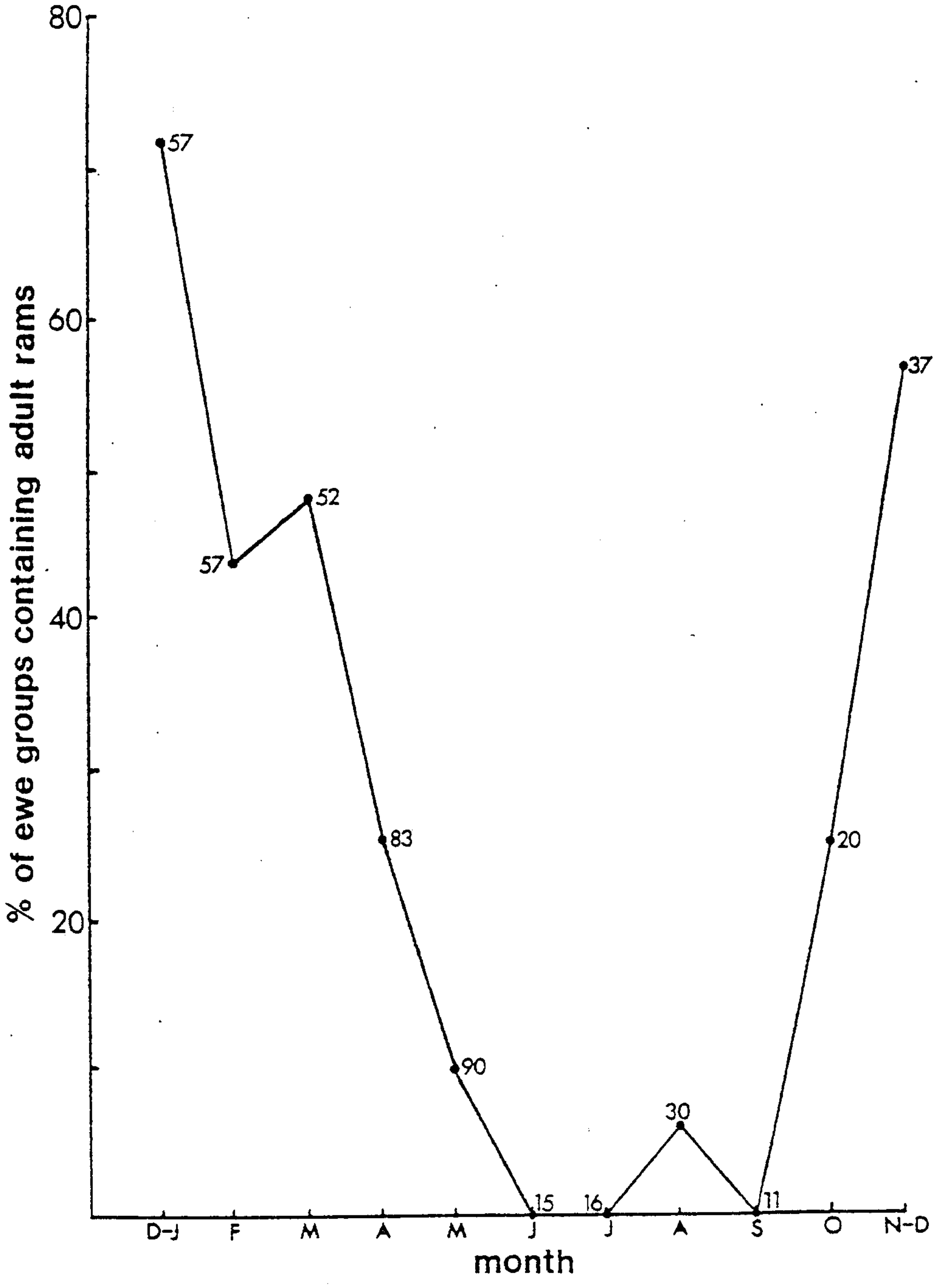
Needlegrass eaten by tule elk on bighorn winter ranges may actually enhance bighorn nutrition the following winter. A considerable amount of old growth must be eaten by bighorn in winter before much of the new growth can be consumed. While this old growth is important sustenance before new growth is present in adequate quantity, it becomes a detriment thereafter. In removing some of this old growth during summer, elk may allow bighorn to consume a higher ratio of new to old growth in winter, thus enhancing their nutrition.

Sex Segregation

Spatial segregation of males and females outside the mating season is common among ungulates (McCullough 1979), including bighorn sheep (Geist 1971, Geist and Petocz 1977, Leslie and Douglas 1979). Yearling rams remain with female groups during their second year, although they are occasionally seen with rams in summer and frequently in late winter as they approach two years of age. As two year olds they assume the patterns of adult rams, except for a small percentage that remain with females for an extra summer. An occasional two-year-old ram was recorded with females in the Baxter herd during every summer of this study.

A complete measure of spatial separation of the sexes would require a representative sampling of both sexes throughout the year, which was not feasible. Alternatively, an index of separation can be developed relative to one sex to elucidate seasonal patterns. This was done for the Baxter herd by plotting the percent of female groups which contain adult rams (Figure 14). Because the occasional 2-

Figure 14. Annual sex segregation pattern of the Baxter herd. Adult rams are considered three-year old and older. Sample sizes are adjacent to points.



year old rams in female groups in summer are not representative of the adult rams population as a whole, adult rams were considered to be three years old and older for this purpose.

The greatest mixing of the sexes occurs in early winter immediately after sheep enter the winter range, but declines steadily until complete segregation occurs in June when winter ranges have been abandoned and high country ranges begin to be occupied (Figure 14). The sharp spring increase in segregation is largely a reflection of ewes and accompanying yearlings and lambs changing habitats for lambing, rather than changes in ram behavior. Nevertheless, separate ram groups are to be found throughout the period they are on winter ranges. Also, within mixed groups in winter, adult rams commonly form subgroups. It would thus appear that, outside of the mating season, mixed groups occur when female and male groups happen to mix where their habitats overlap; this overlap is large in winter. If so, one would predict that mixed groups would be generally larger than groups of either sex if other habitat variables affecting group size are controlled. This was tested on the Sand Mountain winter range, where minimal variation in forage cover (high) and rock cover (low) exist, both of which potentially affect group size (Alexander 1974). For the period from January through April, female and male groups were not significantly different in size (t=.076; d.f.=33), averaging 7.1 and 6.9 sheep respectively. Mixed groups averaged 32.0 individuals, and were barely significantly (P=.05) larger than male and female groups pooled (t=1.99; d.f.=79).

Although habitats used by rams and ewes are largely overlapping in winter, a small difference may exist. Prior to spring greenup on the Sawmill and Sand Mountain winter ranges, ram groups appear to range into the higher forested areas more readily than females. Nevertheless, female groups are occasionally found in these areas also.

The separateness of the ranges of ram and ewe groups during summer has been previously delineated (Figures 6 and 7). This results in the zero values for the summer period in Figure 14. The western boundary of the northwestern section of the Baxter ewe-lamb range in summer (Figure 6) overlaps the eastern boundary of the ram range slightly (Figure 5). On two occasions ram and ewe groups that were temporarily mixed were encountered along this boundary, resulting in the non-zero value for August in Figure 14. In the second week of October, rams begin joining ewe-lamb groups, causing the autumn rise in Figure 14.

Summer and Fall Ranges

The restricted habitat use of ewes at lambing continues through summer until lambs are weaned in early fall. The treeless rocky expanse of the alpine constitutes the summer habitat of ewe-lamb groups. Throughout summer rams exhibit less restrictive habitat use relative to the safety of openness and rocks, and are found almost entirely at or below timberline in the subalpine.

Vegetation Types and Their Use

The most striking feature of the southern Sierran alpine is its barrenness. Large areas are virtually devoid of vegetation due to surface of bare rock or talus with minimal soil between rocks. Consequently, vegetation is very patchy in distribution. Furthermore, existing patches vary greatly in size, composition, and vegetative cover. Many plant associations have been delineated (Major and Taylor 1977). This complexity has precluded any meaningful detailed quantitative vegetation comparison of the alpine ranges of the Baxter and Williamson herds. However, consideration at this level of detail is probably of little merit relative to bighorn, since they appear to key on broad vegetation classes rather than specific associations. Throughout this study vegetation cover of a large variety of alpine vegetation patches was measured to illustrate the diversity of types and the general sparsity of plant cover. Since these transects were subjectively placed in vegetation patches, they are not representative of the overall vegetative cover. However, locations 10 and 21 on Figure 15, whose vegetative cover values are presented in Table 13, represent the sparsity of much of the interpatch vegetation.

In general plant cover on vegetation patches becomes sparser with increasing elevation (Tables 13, 14). When the

Table 13. Vegetative cover measurements for high alpine patches. Locations are plotted on Figures 15 and 16.

	PERCENT COVER																								
PLANT SPECIES Location:	5	9	10	11	12	14	15	16	17	17	18	18	19	19	20	21	22	23	25	26	27	27	27	27	28
Graminoids:																									
*Sitanion hystrix**	.3	.4				.9		.05	.4		.01	.3	.8	.3	.02	.1		.6	1.8	.6			.1	.7	.2
Festuca brachyphylla	.03	.3		.8	.1	.3	.6				.02	.1	.2			.04					.04	.1			
Muhlenbergia richardsonis		9.5				5.2	1.0												.7	1.3					.7
Calamagrostis purpurascens							1.2												.7	1.3					.7
*Stipa pinetorum**		1.5				1.0																			
*Poa rupicola**			.02																						
Poa sp.*																									.3
*Juncus parryi**							3.8	.01																	
Luzula spicata				.1																					
*Carex exserta**		1.8																							
Carex leporinella			.04				1.6													1.3					.5
*Carex helleri**			.2	1.6	.1		1.0														.7	2.6	.2		
*Carex rossii**						.7													1.3	1.9					.1
Carex sp.								.2																	
Forb Species:																									
Erysimum perenne								.07																	
Arabis spp.					.04	.04																			
Potentilla sp.	.4																								.8
Sibbaldia procumbens				.3			.4																		
*Ivesia pygmaea**					1.8															5.0	2.5		2.3	.4	
Ranunculus eschscholtzii				.1																					
Monardella odoratissima																			.9						
Castilleya nana	.02	.3				.1																			
*Polemonium eximium**	.9								1.7	1.4		1.3	1.8	2.3	1.2	.3	2.6	2.6						3.0	
Antennaria spp.				2.4			1.0													1.3					
*Hulsea algida**	.1							1.4	.8	2.1	1.2	.7			.1					.6			.1		
Erigeron compositus						.7			.6	.1			.1		.2				.4					.2	
Erigeron vagus																.2	.1	.7							
Haplopappus macronema																			1.6						.8
Selaginella watsoni																				1.9					
Woody Species:																									
Ribes cereum						2.4							.8						2.7	.6					
Penstemon davidsonii			.3																						
*Leptodactylon pungens**		2.3					.2	.5											3.8						2.9
*Tanacetum canum**																			.2						
Cushion Plants:																									
Eriogonum ovalifolium	4.6	5.3			1.0	7.5	.6	.3	.03		.5	2.4							.7				.7	2.4	
Astragalus kentrophyta	2.3	.5				3.7	.4																		
Draba spp.	.01					.03																			
Total Vegetative Cover	8.7	21.9	.6	5.3	3.0	22.6	11.8	2.5	3.5	3.6	1.7	4.8	3.7	2.6	1.5	.6	2.7	3.9	15.1	14.5	3.2	2.7	3.4	6.7	6.3
Frequently Eaten Species	1.3	4.5	.2	1.6	1.9	2.6	5.0	2.0	2.9	3.5	1.2	2.3	2.6	2.6	1.3	.4	2.6	3.2	7.1	3.6	3.2	2.6	2.6	4.1	3.5
Elevation (X 1000m)	3.96	3.72	3.63	3.60	3.69	3.81	3.44	3.54	3.78	3.78	3.72	3.72	3.69	3.72	3.84	3.72	3.84	3.99	3.69	3.51	3.75	3.72	3.69	3.75	3.38
Sampling Method¹	l	l	l	l	l	l	p	l	l	l	l	l	l	l	l	l	l	l	p	p	l	l	l	l	l
Sample Size² (X 100)	2.44	.12	2.29	.46	.61	.46	5.00	.91	.38	.64	3.05	1.52	1.83	1.83	3.05	1.83	1.83	.61	4.50	1.60	.61	.30	.61	.61	.30

*frequently eaten species

[1] l=line intercept; p=point intercept

[2] meters of transect for line intercept; number of points for point intercept

Table 14. Vegetative cover measurements for low alpine patches. Locations are plotted on Figures 15 and 16.

						PERCENT		COVER					
Location:	1	2	3	4	6	7	7	7	8	13	24	29	30
PLANT SPECIES													
Graminoids:													
*Sitanion hystrix**									1.0	0.1		0.1	
Festuca brachyphylla							1.3		3.3	0.2	0.2		
Muhlenbergia richardsonis		0.7	1.5	0.5	6.8		3.0				5.2		
Calamagrostis breweri		20.0	9.1	20.5			7.6	29.8					
Calamagrostis purpurascens											0.2		
*Stipa occidentalis**												0.1	
*Stipa columbiana**	3.0												
*Stipa pinetorum**					0.4						0.2		
*Poa hanseni**										1.3			
Poa epilis										0.3			
*Poa rupicola**									1.0				
Poa sp.											0.2		
Trisetum spicatum	0.5			2.5			1.3	2.6				0.04	
*Danthonia intermedia**			9.8										
Agropyron sp.	0.2												
unidentified grass							0.7	5.0			0.2		
*Hesperochloa kingii**												0.3	
*Juncus parryi**		3.3	3.9						2.3	1.5			
Juncus mexicanus											0.7		
Juncus mertensianus								0.7					
Luzula spicata									1.0				
Scirpis clementis			0.8										
*Carex vernacula**				17.0									40.3
*Carex exserta**		19.3	15.2			20.6	14.1		5.4		4.1		
*Carex subnigricans**				20.5			0.3	17.5					6.0
*Carex spectabilis**		1.3	6.8										
*Carex congdonii**										2.7		0.5	
Carex leporinella	4.3										0.3		
*Carex helleri**							1.3				1.1		
*Carex rossi**					7.6		1.3				1.3	1.4	
Carex jonesii											0.2		
Carex sp.										0.4			
Forb species:													
Arabis sp.												0.1	
Potentilla drummondii											3.1		
Potentilla sp.	0.2												
Sibbaldia procumbens							2.6	0.7	5.4	0.8			

Table 14 (con't)

PLANT SPECIES / Location:	1	2	3	4	6	7	7	7	8	13	24	29	30
Ivesia santolinoides												0.2	
Galium sp.											0.3		
Trifolium monanthum*	33.0		1.5				6.2	17.5			2.1		
Lupinus formosus*					12.8							2.8	
Lupinus pratensis										0.1			
Lewisia spp.							1.3	1.7					
Gayophytum sp.							0.3						
Sedum rosea										0.1			
Sphenosciadium capitellatum	0.3												
Mimulus primuloides				3.5				2.6					0.5
Collinsia sp.											0.2		
Castilleja nana							0.7						
Dodecatheon redolens		4.0	12.9							6.1			20.9
Silene sargentii*					0.4							0.1	
Monardella odoratissima*					1.2						1.8	0.3	
Eriogonum ovalifolium					2.0	0.5			1.3		0.2		
Linanthus nuttallii*												0.3	
Achillea lanulosa*	3.5										0.8		
Solidago multiradiata	0.8												
Antennaria spp.		3.3	5.3	11.5		0.5	8.9	8.3	4.0	0.4	0.3		
Artemisia ludoviciana	1.8												
Salix nivalis				15.5			0.7	7.6					
Veratrum californicum*	2.2												
Woodsia scopulina											0.2		
Selaginella watsoni		0.7	2.3			2.0			8.4			1.2	
moss				1.0			0.7						4.5
unidentified forb	0.2		0.8										
Woody species:													
Holodiscus microphyllus*											3.6	3.4	
Potentilla fruticosa*							4.3						
Jamesia americana*											8.4	1.0	
Ribes cereum	0.8										3.6		
Ribes montigenum*											0.3		
Symphoricarpus vaccinoides											3.1		
Phyllodoce breweri									0.7	17.6			
Leptodactylon pungens*					7.2						1.0	0.1	
Penstemon heterodoxus							4.9						
Chrysothamnus viscidiflorus					16.0						2.4	6.9	
Salix sp.							3.3						
rock	0.0	11.3	7.6	0.0	21.2	47.2	18.1	0.0	53.0	NA	44.4	NA	17.4
Total vegetative cover	50.8	52.6	69.9	92.5	54.4	23.6	64.8	94.0	33.8	31.6	45.3	18.8	72.2
Cover of * species	41.7	23.9	37.2	37.5	29.6	20.6	27.5	35.0	9.7	5.6	24.9	10.4	46.3
Elevation (X 1000m)	3.14	3.23	3.29	3.47	3.17	3.23	3.23	3.21	3.44	3.41	3.35	3.05	3.51
Sampling method[1]	p	p	p	p	p	p	p	p	p	l	p	l	p
Sample Size[2] (X 100)	6.0	1.5	1.3	2.0	2.5	2.0	3.0	3.0	3.0	0.30	6.1	0.61	2.0

*species frequently eaten in summer or fall

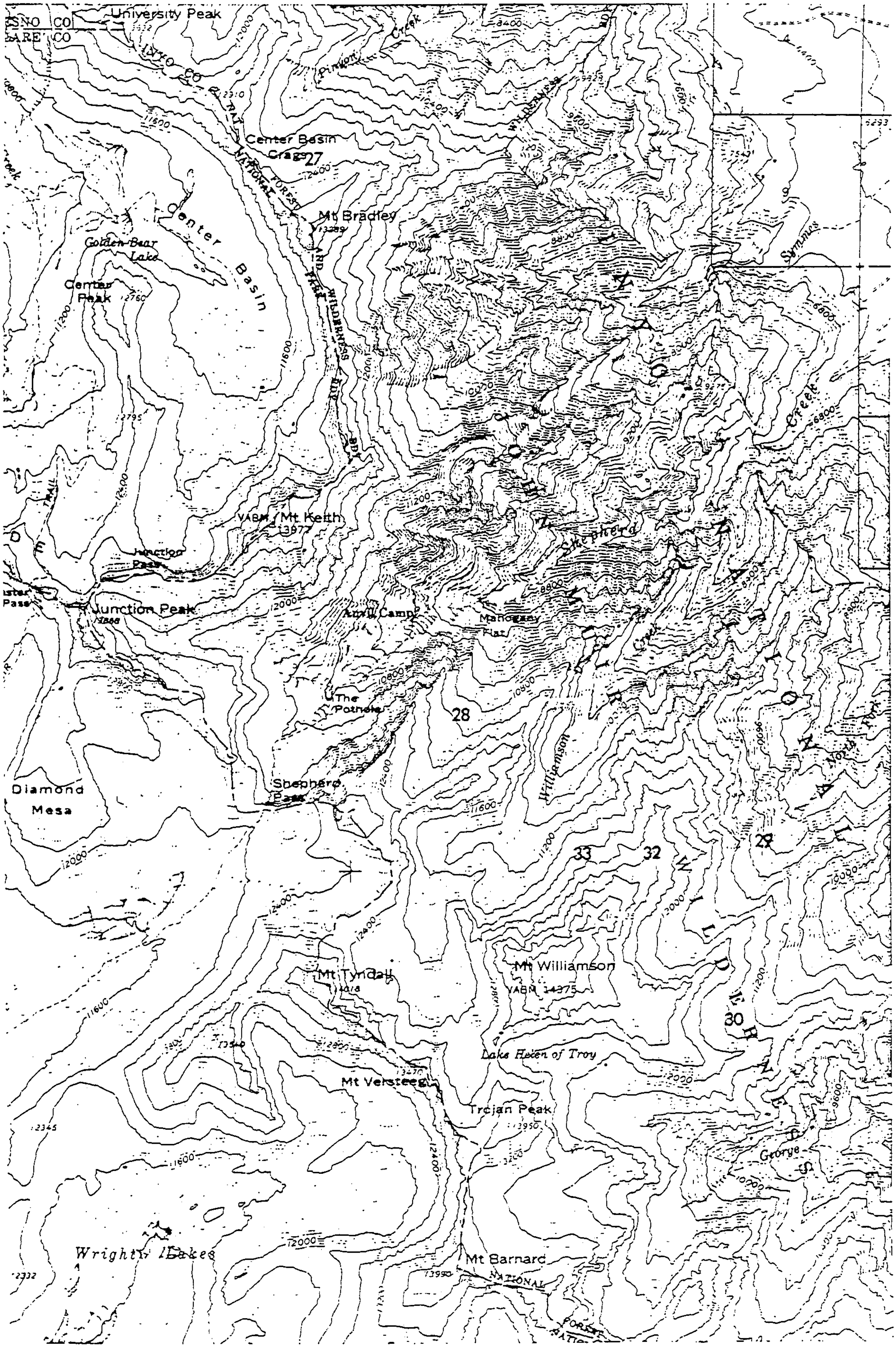
[1] p - point intercept; l - line intercept

[2] points or meters sampled

Figure 15. Locations of alpine vegetation cover and utilization plots in the Baxter herd range.


Sawmill Meadow
Woods Lake
Sawmill Pass
Sawmill Lake
FRESNO CO.
INYO CO.
Stocking Lake
Mt Baxter
1
2
3
4
5
Baxter Lakes
6
7
8
9
10
11
12
Baxter Pass
Summit Meadow
13
Diamond Peak
14
15
16
17
18
19
20
21
22
23
Fin Dome
Rae Lakes
Black Mtn
24
Dragon Lake
Parker Lakes
25
Sardine Lakes
26
Painted Lady
Glen Pass
Dragon Peak
Kearsarge Peak
Rex Montis Mine
Mt Rixford
Mt Gould
Golden Trout Lake
Kearsarge Pass
Bullfrog Lake
Big Pothole Lake
Onion Valley

Figure 16. Locations of alpine vegetation cover and utilization plots in the Williamson herd range.


University Peak
Center Basin Crags
Mt Bradley
Center Basin
Golden Bear Lake
Center Peak
Mt Keith
Junction Pass
Junction Peak
Anvil Camp
Mahogany Flat
The Pothole
Shepherd Pass
Diamond Mesa
Shepherd Creek
Williamson
Mt Tyndall
Mt Williamson
Lake Helen of Troy
Mt Versteeg
Trojan Peak
Wright Lakes
Mt Barnard
George
Symmes Creek
North Fork
INYO NATIONAL FOREST
JOHN MUIR WILDERNESS
27
28
29
30
32
33

total cover values for transects on Tables 13 and 14 are regressed on elevation, a significant ($P<.001$) regression results ($r^2=.434$; $N=38$). When cover of preferred species is used, a slightly better fit is obtained ($r^2=.473$). Biomass rather than vegetative cover would better represent food availability. A steeper slope would be expected for biomass relative to elevation, since the high alpine vegetation consists largely of low tufted graminoids, forbs, and cushion plants, while timberline patches include shrub species of considerably higher stature and biomass; most of these shrub species are preferred dietary items.

Two types of low elevation patches are especially important to bighorn: meadows and brush patches. The best feeding patches mix these two elements, usually in the form of shrub species (notably Holodiscus microphyllus, Ribes montigenum, Jamesia americana, and Potentilla fruticosa) bordering a patch of meadow vegetation. Locations 7, 24, and 30 in Figure 15 are good examples of such mixtures, although only in location 24 did the sampling include the brush component (Table 14). Of these two components, meadows are the rarer, but brush patches are also scarce above timberline. Most canyons of the east slope do not exhibit increased meadow vegetation below timberline because of their steepness and aridity. West of the crest, meadow patches increase substantially in frequency, size, and height of vegetation below timberline. Consequently, summer ram habitat includes frequent meadow and brush patches.

In contrast, low elevation brush and meadow patches used by ewe-lamb groups are small in size and number, and are widely spaced. Most of these low elevation patches used by ewe-lamb groups are in cirque bottoms or similar locations away from rock outcrops, and none of these contain trees other than a few krumholz whitebark pines. Patches in similar juxtaposition to rocks, but containing small stands of trees, have not been used by ewe-lamb groups. Sites used that were adjacent to trees were also immediately adjacent to steep rocks.

Summer feeding patterns of ewe-lamb groups contrast markedly to winter patterns, in which groups may frequently be found in the same location for successive days. During summer ewe-lamb groups move considerable distances while feeding, and rarely are observed feeding in the same drainage for an entire day. This continual movement results from the extreme sparsity of most vegetation. The major exceptions to this are the low elevation patches of high forage abundance, in which bighorn may spend several hours and occasionally longer.

In the Baxter herd most ewe-lamb groups observed in summer were in higher alpine areas. In the Williamson herd the opposite was true; most sightings were in low elevation patches due to the difficulty of locating ewe-lamb groups elsewhere. Assessment of the relative use of the two basic habitat types has not been possible due to the difficulty of obtaining an unbiased sample.

When one examines many high alpine feeding sites following bighorn use, it is striking how little vegetation has been consumed. Certainly a substantially higher consumption rate occurs in low elevation patches. Although small in total area, these low elevation patches may contribute a large fraction to the forage consumed.

Feeding habits of rams in summer contrast strongly with ewe-lamb groups in that little movement occurs. Ram groups commonly spend half a day at a single feeding location and move only short distances between feeding areas. Undoubtedly they expend considerably less energy than ewe-lamb groups in obtaining food.

Food Habits and Plant Phenology

A large number of plant species were recorded to be fed on by bighorn in summer, but this number decreases considerably in fall as the growing seasons ends (Table 15). The timing and length of the growing period vary greatly among communities and were noted to vary within communities between years of this study. Moisture is the critical factor determining both community composition and the length of the growing season in the Sierran alpine (Klikoff 1965, Major and Taylor 1977, Burke 1979). Snow cover patterns have considerable influence on this. The following discussion treats basic community types important to bighorn in terms of timing of growth and forage species preference.

High elevation patches containing *Polemonium eximeum* or

Table 15. Plant species fed on by bighorn in summer and fall.

	Time period:	June - Oct.15			Fall
Species	Group type:	Ewe-lamb		Ram	All
Graminoids:	Herd:	W	B	B	B
Juncus parryi		X	X	X	X
Juncus drummondii			X	X	
Juncus mexicana			X		
Luzula comosa				X	
Carex exserta			X	X	
Carex subnigricans		X	X	X	
Carex spectabilis		X	X		
Carex congdonii		X	X	X	
Carex vernacula		X	X		
Carex rossii		X	X	X	X
Carex helleri			X		
*Carex leporinella**		X	X	X	
Carex heteroneura			X		
Carex incurviformis danaensis			X		
Carex aurea				X	
*Festuca brachyphylla**		X	X	X	
Hesperochloa kingii		X			
Poa hanseni		X	X		
Poa epilis				X	
Poa spp.		X	X		
Sitanion hystrix		X	X	X	X
*Trisetum spicatum**				X	
Danthonia intermedia				X	
*Calamagrostis breweri**		X	X		
*Calamagrostis purpurascens**		X		X	
Phleum alpinum			X	X	
*Muhlenbergia richardsonis**		X		X	
Stipa pinetorum					X
Stipa columbiana				X	
Stipa occidentalis			X	X	

Table 15 (con't)

	June - Oct.15			Fall
	Ewe-lamb		Ram	All
Herbaceous species:	W	B	B	B
Aquilegia pubescens (mostly flrs.)	X	X		
Erysimum perenne		X		
Draba sp.*		X		
Silene sargentii	X	X		
Eriogonum latens			X	
*Oxyria digyna**		X		
Polemonium eximeum (mostly flrs.)	X	X		
Linanthus nuttalii	X			
Phacelia frigida	X	X	X	
Cryptantha circumcissa		X		
Castilleja applegatei			X	
Monardella odoratissima				X
Sedum sp.	X			
Potentilla breweri			X	
Ivesia pygmaea	X	X		
Lupinus formosus	X	X		X
Trifolium monanthum			X	
Epilobium obcordatum		X	X	
Angelica lineariloba		X		
Hulsea algida (mostly flowers)	X	X		
Achillea lanulosa alpicola	X	X	X	
*Erigeron petiolaris**		X		
Erigeron sp.*	X			
Hieracium horridum	X		X	
Artemisia ludoviciana	X			
*Haplopappus macronema**	X		X	X
*Solidago multiradiata**			X	
Veratrum californicum			X	
Allium validum			X	
Pellea breweri			X	

Table 15 (con't)

	June - Oct.15			Fall
	Ewe-lamb		Ram	All
Woody species:	W	B	B	B
Penstemon davidsonii (flowers)		X		
Leptodactylon pungens	X	X	X	X
Phyllodoce breweri (flowers)		X		
Jamesia americana	X	X	X	X
Ribes cereum (flowers & berries)	X	X	X	
Ribes montigenum	X	X	X	
Holodiscus microphyllus	X	X	X	
Potentilla fruticosa		X	X	
Ceanothus cordulatus				X
Symphoricarpus vaccinoides				X
*Salix jepsonii**			X	
Tanacetum canum	X			X
Chrysothamnus nauseosus (flowers)$^{+}$				X
Pinus albicaulus		X	X	

*these species usually avoided in summer

$^{+}$late September 1977 observation in Sawmill winter range

Hulsea algida or both are worthy of discussion because of the high use they receive. The flower heads of both species are highly preferred and their leaves are eaten in late August after the flowers are all eaten, dried up, or in the case of *Hulsea algida*, have dispersed their seeds. These two species usually dominate the vegetation when present (Table 13). *Polemonium eximium* grows on a variety of substrates, while *Hulsea algida* is restricted to granitic soils; thus its absence from the metabasaltic substrates of Mount Mary Austin (location 21-23 on Figure 11). This vegetation grows in patches varying in size from a few meters across to entire slopes, as on the west face of Mount Mary Austin, the north side of Black Mountain, and the summit plateau of Mount Baxter. The Baxter summit patch covers an area of about .1km^2. Utilization of this vegetation is easily measured in late summer by determining the percent of flowers eaten. The use of *Hulsea algida* flowers by pikas (*Ochotona princeps*) is an unimportant factor, since this utilization was found to be a negligible proportion of the flower crop outside of the bighorn range. Flower utilization exceeded 25% for all measurements, and in some cases was predictably very high every year (Table 16). The biomass of forage in these patches is high relative to other high alpine patches, and ewe-lamb groups may spend several hours in one before moving on.

Developmental changes among high alpine species occur rapidly. *Polemonium eximium* changes from a state of 100%

Table 16. Measurements of flower head utilization of *Polemonium eximium* and *Hulsea algida* in different alpine patches. Locations are plotted on Figures 15 and 16. Sample sizes (flower heads sampled) are in parentheses.

	PERCENT OF FLOWER HEADS EATEN								
Location: Species & Year	5	18	19	21	22	23	31	32	33
1975									
Polemonium eximium	98 (152)	78 (246)	68 (556)	43 (237)	26 (396)				
Hulsea algida	97 (132)	93 (268)							
1976									
Polemonium eximium	92 (589)	71 (314)	63 (820)	65 (189)	26 (622)	49 (485)	92 (252)		
Hulsea algida	99 (103)	83 (164)							
1977									
Polemonium eximium	98 (199)		63 (581)	71 (235)	30 (292)	36 (538)		96 (401)	76 (414)
Hulsea algida		98 (377)							
1978									
Polemonium eximium	95 (221)								

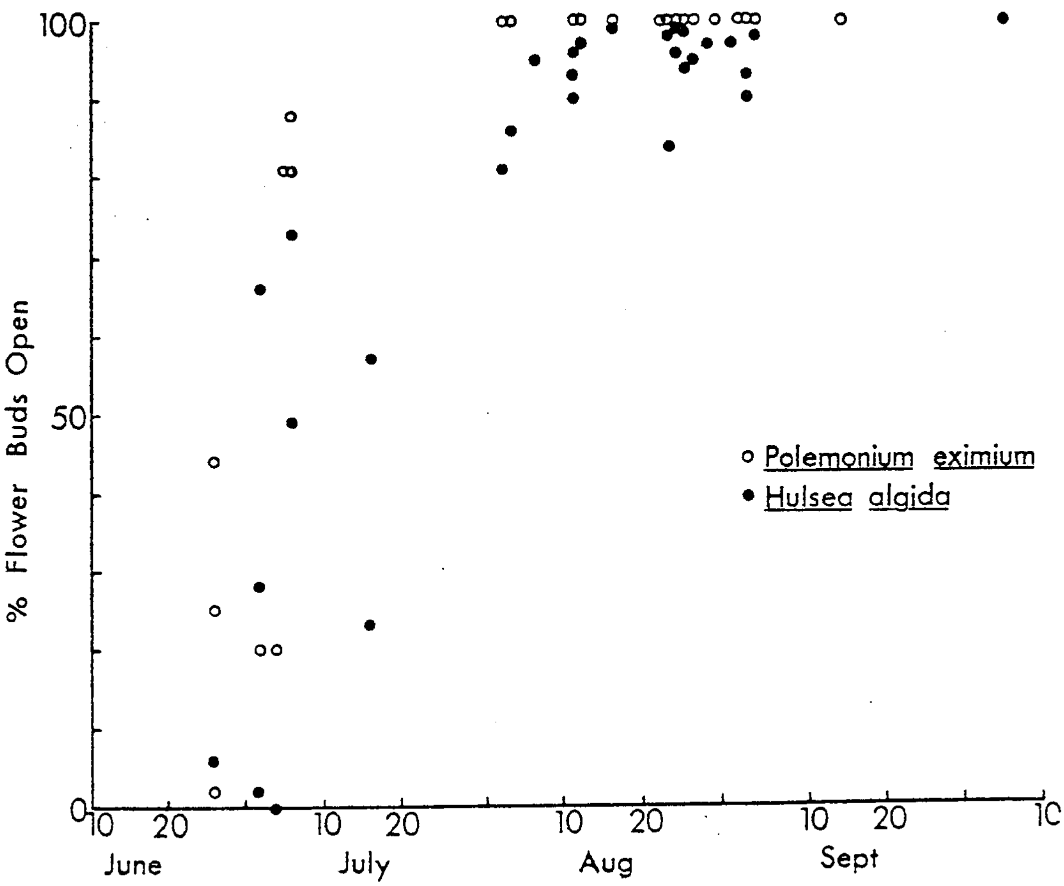
flower buds to nearly 100% flower heads in a period of 2-3 weeks, with peak flowering occurring in mid-July (Figure 18). *Hulsea algida* lags behind slightly and has a longer flowering period (Figure 17). By mid-August flowers of both species are scarce and bighorn begin feeding on their leaves. *Polemonium eximium* leaves first show yellowing in late August. By mid-September *Polemonium* and *Hulsea* communities are virtually unused by bighorn.

Other high alpine forage species preferred by ewe-lamb groups in summer include *Carex helleri*, *Carex rossii*, *Sitanion hystrix*, *Phacelia frigida*, *Silene sargentii*, *Aquilegia pubescens*, and *Ivesia pygmaea*. The last three are more abundant in the Williamson herd summer range, where they are noticeably grazed. Utilization of *Aquilegia pubescens* flowers was 98% in South Bairs cirque in 1978.

Two basic alpine meadow types are considered here: dry *Carex exserta* meadows (see locations 3, 7 on Table 13) and wet meadows characterized by *Calamagrostis breweri*, *Carex subnigricans*, and *Carex vernacula* (locations 2-4,7,30 on Table 14). Wet meadows frequently grade into the dry *Carex exserta* type, but also may occur entirely separate and exhibit very different growth patterns.

Carex exserta attains nearly monospecific stands (e.g., location 7 on Table 13) on dry gravelly sites where water depletion occurs rapidly relative to the wet alpine meadow type (Klikoff 1965, Taylor 1977), and is found only on granitic substrates (Taylor 1977). Its growing period is

Figure 17. The timing of flowering of _Polemonium eximium_ and _Hulsea algida_ in the alpine, 1975-1977. Open buds represent all developmental stages subsequent to flowers opening.



short and annual productivity is only about 30g/m^2 (Rundel et al. 1977). Yellowing has been observed on some sites as early as late June. Few green patches normally persist at the beginning of August, but the timing of the growing season at any site is strongly influenced by snow pack. The difference in the timing of yellowing between drought years and 1978 was 6-8 weeks in most locations. Some patches were still snow covered in 1978 at the same time they were yellow during drought years. *Carex exserta* is a highly preferred forage species when green, but is untouched once yellowing.

Wet meadow patches occur where high soil moisture persists well into summer. The source of moisture may be springs, runoff from late persisting snow patches, and rock glacier melt. *Carex vernacula* grows and dominates the vegetation where moisture is surface water, as along waterways through meadows. It occasionally dominates more than a narrow band of vegetation if water is spread over a considerable surface before becoming channelized, as at location 30 in Table 14. Immediately away from surface water, wet meadows are dominated by mixtures of *Calamagrostis breweri* and *Carex subnigricans* (e.g., locations 4,7 in Table 13). *Carex vernacula* is the preferred forage of bighorn in these wet meadows. *Calamagrostis breweri* is untouched throughout summer and has been found grazed only late in the season when green vegetation is scarce. Protected plots of *Carex vernacula* were clipped late in the season and yielded an average dry weight of $140g/m^2$; this is approximately 4.5 times that of *Carex exserta*. *Carex vernacula* is heavily grazed when present on feeding sites.

Wet meadows remain green considerably longer than *Carex exserta*. Those fed by persistent snow patches have shown clear variation in the timing of yellowing, which depends largely on snowpack. For example, the wet meadows at location 7 in figure 15 were completely dry by mid-September of the drought year 1976, while in 1978 and 1979 they were in the process of yellowing at the end of the first week of October. Wet meadows fed by rock glacier melt usually lose their water in October when temperatures drop to the point where ice melt is insufficient. Because of its unpredictability, summer rainfall probably helps extend the growing season of meadows only occasionally and for short periods when optimally timed relative to the development of water stress. Wet meadow species cease to be taken by bighorn when yellow.

Subalpine meadows in ram habitat are also variable in the timing of yellowing, depending on how directly their water sources are tied to snow and ice melt. Rams have considerable choice in where they feed and are found feeding in a large variety of meadow types. In early summer, green *Carex exserta* patches are frequently used until yellowing begins. Wet meadows are used by rams throughout summer. In 1976, after many meadow systems yellowed early in summer, rams were still feeding in green meadows that were fed by predictable spring water. Also, during the drought years, rams were still feeding in small persistent green meadow patches in September and early October when similar vegetation was largely unavailable to ewe-lambs groups. This greater availability and utilization of meadow vegetation by rams is reflected in the high graminoid content of their summer diet compared to ewes (Table 17).

Four deciduous brush species, *Holodiscus microphyllus*, *Jamesia americana*, *Ribes montigenum*, and *Potentilla fruticosa*, are fed on by all sex and age classes of bighorn in summer. Leaf yellowing on these begins in late August and by mid-September their use as bighorn forage has ceased, except for *Jamesia*, whose twigs are occasionally eaten later in fall.

A short growing season and rapid plant development are characteristic of most Sierran alpine species and are generally typical of arctic and alpine plants (Bliss 1956, Mooney and Billings 1960, Klikoff 1965, Billings and Bliss 1959, Holway and Ward 1963). That water is the factor governing growing season in the Sierran alpine is suggested by the fact that temperatures are commonly sufficient for plant growth after most species have dried up. Since snow melt is the primary water source during the growing season, winter precipitation is the major factor determining the summer growth pattern in the alpine. This might act as a tradeoff for bighorn in which higher nutrition of green vegetation in late summer is gained at the cost of early

Table 17. Results of fecal microhistological analysis of summer and fall diets.

Date	Herd[1]	Group Type	% Graminoids	% Nongraminoids	Number of Fragments Sampled	Number of Pellet Groups Composited
6/23/78	W	Ewe	43	57	239	9
6/29/78	B	Ewe	54	46	202	6
8/7/78	W	Ewe	58	42	226	8
8/2/78	B	Ewe	53	47	178	10
8/11/76	B	Ewe	68	32	215	7
8/7/76	B	Ram	90	10	175	4
8/9/76	B	Ram	85	15	201	9
9/12/78	W	Ewe	72	28	206	8
10/6/78	B	Ewe	85	15	250	4
11/15/77	B	Mixed	70	30	180	1
12/6/76	B	Mixed	72	28	205	1

[1] W=Williamson, B=Baxter

summer growth due to snow covering vegetation. In fact, this tradeoff probably does not occur for two reasons. First, to some extent bighorn can simply migrate upslope more slowly in years of high snowpack, thereby remaining in the region of active plant growth. Second, snow distribution is highly variable due to topographic relief and wind patterns. Thus, even under conditions of a large snowpack, such as in 1978, many alpine patches are free of snow early in the season. A large snowpack consequently has the effect of (1) extending the growing season of vegetation dependent on its runoff, and (2) temporally spreading out the growing season of snowbank communities that characteristically have short growing seasons once snow-free (Holway and Ward 1963).

Ewe-lamb groups exhibit a change in diet in late September and October as green vegetation becomes scarce. The diet shifts to include those species remaining green. Some of these, such as *Calamagrostis breweri* and *Carex leporinella*, are ungrazed prior to this period, and may be taken for only a short period until yellow. A few species remain green or partially green well into or throughout fall and are highly preferred at that time. These are *Carex rossii*, *Juncus parryi*, *Sitanion hystrix*, *Stipa pinetorum*, *Leptodactylon pungens*, and *Lupinus formosus*. The fall diet also includes *Haplopappus macronema* and *Monardella odoratissima* as important dietary components. *Carex rossii* is the only one that is consistently green throughout fall and is consequently heavily grazed; but it probably constitutes only a small portion of the total diet due to its low overall occurrence (Tables 13,14) and low available biomass per plant.

Species fed on in fall are more abundant in the lower elevations of the alpine (e.g., locations 6, 8, 29 on Figures 15 and 16; see Table 14). High elevations become little used by ewe-lamb groups and the elevational distribution of their feeding centers around timberline, extending down to 2900m elevation and occasionally lower. These include open areas surrounded by trees at timberline, as well as within some timbered habitats. Nearby rocky slopes continue to be a consistent habitat component. This shift in habitat selection coincides with the completion of weaning in early October.

In terms of growth stage of plants, fall range is comparable to early winter on winter ranges, when green growth of needlegrass is unavailable. In terms of quantity of available forage, the fall range is decidedly sparser than the winter range, since it still encompasses alpine communities to a large extent. This shortage of vegetation is illustrated by utilization measurements of the two most preferred fall species, <u>Carex rossii</u> and <u>Juncus parryi</u> taken in the area of location 6 on Figure 15 in mid-December 1976. For 797 <u>Carex rossii</u> plants sampled, 90% were grazed, of which 87% were grazed to ground level. Of 470 <u>Juncus parryi</u> plants sampled, 99% were grazed, of which 89% were completely grazed. The fall diet exhibits a predominance of graminoid species similar to what was found for the winter diet (Tables 17,9).

Nutrition

Nutritional Content of Individual Plant Species

An approach to ruminant nutrition that has received considerable attention for many years has been an attempt to partition forage plants into components that have predictive value in terms of animal nutrition. Proximate analysis has been the standard method for over 100 years, but is not particularly meaningful in terms of digestibility of the components (Van Soest 1967). In particular, crude fiber and nitrogen free extract are not the relatively indigestible cell wall material and highly digestible sugars, respectively, that they were thought to be (Van Soest 1967). They have been recently replaced by a more predictive system in which the cell is first partitioned into cell wall constituents (neutral detergent fiber) and cell solubles, then the cell wall is further partitioned into hemicellulose, cellulose, and lignin (Van Soest 1966). This system has the advantage of better predictability in terms of digestibility, yielding low standard errors for equations involving lignification indices (Van Soest 1967), which hold across basic forage classes (Van Soest 1965,1967). However, these equations hold only for forages that lack essential oils which are inhibitory to rumen microbes (Nagy et al. 1964), and thus are of questionable value for many rangeland forage species. This makes precise energy considerations of wildlife diets largely impossible without running <u>in vitro</u> or <u>in vivo</u> digestibility trials on major forage species. Consequently, this section considers forage nutrition in the Sierra Nevada only in terms of protein, phosphorus, and calcium.

Basis of Diet Selection

Ruminants are highly selective in the plant species and plant parts they eat (Gwynne and Bell 1968, Westoby 1974, Belovsky 1978). This is apparent among Sierra bighorn, even in alpine areas of very sparse vegetation. The many models of optimum foraging to emerge in recent years have avoided consideration of herbivores due to the potential complexity of their diet selection (Belovsky 1978). Belovsky and Jordan (in press, Journal of Mammalogy) and Botkin et al. (1973) showed that sodium is the limiting mineral for moose on Isle Royale, and Belovsky (1978) found the diet selection of Isle Royale moose to closely match the prediction of a model based only on sodium needs and energy maximization. Similar results were obtained for an array of herbivores on the National Bison Range of Montana (Belovsky, pers. comm.). Belovsky's model considers only basic forage classes (graminoids, forbs, browse). In the context of Levin's (1968) argument concerning models, it sacrifices precision for generality and realism. It does not tell us which species within any particular forage class will be eaten, or which parts of them will be eaten, since parameters such as secondary compounds and specific nutrients, other than energy and sodium (in the case of moose), are not considered. For herbivores the size of bighorn sheep, sensitivity analysis of his model indicated that considerable variation in proportions of the various forage classes in the diet was possible (Belovsky, pers. comm.). This suggests that rather than selecting first on the basis of forage class, ungulates of this general size class may select first on the basis of plant chemistry.

Nagy et al. (1964) showed the inhibitory effects of essential oils of sagebrush on rumen microbes of deer, and subsequent studies have demonstrated similar effects of other aromatic species (Oh et al. 1967, Schwartz et al. 1980). Longhurst et al. (1968) concluded that diet selection by blacktailed deer (_Odocoileus hemionus columbianus_) was strongly influenced by secondary compounds detrimental to rumen fermentation. Beyond that, they found only that nitrogen fertilization of plants increased their palatability.

The basis of diet selection by bighorn in the Sierra has been investigated relative to phosphorus, calcium, and protein content and the Ca:P ratio. Ratios of Ca:P in excess of 2:1 are considered less than optimal due to the precipitation of tricalcium phosphate in the gut and thus its loss to the animal (Maynard and Loosli 1969). This investigation sought to determine whether Sierra bighorn exhibited any consistent preference relative to these forage components.

It has been necessary to define preference of one species or plant part over another in an unambiguous way, and to control as much as possible for other variables such as secondary compounds. Preference was defined as cases where one species was clearly avoided while one was clearly eaten. Furthermore, this was considered only for species growing together in a particular patch type where a preference for one over another could be exercised. Thus, for instance, a species fed on regularly in the high alpine was not considered preferred over one avoided in a timberline meadow type. To control for other variables, all comparisons were either made within the graminoid class in which the problem of secondary compounds was minimal, or were made between plant parts of the same species. All 29 pairs that resulted involved alpine species in summer or fall condition. Comparisons were made by subtracting protein, P, Ca, and Ca:P values of the avoided species from the preferred one and looking at the signs of the results relative to the expected sign. Since nutritional status is normally improved by increases in protein and phosphorus, positive values would be expected for them. Since calcium is normally overabundant relative to phosphorus, a negative sign was expected for calcium and the Ca:P ratio.

The results suggest that the basis of forage preference is strongly correlated with phosphorus level (Table 18). Only two comparisons existed in which phosphorus content was lower in the preferred species. Both involved Carex rossii in summer condition. There is good reason to suspect that the summer phosphorus value of this species is in error, since the fall value when leaves were partially dry is higher rather than lower (Table 19). A drop in phosphorus level with more advanced maturity is the rule and is exhibited by other alpine species in the Sierra (Table 19). Consequently, comparisons were also made after excluding all pairs involving Carex rossii in summer condition. The results exhibit the same pattern of high selectivity on the basis of phosphorus, no apparent selectivity on the basis of calcium, and weak selectivity on the basis of protein and the Ca:P ratio. If ranking of the magnitude of the differences between pairs is considered by using a Wilcoxen matched-pairs signed-ranks test (Siegel 1956), the same pattern is apparent; protein and Ca:P ratio each exhibit significance in the expected direction ($p=.02$ for each), while phosphorus is much higher in both the magnitude and significance ($P<.0001$) of its difference, and calcium shows no significant deviation ($P=.24$) from a zero difference between pairs.

The significance of the values for the Ca:P ratio is to be expected if phosphorus or a close correlate is the basis of diet preference, since phosphorus constitutes the denominator of the ratio. Similarly, protein and phosphorus

Table 18. Comparison of nutrient content of 29 alpine species pairs for which one species was clearly preferred over the other.

	Δ[1]Protein	ΔP	ΔCa	ΔCa:P
Expected sign	+	+	-	-
All species pairs:				
No. with expected sign	18	27	15	18
No. with other sign	10	2	14	10
No. of ties	1	0	0	1
% with expected sign	62	93	52	62
Level of significance[2]	.093	.00003	.500	.093
Exclusive of *Carex rossii*:				
No. with expected sign	16	24	13	16
No. with other sign	8	0	11	7
No. of ties	0	0	0	1
% with expected sign	67	100	54	67
Level of significance[2]	.076	.00003	.419	.047

[1] Δ = preferred - other

[2] probability that the values are not different from a 50:50 ratio as computed by the sign test (Siegel 1956)

Table 19. Nutrient content of some plant species available to bighorn in the Sierra Nevada.

Species	Month	Phenological State	% Crude Protein	% P	Ca/P
WINTER					
Stipa speciosa (leaves)	Dec.	dry	4.5	.04	9.2
Artemisia tridentata (gr. lvs, stem tips)	March	dormant	11.3	.24	2.6
Purshia (hybrids) (leaders)	March	dormant	11.1	.14	4.1
Eriogonum fasciculatum (leaves + stem)	March	dormant	13.6	.18	4.1
Keckiella breviflorus (green stems)	March	dormant	5.8	.12	2.3
Ephedra viridis (green stems)	March	dormant	11.5	.11	34.7
Ephedra nevadensis (green stems)	March	dormant	10.5	.10	30.1
Chrysothamnus nauseosus (green stems)	March	dormant	5.2	.12	3.3
Haplopappus cuneatus (lvs. + leader stems)	March	dormant	7.0	.07	25.3
Ceanothus greggii (lvs. + leader stems)		dormant	8.7	.12	10.5
Ceanothus cordulatus (green leaves)	Jan.	dormant	16.9	.20	3.1
Lupinus excubitus (lvs. + stem tips)	Feb.	dormant	21.6	.18	9.7
Cercocarpus ledifolius (green leaves)	March	dormant	9.2	.13	7.5

Table 19 (con't)

Species	Month	Phenological State	% Crude Protein	% P	Ca/P
SPRING					
Stipa speciosa (green leaves)	May	growing	13.6	.19	1.5
Stipa coronata (green leaves)	April	growing	16.0	.26	.9
Oryzopsis hymenoides (green leaves)	April	growing	17.9	.24	1.3
Bromus tectorum (green leaves)	March	growing	22.2	.43	1.9
Eriogonum nudum (green leaves)	March	growing	18.6	.36	2.3
Eriogonum fasciculatum (new growth)	April	growing	19.8	.42	2.0
Ephedra viridis (new growth)	May	growing	23.1	.48	1.8
Artemisia tridentata (new growth)	June	growing	17.5	.38	2.0
Purshia (hybrids) (new leaders)	May	growing	13.9	.25	3.4
Chrysothamnus nauseosus (new growth)	May	growing	19.7	.50	2.0
Prunus andersonii (green leaves)	May	growing	15.8	.51	1.5
Lupinus excubitus (green lvs. + flowers)	April	growing	17.5	.45	1.9
Dalea fremontii (green leaves)	April	growing	15.7	.48	4.0
Tauschia parishii (green leaves)	May	growing	20.6	.46	4.3

Table 19 (con't)

Species	Month	Phenological State	% Crude Protein	% P	Ca/P
Convolvulus aridus (green lvs. + stems)	April	growing	28.7	.39	2.5
Penstemon bridgesii (green leaves)	June	growing	18.7	.30	2.7
Arctostaphylos patula (leaves)	May	growing	5.9	.09	8.1
Arctostaphylos patula (flowers)	May	growing	7.1	.21	2.2
SUMMER					
Graminoids:					
Juncus parryi (stems + flowers)	July	green	16.5	.22	.9
Juncus parryi (stems + seed heads)	Aug.	green	13.8	.20	1.1
Juncus drummondii (stems + seed heads)	Aug.	green	14.5	.17	1.4
Luzula comosa (leaves + flr. stems)	Aug.	green	15.7	.24	2.7
Carex exserta (leaves)	June	green	24.3	.25	1.6
Carex exserta (leaves + seed heads)	Sept.	partly green	7.0	.10	4.6
Carex subnigricans (lvs., stems, flwrs.)	Aug.	green	13.5	.18	3.2
Carex spectabilis (leaves + flr. stems)	July	green	19.3	.22	1.2
Carex congdonii (leaves)	July	green	18.0	.19	1.2

Table 19 (con't)

Species	Month	Phenological State	% Crude Protein	% P	Ca/P
Carex vernacula (leaves + flr. stems)	July	green	20.6	.25	.9
Carex vernacula (leaves + seed heads)	Sept.	partly green	15.4	.14	3.5
Carex rossii (leaves)	July	green	17.0	.12?	2.5
Carex helleri (leaves + flr. stems)	Aug.	green	19.2	.21	2.6
Carex leporinella (leaves + flr. stems)	Aug.	green	13.1	.17	2.6
Festuca brachyphylla (leaves + flr. stems)	Aug.	green	13.9	.14	1.7
Poa incurva (leaves + flr. stems)	Aug.	green	22.4	.21	2.2
Poa rupicola (leaves + flr. stems)	Aug.	green	10.5	.14	1.9
Poa hanseni (leaves + flr. stems)	Aug.	green	11.5	.21	1.4
Stipa occidentalis (leaves + flr. stems)	July	green	13.6	.27	1.1
Stipa pinetorum (leaves + flr. stems)	Aug.	green	15.9	.17	3.1
Stipa columbiana (leaves + flr. stems)	Aug.	green	16.5	.17	2.4
Oryzopsis kingii (leaves + flr. stems)	Aug.	green	10.1	.20	.8
Calamagrostis breweri (leaves)	Aug.	green	17.4	.20	1.9
Calamagrostis purpurascens (leaves)	Aug.	green	17.0	.10	1.9

Table 19 (con't)

Species	Month	Phenological State	% Crude Protein	% P	Ca/P
Calamagrostis inexpansa (leaves)	Sept.	green	12.9	.15	2.0
Muhlenbergia richardsonis (leaves)	Aug.	green	11.2	.15	3.7
Sitanion hystrix (leaves + flr. stems)	Aug.	green	17.6	.18	3.9
Trisetum spicatum (leaves)	Aug.	green	17.8	.19	4.6
Deschampsia caespitosa (leaves)	Aug.	green	12.6	.10	5.2
Phleum alpinum (leaves)	Sept.	green	14.0	.18	1.9
Hesperochloa kingii (leaves)	Sept.	green	15.2	.26	3.2
Danthonia intermedia (leaves + flr. stem)	Aug.	green	10.0	.19	2.4
Herbaceous Species:					
Allium validum (leaves + stems)	Sept.	green	13.2	.19	8.2
Allium validum (flowers)	Aug.	green	29.3	.73	1.0
Dodecatheon redolens (leaves)	July	green	25.8	.31	2.5
Lupinus formosus (leaves)	Sept.	green	23.5	.32	.6
Oxyria digyna (leaves + flr. stems)	Aug.	green	22.0	.32	8.0
Phacelia frigida (leaves + flr. heads)	Aug.	green	22.3	.35	13.4

Table 19 (con't)

Species	Month	Phenological State	% Crude Protein	% P	Ca/P
Achillea lanulosa (flowers)	Aug.	green	13.4	.37	2.2
Polemonium eximeum (leaves)	Aug.	green	16.8	.28	9.6
Polemonium eximeum (flowers)	Aug.	green	13.1	.43	2.6
Polemonium eximeum (seed heads)	Aug.	green	12.0	.34	2.3
Hulsea algida (leaves)	Aug.	green	19.4	.28	9.0
Hulsea algida (flowers)	Aug.	green	15.4	.43	2.0
Cryptantha circumcissa (flowers)	July	green	16.4	.20	10.2
Sphenosciadium capitellatum (leaves)	Aug.	green	14.7	.17	11.6
Silene sargentii (Leaves + flr. stems)	July	green	17.0	.27	4.8
Aquilegia pubescens (flowers)	July	green	18.5	.33	1.1
Trifolium monanthum (leaves + stems)	June	green	16.9	.17	21.7
Ivesia pygmaea (leaves + flrs.)	Aug.	green	13.4	.30	4.6

Table 19 (con't)

Species	Month	Phenological State	% Crude Protein	% P	Ca/P
Woody Species:					
Leptodactylon pungens (new leaves)	July	green	13.6	.28	3.0
Leptodactylon pungens (leaves with stem)	July	green	12.9	.23	4.4
Potentilla fruticosa (leaves)	Aug.	green	18.8	.25	2.7
Potentilla fruticosa (flowers)	Aug.	green	11.0	.21	3.0
Potentilla fruticosa (leaves)	Sept.	yellowing	10.8	.11	14.0
Holodiscus microphyllus (leaves)	July	green	16.3	.36	4.2
Jamesia americana (new leaves)	June	green	17.7	.30	8.8
Jamesia americana (leaves + flowers)	July	green	17.3	.27	13.6
Ribes montigenum (leaves)	July	green	23.0	.40	3.0
Monardella odoratissima (leaves + flowers)	Aug.	green	18.9	.25	8.1
Penstemon davidsonii (flowers)	Aug.	green	11.8	.28	1.9
Tanacetum canum (leaves with stem)	July	green	19.6	.39	1.8
Salix jepsonii (leaves)	Sept.	green	17.7	.11	8.4

Table 19 (con't)

Species	Month	Phenological State	% Crude Protein	% P	Ca/P
FALL					
Carex exserta (leaves + seed heads)	Dec.	dry	7.8	.09	5.9
Carex rossii (leaves)	Nov.	partly green	11.1	.14	3.8
Carex leporinella (leaves)	Nov.	partly green	6.5	.06	8.2
Juncus parryi (stems + seed heads)	Dec.	partly green	7.6	.10	2.7
Festuca brachyphylla (leaves + seed heads)	Dec.	partly green	9.6	.09	2.5
Stipa pinetorum (leaves)	Nov.	partly green	8.7	.05	7.0
Calamagrostis purpurascens (leaves)	Dec.	dry	4.4	.11	1.8
Muhlenbergia richardsonis (leaves)	Nov.	partly green	6.9	.12	5.6
Sitanion hystrix (leaves)	Nov.	partly green		.14	3.2
Lupinus formosus (leaves)	Nov.	partly green	19.3	.18	17.4
Haplopappus macronema (leaves + stem)	Oct.	mostly dry	11.4	.16	8.0
Chrysolepis sempervirons (green leaves)	Nov.	green	7.6	.09	12.8

are well-known correlates, thus the significance of the results for protein. Correlations of protein and phosphorus values in Table 19, stratified by forage classes, all yielded highly significant values (P<.001). Since protein content is also correlated with apparent digestibility (Hebert 1973), phosphorus should also correlate with it to some degree. Overall, phosphorus content should be a good measure of forage quality and thus a good basis for preference.

Two independent findings suggest that phosphorus might be in short supply to bighorn in the Sierran alpine. Klikoff (1965) investigated soil chemistry at multiple sites for 8 different alpine vegetation types in the Yosemite area of the Sierra and found all to be deficient in phosphorus. Secondly, Hicks (pers. comm.) conducted a chemical analysis of rocks used by bighorn as a salt lick on Baxter Pass, and concluded that phosphorus was the most likely element being sought.

Seasonal Phosphorus and Protein Levels

Based on food habits data in Table 9 and forage nutrient values in Table 19 it is possible to calculate approximate dietary levels of phosphorus and protein for winter and spring. Since relative proportions of new and old growth of needlegrass in the diet are not known for most of the period, calculations were made only for the early winter situation of all old growth and for the May situation of all new growth. For sheep in Sawmill Canyon in early winter the calculated protein level of the diet was 7% and the phosphorus level was .095%. The actual values can be expected to be higher, since selectivity by bighorn for more nutritious plants is not taken into account in the calculations. Hebert (1973) found that bighorn did not lose weight until the winter diet dropped below 5% protein, and .11% phosphorus was considered a winter maintenance level (Hebert 1972). Early winter protein level appears to be above maintenance, while the calculated phosphorus level is slightly below. It is doubtful that the true phosphorus level is below maintenance, given (1) the apparent ability of the bighorn to select forage on this basis, and (2) that among their preferred winter forage species are some (e.g., Artemisia tridentata and Eriogonum fasciculatum) that have phosphorus values well above 11% (Table 19).

Calculations for the May diet in Sawmill Canyon yielded values of 17% protein and .32% phosphorus. The minimum protein requirement for a domestic ewe in early lactation is about 1.9 g. digestible crude protein per kg body weight for body sizes in the 50-60 kg range found for bighorn ewes in the Sierra (National Research Council 1964). Hebert (1973) found a close fit to a linear relationship between percent crude protein in the diet and digestible crude protein per gm body weight for bighorn. Using his equations, the minimum protein requirement of Sierra bighorn in early lactation would be about 9% on a forage intake basis.

Minimum phosphorus requirement for domestic ewes is .20% (National Research Council 1964). The May values for Sawmill Canyon greatly exceed these minimum requirements. Calculations for the mid-May diets of the ewes that lambed in South Bairs Canyon yielded approximately 11.5% protein and .20% phosphorus. These values are considerably below those for Sawmill Canyon, but nevertheless appear to meet the minimum requirements cited for domestic ewes in early lactation.

Lack of precise data on food habits in the high country and the problem of rapid changes in growth stage of alpine plants preclude calculation of approximate nutrient budgets for summer and fall. However, comparison of nutrient values in Table 19 for preferred species in different seasons is meaningful. Preferred summer graminoids are primarily *Juncus parryi*, *Carex exserta*, *Carex spectabilis*, *Carex vernacula*, *Carex congdonii*, *Carex helleri*, *Carex rossii*, and *Sitanion hystrix*. With the exception of *Carex rossii*, whose phosphorus value is in question, these species are comparable to spring perennial grasses in protein and phosphorus content. *Carex exserta* is notable among them as an excellent forage species. However, its availability to ewe-lamb groups is small due to its short growing season and low abundance above timberline. Once yellowing, its nutritional value plummets (Table 19), which explains its unpalatability in that condition.

Of the preferred summer browse species (*Holodiscus* *microphyllus*, *Jamesia americana*, *Ribes montigenum*, and *Potentilla fruticosa*), only *Ribes* approaches the high phosphorus values available in spring range browse species, but protein values appear similar (Table 19).

Of the summer forb species in Table 19, *Allium validum* flowers have exceptionally high phosphorus and protein values. These are clearly preferred by rams, but are unavailable to ewe-lamb groups. Of the species consumed by ewe-lamb groups, only *Phacelia frigida* and *Lupinus formosus* (eaten mostly by the Williamson herd in summer) have both high phosphorus and protein values such as found in the spring range forbs *Tauschia parishii* and *Convolvulus aridus*; other forbs are high in one or the other, but not both (Table 19). *Oxyria digyna* has high protein and phosphorus values, but is avoided by ewe-lamb groups, perhaps because of its high content of oxalic acid. Phosphorus values of summer forb species are lower than spring broad-leaved species in general, with the exception of the flower heads of *Polemonium eximium* and *Hulsea algida*, both of which are highly preferred, as discussed previously.

Phosphorus content is clearly lower among alpine species compared to spring range species. Protein differences are not so clear cut. The apparent tradeoff of protein for phosphorus in the alpine may result in a lower protein level in the early summer diet than in spring. The high percentage of high quality broad-leaved species in the spring diet (Table 9) had the effect of considerably raising the overall diet quality over one consisting primarily of graminoids. The summer diet exhibits a shift back to a predominance of graminoids (Table 17) and a concomitant drop in quality would be expected since spring and summer range graminoids appear equivalent in quality. The rapid developmental changes in alpine plants can be expected to cause a continuously decreasing diet quality until it reaches a stable low point in late October, or earlier in dry years. The magnitude of this drop can be seen by examining nutritional values for species available in fall (Table 19). Both phosphorus and protein values are similar to those found in early winter on winter ranges.

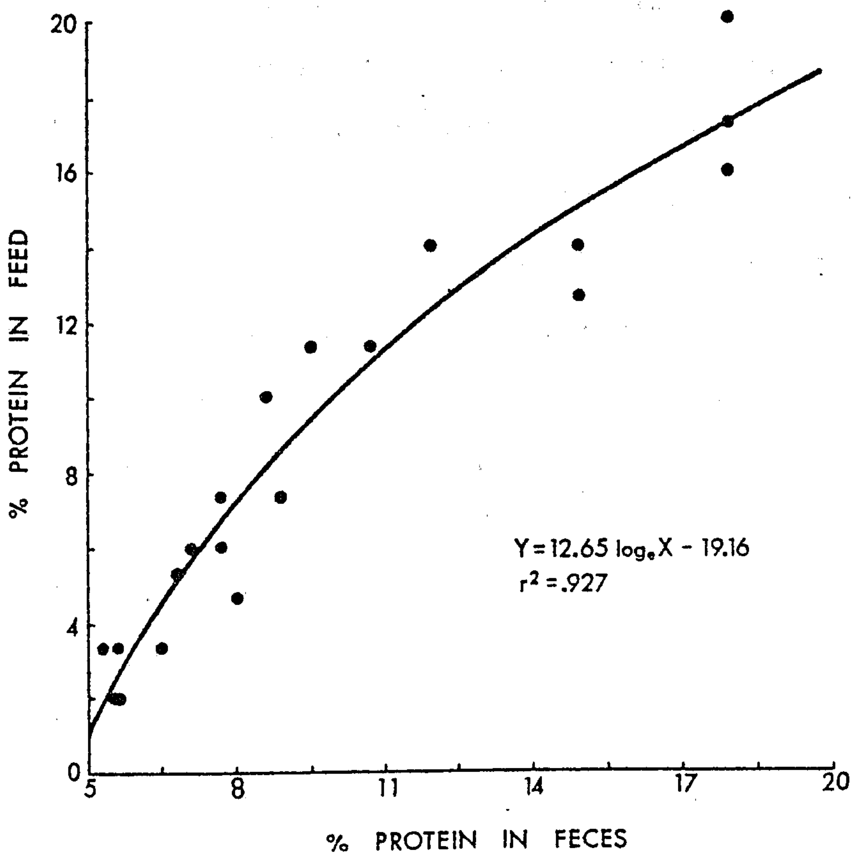
Fecal Protein

Background

Fecal nitrogen is derived from undigested nitrogen of the feed and metabolic nitrogen (e.g., enzymes, intestinal cells) contributed by the body in the process of digestion (Maynard and Loosli 1969). Since most forage nitrogen is soluble (93%) and readily digested (Van Soest 1967), the majority of nitrogen in feces is of metabolic origin and its quantity is directly proportional to the amount of forage consumed (Mitchell 1926). Its concentration (% dry matter) in feces should thus reflect the fraction of the feed that becomes fecal matter, i.e. the digestibility of the forage. This relationship is well-known among domestic ruminants (Blaxter and Mitchell 1948, Lancaster 1949). Digestibility itself correlates well with forage nitrogen content (Gallup and Briggs 1948, Hebert 1973). Thus a correlation between forage nitrogen content and fecal nitrogen would be expected. This has been demonstrated for domestic ruminants (Blaxter and Mitchell 1948) including domestic sheep (Raymond 1948). Hebert (1973) found the same relationship for captive bighorn fed known major dietary items from bighorn ranges in Canada. In his study, two groups of bighorn were fed different diets through one year; one simulated normal migratory patterns and the other simulated year round occupation of winter ranges. Using linear regression and covariance analysis, Hebert (1973) concluded that slopes of the regressions of % dietary protein on % fecal protein differed slightly for the two annual dietary regimes of his experiment. Examination of his data suggest that this conclusion is an artifact of using a linear model. With a simple curvilinear model (Figure 18) the two treatments do not differ significantly and the overall fit of the data is significantly better than a linear model ($P<.025$). Hebert (1973, 1978) also found fecal protein level to correlate significantly with percent digestibility and blood urea nitrogen. Fecal protein would thus appear to have considerable potential as a relative measure of diet quality.

Its use for Sierra bighorn has born this out, providing the opportunity to further investigate patterns of diet quality suggested to exist on the basis of growth condition

Figure 18. The relationship between fecal and dietary protein levels for Rocky Mountain bighorn fed natural diets. Data are from Hebert (1973).



and nutrient content of forage species. Comparisons between the Baxter and Williamson herds within years, as well as comparisons between years mostly involving the Baxter herd have been investigated (Figure 19).

Fecal samples analysed for protein for comparisons between herds and years were selected to correspond as closely as possible in time so that statistical pairwise comparisons could be made. In most cases comparisons spanned a week or less. All samples were from groups containing ewes.

Replicate samples for many samplings came from a single bighorn group and may not be representative of the entire herd. The high mobility of ewe-lamb groups in the alpine probably integrates much spatial variability in forage quality, thus increasing the representativeness of high country samples. This has been born out by the closeness of values sampled at different locations in some samplings.

The winter samples from the Williamson herd in 1978 came from a group that constituted 75% of the census total, thus should represent the herd well. Other winter samples may be less representative. Nevertheless, daily movement patterns of sheep in winter frequently cover much elevation, thus may also integrate much of the variance in forage quality. Samples from lambing ranges are representative of only the specific ranges on which they were collected.

Figure 19. Fecal protein levels for ewe-lamb groups, 1976-1978.

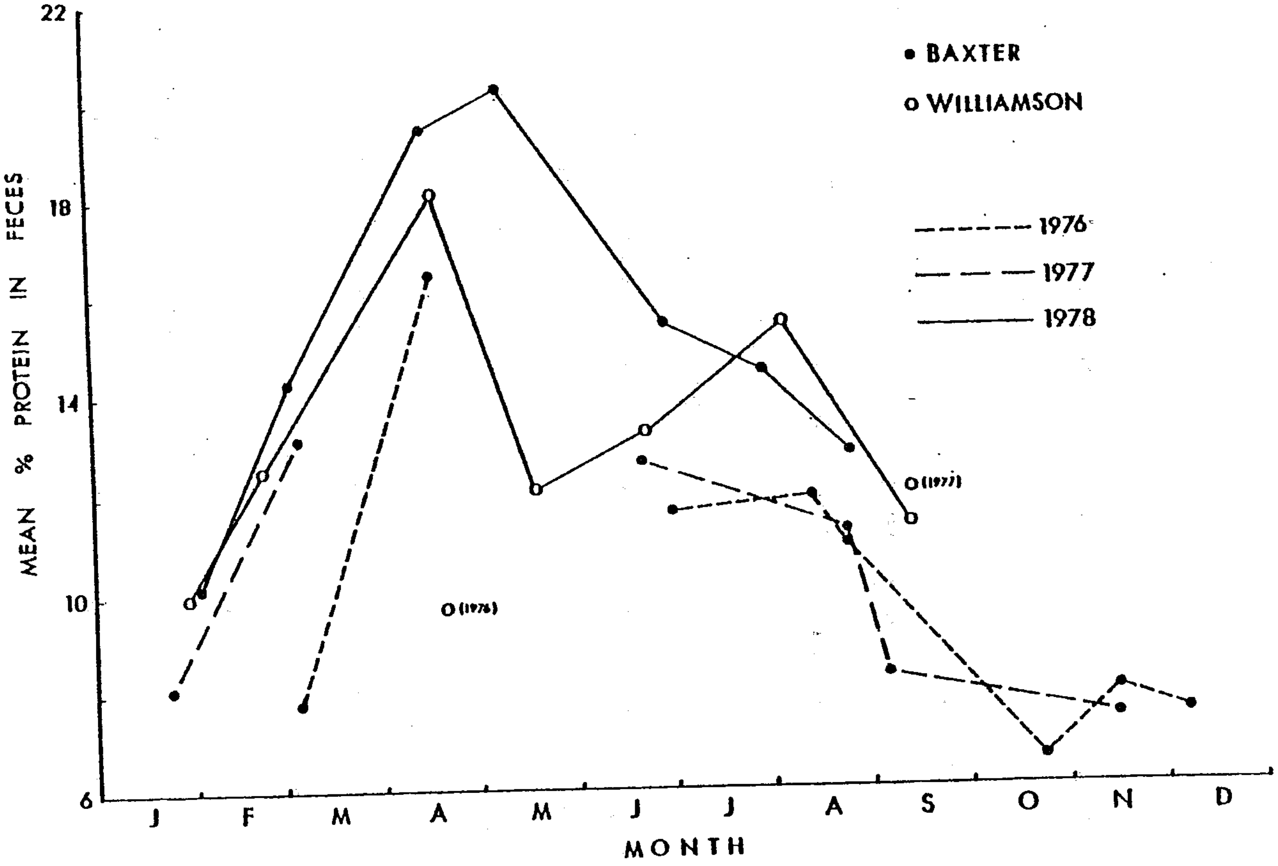


Table 20. Fecal protein values for ewe-lamb groups in the Baxter and Williamson herds, 1976-1978.

Herd[1]	Season	Date	Mean	S.E.	N	t value
W	winter	2/1/78	10.06	.140	10	1.08
B		2/2/78	10.22	.048	4	2.76*
B		1/23/77	8.13	.756	4	
W	winter	2/27/78	12.55	.563	6	2.20*
B		3/3/78	14.27	.544	6	1.30
B		3/5/77	13.08	.768	4	8.49***
B		3/4/76	7.86	.414	4	5.98***
W	spring	4/20/78	18.11	.513	7	1.61
B		4/16/78	19.52	.749	5	3.99* 8.25***
B		4/17/76	16.38	.238	4	6.62**
W		4/21/76	9.70	.981	5	
W	spring	5/18/78	12.11	.475	9	9.73***
B		5/12/78	20.24	.706	8	
W	summer	6/23/78	13.34	.678	8	2.93*
B		6/29/78	15.41	.195	8	8.49***
B		6/20/77	12.67	.232	4	4.62*
B		7/1/76	11.63	.794	3	1.45
W	summer	8/7/78	15.54	.427	9	1.36
B		7/29/78	14.42	.616	13	
B	summer	8/25/78	12.76	.500	2	1.55
B		8/23/77	11.24	.565	5	2.62
B		8/23/76	10.87	.479	3	.44
W	fall	9/12/78	11.32	.125	2	1.89
W		9/13/77	12.03	.355	11	***
B		9/5/77	8.30	--	1	
B	fall	11/15/77	7.36	.270	5	1.38
B		11/15/76	7.95	.318	6	

[1] W=Williamson; B=Baxter

* $P \leq .05$
** $P \leq .01$
*** $P \leq .001$

Winter

Winter fecal protein levels exhibited the expected rise beginning in early February of 1978 with the initiation of green needlegrass growth (Figure 19). A slight difference between the two herds in the early March sampling (Figure 19, Table 20) presumably reflects elevational effects on plant development. In 1977, the early winter Baxter sample was somewhat lower than 1978, while the early March sample was not significantly different (Figure 19, Table 20). This slight difference probably reflects different timing of the first winter storm. The first storm in 1977 was about two weeks later than in 1978. In 1976 it was about two months later than 1978 (thus the lack of an early winter sample) and the effect appears to be demonstrated by the early March sampling (Figure 19, Table 20).

The rise in nutrition during winter is probably attributable to a number of factors. The existence of green needlegrass alone does not easily explain it, since in 1976 and 1977 needlegrass began growing after heavy early fall rains. Nevertheless, although the new growth did not yellow, the long dry period before the the first winter storms may have caused some drop in nutrient content. Also, bighorn nutrition may be influenced by how early they begin feeding on winter ranges, since the dry needlegrass of the previous season must be consumed to a considerable extent before new growth can be fed on. Hebert (1973) noted this problem on spring ranges in Canada. Lastly, nutrient content of other forage species is probably involved, despite lack of visible evidence. Jones (1954) found that the protein content of sagebrush in Owens Valley increased one percent per month from December through March then rose rapidly with spring growth. However, neither *Purshia* spp. nor *Eriogonum fasciculatum* showed protein changes until April.

Spring

The April sampling shows a continuing rise in nutrition with the flush of spring growth (Figure 19). The 1978 values for the Baxter and Williamson herds are not significantly different, but the 1976 values differ significantly from each other and from 1978 values (Table 20). However, the 1976 Baxter herd value shows less difference from the 1978 value than does the March sampling. Apparently spring nutrition in the Baxter herd is less sensitive to precipitation than winter nutrition. The 1976 April value for the Williamson herd is exceedingly low. The explanation for this is that these sheep inhabited considerably higher elevations than the Williamson sheep sampled in 1978 at that time, or the Baxter sheep sampled at the same time. The paucity of snow in 1976 compared with 1978 allowed the Williamson sheep to exist at much higher elevations in April, but at an apparent nutritional cost. The relative closeness of winter and early spring fecal protein values for the two herds in 1978 may be the exception rather than the rule due to the deep snow that winter. Only half the winter snowfall recorded in 1978 fell in 1979 (Table 1), and neither bighorn nor their sign could be located at any known escarpment base wintering areas in the Williamson range. Presumably the lesser snow depths allowed them to remain at higher, safer elevations, but undoubtedly at a cost in terms of nutrition, such as suggested by the 1976 fecal protein value.

The 1978 May samplings are from Sawmill Canyon and South Bairs Canyon lambing grounds. The nutritional differences predicted previously on the basis of food habits and stage of plant development are clearly apparent (Figure 19). On the basis of the rate at which greenup rises with elevation it was previously predicted that these sites would differ in stage of plant development by about two months. The fecal protein levels suggest the difference is even somewhat greater, since the Williamson mid-May sampling is about equivalent to late February (Figure 19).

Summer and Fall

Early summer (late June) samples from ewe-lamb groups in the alpine show a much less, but still significant, advantage for the Baxter herd (Figure 19, Table 20). The reason for this is not clear, but may be the result of greater availability to the Baxter herd of patches of meadow vegetation. The low summer values for the Baxter herd in 1976 and 1977 (Figure 19) reflect the winter drought during those years (Table 1), and the consequent lack of moisture in the alpine. Mid-summer values for the Baxter and Williamson herds were not significantly different in mid-summer of 1978 (Table 20). The unreplicated September 1977 sample from the Baxter herd fell outside of the 99.9% confidence limits of the Williamson herd sample from the same time period, but conclusions based on this single sample seem unjustified. It is nevertheless significant that the September Williamson herd samples from 1977 and 1978 did not differ (Table 20). In both cases a large percentage of the Williamson herd ewes, lambs, and yearlings were feeding considerably in a meadow fed by rock glacier melt at the head of South Bairs Creek cirque. Water runs late in this meadow, thus it remains green into October regardless of precipitation. It is possible that the Williamson herd regularly maintains a high diet quality through September by the use of these meadows.

Fall levels of fecal protein in 1976 and 1977 were similar to those found in early winter on winter ranges (Figure 19), as was suggested on the basis of protein content of individual forage species.

Comparison with Other Populations

The only other fecal protein data available are those from Hebert's (1973) study of captive bighorn in Canada. While the species composition of the diet of these sheep was representative of what they would eat if free ranging in the

Canadian Rockies, the vegetation they were fed could not be collected with the selectivity with which bighorn would feed. The annual pattern differed from that observed in the Sierra in that peak nutrition occurred in the month of July after migration into the alpine rather than in spring, although a small peak (12% fecal protein) occurred in April on winter range forage. Since these northern Rocky Mountain bighorn populations bear their lambs about a month later than in the Sierra (Geist 1971), their peak nutrition would occur just after lambing, rather than during, as was apparent in the case of the Baxter herd. Both populations exhibit a steady drop in nutrition in the second half of summer with an October leveling at a low value. This low nutritional plane extends through March in the northern populations, which is two months longer than normally occurs in the Sierra. Thus the overall yearly pattern of diet quality, as would be measured by integrating the fecal protein curves over a year, would be expected to be less among northern populations than in the Sierra.

Milk Consumption

Background

A considerable amount of agricultural research has been directed toward understanding the influence of nutrition on milk production of domestic ewes, which in turn influences lamb growth rates and survival. Many studies have shown that milk production is clearly a function of diet quality.

Horejsi (1976) and Berger (1979) provided reviews of this literature as it applies to the use of measures of suckling to assess different nutritional regimes of bighorn sheep. The following summary of pertinent points is based on these reviews and concerns non-dairy domestic sheep.

Quantity and quality of milk consumed determine the amount of nutrition a lamb receives from its mother through her milk. In terms of quality, fat content shows the most variation, and generally varies inversely with diet quality. However, total milk fat production is positively correlated with quality of the diet. Variation in milk quality generally has been found to be of little importance, compared with quantity, in effecting weight gain in lambs. This is convenient, since variation in milk quality cannot be measured in most field studies. Quantity of milk produced has been found to depend on the quality of the diet during lactation and on the amount of mammary tissue. Mammary development takes place mostly during the last 20% of gestation, and nutrition during that period strongly affects mammary size and, hence, the potential for milk production. Thus it is meaningful to consider prepartum and postpartum nutrition separately.

Postpartum nutrition exerts the greatest influence on total milk yield and is more critical to the ewe than prepartum nutrition, judging from the amount of weight lost by ewes fed different pre- and postpartum diets. Postpartum nutrition largely determines total milk production through its influence on early lactation when production rate is highest. Prepartum nutrition influences the level of late lactation.

Geist (1971), Shackleton (1973), Horejsi (1976), Berger (1978, 1979), and Smith and Wishart (1978) provided quantitative results of suckling from field studies of a variety of bighorn populations. However, many of these results differ in their units of measure, making comparisons difficult. All of the studies quantified duration of suckles, but many have done so on a monthly basis rather than on the basis of lamb age. The span of lamb ages within any month may cause considerable variance in suckling measurements. Since ages of lambs in a particular month vary among populations due to variation in the timing and length of lambing seasons, transformation of month-based data to age-based data, where possible, is necessary for purposes of interpopulation comparison.

Suckle frequencies have not always been measured, and where they have been, the time basis has varied. Geist (1971), Berger (1979), and Horejsi (1976) all measured frequency on the basis of hours of ewe activity, while only Shackleton (1973) measured it on a total hourly basis. A basis of total hours seems more meaningful since (1) this is what matters to lambs in terms of total milk consumption, (2) comparisons between populations need to be corrected for variation in activity patterns of ewes, and (3) activity patterns may vary considerably within populations. Belovsky

(1978 and pers. comm.) found ungulate activity patterns to be dependent on ambient temperature. Variation on this basis has been evident among ewes with young lambs in Sawmill Canyon. On hot days (30-35°C) in May bedding periods of ewes were so long (up to 140 min.) that their lambs would force their mothers to rise briefly for a suckle by attempting to suckle while they were bedded. To base suckle frequency measures on the basis of ewe activity seems questionable.

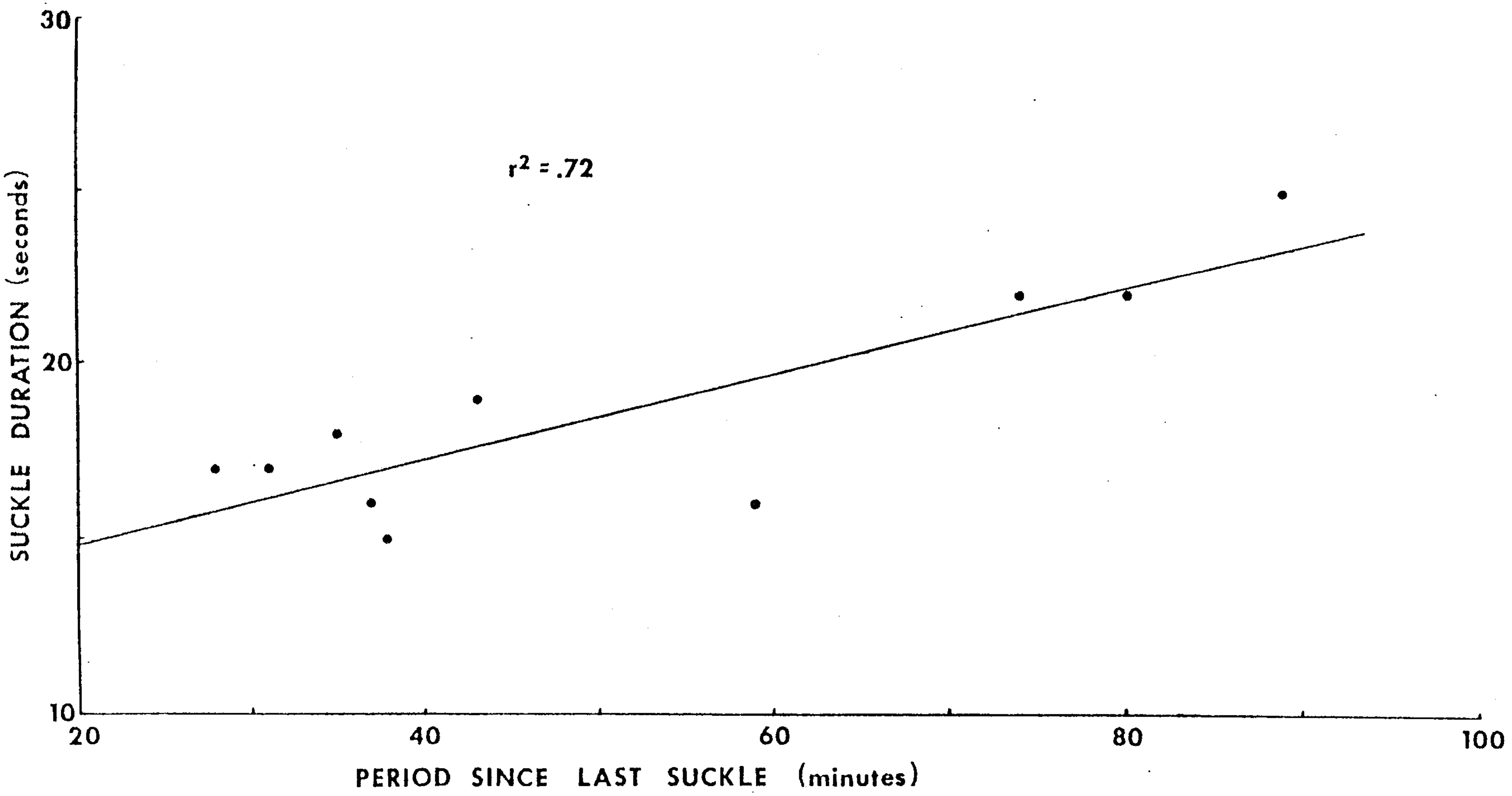
Previous studies have also failed to follow suckling to the completion of weaning, although Horejsi (1976) presented data extending through December for 1969. This may be a particular problem in some populations where alternate year breeding (Heimer 1978) causes some ewes to nurse their lambs considerably longer than others (Geist 1971).

Lastly, none of the above studies has looked at the relationship of suckle duration and frequency for individual lambs. A significant relationship between suckle duration and the length of the period since the previous suckle would mean that much of the observed variation in these parameters could be eliminated by measuring rate of milk consumption on an individual lamb basis, rather than on the basis of average suckle durations and average overall frequency of suckles for all lambs.

The Relationship Between Suckle Duration and Frequency

The purpose of collecting data on suckling was to make a comparison of the Baxter and Williamson herds as a measure of possible nutritional differences. In light of the above discussion, it was considered desirable to make separate measures for individual lambs at each sampling, and to express the results on the basis of lamb age. Whether a statistical relationship existed between suckle duration and period since the previous suckle was an important question. Its answer depended on obtaining numerous points for a single lamb within a short period of time, over which rate of milk consumption was not changing. Since suckle frequency declines rapidly with lamb age and bighorn groups could only rarely be observed over more than a single day, it was necessary to investigate this question using a young lamb, since its high suckling frequency would allow numerous suckles to be recorded in a single day. Another variable that had to be controlled was disturbance, since ewes were frequently observed to rapidly terminate suckles if another lamb approached too closely while she was nursing. Adequate data were obtained on only a single occasion involving a Williamson herd group containing a single lamb, for which 12 hours of continuous observation were logged over the course of one day and the following morning. The results clearly demonstrate the expected relationship between the duration of a suckle and the period since the previous suckle (Figure 20).

Figure 20. The relationship between suckle duration and frequency for a single lamb three weeks of age.

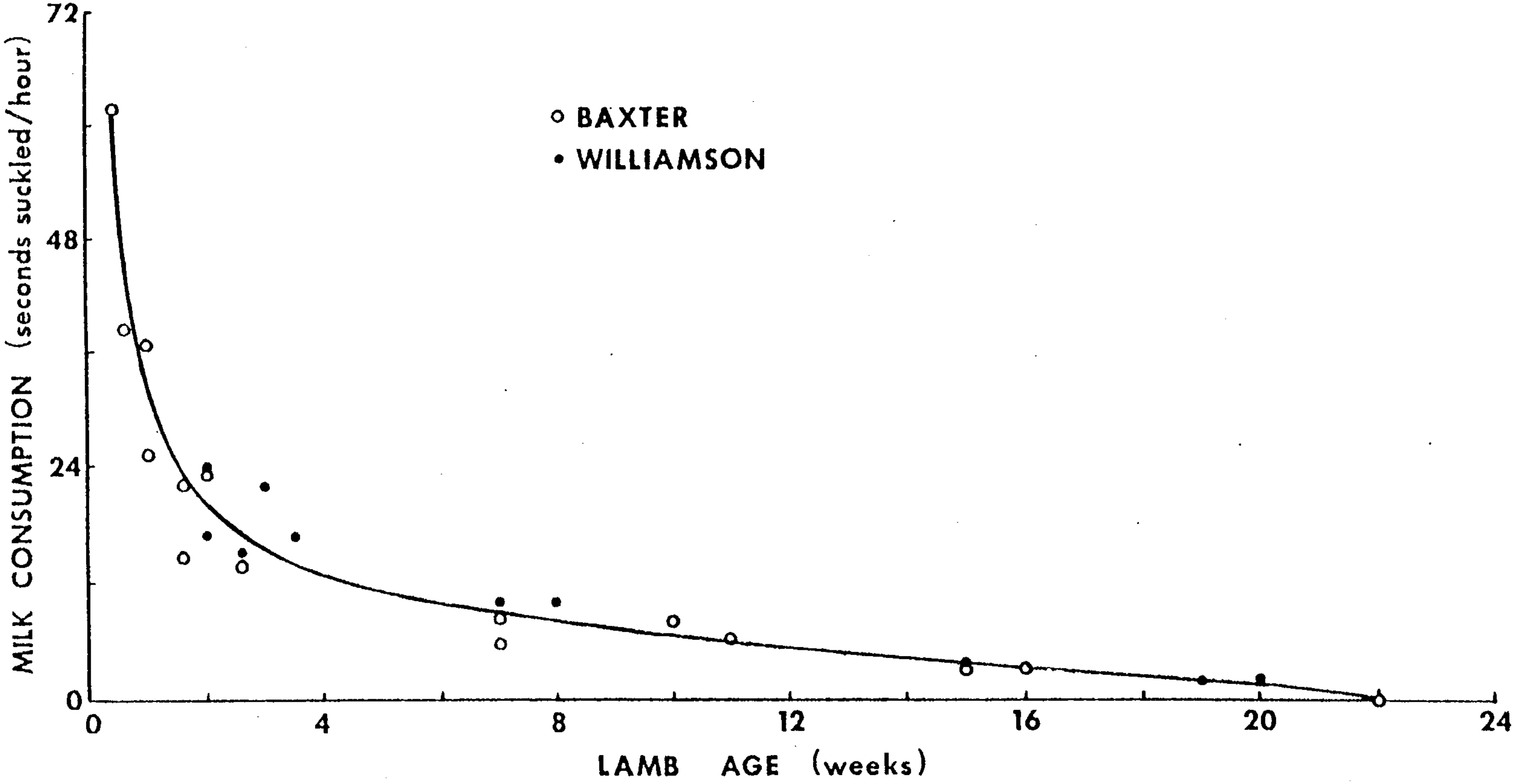


Milk Consumption Rate

Rate of milk consumption for each lamb sampled was measured by summing the durations of suckles after the first observed suckle and dividing by the total period elapsed between the first and last suckle. Since suckles occurred only about once every three hours in late summer, it was usually possible to observe only two suckles per lamb toward the end of weaning. The values for all lambs sampled have been plotted as a function of lamb age (Figure 21). The resultant curve shows no clear difference between the two herds. When the samples from 1.5 to 3.5 weeks of age are compared, no significant difference between herds was found (t=.297, d.f.=7). This lack of difference is of interest since these samples of young lambs were mostly from sheep in Sawmill Canyon and South Bairs Canyon, whose diets have previously been shown to be quite different in quality. The lack of difference in milk consumption probably reflects the finding that neither diet appeared deficient relative to minimum protein and phosphorus requirements set for domestic sheep.

The shape of the milk consumption curve exhibits a rapid early decline during the first 1.5 weeks of age then a long nearly linear decline (Figure 21). Completion of weaning occurred in October coincident with the sheep approaching the low point in their annual nutrition curve. Ewes clearly control the decline in milk consumption by refusing suckle attempts and controlling the duration of

Figure 21. Rates of milk consumption for the Baxter and Williamson herds in 1978.

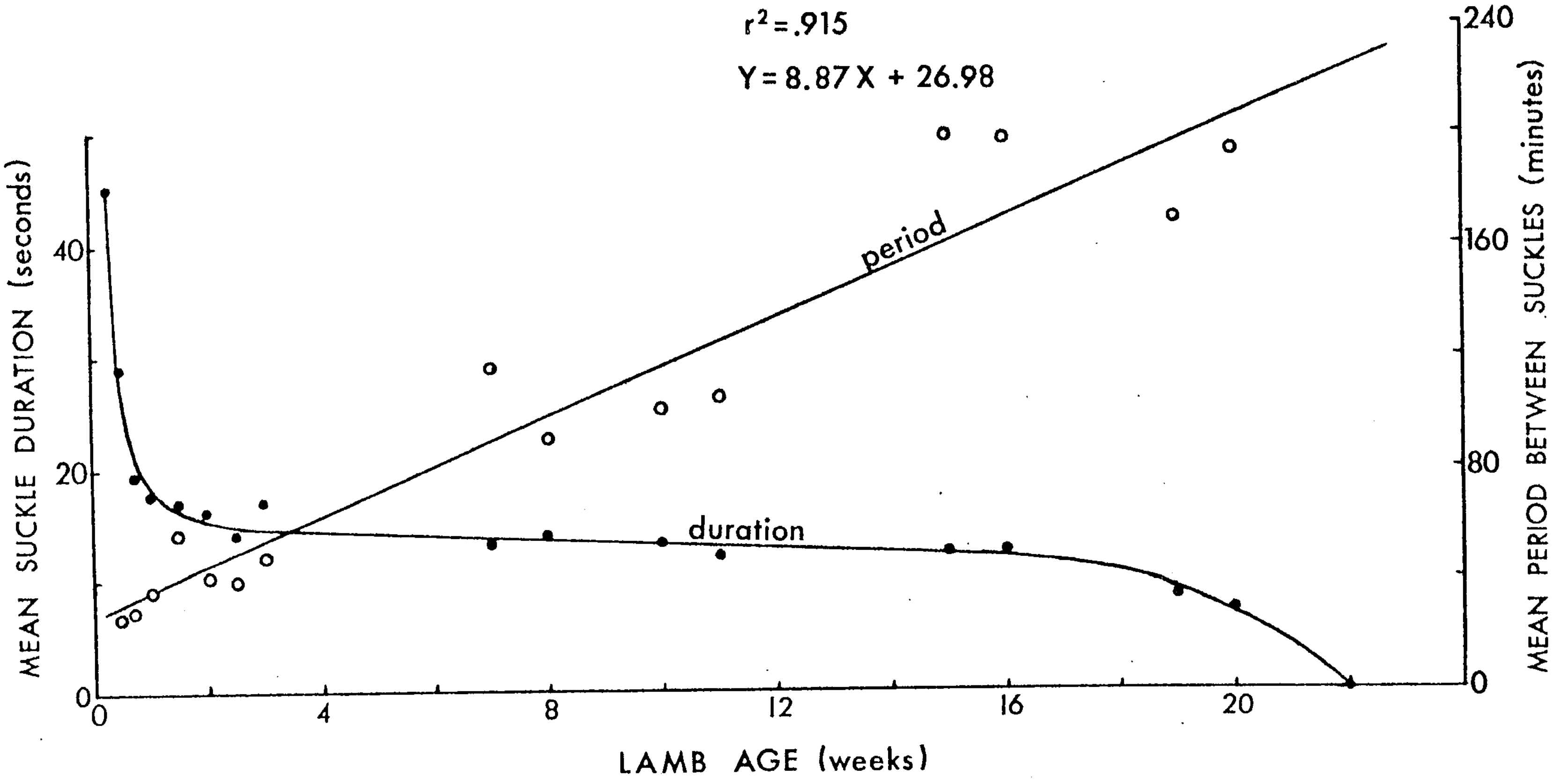


suckles. Lambs have been observed to terminate suckles, presumably due to satiation, only during the first week of their lives when long suckles are apparent (Figure 22). Early long suckles do not necessarily mean that lambs are receiving more milk than a few days later, but may simply reflect a young lamb's inability to consume milk as rapidly.

When the curve of total milk consumption (Figure 21) is broken into its component curves of suckle duration and frequency, the importance of frequency in determining milk consumption is apparent (Figure 22). Suckle duration declines very slowly between week 2 and 16, while the period between suckles rises substantially. If duration alone had been considered, a misleading picture would have clearly resulted.

When compared with suckle durations recorded for other populations (Geist 1971, Shackleton 1973, Horejsi 1976, Smith and Wishart 1978, Berger 1979), the 1978 values from the Sierra coincide with the lowest values reported, and are notably lower in the first couple of weeks of life. According to Geist (1971), Shackleton (1973), and Horejsi (1976), the Sierran herds should represent a situation of a static or declining population in which nutrition and lamb survivorship are poor (low quality population in Geist's terms). Yet, no differences were apparent between the two Sierran herds despite considerable nutritional differences at the most critical time of lactation. Furthermore, although recruitment in the Baxter herd was low in 1978, it

Figure 22. Suckle duration and frequency as a function of lamb age.



represented a high survivorship, since lamb production was low (Table 4).

These results point out the danger of using suckling measurements as meaningful measures of population nutrition and demographic status, except within similar environments. Native bighorn range encompasses a wide variety of environments. Ewes should be expected to exhibit different reproductive patterns, including lactation, in different environmental circumstances (Lenarz 1978). Berger (1979) found a considerable difference in patterns of lactation between one desert and two northern populations.

Resource Predictability and Reproductive Pattern

Investment by a female in a current reproductive effort entails some cost in terms of her future reproduction (Williams 1966a,b, Cody 1966, Shaffer 1974, Bradbury and Vehrencamp 1977). This cost may vary considerably depending on the intake of nutrients and the nutritional demands of reproduction. Natural selection can be expected to favor a tactic (sensu Stearns 1976) that on the average nets individual females the most descendents in future generations (Williams 1966a, Shaffer 1974, Goodman 1974, Pianka and Parker 1975). Whether a ewe can successfully rear a lamb depends on whether the combination of her body reserves and nutrient intake can meet the needs of gestation and lactation. Natural selection will favor abandoning reproductive efforts when future reproductive possibilities are jeopardized due to excessive demands on body reserves. However, the physiological state at which reproduction will be discontinued may vary with reproductive value (Fisher 1958) of the individual (Williams 1966b, Fagen 1972, Shaffer 1974). Any reproductive effort that does not lead to a reproductively successful offspring represents effort wasted by the ewe. Reproductive tactics exhibited by different bighorn populations can be expected to minimize such costs.

At the time of ovulation and conception, a ewe's physiology must decide whether her physical condition is adequate to carry a reproductive effort to successful completion. How well this prediction can be made will depend on the variability of the curves of nutrient intake and expenditure throughout the period of the reproductive effort. The reproductive effort may be terminated at various stages by fetal resorption, abortion, or offspring abandonment following birth (Bradbury and Vehrencamp 1977, Low 1978), but, respectively, each represents a greater cost in wasted nutrients. Ramsay and Sadleir (1979) presented evidence suggesting that a bighorn ewe resorbed a fetus near term. This should reduce costs relative to the alternative of abortion, but is still more costly than earlier termination (Low 1978).

Nutritional requirements of domestic, and presumably bighorn, ewes are highest during early lactation, followed by the last 6 weeks of gestation and the latter part of lactation, with early gestation and nongestation having the lowest requirements (Maynard and Loosli 1969). The different timings of lambing seasons among bighorn populations presumably reflect environment-specific solutions for the tradeoff between (1) maximizing the period of growth available to the lamb before the onset of the thermally and nutritionally harsh season of the year (winter in the mountains, summer in the deserts) and (2) coinciding births with the timing of optimal nutritional and thermal conditions. In many southern desert bighorn ranges the predictability of the timing and magnitude of vegetation greenup and the concomitant nutritional rise is low, and the season of births is consequently spread throughout the year (Lenarz 1979). Thus, conception represents a gamble (Lenarz 1979) and reproductive efforts are undoubtedly frequently terminated when favorable environmental circumstances do not materialize. Among northern bighorn populations, winter severity represents a major environmental variable. Hebert (1973) found that winter forage quality dropped below maintenance, and noted that, depending on snow cover, nutrition could drop further. Also, thermal stress in cold winters can additionally deplete nutrient reserves. Smith and Wishart (1978) reported a significant negative correlation between winter precipitation and recruitment rate for a population in the Canadian Rockies.

Environmental conditions of the Baxter herd range, and to a large extent the southern Sierra, appear to offer a favorable blend of desert and mountain conditions in the following ways: (1) through altitudinal migration the sheep are able to maintain a prolonged period of high diet quality, (2) nutrition appears rarely to drop below maintenance, (3) the short period of low diet quality coincides with a time of low nutritional requirements by the sheep, (4) the annual temperature regime is mild (Figure 3) and snow depths are rarely sufficient to significantly hinder feeding activities, and (5) a spring rise in nutrition is predictable and peak nutrition is excellent. Even during the extreme winter drought year of 1976, nutrition in April was high, judging from the fact that the fecal protein level was substantially higher than the Williamson herd sample of May 1978, which appeared to adequately meet nutritional requirements of early lactation.

Since diet quality appears to be predictably high during late gestation and most of lactation, when nutrient requirements are greatest, lambs should be well-nourished both pre- and postnatally, and their survivorship should be high. That postnatal nutrition is high is suggested by the fact that, despite considerable difference in diet quality, milk consumption was the same in both herds in 1978. I interpret this to mean that lambs were receiving the maximum milk ration allowable under the long term reproductive tactic of the ewes; thus lamb survival would be expected to be high.

This expectation of high survivorship is born out by comparing summer and winter lamb:ewe ratios during this study (Table 4). The number of lambs born on the Sawmill Canyon winter range can be used as an index of actual lamb production for studying the possibility of early lamb mortality as the cause of differences in summer lamb:ewe ratios. In 1977, when the summer lamb:ewe ratio was high (Table 4), 10 lambs were born in Sawmill Canyon (Figure 12). In 1978 the summer ratio was low (Table 4) and only 4 lambs were born in Sawmill Canyon (Figure 12). This suggests that early lamb mortality was not a significant factor, but the sample size is only two.

Calculation of the early winter level of dietary protein, and comparison of fecal protein values at that time with values presented by Hebert (1973) suggest that the diet during early gestation has been above maintenance. Since nutritional requirements of ewes at this time are low, prenatal mortality would be expected to be low. This is born out by considering that lamb production in 1976 was high (Table 4) despite an apparent prolonged period of low nutrition in early winter (Figure 22).

In summation, the above considerations suggest that the environmental regime in the Baxter herd range is such that once a ewe has initiated a reproductive effort by conceiving in fall, it is unlikely that conditions will occur necessitating early termination of or suboptimal investment in the effort. Recruitment rates measured during winter would thus be expected to correlate strongly with ovulation rates during the rut approximately 15 months prior.

Ovulation rates of domestic ewes are strongly influenced by body weight, which reflects nutrient reserves and, hence, prior nutrition (van Tienhoven 1968). It would thus be predicted that recruitment rate in the Baxter herd should be strongly influenced by factors affecting nutrition during the year prior to ovulation. Two such factors have been previously discussed: late summer nutrition is dependent on winter snow pack and winter nutrition is influenced by early winter precipitation. Thus winter precipitation would be expected to influence recruitment rate two years later. This was tested using ten years of recruitment data available for the Baxter herd and precipitation data from the Cottonwood Lakes Basin, the only data set complete for all years of recruitment records. Since many previous investigators did not distinguish yearling ewes, recruitment was measured as a ratio to all ewes. The analysis investigated precipitation for individual months and combinations of months.

Precipitation in single and blocks of months during the postovulation period exhibited no significant correlations with recruitment, and explained no more than 4% of the variance. In contrast, preovulation precipitation yielded some highly significant correlations. One month, December, yielded a significant ($P<.05$) regression with recruitment, and explained 43% of the variation, while blocks of months explained as much as 61% (Table 21). Examination of Table 21 reveals some interesting patterns. For the period of

Table 21. Results of regressions of recruitment rate on preovulation precipitation.

Variable	Mean ppt (cm)	CV	Regression slope	r^2	Significance level
single months:					
October	1.74	154.1	-.56	.022	.679
November	3.78	93.1	1.55	.299	.102
December	6.26	104.2	1.00	.426	.041
January	6.21	73.1	-.30	.018	.708
February	5.44	67.2	-.50	.033	.615
March	6.75	83.8	.74	.178	.224
April	2.21	72.4	.92	.022	.683
May	3.14	70.7	-1.86	.173	.231
June	1.84	131.6	-1.60	.151	.267
July	2.92	93.8	.11	.001	.931
August	2.19	86.8	-.47	.008	.806
September	3.21	154.4	-.35	.000	.962
October	2.02	142.8	.48	.019	.704
month pairs:					
Nov - Dec			.80	.499	.022
Dec - Jan			.97	.354	.069
Jan - Feb			-.30	.038	.590
Feb - Mar			.41	.071	.457
Mar - Apr			.63	.166	.243
Apr - May			-.98	.068	.466
May - Jun			-1.77	.333	.081
month blocks:					
Nov - Jan			.82	.459	.031
Nov - Feb			1.06	.524	.018
Nov - Mar			.83	.611	.008
Nov - Apr			.71	.539	.016
Nov - Jun			.61	.349	.072
Jan - Mar			.14	.016	.729

most precipitation (November - March), those months with higher coefficients of variation (CV) of precipitation exhibit the non-trivial r^2 values. However, in terms of total snow pack, the relative average contribution of each month must be considered. November contributes least of the five important months, yet has the second highest r^2 value. It is not clear how its CV alone can account for this relatively high r^2 value. This is pointed out in light of the possibility that November and December precipitation may influence nutrition and thus ovulation by contributing to the high country snowpack, in addition to influencing winter range nutrition. Precipitation in these two months is not entirely additive in its influence on recruitment. When each month is used as an independent variable in a multiple regression, the significance of each is considerably reduced relative to being considered alone and the overall regression is not significant (P=.09). When precipitation in these two months is added, the percent of recruitment variance explained rises only to 50%. This percent declines when January precipitation is added, but rises progressively with the addition of February and March precipitation (Table 21).

January through March precipitation alone explains only 1.6% of the variance in recruitment (Table 21), but explains an additional 11% when added to Nov - Dec precipitation (Table 21). That Nov - Dec precipitation influences recruitment in more ways than just through high country snow pack is suggested by the fact that when considered separately with January - March precipitation in a multiple regression, the percent of recruitment variance explained increases an additional 12% to 73% (R=.855) and the contribution of each independent variable is significant (P=.0035 for Nov - Dec, P=.044 for Jan - Mar).

Another interesting pattern in Table 21 is the strongly negative slope and rise in r^2 values for May and June. When these months are lumped their regression approaches significance (P=.081, Table 21). Covariance analysis indicates that the May - June slope differs significantly from Nov - Dec slope (P=.01) and from Nov - Mar slope (P=.007). The reason for this strongly negative slope may be explained by the fact that precipitation in the high country during this period occurs largely as rain rather than snow; thus it acts to decrease the snowpack, which would hasten summer decline in nutrition. However, when added to Nov - Dec and Jan - Mar precipitation as a third independent variable, May - June precipitation raises the R^2 value only to .77 (R=.88) and its contribution to the regression is not significant (P=.30).

Population density was also considered as an independent variable by using the curve fitted to the values in Figure 9 as a density index. As a single independent variable, this index explained only 2.7% of the variance in recruitment and was not significant (P=.649). As an independent variable in a multiple regression with Nov - Dec and Jan - Mar precipitation, its contribution was also not significant (P=.60).

Another variable likely to influence recruitment rate is the previous year's recruitment rate. Since nutrients provided to lambs during gestation and lactation would otherwise be funneled into body reserves, whether or not a ewe has just completed a reproductive effort is likely to have considerable influence on whether she ovulates in fall. Heimer (1978) reported alternate year breeding in Dall sheep in Alaska. This variable could not be considered in the above model because recruitment data were not always from successive years.

Internal Parasites

Gastrointestinal Nematodes

Sugar flotation yielded only ova of a single nematode. These ova were large (mean length=241.8microns, S.D.=14.52, N=41), which would place them in either the genus *Nematodirus*, as reported by McCullough and Schneegas (1966), or the species *Ostertagia marshalli* according to Shorb (1939, 1940), and Kates and Shorb (1943). The length measurements obtained are significantly (P<.001) longer than any of the measurements provided by Shorb (1939) for *Nematodirus* and *Ostertagia marshalli* from domestic ruminants. However, the ova from Sierra bighorn exhibited the tapered thickened ends that Shorb (1940) and Kates and Shorb (1943) consider diagnostic of *Nematodirus spathiger*.

The larger size presumably reflects differences between domestic and bighorn sheep as hosts.

The presence of this single intestinal nematode allowed its quantification to be carried out simultaneously with that of lungworms using a Baermann apparatus. This was done by allowing fresh fecal samples to air dry and age for at least 6 weeks before analysis. Thereafter, Nematodirus ova had embryonated and the larvae emerged upon soaking.

The average densities of Nematodirus larvae in winter pellet samples were 2.6 larvae per gram dry feces (N=49) in the Baxter herd and 13.2 (N=47) in the Williamson herd. These two values are significantly different ($P<.001$). In domestic sheep 50-100 Nematodirus ova per gram wet feces represent a light infection defined as probably having "little or no effect on health or productivity" (unpubl. mimeo, School of Veterinary Medicine, University of California, Davis). Evaluation of infection rates on the basis of their significance relative to other species may be questionable. Nevertheless, the exceedingly low values for Nematodirus infection in both herds in the Sierra suggest that both are insignificant.

One adult pinworm (Skrjabinema ovis) was found in a fecal pellet from the Williamson herd by chance while preparing samples for other analyses. Due to the life cycle of pinworms, there is no way of assessing the level of infection of this parasite. Pinworms are, in general, largely non-pathogenic.

Lungworms

Lungworms of the genus Protostrongylus have been found to play an important role in the population dynamics of Rocky Mountain bighorn populations. Buechner (1960) discussed various die-offs of Rocky Mountain bighorn herds in which a lungworm-pneumonia complex was an important factor. Stelfox (1971) showed that such die-offs of Rocky Mountain bighorn in Canada result in the loss of 75% or more of the sheep in the herds involved, and are part of a cycle of about a 25-year periodicity. As herds recover, density effects cause increasing lungworm loads and a decreasing plane of nutrition. The population crashes occur at high densities and are generally precipitated by the additional stress of a severe winter (Stelfox 1971, 1976). Cause of death is pneumonia, and usually involves a secondary bacterial infection for which lungworms are a predisposing factor (Post 1971, Woodard et al. 1974, Hibler et al. 1976).

Some recent lungworm related population declines in Colorado have been attributed to very poor lamb survival, rather than sudden die-offs (Hibler et al. 1976). High lamb mortality occurred in summer during the least stressful season of the year. Pneumonia again has been the cause of death (Woodard et al. 1974, Hibler et al. 1976), and the heavy lungworm burdens in the lambs are of transplacental origin (Hibler et al. 1972, 1974, 1976).

The life cycle of Protostrongylus spp. infecting bighorn involves a snail as intermediate host (Forrester

1971, Monson 1971). The shedding of larvae, as measured by larval concentration in bighorn feces, has been found to be cyclic on an annual basis, with peak larval output coinciding with the spring period when temperature and moisture conditions are favorable for snail activity (Uhazy et al. 1973). Additionally, Forrester and Littell (1976) found that the level of lungworm infection in Rocky Mountain bighorn herds in Montana correlated with the level of rainfall in the spring period from April through June. Spring range thus appears to be the range where infection occurs.

On Sierra Nevada bighorn ranges, temperature and moisture conditions favorable to snail activity probably occur throughout the period that winter ranges are occupied. Thus highest output of lungworm larvae would be expected during this period. Samples from the Williamson herd illustrate this clearly. Those collected from January through May (N=68) averaged 132.2 larvae per gram of feces, while the average from June through August, when sheep were in the high country was 3.4 larvae per gram (N=17). The difference is highly significant (t=10.1, P<.001). Winter range samples were consequently used for comparing herd infection levels.

Winter samples were stratified into three pellet weight classes, which correspond to lambs, yearlings, and adults, but with some overlap at the cutoff points. The Williamson herd exhibits substantially higher levels of lungworm infection overall (Table 22), as well as a different pattern of infection. When each of the three pellet size strata are compared between herds, the differences are all highly significant ($P<.001$ in each case). For the adult class the infection level of the Williamson herd is about 10 times that of the Baxter herd, while this factor approaches 100 for the younger age classes combined.

When analysis of variance is applied to the lungworm data from each herd, the Williamson herd yields no significant difference among strata ($F_{2,65}=1.96$), while the Baxter herd exhibits highly significant ($P<.001$) differences ($F_{2,44}=9.18$). The noteworthy difference in patterns of infection lies with lambs and yearlings, which carry adult infection levels in the Williamson herd, but near-zero values in the Baxter herd. Two hypotheses might account for this difference: (1) habitat differences between the two herds might expose Williamson herd lambs to infected snails at a younger age, or (2) the Williamson herd lambs were obtaining infections prenatally. The two hypotheses are not exclusive. Since the summer ewe-lamb habitats of the two herds do not differ appreciably, the second hypothesis was suspected.

Whether prenatal infection was occurring in the Williamson herd was investigated by analysing summer lamb pellets. Of nine summer lamb samples from the Baxter herd, none yielded any lungworm larvae. Of 15 such samples from the Williamson herd, 11 yielded lungworm larvae, with an

Table 22. Winter-spring lungworm (*Protostrongylus* spp.) levels in the Baxter and Williamson herds. The three pellet size classes correspond to lamb, yearling, and adult. Analysis was by the Baermann method using air-dried pellets broken in half. All samples were collected fresh.

Pellet Size Class	LARVAE PER GRAM OF FECES Mean	Range	S. D.	Sample Size
BAXTER				
< .15 gm/pellet	1.8	0-6.8	3.325	4
.15-.20 gm/pellet	1.0	0-3.5	1.281	11
≥.20 gm/pellet	15.9	0-59.6	12.956	32
WILLIAMSON				
< .15 gm/pellet	95.5	4.4-428.0	110.430	16
.15-.20 gm/pellet	124.5	20.5-344.0	97.312	22
≥.20 gm/pellet	157.4	25.8-503.3	103.788	30

average density (for all 15 samples) of 32.9 larvae per gram. To distinguish between prenatal infection and the ingestion of infected snails as possible sources of these summer results, it was necessary to establish whether lambs were passing larvae at ages less than the prepatent period for infection via snail ingestion. Monson (1971) experimentally infected bighorn-mouflon hybrids and found the prepatent period to vary from 63 to 122 days. Since lambs as young as three weeks of age were found to be passing larvae, prenatal infection is probably a major factor responsible for the different patterns of infection among age groups of the two herds.

The lungworm sampling in this study involved breaking fecal pellets only in half, whereas Baermann analysis commonly involves breaking pellets into many pieces. Before meaningful comparisons with data from bighorn populations outside of the Sierra could be made, an analysis of the influence of the methodology was necessary. This involved splitting some samples and applying different procedures to each. Two comparisons were made: (1) unbroken pellets vs. pellets broken in half, and (2) pellets broken in half vs. pellets broken into many pieces. The data were analysed by regressing the more-broken sample on the less-broken sample in each experiment. The resulting slopes represent the factor by which the results of one procedure may be transformed for comparison with results of the other procedure. In the first experiment the regression was highly significant ($P<.005$, $r^2=.609$, $N=32$) and the resulting slope was steep (4.33). In the second experiment the regression was also highly significant ($P<.005$, $r^2=.818$, $N=8$), but the slope was only 1.11, which was not significantly different from 1.00 ($t=.51$, d.f.=6). The sample size in this second experiment was small. A larger sample size may yield a slope significantly different from unity, but the difference is probably not important relative to the large spread of means among populations.

While the differences in lungworm infections between the Baxter and Williamson herds appear great, both are quite low when compared with values reported for other bighorn herds in North America. Forrester and Senger (1964) report average values ranging from less than 10 to 970 larvae per gram of dry feces for 10 Rocky Mountain bighorn herds in Montana. Uhazy et al. (1973) reported average values ranging from 439 to 2,375 larvae per gram of dry feces for 6 Rocky Mountain bighorn herds in Canada. Hibler et al. (1976) reported average levels of 3,000 larvae per gram for adults and 7-9,000 per gram for lambs in the Pikes Peak herd in Colorado when prenatal infection was killing most lambs. In light of these values, it is unlikely that the lungworm infections of the herds in Sierra are of any significance. This is corroborated by the lack of any clinical signs of lungworm infection and its associated pneumonia (see Forrester 1971) in either herd.

The low lungworm levels in the Sierra probably reflect low snail populations due to the aridity of the habitat. It was Buechner's (1960) contention that all bighorn ranges outside of the Rockies were probably too arid to support sufficient snail populations for lungworms to be of any significance. To date this prediction has been good. The difference in lungworm infection levels between the Baxter and Williamson herds probably reflects habitat differences. In particular, snails may be most prevalent in the understory of forested areas. This is suggested in light of the finding that the only Nevada bighorn herds carrying lungworms are those that inhabit higher elevations where tree cover and duff are present (McQuivey 1978).

Human Disturbance

The question of human disturbance is similar to resource competition in that, if significant, its ultimate influence will be a lowering of carrying capacity. This would happen because the population was unable (1) to obtain as much resource from its environment and/or (2) to convert as much of its resources into biomass. The first of these might occur through long term abandonment of areas of frequent human presence or frequent disruption of feeding patterns so that nutrient intake suffered. The second would result from resources expended in flight.

In examining the hypothesis of human disturbance, two predictions were made. First, if long term displacement were occurring, it should be apparent in areas of frequent human use either known historically to be bighorn range or suspected to have been used historically on the basis of present habitat use nearby. Secondly, if carrying capacity were being lowered through causes other than long term displacement, it should show up as a declining population. However, this does not test the possibility that a population decline has already occurred followed by a leveling due to density dependent influences on nutrition. While the prediction of a declining population may be clearly refuted, data indicating a population decline will be ambiguous relative to human disturbance since numerous causes may be involved. Consequently, acceptance of human disturbance as a cause of herd decline in the absence of clear long term spatial displacement, such as envisioned by DeForge (1976), will be possible only in the context of a large scale study of numerous potential controlling factors.

Baxter Herd

Ewes were the focus of human disturbance studies because they carry the burden of reproduction. Ewes exhibited noticeably heightened wariness once new lambs were present, which continued until they reappeared on winter ranges; no seasonal difference was apparent in ram behavior in this regard. Simple analysis of distance between bighorn and myself associated with different reaction categories illustrates the differences between seasons and sexes (Figures 23, 24, Table 23).

Figure 23. Seasonal comparisons of reaction distances of groups containing ewes. Boxes represent ± one standard error.

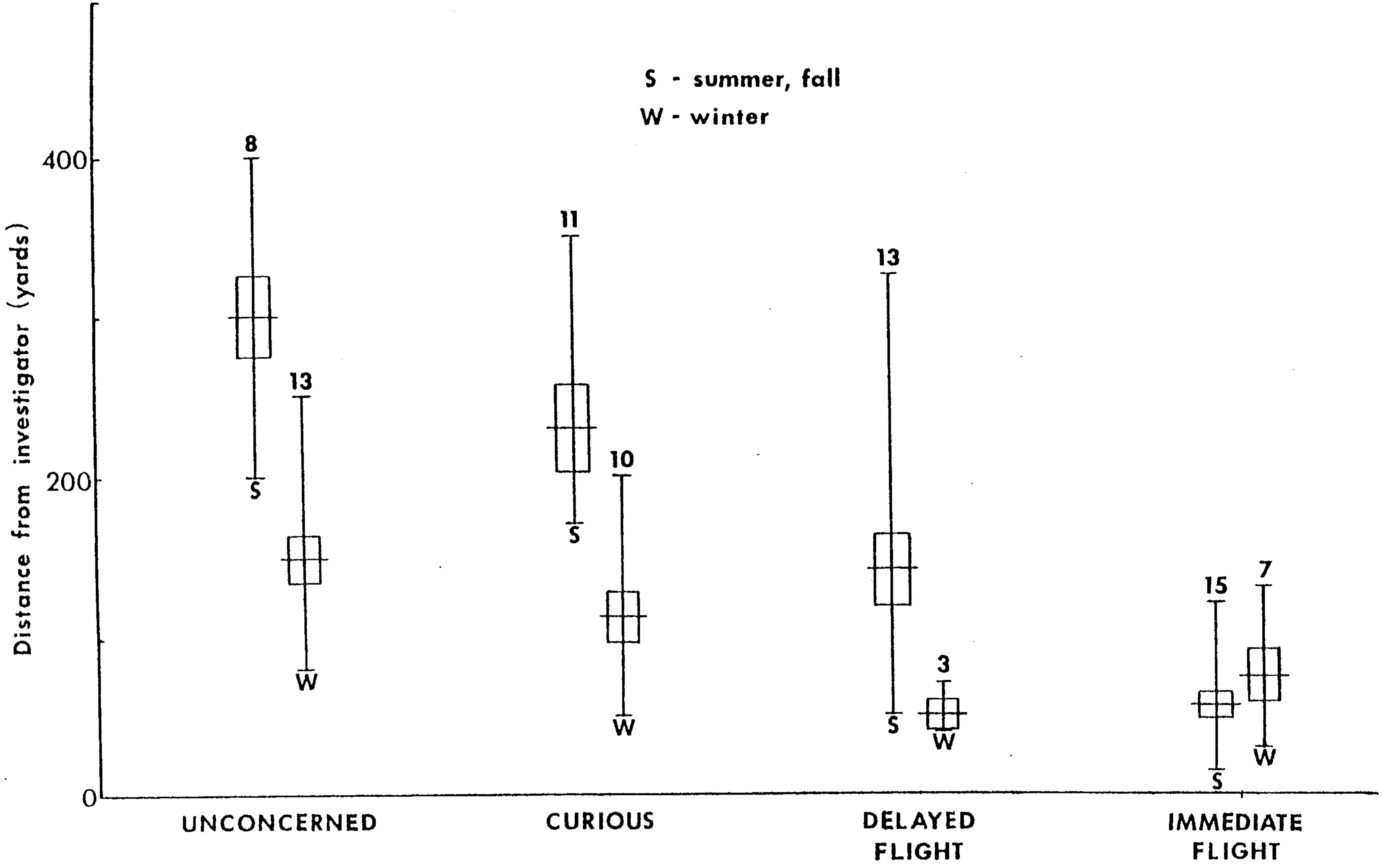


Figure 24. Comparisons of reaction distances of ewe and ram groups in summer. Boxes represent ± 1 s.e.

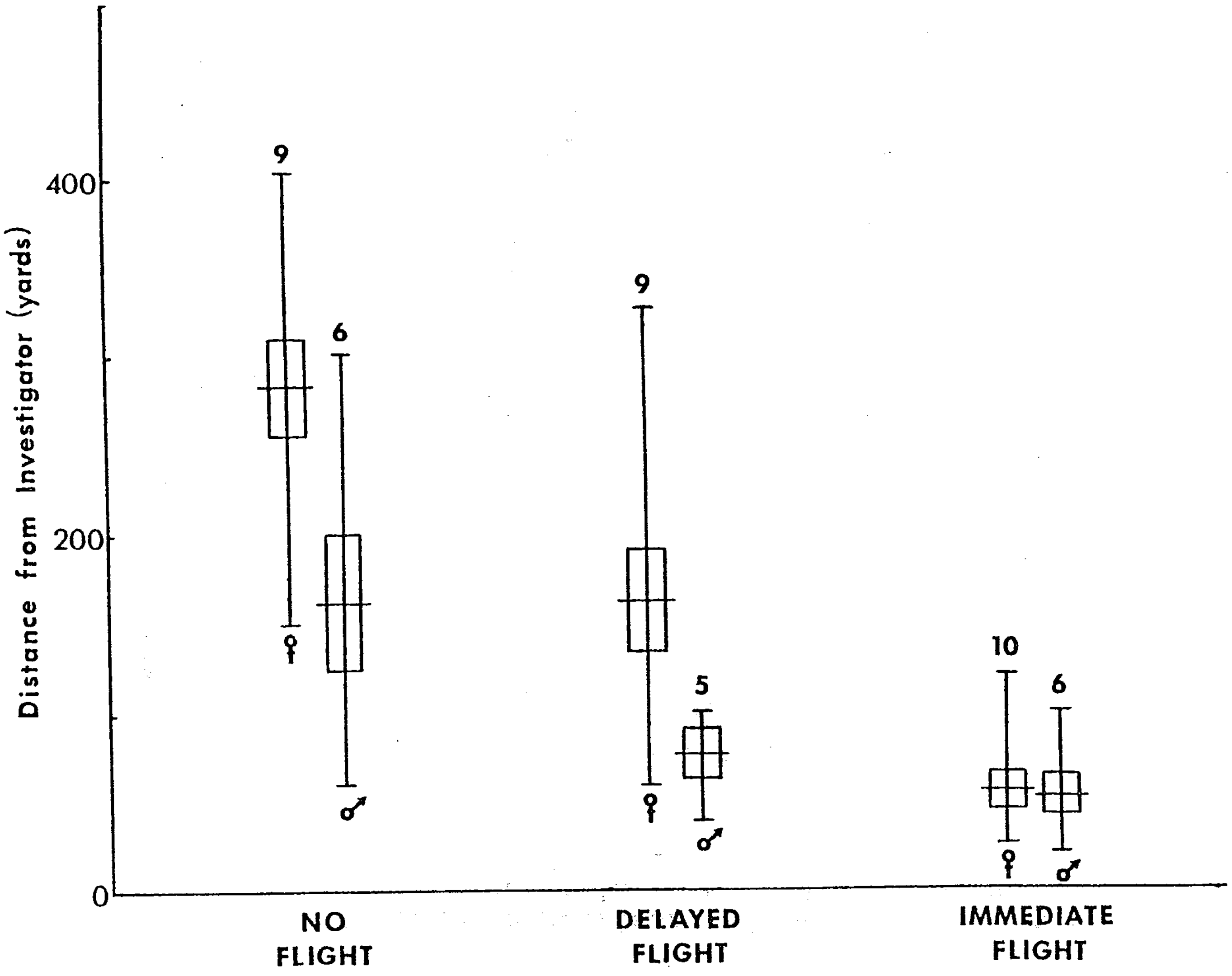


Table 23. Values of the t statistic for reaction comparisons.

	Unconcerned	Curious	No Flight	Delayed Flight	Immediate Flight
Rams vs. Ewes (winter)			0.034	2.18^{+}	1.65
Winter vs. Summer (rams)			0.67	1.61	0.80
Winter vs. Alpine (ewes)	5.59***	3.67**		1.87^{+}	1.03
Rams vs. Ewes (summer)			2.66*	2.13*	0.26
Above vs. level + below (ewes in alpine)			1.11	2.22*	1.66
Rams vs. Ewes (summer) (compound distance variable)			4.10**	4.66***	0.99

+ P≤.10
* P≤.05
** P≤.01
*** P≤.001

Sample sizes were too small to investigate many of the variables suspected to influence reactions. Distance between bighorn and safe rocks was entered into the analysis by creating a new variable, distance between bighorn and myself minus distance between bighorn and safe rocks. A zero value for this variable means that bighorn were midway between myself and rocks; negative values indicate greater danger, while positive values mean less danger. The importance of including distance from safe rocks in this way is suggested by the influence the new variable has in accentuating the differences between ram and ewe groups in summer (Figure 25, Table 23).

Relative elevational positions of ewe-lamb groups and myself in summer also exhibited a significant difference in one of the reaction categories (Figure 26, Table 23). The reason for this is that, in most cases in the summer range, bighorn move up to find safer positions. This is not always the case; the opposite is true for some winter range areas.

In the various comparisons in Table 23, the middle categories are the most meaningful for comparisons in that they are bounded by categories on either side. The "unconcerned" and "no flight" categories are bounded on one side only by maximum distances at which bighorn and the investigator can observe each other. Minimum values of these categories are perhaps more meaningful than means. The immediate flight category is bounded by zero in all comparisons except the compound distance variable. In no

Figure 25. Comparisons of reaction distances of ewe and ram groups in summer using a compound distance variable. Boxes represent ± 1 s.e.

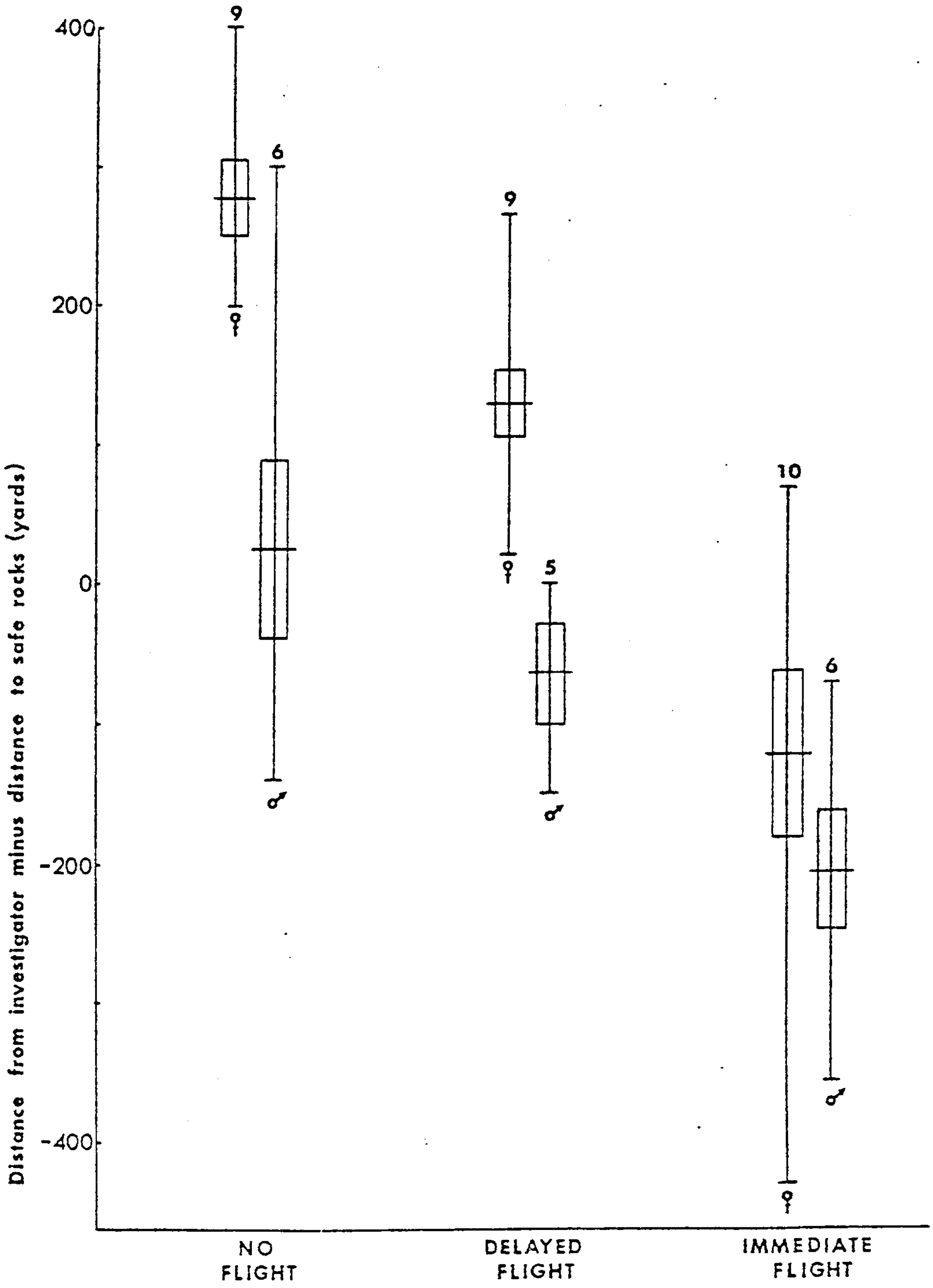
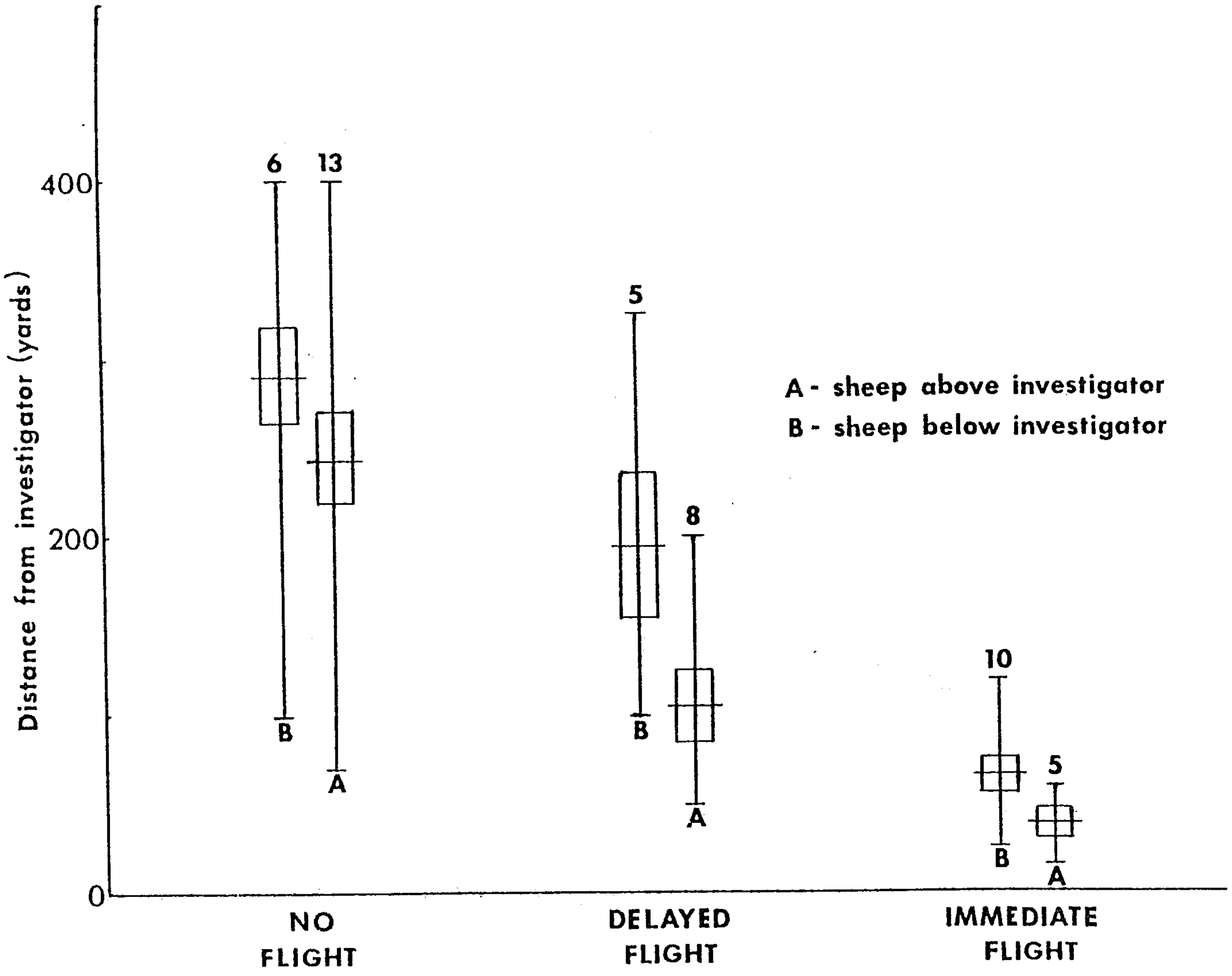


Figure 26. Comparisons of reaction distances of ewe groups in summer for different relative elevational positions. Boxes represent ± 1 s.e.



case was there a significant difference in this category (Table 23), but maximum values have generally exhibited the same directions of differences as the "delayed flight" category (Figures 23-26).

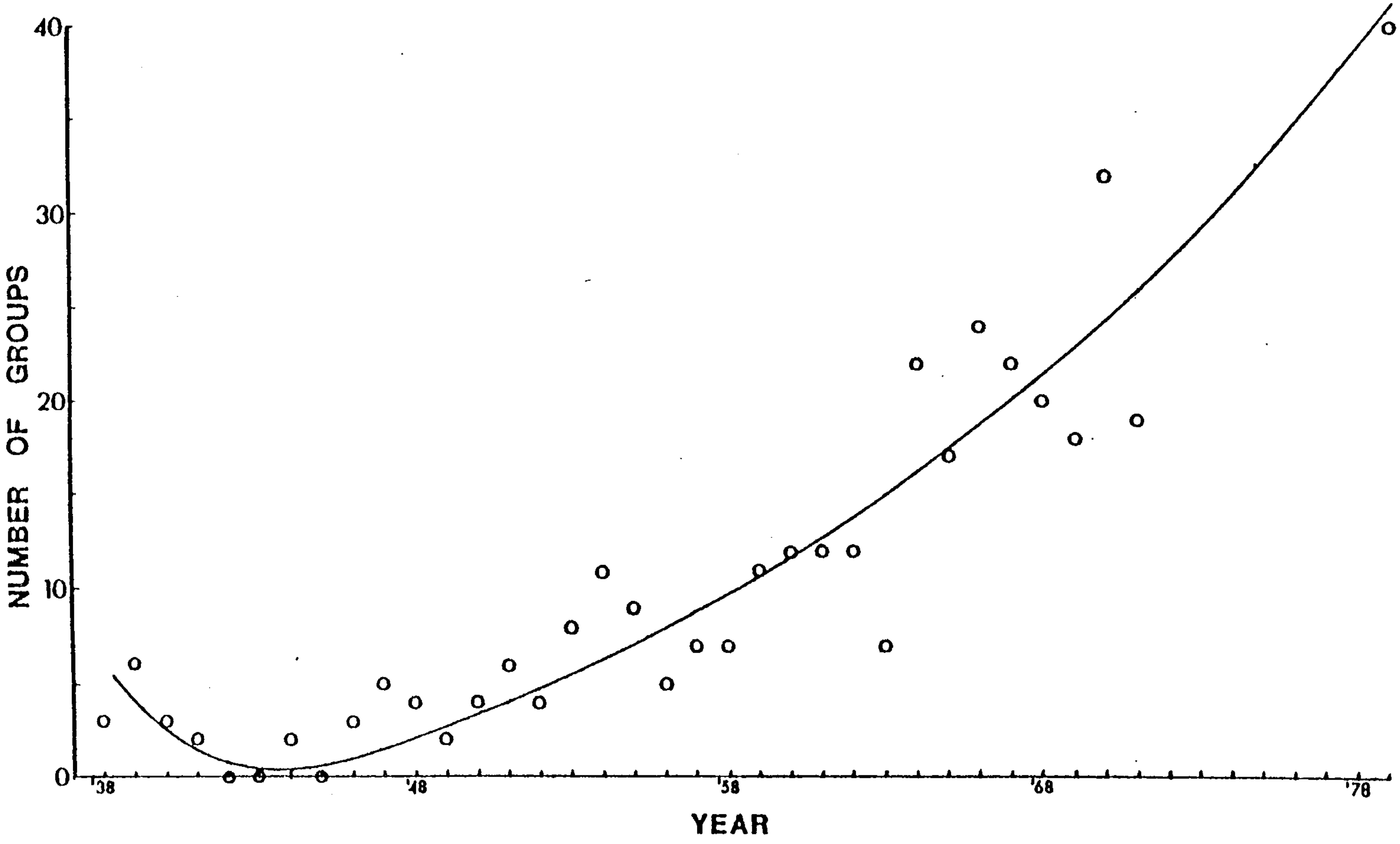
The significance of human disturbance in the Baxter herd was investigated relative to ewe-lamb groups in summer. In addition to exhibiting the greatest disturbability in summer, ewe-lamb groups have the greatest contact with humans backpacking and climbing peaks during that season. The most human use of ewe-lamb range in summer occurs on Baxter Pass. Hicks (1977) studied bighorn-human interactions there in 1976 and found a high interaction rate; half the bighorn groups appearing in the Baxter Pass area encountered backpackers. However, no long term displacement is apparent there. Also, there are no other areas in which displacement is evident. Throughout their summer range, ewe-lamb groups are consistently bounded by timberline and topography regardless of human use patterns. Since human use is largely below timberline, interactions with ewe-lamb groups are confined to a few localized areas. The increasing trend of the Baxter herd refutes the hypothesis that the annual nutrient budget has been adversely affected by interactions with people.

Williamson Herd

Except for three, all summer sightings of ewe-lamb groups in the Williamson herd have been at long distances which precluded any interaction. The three cases of recorded interactions were compared with reactions of ewe-lamb groups in the Baxter herd using the compound distance variable used in Figure 25. One of the interactions was at close range and produced the expected immediate flight. The other two were an immediate flight and a delayed flight at greater distances than recorded for the Baxter herd. While the sample size is too small to make firm conclusions, the results suggest a greater wariness in the Williamson herd and hence a greater potential for significant disturbance. In addition, the number of groups of people climbing Mount Williamson since World War II has increased exponentially at an average annual rate of 9.7% (r^2=.825; Figure 27).

Due to the lack of data on the population trend of the Williamson herd, human disturbance has been investigated only through the hypothesis of long term displacement. Loss of summer range of ewe-lamb groups south and west of Mount Williamson from Mount Barnard to Mount Tyndall, and north of Shepherd Pass since the 1940's was discussed previously. It is noteworthy that the new range boundaries in the areas of range losses coincide with the usual routes of human use in the region. Two of these, upper Georges Creek and the middle of the Williamson Lakes Basin (Figure 4) are the routes by which peak climbers reach Mount Williamson. The third is the Shepherd Pass trail (Figure 4). Long term displacement may be responsible for this correlation.

Figure 27. Number of groups of people climbing Mount Williamson from May 1 to December 1 since 1938.



CONCLUSIONS

Herd Trends

The lack of significance of correlations between recruitment rate and an index of population size in the Baxter herd was surprising considering recent large population gains; a negative correlation would be expected (McCullough 1978, 1979, Caughley 1976, 1977). Geist (1971) presented data illustrating such a relationship for Rocky Mountain bighorn in Banff National Park in Canada. A similar relationship is apparent for bighorn introduced to Wildhorse Island in Montana (Woodgerd 1964). The lack of such a relationship for the Baxter herd suggests that it is still well below carrying capacity, despite recent population gains, and is not yet showing significant density effects. Average recruitment rate for the Baxter herd has been 41.5 lambs per 100 ewes (including yearlings). At carrying capacity, this average can be expected to drop to about 25-30. Total variance in recruitment will thereby increase, and population density should account for this additional variance. Considering the large range of recruitment values recorded since 1965 and the strong influence precipitation has on recruitment, considerable variation in recruitment is also to be expected when the population reaches carrying capacity.

It is not clear where the Williamson herd stands relative to carrying capacity, due to the meager data available. It is also not clear what caused the Baxter herd to be substantially below carrying capacity allowing the observed population increase to occur. Long term population cycles may be involved.

Carrying Capacity

A number of definitions of carrying capacity exist; the carrying capacity referred to here is K carrying capacity as defined by McCullough (1979). Ignoring overshoots and oscillations (Caughley 1970), this is the population size at which recruitment equals mortality of adults, and reflects the influence of population density on individual nutrition (Caughley 1976, McCullough 1979). It is customary to regard carrying capacity of migratory ungulates as being set by population density on one seasonal (often winter) range, where nutrient quantity (an interaction of quantity and quality of vegetation) is most limited. While this view frequently has merit, it can be short-sighted. Carrying capacity for large mammals will be set by the year-round nutritional regime, such as might be measured by the integration of annual curves of fecal protein levels. The reason for this is that body reserves built up during nutritionally favorable seasons act to buffer against seasons of resource shortage. Hebert (1973) found that better body reserves also led to better efficiency in utilization of poor quality forages in winter by bighorn. This suggests that the carrying capacity on the most limiting seasonal range will depend on nutrition during the remainder of the year, everything else being equal. Hence the short sightedness of looking at carrying capacity relative only to a single seasonal range. This concept is of importance in comparing the Williamson and Baxter herds.

Bighorn winter ranges in the Sierra were found to offer sufficient quantity and increasing quality of forage. Fall range was most limiting in both quantity and quality of forage. When densities of the two herds are calculated relative to approximate sizes of fall ranges, the Baxter:Williamson density ratio is only about 2:1 (Table 7), as compared with an approximate herd size ratio of 7:1. It appears then that the relative sizes of fall ranges alone can explain much of the difference in herd sizes.

Comparisons of annual nutritional regimes indicate that the Williamson herd obtains less nutrition from its range per year on an individual basis than the Baxter herd due to habitat differences. Since parasites extract nutrition from their hosts, the higher parasite burden of the Williamson herd effectively increases the nutritional differences between the two herds, although this influence may be of little significance at the parasite levels recorded. Different carrying capacities, as measured by fall densities, are thus to be expected for the two herds on the basis of nutritional differences in other seasons.

In comparing fall densities, an implicit assumption was that the herds were at carrying capacity. Since the Baxter herd does not appear to be at carrying capacity, the ratio of fall densities may shift. Nevertheless, the qualitative conclusions should hold.

Limiting Factors

Wildlife management is concerned with the manipulation of demography, either directly or indirectly, through changes in habitat (Caughley 1976). The concept of managing limiting factors that will provide justifiable returns was formulated by Leopold (1933). The limited quantity and quality of vegetation on fall ranges would qualify as a major limiting factor of Sierra bighorn herds. The possibility of manipulation of this resource to increase carrying capacity is remote, except through range expansion by reintroduction.

For the Williamson herd the abundance of pinyon forest represents another major limiting factor, whose manipulation is possible and likely to yield a return in terms of increased carrying capacity. Removal of trees in areas of topographically desirable winter and lambing range might significantly increase the average annual nutrition of the sheep by (1) encouraging them to winter at lower elevations more frequently, and (2) allowing lambing to occur at lower elevations.

MANAGEMENT CONSIDERATIONS

Management questions concerning Sierra Nevada bighorn have been dealt with in detail elsewhere (Wehausen 1979) and touched on in the conclusions of this report. This section is a brief overview of that subject.

Caughley (1976) considered wildlife management to be concerned with three possible goals of manipulation of demographic characterisitcs of wildlife populations: (1) to increase a desirable but rare species, (2) to decrease an undesirable species, and (3) to extract a sustained yield from a population. These goals are attained either through direct manipulation via removal or addition of animals, or indirectly through manipulation of habitat.

Sierra Nevada bighorn are classified as rare within the state of California. This classification mandates the first of the above goals for this population. Reintroduction to historic ranges is the primary tool for achieving that goal due to the rarity of natural colonization by bighorn (Geist 1971). Consequently, the third goal above becomes linked with the first, since reintroduction involves the harvesting of sheep from one population to initiate another. The size and productivity of the Mount Baxter herd makes it a good source of stock for reintroductions. In the winters of 1979, 1980, and 1982, a total of 59 bighorn were transplanted to other ranges from this herd.

The first priority of management of bighorn in the Sierra Nevada should be the assurance of perpetuation of the two native herds. As such, careful monitoring of the Mount Baxter herd has been an integral part of the reintroduction program, and must continue to be so. A related question is what constitutes an optimal harvesting strategy for reintroduction. Harvesting theory dictates that the determination of this optimum necessarily requires allowing the Mount Baxter herd to grow in size to the point where the influences of density on recruitment rate can be clearly discerned. Elucidation of this relationship is necessary for the calculation of maximum sustained yield and the population level where this occurs (Caughley 1976, McCullough 1979). The present study indicated that density was not yet influencing recruitment rate. Removal of bighorn for reintroduction has caused a lowering of the population size since 1978; thus the current program of animal removal is probably somewhat below maximum sustained yield.

A major finding of this study was a sacrifice of diet quality for safety in winter and spring by members of the Mount Williamson herd. Obstruction of vision by pinyon pines was considered the major factor dictating this tradeoff; and it was suggested that removal of these trees should lead to an increase in carrying capacity. However, such habitat manipulation begs the question of justification, particularly considering that such alteration of the ecosystem will necessarily impact other species. To the extent that bighorn are not hunted in the state of California, harvest as a justification for management to increase the population is limited to bighorn removal as reintroduction stock. This will not be arguable, since (1) it is unlikely that habitat manipulation will increase the size of the Mount Williamson herd to where managers can feel comfortable about removing sheep, and (2) the Mount Baxter herd already serves this end.

The remaining rationale for habitat manipulation would involve loss of habitat through vegetational succession such that it threatened the persistence of the Mount Williamson herd. This would be particularly defensible if suppression of natural fires was at cause. Future monitoring of the Mount Williamson herd is advisable to clearly establish its trend; but the existing pinyon woodland probably represents a natural climax community unlikely to further limit existing bighorn habitat.

In summary, I see no justification for manipulation of the habitat on Mount Williamson beyond the scientific testing of predictions from this study. However, a policy of allowing natural fires to burn is justifiable both in terms of potential benefits to bighorn and monetary savings relative to fire suppression costs.

LITERATURE CITED

Anonymous. 1924. Yosemite's vanished mountain sheep. Yosemite Nature Notes 3:3-4.

Anonymous 1926. Area added to Sequoia National Park. Calif. Fish and Game 12:188.

Aldous, M.C. 1957. Status of bighorn sheep on the Desert Game Range. Trans. Desert Bighorn Council 1:35-37.

Alexander, R.D. 1974. The evolution of social behavior. Ann. Rev. Syst. and Ecol. 5:325-383.

Bailey, V. 1932. Can we bring back the Sierra bighorn? Sierra Club Bull. 17(2):135-136.

Baumann, T.G. and D.R. Stevens 1978. Winter habitat preference of bighorn sheep in the Mummy Range, Colorado. In: Hebert, D. and M. Nation (eds.). Proc. Biennial Symp. N. Wild Sheep and Goat Conf. pp. 320-330.

Belovsky, G.E. 1978. Diet optimization in a generalist herbivore: the moose. Theor. Pop. Biol. 14:105-134.

Berger, J. 1978. Social development and reproductive strategies in bighorn sheep. Ph.D. diss. Univ. of Colorado.

Berger, J. 1979. Weaning conflict in desert and mountain bighorn sheep (Ovis canadensis): an ecological interpretation. Z. Tierpsychol. 50:188-200.

Billings, W.D. and L.C. Bliss 1959. An alpine snowbank environment and its effect on vegetation, plant development, and productivity. Ecology 40:388-397.

Blake, A.H. 1940. Conference on Sierra bighorn planned. Sierra Club Bull. 25(6):7

Blake, A.H. 1941a. Mountain sheep conference held. Sierra Club Bull. 26(2):3

Blake, A.H. 1941b. Some reports of Sierra bighorn seen in 1940. Sierra Club Bull. 26(1):125-126.

Blake, A.H. 1942. Some records of mountain sheep. Sierra Club Bull. 27(4):120-121.

Blake, A.H. 1949. Will the Sierra bighorn survive? Sierra Club Bull. 34(6):119-122.

Blaxter, K.L. and H.H. Mitchell 1948. The factorization of the protein requirements of ruminants and of the protein values of feeds, with particular reference to the significance of metabolic nitrogen. J. Anim. Sci. 7:351-372.

Bliss, L.C. 1956. A comparison of plant development in microenvironments of arctic and alpine tundras. Ecol. Monogr. 26:303-337.

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

Bradbury, J.W. and S.L. Vehrencamp 1977. Social organization and foraging in emballonurid bats IV. Parental investment patterns. Behav. Ecol. and Sociobiol. 2:19-29.

Buechner, H.K. 1960. The bighorn sheep in the United States, its past, present, and future. Wildl. Monogr. No. 4.

Bunch, T.D., S.R. Paul, and H. McCutchen 1978. Chronic sinusitus and osteonecrosis in desert bighorn sheep (<u>Ovis canadensis nelsoni</u>). In: Hebert, D. and M. Nation (eds.). Proc. Biennial Symp. N. Wild Sheep and Goat Council pp. 261-273.

Burke, M.T. 1979. The flora and vegetation of the Rae Lakes Basin, southern Sierra Nevada: an ecological overview. M. S. thesis. Univ. of Calif., Davis.

Caughley, G. 1966. Mortality patterns in mammals. Ecology 47:906-918.

Caughley, G. 1967. Parameters for seasonally breeding populations. Ecology 48:834-839.

Caughley, G. 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. Ecology 51:54-72.

Caughley, G. 1974. Interpretation of age ratios. J. Wildl. Manage. 38:557-562.

Caughley, G. 1976. Wildlife management and the dynamics of ungulate populations. Adv. Appl. Biol. 1:183-245.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, Bath. 234pp.

Caughley, G. and L.C. Birch 1971. Rate of increase. J. Wildl. Manage. 35:658-663.

Chamrad, A.D. and T.W. Box 1964. Food habits of white tailed deer in south Texas. J. Range Manage. 21:158-164.

Clyde, N. 1936. A survey of mountain sheep. Sierra Club Bull. 21(1):87-88.

Clyde, N. 1971a. Norman Clyde of the Sierra Nevada, rambles through the range of light. Scrimshaw Press, San Francisco.

Clyde, N. 1971b. 23 March letter to Vern Burandt titled "The bighorn in the Southern Sierra, mostly a half century of casual recollections".

Cody, M. 1966. A general theory of clutch size. Evolution 20:174-184.

Colby, W.E. 1940. Sanctuary for mountain sheep. Sierra Club Bull. 25(5):3-4.

Curtis, B., L. Mangan, B. Hines, D. Babb, R. Rawson, and D. Garber 1977. Owens Valley tule elk habitat management plan. Calif. Dept. Fish and Game.

DeForge, J.R. 1976. Stress: is it limiting bighorn? Trans. Desert Bighorn Council 20:30-31.

Dixon, J.S. 1936. The status of the Sierra bighorn sheep. Proc. N. Amer. Wildl. Conf. 1:641-643.

Dunaway, D.J. 1970. Status of bighorn sheep populations and habitat studies on the Inyo National Forest. Trans. Desert Bighorn Council 14:127-146.

Dunaway, D.J. 1971a. Bighorn sheep habitat management on the Inyo National Forest, a new approach. Trans. Desert Bighorn Council 15:18-23.

Dunaway, D.J. 1971b. Human disturbance as a limiting factor of Sierra Nevada bighorn sheep. Trans. N. Amer. Wild Sheep Conf. 1:165-173.

Dunaway, D.J. 1972. Winter food habits of California bighorn sheep in the Sierra Nevada. Trans. Desert Bighorn Council 16:21-29.

Eccles, T.R. and D.M. Shackleton 1979. Recent records of twinning in North American mountain sheep. J. Wildl. Manage. 43:974-976.

Elder, J.M. 1977. Human interaction with Sierra Nevada bighorn sheep: the Mt. Baxter herd. M. S. thesis, Univ. of Michigan.

Fagen, R.M. 1972. An optimal life-history strategy in which reproductive effort decreases with age. Amer. Natur. 106:258-261.

Fisher, R.A. 1958. The genetical theory of natural selection. Dover, New York.

Forrester, D.J. 1971. Bighorn sheep lungworm-pneumonia complex. In: Davis, J.W. and R. Anderson (eds.). Parasitic diseases of wild mammals. Iowa St. Univ. Press. pp. 158-173.

Forrester, D.J. and C.M. Senger 1964. A survey of lungworm infection in bighorn sheep of Montana. J. Wildl. Manage. 28:481-491.

Forrester, D.J. and R.C. Littell 1976. Influence of rainfall on lungworm infections in bighorn sheep. J. Wildl. Dis. 12:48-51.

Gallup, W.D. and H.M. Briggs 1948. The apparent digestibility of prairie hay of variable protein content, with some observations of fecal nitrogen excretion by steer in relation to their dry matter intake. J. Anim. Sci. 7:110-116.

Garcia, E.R. 1977. Range, distribution, and habitat selection by the Williamson herd of Sierra Nevada bighorn sheep. M. S. thesis, Univ. of Michigan.

Geist, V. 1966. Validity of horn segment counts in aging bighorn sheep. J. Wildl. Manage. 30:634-635.

Geist, V. 1967. A consequence of togetherness. Nat. Hist. 76(8):24,29-30.

Geist, V. 1971. Mountain sheep, a study in behavior and evolution. The Univ. of Chicago Press, Chicago.

Geist, V. 1975. On the management of mountain sheep: theoretical considerations. In: Trefethen, J.B. (ed.). The wild sheep in modern North America. The Winchester Press, New York. pp. 77-105.

Geist, V. and R.G. Petocz 1977. Bighorn sheep in winter: do rams maximize reproductive fitness by spatial and habitat segregation? Can. J. Zool. 55:1802-1810.

Goodman, D. 1974. Natural selection and a cost-ceiling on reproductive effort. Amer. Natur. 108:247-268.

Grinnell, J. 1912. The bighorn of the Sierra Nevada. Univ. of Calif. Publ. Zool. 10:143-153.

Grinnell, J. 1935. A way to bring back the native bighorn to the Yosemite. Sierra Club Bull. 20(1):28-31.

Grinnell, J. and T.I. Storer 1924. Animal life in the Yosemite. The Univ. of Calif. Press, Berkeley.

Gwynne, M.D. and R.H.V. Bell 1968. Selection of vegetation components by grazing ungulates in the Serengeti National Park. Nature 220:390-393.

Hansen, C.G. 1970. Tongue color in desert bighorn. Trans. Desert Bignorn Council 14:14-22.

Hansen, C.G. and O.V. Deming 1971. Reproduction. In: Sumner, L. and G. Monson (eds.). The desert bighorn, its life history, ecology and management. Preliminary edition.

Hebert, D.M. 1972. Forage and serum phosphorus values for bighorn sheep. J. Range Manage. 25:292-295.

Hebert, D.M. 1973. Altitudinal migration as a factor in the nutrition of bighorn sheep. Ph.D. diss. Univ. of British Columbia.

Hebert, D.M. 1978. Blood chemistry as an indicator of nutritional condition in bighorn sheep. In: Hebert, D. and M. Nation (eds.). Proc. Biennial Symp. N. Wild Sheep and Goat Council. pp. 365-387.

Heimer, W.E. 1978. Alternate year reproduction in a low quality, declining Dall sheep population: management considerations. In: Hebert, D. and M. Nation (eds.). Proc. Biennial Symp. N. Wild Sheep and Goat Council. pp. 30-41.

Hibler, C.P., R.E. Lange, and C.J. Metzger 1972. Transplancental transmission of Protostrongylus spp. in bighorn sheep. J. Wildl. Dis. 8:389.

Hibler, C.P., C.J. Metzger, T.R. Spraker, and R.E. Lange 1974. Further observations on Protostrongylus spp. infection by transplacental transmission in bighorn sheep. J. Wildl. Dis. 10:39-41.

Hibler, C.P., T.R. Spraker, and R.L. Schmidt 1976.

Treatment of bighorn sheep for lungworms. Trans. N. Amer. Wild Sheep Conf. 2:66-68.

Hicks, L.L. 1977. Human disturbance of the Mt. Baxter herd of Sierra Nevada bighorn sheep. M.S. thesis, Univ. of Michigan.

Hill, M. 1975. Geology of the Sierra Nevada. The Univ. of Calif. Press, Berkeley. 232pp.

Hoefs, M. 1978. Twinning in Dall sheep. Can. Field Natur. 92:292-293.

Holway, J.G. and R.T. Ward 1963. Snow and meltwater effects in an area of Colorado alpine. Amer. Midl. Natur. 69:189-197.

Horejsi, B.L. 1976. Suckling and feeding behavior in relation to lamb survival in bighorn sheep (_Ovis canadensis canadensis_ Shaw). Ph.D. diss., Univ. of Calgary, Alberta.

Hormay, A.L. 1943. Bitterbrush in California. U. S. Forest Service, Calif. Forest and Range Expt. Sta. Note 34. 13pp.

Jones, F.L. 1949. A survey of the Sierra Nevada mountain sheep. M. A. thesis, Univ. of Calif., Berkeley.

Jones, F.L. 1950a. A survey of the Sierra Nevada bighorn. Sierra Club Bull. 35:29-76.

Jones, F.L. 1950b. The Sierra Nevada bighorn in Yosemite. Yosemite Nature Notes 24:1

Jones, F.L. 1954. The Inyo-Sierra deer herds. Calif. Dept. Fish and Game, Fed. Aid in Wildl. Restor. Proj. W-41-R Report. 84pp.

Jorgensen, R.D. and D.B. Schaub 1972. California bighorn sheep survey - Mt. Langley herd unit. Calif. Dept. Fish and Game, Fed. Aid in Wildl. Restor. Proj. W-54-R Report.

Kates, K.C. and D.A. Shorb 1943. Identification of eggs of nematodes parasitic in domestic sheep. Amer. J. Vet. Res. 4:54-60.

Klikoff, L.G. 1965. Microenvironmental influences of vegetational pattern near timberline in the central Sierra Nevada. Ecol. Monogr. 35:187-211.

Kornet, C.A. 1978. Status and habitat use of California bighorn sheep on Hart Mountain, Oregon.

M. S. thesis, Oregon State Univ.

Krebs, C.J. 1972. Ecology. Harper and Row, New York. 694pp.

Lancaster, R.J. 1949. Estimation of digestibility of grazed pasture from faeces nitrogen. Nature 163:330-331.

Lenarz, M.S. 1979. Social structure and reproductive strategy in desert bighorn sheep (Ovis canadensis mexicana). J. Mammal. 60:671-678.

Leopold, A. 1933. Game management. Charles Scribner's Sons, New York.

Leslie, D.M. and C.L. Douglas 1979. Desert bighorn sheep of the River Mountains, Nevada. Wildl. Monogr. No. 66.

Levins, R. 1968. Evolution in changing environments: some theoretical explorations. Princeton Univ. Press, Princeton.

Light, J.T. and R. Weaver 1973. Report on bighorn sheep habitat study in the area for which an application was made to expand the Mt. Baldy winter sports facility. Admin. Report, San Bernadino National Forest.

Longhurst, W.M., H.K. Oh, M.B. Jones, and R.E. Kepner 1968. A basis for the palatability of deer forage plants. Proc. N. Amer. Wildl. and Nat. Res. Conf. 33:181-192.

Low, B.S. 1978. Environmental uncertainty and the parental strategies of marsupials and placentals. Amer. Natur. 112:197-213.

Major, J. 1977. California climate in relation to vegetation. In: Barbour, M.G. and J. Major (eds.). Terrestrial vegetation of California. John Wiley and Sons. pp. 11-73.

Major, J. and S.A. Bamberg 1967. Comparison of some North American and Eurasian alpine ecosystems. In: Wright, H.E. and W.H. Osborn (eds.). Arctic and alpine environments. Indiana Univ. Press. pp. 89-118.

Major, J. and D.W. Taylor 1977. Alpine. In: Barbour, M.G. and J. Major (eds.). Terrestrial vegetation of California. John Wiley and Sons. pp. 601-675.

Maynard, L.A. and J.K. Loosli 1969. Animal nutrition. McGraw-Hill, New York 613pp.

McCullough, D.R. 1969. The tule elk, its history, behavior, and ecology. Univ. of Calif. Publ. Zool. The Univ. of Calif. Press, Berkeley.

McCullough, D.R. 1978. Essential data required on population structure and dynamics in field studies of threatened herbivores. In: Threatened Deer. IUCN, Morges. pp. 302-317.

McCullough, D.R. 1979. The George Reserve deer herd. Univ. of Michigan Press, Ann Arbor. 271pp.

McCullough, D.R. and E.R. Schneegas 1966. Winter observations on the Sierra Nevada bighorn sheep. Calif. Fish and Game 52:68-84.

McCutchen, H.E. 1977. A minimum breeding age for a desert bighorn ewe. Southwest Naturalist 22:153.

McQuivey, R. 1978. The desert bighorn sheep of Nevada. Nevada Dept. of Fish and Game Biol. Bull. No. 6. 81pp.

Mitchell, H.H. 1926. The determination of the protein requirements of animals and of the protein values of farm feeds and rations. Bull. Nat. Res. Counc. No. 55. 44pp.

Monson, R.A. 1971. The life cycle of Protostrongylus stilesi in bighorn sheep. Trans. N. Amer. Wild Sheep Conf. 1:76-86.

Mooney, H.A. and W.D. Billings 1960. The annual carbohydrate cycle of alpine plants related to growth. Amer. J. Bot. 47:594-598.

Moore, J.G. 1963. Geology of the Mount Pinchot quadrangle, southern Sierra Nevada, California. Geological Survey Bull. 1130. U. S. Government Printing Office, Washington.

Muir, J. 1894. The mountains of California. The Century Co., New York.

Muir, J. 1898. Among the animals of the Yosemite. Atlantic Monthly 82:617-631.

Murie, A. 1944. The wolves of Mount McKinley. Fauna of the National Parks of the United States No. 5.

Murphy, E.C. and K.R. Whitten 1976. Dall sheep demography in McKinley Park and a reevaluation of Murie's data. J. Wildl. Manage. 40:597-609.

Nagy, J.G., H.W. Steinhoff, and G.M. Ward. 1964. Effects of essential oils of sagebrush on deer rumen microbial function. J. Wildl. Manage. 28:785-790.

National Research Council 1964. Committee on animal nutrition. Nutrient requirements of sheep. National Academy of Sciences, Washington, D.C. Publ. 1193.

Nichols, L. 1978. Dall sheep reproduction. J. Wildl. Manage. 42:570-580.

Nord, E.C. 1965. Autecology of bitterbrush in California. Ecol. Monogr. 35:307-334.

Ober, E. 1911. 20 November letter to the Calif. Fish and Game Comm.

Ober, E. 1914. Fish and game conditions in the "land of little rain". Twenty-third Biennial Report of the State of Calif. Fish and Game Comm.

Ober, E. 1915. Sierra mountain sheep on the increase. Calif. Fish and Game 1:236-237.

Ober, E. 1916. Mountain sheep seen in Oak Creek Pass. Calif. Fish and Game 2:213.

Ober, E. 1931. The mountain sheep of California. Calif. Fish and Game 17:27-39.

Oh, H.K., T. Sakai, M.B. Jones, and W.M. Longhurst 1967. Effects of various essential oils isolated from Douglas fir needles upon sheep and deer rumen microbial activity. Appl. Microbiol. 15:777-784.

Pianka, E.R. and W.S. Parker 1975. Age-specific reproductive tactics. Amer. Natur. 109:453-464.

Post, G. 1971. The pneumonia complex in bighorn sheep. Trans. N. Amer. Wild Sheep Conf. 1:98-106.

Ramsay, M.A. and R.M.F.S. Sadleir 1979. Detection of pregnancy in living bighorn sheep by progestin determination. J. Wildl. Manage. 43:970-973.

Raymond, W.F. 1948. Evaluation of herbage for grazing. Nature 161:937-938.

Riegelhuth, R. 1965. A reconnaissance of Sierra bighorn and bighorn ranges in the Sierra Nevada. Trans. Desert Bighorn Council 9:35-39.

Rundel, P.W., D.J. Parsons, and D.T. Gordon. Montane and subalpine vegetation of the Sierra Nevada and

Cascade ranges. In: Barbour, M.G. and J. Major (eds.). Terrestrial vegetation of California. John Wiley and Sons. pp. 559-599.

Schwartz, C.C., J.G. Nagy, and W.L. Regelin 1980. Juniper oil yield, terpenoid concentration, and antimicrobial effects on deer. J. Wildl. Manage. 41:107-113.

Shackleton, D.M. 1973. Population quality and bighorn sheep (Ovis canadensis canadensis Shaw). Ph.D. diss. Univ. of Calgary, Alberta.

Shaffer, W.M. 1974. Selection for optimal life histories: the effect of age structure. Ecology 55:291-303.

Shannon, N.H., R.J. Hudson, V.C. Brink, and W.D. Kitts 1975. Determinants of spatial distribution of Rocky Mountain bighorn sheep. J. Wildl. Manage. 39:387-401.

Shorb, D.A. 1939. Differentiation of eggs of various genera of nematodes parasitic in domestic ruminants in the United States. U. S. D. A. Tech. Bull. No. 694.

Shorb, D.A. 1940. A comparative study of the eggs of various species of nematodes parasitic in domestic ruminants. J. Parisit. 26:223-231.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York. 312pp.

Smith, D.R. 1954. The bighorn sheep in Idaho. Idaho Dept. of Fish and Game Wildl. Bull. No. 1.

Smith, K.G. and W.D. Wishart 1978. Further observations of bighorn sheep non-trophy seasons in Alberta and their management implication. In: Hebert, D. and M. Nation (eds.). Proc. Biennial Symp. N. Wild Sheep and Goat Council. pp. 52-76.

Smith, R.L. 1974. Ecology and field biology. Harper and Row, New York. 850pp.

Spalding, D.J. 1966. Twinning in bighorn sheep. J. Wildl. Manage. 30:207.

Stearns, S.C. 1976. Life-history tactics: a review of the ideas. Quart. Rev. Biol. 51:3-47.

Stelfox, J.G. 1971. Bighorn sheep in the Canadian Rockies: a history 1800-1970. Can. Field Natur. 85:101-122.

Stelfox, J.G. 1976. Range ecology of Rocky Mountain bighorn sheep. Can. Wildl. Serv. Series No. 39.

Storer, T.I. and R.L. Usinger 1970. Sierra Nevada natural history. The Univ. of Calif. Press, Berkeley. 374pp.

Streeter, R.G. 1970. A literature review on bighorn sheep population dynamics. Colorado Div. Game, Fish and Parks Spec. Report No. 24.

Sugden, L.G. 1961. The California bighorn in British Columbia, with particular reference to the Churn Creek herd. Brit. Columb. Dept. Recreat. and Conserv., Victoria. 58pp.

Taylor, D.W. 1977. Ecology of the timberline vegetation at Carson Pass, Alpine County, California. Ph.D. diss. Univ. of Calif., Davis.

Trefethen, J.B. (ed.) 1975. The wild sheep in modern North America. The Winchester Press, New York.

Trivers, R.L. 1972. Parental investment and sexual selection. in: Campbell, B. (ed.). Sexual selection and the descent of man. Aldine, Chicago. pp. 136-179.

Turner, J.C. 1977. Cemental annulations as an age criterion in north American sheep. J. Wildl. Manage. 41:211-217.

Uhazy, L.S., J.C. Holmes, and J.G. Stelfox 1973. Lungworms in the Rocky Mountain bighorn of western Canada. Can. J. Zool. 51:817-824.

Van Soest, P.J. 1965. Comparison of two different equations for prediction of digestibility from cell contents, cell-wall constituents, and lignin content of acid detergent fiber. J. Dairy Sci. 48:815.

Van Soest P.J. 1966. Nonnutritive residues: a system of analysis for the replacement of crude fiber. J. Assn. Off. Anal. Chem. 49:546.

Van Soest, P.J. 1967. Development of a comprehensive system of feed analysis and its application to forages. J. Anim. Sci. 26:119-128.

van Tienhoven, A. 1968. Reproductive physiology of vertebrates. W. B. Saunders Co., Philadelphia.

Vankat, J.L. 1970. Vegetation change in Sequoia National Park, California. Ph.D. diss. Univ. of Calif., Davis.

Vankat, J.L. and J. Major 1978. Vegetation changes in Sequoia National Park, California. J. Biogeogr. 5:377-402.

Vasek, F.C. and R.F. Thorne 1977. Tranmontane coniferous vegetation. In: Barbour, M.G. and J. Major (eds.). Terrestrial vegetation of California. John Wiley and Sons. pp. 797-832.

Weaver, R.A. 1972. California bighorn in the Sierra Nevada mountain range. Calif. Dept. of Fish and Game Wildl. Mgmt. Admin. Rep. No. 72-7.

Wehausen, J.D. 1979. Sierra Nevada bighorn sheep: an analysis of management alternatives. Admin. Rep., Inyo National Forest. 92pp.

Wells, R.E. and F.B. Wells 1961. The bighorn of Death Valley. Fauna of the National Parks of the United States No. 6. 242pp.

Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. Amer. Natur. 108:290-304.

Williams, G.C. 1966a. Adaptation and natural selection. Princeton Univ. Press, Princeton. 307pp.

Williams, G.C. 1966b. Natural selection, the cost of reproduction, and a refinement of Lack's principle. Amer. Natur. 100:687-690.

Woodard, T.N., R.J. Gutierrez, and W.H. Rutherford 1974. Bighorn lamb production, survival, and mortality in south central Colorado. J. Wildl. Manage. 38:771-774.

Woodgerd, W. 1964. Population dynamics of bighorn sheep on Wildhorse Island. J. Wildl. Manage. 28:381-391.

Wright, G.M., J.S. Dixon, and B.H. Thompson 1933. A preliminary survey of faunal relations in national parks. Fauna of the National Parks of the United States No. 1. 157pp.

Young, T.A., R.A. Evans, and J. Major 1977. Sagebrush steppe. In: Barbour, M.G. and J. Major (eds.). Terrestrial vegetation of California. John Wiley and Sons. pp. 763-796.

APPENDIX

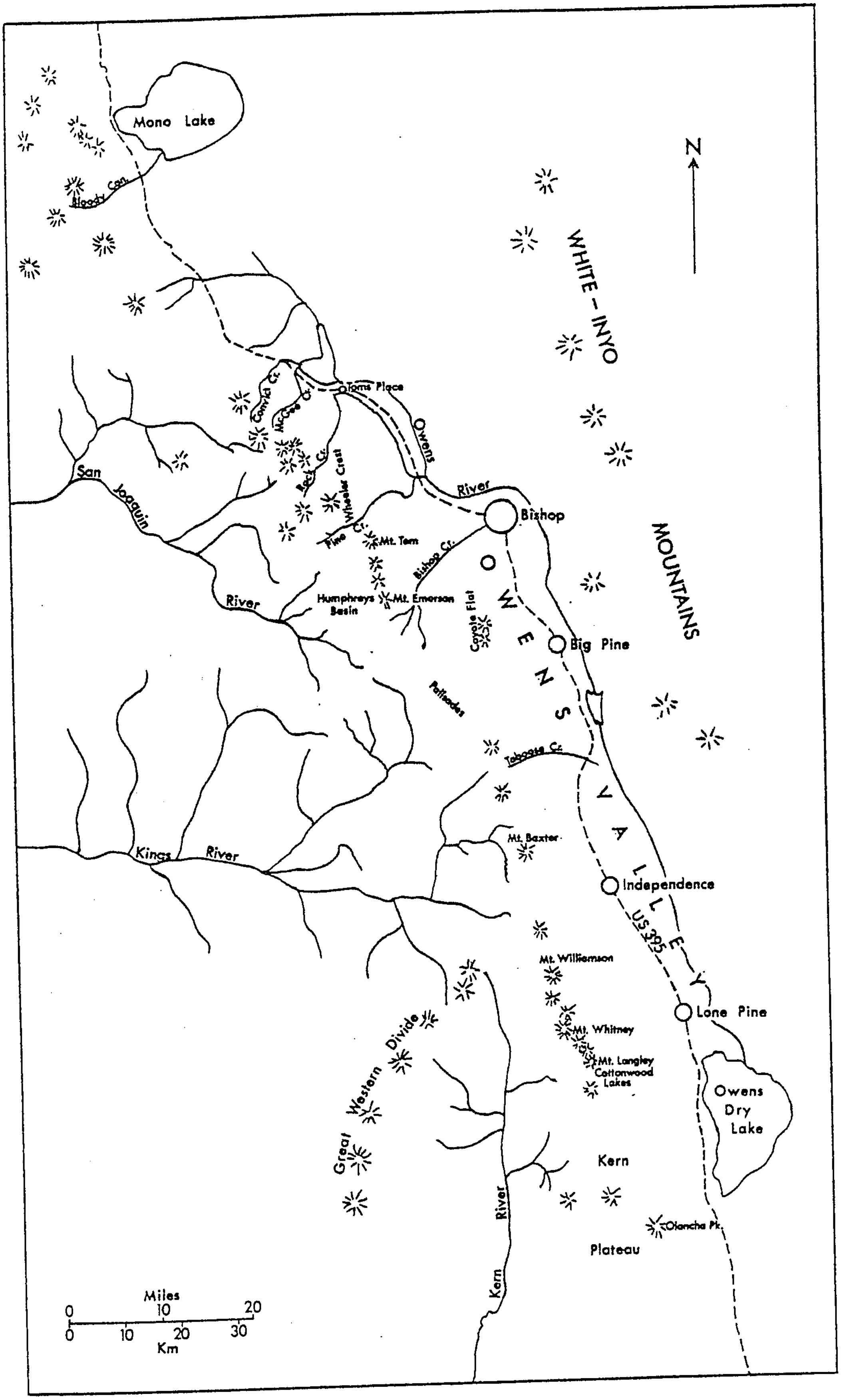
Historic Range

Historically, bighorn were distributed in the Sierra Nevada from the Sonora Pass area about 40 miles north of Mono Lake (Figure 1) south to approximately the southern end of the range (Jones 1950a). An additional disjunct population occurred in the Truckee River drainage just north of Lake Tahoe (Figure 1)(Buechner 1960). Summer ranges were along the mountain crest and winter ranges on the east side (Muir 1894, 1898), where topography and snow conditions permitted. The only known exception to this was the Great Western Divide (Jones 1950a), a western spur of high peaks in the south end of the range (Figure 1), which contained both summer and winter range. Winter ranges in this case were probably along the Kern River at the eastern base of the divide. Figure 28 is a map of landmarks pertinent to the following discussions.

Ignoring the disjunct population in the Truckee River drainage, historic bighorn range in the Sierra can be divided into four separate regions on the basis of topography: (1) the Owens Valley region, (2) the region north of Owens Valley, (3) the region south of Owens Valley, and (4) the Great Western Divide.

The section of the range adjacent to Owens Valley offers the best habitat because (1) the low elevation of the escarpment base provides winter ranges of low snow cover below the pinyon pine belt in nutritionally rich sagebrush steppe vegetation, and (2) extensive alpine habitat is

Figure 28. Landmarks pertinent to discussion of historic bighorn range in the southern Sierra Nevada.


Mono Lake
Bloody Can.
N
WHITE – INYO
MOUNTAINS
Convict Cr.
McGee Cr.
Toms Place
Owens
River
Rock Cr.
Wheeler Crest
Pine Cr.
Mt. Tom
San
Joaquin
River
Bishop
Bishop Cr.
Humphreys
Basin
Mt. Emerson
Coyote Flat
O W E N S
V A L L E Y
Big Pine
Palisades
Taboose Cr.
Mt. Baxter
Kings
River
Independence
US 395
Mt. Williamson
Mt. Whitney
Mt. Langley
Cottonwood
Lakes
Lone Pine
Owens
Dry
Lake
Great Western Divide
Kern
Plateau
Olancha Pk.
Kern
River
Miles
0
10
20
0
10
20
30
Km

available for summer range.

North of Owens Valley the escarpment base rises about 900m in elevation with a disproportionate rise in snow cover due to increasing severity of winter storms. No information has been found that specified locations of historic winter ranges in this region. The large number of skulls reported for the area were obtained in the high country (Wehausen 1979). Snow conditions encountered on potential escarpment base winter ranges during this study have been severe. This has led to the conclusion that it is unlikely that historic winter ranges were located in the Sierra Nevada, but instead occurred in suitable topography to the east. This would have entailed more complex migratory patterns than necessary in the Owens Valley region. In 1911 H. A. Carr of the Museum of Vertebrate Zoology at Berkeley quoted local inhabitants as saying that bighorn in the Sierra west of Independence in Owens Valley did not leave the escarpment in winter, whereas those north of Owens Valley around McGee Creek did (Jones 1950a). This is the only historical evidence pertinent to and in support of this hypothesis. A few winter sightings in recent decades of individuals and groups of two or three bighorn east of the Sierra north of Owens Valley (Wehausen 1979) support the contention that snow conditions there are too severe for bighorn. These sightings presumably represent the last vestiges of remnant herds in this region. Alpine summer range is abundant along the crest north of Owens Valley.

The third region of historic bighorn range begins south of the Cottonwood Lakes Basin at the south end of Owens Valley and extends as far as Jawbone Canyon. The evidence for this historic range comes from early sightings and skull remains listed by Jones (1949 - Appendix A). This region is characterized by adequate low elevation winter areas, but a general lack of alpine summer range; a small amount of alpine range exists in the area of Olancha Peak, which contains the southernmost alpine in the Sierra Nevada. Most of the Kern Plateau is topographically unsuitable as bighorn habitat. However, rocky ridge systems extending onto the east side of the Kern Plateau from the top of the eastern scarp apparently provided bighorn access to the abundant subalpine meadow systems. Jones (1949 - Appendix A) provided historical sightings in locations such as Monanche Meadows supporting this contention. South of the Kern Plateau this summer option disappears and the habitat increases in aridity, resembling that of desert bighorn to the east. Summer water sources were probably important to bighorn in this most southern area of the Sierra, whereas they appear to be of little importance for water consumption in alpine summer range.

The fourth region of historic bighorn range is the Great Western Divide. It is considered as a separate region because it lies west of the main crest. However, it resembles the Owens Valley region in that a large expanse of alpine summer range is present and winter ranges were undoubtedly at the base of its east side along the Kern River at elevations as low as 2150m. This is nevertheless 600m higher than the lowest winter range in Owens Valley.

A History of Herd Decline

The decline of the Sierran bighorn population appears to fall into two periods: one of rapid decimation occurring over two to three decades beginning about 1860, followed by a lengthy period of slower decline. Historical records from the 1800's are few. Many bighorn herds disappeared during that century without any or much trace of their existence being recorded. Skull remains found much later are often the only evidence of previous occupation. It is thus necessary to treat general regions as units of discussion.

The north end of historic bighorn range from Sonora Pass south through Yosemite apparently lost its bighorn rapidly. A group of three reported killed about 1870 in the Yosemite area is the only record provided by Muir (1894). A packer reported sighting about a dozen each year from 1876 to 1878 on the eastern slope of Sonora Pass (Grinnell and Storer 1924). Muir (1894, 1898) never mentioned personally seeing bighorn except in the southern Sierra. This suggests their early demise in the northern section. The conclusion of Grinnell and Storer (1924) that their disappearance predated the early 1880's seems justified. Jones' (1950a,b) statement that Muir claimed some still existed in 1898 appears to be an overstatement of Muir's words, "Few wild sheep, I fear, are left hereabouts".

On the basis of discussions with people present during the extirpation of bighorn from the Yosemite area, Grinnell (1935) concluded that the primary cause was uncontrolled hunting by miners and sheepherders. The former shot bighorn for food, while the latter regarded them as undesirable competitors with their domestic stock. Muir (1898) pointed out that Yosemite bighorn were particularly vulnerable to hunters when snow forced them down the east side of the range. This was probably particularly true of this northern region, where adequate winter range in the Sierra Nevada proper seems to be absent. Two intense periods of mining in the area, the first beginning in 1857 and the second in the 1870's (Anon. 1924) could well account for the early demise of bighorn in the area. Grazing by domestic sheep appeared later than mining and was terminated on Yosemite Natonal Park lands in the 1890's (Grinnell 1935). Grinnell (1935) raised the possibility that competition for forage and transmission of diseases such as scabies from domestic sheep might have played some role in the extirpation of bighorn from the area.

A second area known to lose its bighorn early was the Great Western Divide region. A die-off of bighorn due to scabies contracted from domestic sheep in the 1870's is recorded for this area (Jones 1950a). This southern section of the Sierra was one of the earliest to receive grazing by livestock. Cattle were already present in 1861, but were replaced rapidly by domestic sheep (Vankat and Major 1978). Stocking rates were excessive and few areas went ungrazed. By the early 1870's results of severe overgrazing were already apparent. Clarence King of the 1864 geological survey party noted the great destruction of grazeable areas on the Kern Plateau upon his return in 1873, and Magee wrote in 1885 that severe overgrazing was more evident in the Mount Whitney region than elsewhere in the Sierra (Vankat and Major 1978). Domestic sheep herded through the area every summer apparently numbered in the hundreds of thousands (Vankat 1970).

The Great Western Divide is the only area in which a die-off of bighorn from scabies is recorded. Scabies outbreaks probably occurred unrecorded throughout this southern region in the 1870's. No mention was made of bighorn in this southern region in the early twentieth century, when other herds in the Owens Valley region were discussed. This suggests that these herds were gone or in a decimated state.

A number of Sierran bighorn herds clearly persisted into the twentieth century. Ober (1914) considered only three to exist in 1914: the Mount Baxter, Taboose Creek, and Mount Tom herds. The Taboose Creek herd was mentioned in both the 1921 and 1923 Inyo National Forest Annual Fish and Game reports, with population estimates as high as 70. No reference to it occurs thereafter in any discussion of Sierra bighorn, until Jones (1950a) resurrected it with very unconvincing evidence. Presumably the Taboose Creek herd disappeared in the 1920's.

Ober (1931) again noted the existence of the Mount Tom herd, although with a population estimate of 35 instead of his previous 40-50. In both discussions (1914 and 1931) he stated that this herd both wintered and summered on Mount Tom. In an earlier discussion (1911) Ober considered this herd to summer as far north as McGee Creek as well as west of the crest. At that time (1911), Ober also considered the Taboose Creek and the Baxter herds as a single herd. Clearly some confusion existed then as to what constituted a demographic unit.

The Mount Tom herd persisted into at least the 1930's. Ober (1931) estimated it at 35 animals. Fred Ross reports (pers. comm. 1979) having occasionally sighted bighorn and frequently seen their sign in the 1930's west of Mount Tom across Humphreys Basin in the area of Mount Senger. Six bighorn were seen in 1934 just west of Piute Pass in Humphreys Basin (Jones 1949), and five on Mount Emerson in 1936 (1936 Inyo National Forest Fish and Game Report). These seem to be the last evidence of the existence of the Mount Tom herd.

The 1921 and 1923 Inyo National Forest Annual Fish and Game Reports each mentioned a herd referred to as the Pine Creek-Rock Creek band, which wintered at the base of Wheeler Crest. Although immediately adjacent to Mount Tom, this probably constituted a separate herd, considering Ober's

(1914) clear statement that the Mount Tom herd wintered on Mount Tom itself. The Pine Creek-Rock Creek band was believed to summer as far north as McGee Creek. This is doubtful, since about 12 miles of crest would have to be traversed. It is more probable that a separate herd later referred to by Jones (1950a) as the Convict Creek herd summered in the McGee Creek country. A couple of sightings of 20 and 24 sheep in this area in 1911-13 (Jones 1949) would seem to support the contention that the Convict Creek herd was still viable at that time. The comments by local residents in 1911 (discussed earlier) that bighorn in the McGee Creek area left the Sierra in winter also suggests this was a separate herd from those wintering on Wheeler Crest. The Convict Creek herd probably wintered in the Owens River Gorge and migrated between there and the Sierra just north of Toms Place, where the Bishop Tuff provides rocky terrain. Mention of the Pine Creek-Rock Creek herd ceased after 1923. Presumably it also disappeared during the 1920's.

The timing of the disappearance of the Convict Creek herd is less certain, partly because early writers did not distinguish it as a separate herd. No sightings are recorded from the area between 1913 and 1935, but scattered sightings of small groups exist for approximately 15 years thereafter (Wehausen 1979). Sightings since 1950 are few and have been mostly lone rams. Interpretation of these data is difficult. They suggest that the major demise of the herd occurred during the first couple decades of the century, while later sightings were probably of a small remnant herd that persisted until about 1950.

An additional herd probably existed between the Taboose Creek herd and the Mount Tom herd. This herd would have wintered at the eastern base of Coyote Flat where extensive winter range exists, and probably migrated to summer range via the south fork of Bishop Creek. A large section of the crest between the Palisades and Humphreys Basin, including divides extending west, would have constituted summer range. Ample evidence in the form of skulls (Jones 1949 - Appendix A) verifies historic bighorn occupancy of this section of the crest. However, sightings are lacking, suggesting early extirpation of this herd. This is not surprising considering the easy accessibility of its winter range and its close proximity to the towns of Bishop and Big Pine.

The persistence of the Baxter herd through time is indicated by numerous references to the presence of bighorn in locations presently occupied (Ober 1911, 1914, 1915, 1916, 1931, Clyde 1936, Blake 1941b, 1949). Its size has apparently been substantial for many years, judging from herd size estimates and group sizes reported over time. It was the abundance of sheep in this herd that allowed Grinnell to collect five bighorn on the the slopes of Mount Baxter in 1911 (Grinnell 1912); a group of forty was reported from the summer range that year (Ober 1911). In 1914, Ober (1914) counted 65 different individuals in this herd at one time during winter and estimated its population at 85-90. The following year he encountered over 200 in a two week period during spring, and intimated the population was considerably larger than his previous estimate (Ober 1915).

A question of interest is whether the factor(s) that brought about the decline of the previously-mentioned herds in the 1920's and 1930's also adversely affected the Baxter herd at that time. Mention of the Baxter herd is essentially lacking between 1916 and 1931. The only reference to it in Annual Fish and Game Reports of Inyo National Forest is mention of a small number of bighorn in the Thibaut Creek area. In 1931, Ober estimated the total Sierran bighorn population at 200, 35 of which were on Mount Tom, while most of the others were in the Baxter herd (Ober 1931). Weaver (1972) reported that California Department of Fish and Game personnel observed a group of 34 bighorn in Sawmill Canyon during the winter of 1935. This is comparable to maximum group sizes seen there today. It is doubtful that the Baxter herd has ever reached a dangerously low point due to activities of modern man. Judging from numerous sightings reported over time, there is also no apparent decline in the range of use by this herd during this century.

No mention of the Mount Williamson herd exists in early discussions of Sierra bighorn. The first evidence of a herd in the region of Mount Williamson came with the publication of sightings solicited by the Sierra Club in the 1940's (Blake 1941b, 1942, 1949). Jones (1949) was the first to clearly identify this herd, and listed sightings dating back to 1925. The reason for the anonymity of this herd for so long probably lies in the extreme ruggedness of the terrain it inhabits. Only a few ardent mountain climbers would have entered this country in early years. The most famous climber of that era, Norman Clyde, is responsible for most bighorn sightings in this area prior to 1940 (Jones 1949 - Appendix A). Clyde (1971a,b) discussed bighorn use of this area based on observations beginning early in the century.

Another herd unmentioned in early reports was located immediately north of the Cottonwood Lakes Basin. Dixon (1936) first mentioned the possibility of a herd there; Jones (1950a) named it the Mount Langley herd. Sightings in the area of Mount Langley did not occur until 1930. Scattered sightings thereafter have been mostly on Mount Langley itself (Jones 1949 - Appendix A), and occasional sightings in the area continue to the present (Wehausen 1979). With the abundance of good winter range at the base of the eastern scarp in this area and extensive summer range, particularly west of the crest, a substantial bighorn herd would be expected. Evidence of it this century is very patchy, suggesting that only a remnant survived early decimation. Clyde (1971b) notes having encountered little bighorn sign in the Mount Langley area over the years. This is in strong contrast to his comments (Clyde 1971a,b) about the Mount Williamson herd range, as well as to what one finds in general where an established herd exists.

Causes of Herd Losses

Why did most herds in the Owens Valley region survive so much longer than in the other regions? This question reduces to an analysis of causes of herd losses. Extirpation of North American bighorn herds is generally attributed to one or a combination of three causes: overhunting, competition from domestic sheep, and diseases (notably scabies) contracted from domestic sheep (Buechner 1960). Both hunting and domestic sheep appear to be factors in the early period of extirpations in the Sierra Nevada. If Grinnell (1935) is correct, the demise of the northern herds is largely a function of uncontrolled hunting during an early rush of miners to the area. In contrast, there is no indication that excessive hunting was involved in the southern region. Domestic sheep instead seem to be the cause. It appears unlikely that excessive hunting was the cause of later herd losses in the Owens Valley region. Some law enforcement came into effect shortly after the turn of the century. Ober (1911) reported catching a bighorn poacher as early as 1911. Some poaching nevertheless continued well into the century. As late as the 1930's Dixon (1936) expressed concern over poaching on the Baxter herd, where deer hunters reputedly shot bighorn every year for camp meat. It is doubtful that this sort of casual hunting could account for the extirpation of entire herds. It is also unlikely that more intensive hunting, such as market hunting to supply mining camps, was possible at that time, due to its unlawfulness. Domestic sheep grazing seems the more likely candidate as the cause of later herd losses. This would suggest that the northern Owens Valley herds were impacted by domestic sheep much later than those in the Great Western Divide and Kern Plateau area.

It is known that stock grazing began on the west side of the Sierra. The use of the mountains for summer grazing became established in the 1860's during severe droughts that prevented summer cattle grazing in the Central Valley (Vankat 1970). The rapid and severe overgrazing in the Kern River drainage that followed has been previously discussed. Magee's comment in 1885 (cited by Vankat and Major 1978) that this area was notably more impacted than the rest of the Sierra is significant relative to the early losses of bighorn herds in this region.

Geographic features probably also played a role. First, domestic sheep in the Kern drainage would have grazed winter ranges of the herds residing along the Great Western Divide; winter ranges east of the main crest of the Sierra would not have been impacted by grazing on the west side. Secondly, those herds south of the Cottonwood Lakes Basin that depended on meadows of the Kern Plateau for summer forage would have been much more severely impacted than herds to the north that summered along the crest in the alpine. Domestic sheep grazing was probably limited largely to less steep slopes and firm substrates where herdability and vegetative cover made grazing worthwhile. In the southern Sierra this would have limited grazing to the subalpine, except for some cirque bottoms that extend above timberline. This would have overlapped summer habitat of bighorn rams to some extent. Steep alpine habitat used by ewe-lamb groups would have received domestic sheep use only at its lower western extremes, while all summer ewe-lamb range on the east side would have been untouched by domestic sheep. This may account for the survival of most Owens Valley bighorn herds into the twentieth century.

Control of domestic stock grazing in the Sierra came after federal land designation. In 1890 Yosemite and Sequoia National Parks were established (Storer and Usinger 1970). In 1893 most remaining land in the southern Sierra was placed in the Sierra Forest Reserve, later to be divided into National Forests as well as additional park lands (Vankat 1970). Attempts to control domestic sheep grazing on these newly-designated federal lands met with varied success for the first decade (Vankat 1970). For instance, grazing in the heavily overgrazed upper Kern River region was not successfully reduced until just after the turn of the century (Vankat and Major 1978).

Reduction in livestock grazing on the east slope of the Sierra apparently occurred much later. Harry Scott (pers. comm. 1979) reported that he had charge of 3000 domestic sheep that grazed in part of the Convict Creek drainage in 1918, and that the Deadman Creek allotment to the north had 10,000 sheep. This was apparently typical of most east side drainages at the time. Wright et al. (1933) and Grinnell (1935) both pointed out that considerable domestic sheep grazing continued on the east slope in the early 1930's. Dixon reported in 1936 that Inyo National Forest was just then withdrawing domestic sheep from areas where they might compete with bighorn. This was apparently too late for most Owens Valley bighorn herds.

It is evident that considerable domestic sheep grazing along the east slope was present at the time of bighorn herd losses in the Owens Valley region. The question of why this occurred so much later than elsewhere requires information on when grazing of the east slope began. This information has not been found. It is probable that intensive grazing of the east slope began this century in response to reduction of grazing west of the crest.

The most significant distinguishing feature of east slope grazing is that bighorn winter ranges would have been grazed. Dixon (1936) noted that this left little of the previous season's growth for bighorn when they descended to winter ranges. Additionally, overgrazing would have reduced the populations of perennial grasses important in bighorn winter diets. East side summer ranges would have been much less impacted than winter ranges due to their extreme ruggedness.

The role of domestic sheep disease in the demise of Owens Valley bighorn herds is unclear. The practice of sheep dipping was considered to have eliminated scabies in California by 1934 (Jones 1950a). Chronic frontal sinusitus (Bunch et al. 1978) may have played a role. The skull of a ewe shot by Grinnell's assistant in 1911 on Mount Baxter, now in the collection at the Berkeley Museum of Vertebrate Zoology, shows clear sign of this debilitating disease.

Remnant Herds

Temporal patterns of extirpation of bighorn herds probably vary considerably depending on causation. Many exhibit a lengthy period between initial rapid decline and final disappearance, as indicated by cessation of records of bighorn in an area. Herds in this latter period of disappearance have come to be called remnant herds. A number of examples of this pattern are apparent in the Sierra. It was previously mentioned that the patchy evidence of the Langley and Convict Creek herds in this century suggests they have been remnants of much more substantial herds. Likewise, a small number of bighorn survived along the Great Western Divide until about 1920 (Jones 1949). Evidence of a few bighorn remaining in the northern Yosemite region also appeared early this century (Jones 1950b); additional sightings in the Yosemite area have been reported in recent decades (Wehausen 1979).

Characteristics of remnant herds seem to be: (1)

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come predictable viable
dictable seasonal
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een confusing to
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the traditional
exhibited by bighorn
and copying the patterns
ion from these patterns,
ars to be a very rare
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behaviors, presumably
ers, except under rare
Geist (1975) suggested
he appearance of hostile
rly white people.
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the only survivors would
iderably different
imating factor(s). These

survivors were presumably the more wary individuals that did not venture from the complete safety of precipitous terrain that was inaccessible to hunters as well as domestic sheep. According to Geist's (1967, 1971) hypothesis, these new patterns would be perpetuated as a learned behavior, and knowledge of previously-used range would disappear. Additionally, decimating factors may have selected for a wary genotype (Geist 1975). This is suggested by Hansen's (1970) observation of such a genotype in bighorn in Nevada. The tradeoff would be a climatically and nutritionally harsher environment. The longevity of a small herd of this sort would depend on how nearly recruitment matched adult mortality; recruitment would not be expected to exceed mortality on the average, and herd size would remain small and most likely diminish over time.

Abandonment of winter ranges by mountain bighorn is probably a common source of remnant herds, since winter ranges are usually the most accessible to man. An example of the possible severity of this may be illustrated using the Yosemite area as example. The probable migration of Yosemite bighorn to winter ranges east of the Sierra has been previously noted. Migrations would have crossed unsuitable bighorn range where they would be considerably more vulnerable. Heavy hunting during migration or on winter ranges could easily dissuade surviving members of a herd from making the migration, instead wintering in the deep snow of the Sierra. The sighting about 1870 in the

Yosemite area reported by Muir (1894) appears to illustrate the consequences. This sighting consisted of three bighorn in Bloody Canyon on the east side of Yosemite that were so snowbound in winter that the mountaineers that chanced upon them were able to kill the sheep with an axe.

In Rocky Mountain Natonal Park, loss of bighorn winter range has resulted in successful wintering on alpine windswept slopes (Baumann and Stevens 1978). This option was not available to bighorn in the Sierra due to the extreme sparsity of alpine vegetation on such slopes.