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Ecology of Mountain Sheep Reintroduced in the Sierra Nevada of California

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Abstract. From March 1986 through September 1991, we evaluated a mountain sheep (*Ovis canadensis californiana*) reintroduction to Lee Vining Canyon, Sierra Nevada, California. Natality, mortality, and habitat suitability were studied. We monitored movements and distribution to learn how reintroduced sheep explore and colonize an unfamiliar location. Data were collected at ewe forage sites to develop a discriminant model for classifying foraging habitat.

Twenty-seven sheep were translocated in March 1986. Eleven were added in March 1988, raising the number introduced to 38. The herd grew to 62 sheep after 6 years, with at least 56 lambs born during the study. Survival to 1 year of age averaged 72%. Most of the increase occurred during the last 2 years when the annual growth rate averaged 24.5%. We confirmed 22 deaths, although the actual mortality was more likely 32 sheep. Mountain lion (*Felis concolor*) predation and severe winter weather caused most of the deaths. The age structure of the herd at the end of the study suggests a potential for rapid population growth.

The herd colonized Lee Vining Canyon in two phases. The first phase was characterized by small home range sizes, failure to disperse from the release site, and limited sexual segregation. During the second phase, behavior was more typical of established herds.

The discriminant model correctly classified ewe foraging sites 72% of the time. Distance to escape terrain, herbaceous cover, and presence of surface water were the most useful parameters for classifying a site. Fecal crude protein levels, in conjunction with natality and survival rates, suggested that the habitat was suitable for reproduction and survival of the herd.

Key words: Mountain sheep, reintroduction, population dynamics, movement patterns, habitat use, nutrition, *Ovis canadensis californiana*.

Mountain sheep (*Ovis canadensis californiana*) were once widely distributed throughout the Sierra Nevada of California. A rapid decline in numbers began about 1850 and continued for the next 3 decades. During that time, many of the Sierra herds were reduced to remnant status. A long period of attrition followed, during which most remnant herds disappeared (Wehausen 1980). The major causes of decline include overhunting (Grinnell and Storer 1924:243), forage competition with domestic sheep (Dixon 1936), and diseases contracted from domestic stock (Jones 1950; Wehausen 1988).

In 1974, Wehausen (1979, 1980) began to assess the status of mountain sheep in the Sierra Nevada. After an extensive literature review and field surveys throughout likely mountain sheep habitat, he concluded that only the Mount Baxter and Mount Williamson herds had survived (Fig. 1). The Mount Williamson herd seemed stable at approximately 30 animals. The Mount Baxter herd, however, contained approximately 220 sheep and had been growing for nearly a decade.

Wehausen (1979) developed a series of management alternatives for Sierra Nevada mountain sheep. Major recommendations were that the Mount Baxter herd provide transplant stock for repopulating historic ranges in the Sierra Nevada and that an interagency advisory panel be established to coordinate management of the herds.

The Sierra Nevada Bighorn Sheep Interagency Advisory Group (SNBSIAG) was formed in 1981 to foster cooperation between federal and state agencies involved with Sierra Nevada mountain sheep management.

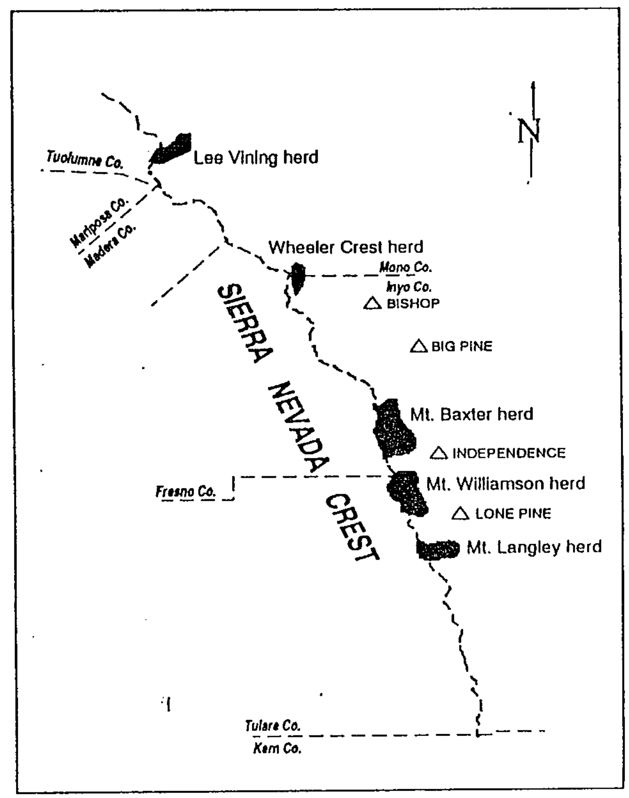

Fig. 1. Distribution of bighorn sheep herds in the Sierra Nevada, California, as of January 1992.

Participants included biologists from the California Department of Fish and Game, National Park Service, U.S. Forest Service, and the Bureau of Land Management. John Wehausen acted as a consultant (Keay et al. 1987).

In 1984, the advisory group issued the Sierra Nevada Bighorn Sheep Recovery and Conservation Plan (Sierra Nevada Bighorn Sheep Interagency Advisory Group 1984). The goal of Sierra Nevada mountain sheep management was to ensure the continued existence of the sheep. This objective was to be achieved by maintaining the health and viability of all existing populations and by promoting the establishment of at least three reintroduced populations that would be large (exceeding 100 animals) and geographically distant from one another (Sierra Nevada Bighorn Sheep Interagency Advisory Group 1984). Lee Vining Canyon, near Yosemite National Park, was identified as the best possible reintroduction site in the northern Sierra Nevada (Wehausen 1979).

History of Mountain Sheep in the Yosemite Region

Mountain sheep historically occupied the Yosemite region (Jones 1950), where they summered along the main crest of the Sierra Nevada (Fig. 2). Most of them disappeared by the early 1880's (Grinnell and Storer 1924). In 1914, Yosemite's mountain sheep were declared extinct (Jones 1950).

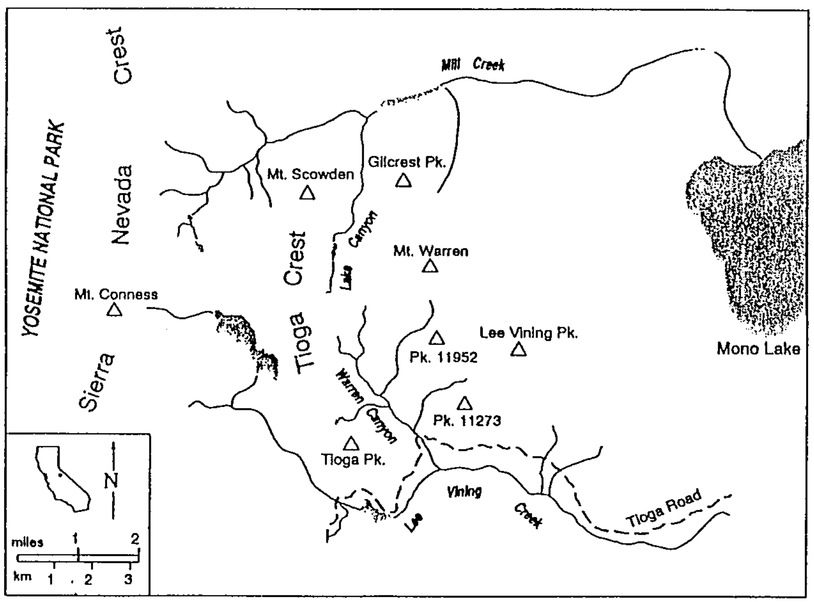

Fig. 2. Map of the Lee Vining Canyon bighorn sheep reintroduction study area showing significant topographic features.

Although the idea of restoring mountain sheep to Yosemite gained early support (Blake 1941, 1949), biologists at the time preferred natural recolonization to reintroduction (Wright et al. 1932; Grinnell 1935). More than 50 years elapsed, however, without mountain sheep recolonizing Yosemite. Spurred by objectives in the recovery and conservation plan (Sierra Nevada Bighorn Sheep Interagency Advisory Group 1984) and recognition that mountain sheep dispersal is limited by their fidelity to traditional ranges (Geist 1971:99), managers began reconsidering reintroduction as an alternative (Keay et al. 1987).

On 5 and 6 March 1986, the California Department of Fish and Game translocated 27 native Sierra Nevada mountain sheep from Mount Baxter to Lee Vining Canyon, just east of Yosemite. The Lee Vining herd was augmented with 11 more sheep from Mount Baxter in March 1988 because the number of adult ewes in Lee Vining Canyon had declined to only five individuals.

The primary objective of our study was to evaluate the reintroduction and identify factors contributing to its success or failure. We planned to monitor population dynamics, identify important components of mountain sheep habitat, assess the suitability of habitat in Lee Vining Canyon, and document how mountain sheep explore and colonize an unfamiliar location.

Study Area

Description

The 46-km^2 study area adjoins the eastern edge of Yosemite National Park along the Sierra Nevada crest. It is bounded on the north by Mill Creek in Lundy Canyon and on the south by Lee Vining Creek (Fig. 2). Elevation ranges from 2,188 m at the eastern end of Lee Vining Canyon to 3,758 m atop Mount Warren. Lands in the study area are managed by the U.S. Forest Service as parts of Inyo National Forest, Hoover Wilderness, and the Harvey Monroe Hall Natural Area.

Fault block uplift and early-to-mid-Pliocene riverine cutting combined to produce the area's complex physiography (Bateman and Wahrhaftig 1966). The landscape was further shaped by at least five glacial sequences (Blackwelder 1931; Sharp and Birman 1963). Substrates on the eastern half of the study area are primarily granitic while those on the west are metasedimentary (Kistler 1966; Bateman et al. 1983). Soils are generally shallow and poorly developed.

Climate

Climate is characterized by cold, wet winters and warm, dry summers. Long periods of clear, sunny weather are broken by storms that are usually short-lived. Mean monthly temperatures range between 1 and 20° C in summer ($\bar{x}$ = 13° C) and 2 and −12° C ($\bar{x}$ = −5° C) during winter. Annual precipitation averages 76 cm and is deposited primarily as snow falling between November and April.

Vegetation

Lower elevations (2,180–2,590 m) used by the Lee Vining herd as winter range are characterized by sagebrush steppe (Young et al. 1977) and pinyon–juniper woodland communities (Munz and Keck 1973; Laudenslayer and Boggs 1988). Summer ranges extend from 3,232 to 3,437 m elevation and consist of subalpine forest and alpine communities (Benson 1977; Major and Taylor 1977).

Methods

Movement and Distribution

We monitored movement and distribution patterns from March 1986 through September 1991 by equipping 36 of the 38 transplanted sheep with radiotelemetry collars. Seasonal movement data were analyzed using the 100% minimum convex polygon method (Hayne 1949). Although the method has shortcomings (Van Winkle 1975; Schoener 1981; Worton 1987), it delineated the extent of movements and allowed comparisons with other studies. When sample sizes were adequate (≥ 80), we also examined location data using the program PDF-XYZ 1.0 (Crabtree 1988) to describe the extent and intensity of space use.

Population Dynamics

We conducted a complete census every 10 days to document reproduction and survival. Motion sensors in the collars alerted us to deaths and enabled us to recover carcasses to determine causes of death.

Habitat

The polygynous mating system of mountain sheep makes ewes the most important reproductive component in sheep populations. Balancing lamb safety and the nutritional demands of lactation forces ewes to be more selective when choosing forage sites (Wehausen 1980). Consequently, we focused on evaluating habitat at sites used by the ewe–juvenile component of the herd.

We conducted fieldwork to evaluate habitat in the summers of 1988 and 1989. We sampled habitat characteristics at 52 forage sites used by ewe–juvenile groups and at 55 randomly selected sites. A forage site was an area, ≤ 40 m in diameter, where a ewe–juvenile band foraged for at least 5 min. We measured elevation, aspect, slope, visibility, distance to escape terrain, vegetative cover, and whether or not water was present at each site.

Visibility was defined as the percentage of each quarter of the compass over which a 90-cm-tall object could be seen from 40 m away (Risenhoover and Bailey 1980). Escape terrain was steep, broken, rocky terrain that would allow sheep to outmaneuver or outdistance predators (Gionfriddo and Krausman 1986). Cover along three line-point transects on each plot was recorded as absolute vegetative cover by species, litter, or bare ground. At each point covered by vegetation, we measured the height of the tallest plant (in centimeters).

Random sites were areas located within ewe summer range, but where sheep were not observed foraging. Their number and location were determined by stratified random sampling. The number of random sites within each habitat type was based on the proportion of ewe–juvenile forage sites occurring within that habitat. Precise locations were determined from randomly selected 0.1-km Universal Transverse Mercator grid intersections within a composite home range of adult ewes. Sampling protocols for random sites followed those used at forage sites.

We used two-way indicator species analysis (TWINSPAN; Hill 1979) to define the plant communities at forage and random sites. Discriminant analysis was used to identify habitat characteristics that best distinguished between forage and random sites, develop a model describing forage site use by ewe–juvenile groups, and test the model's accuracy (Norusis 1988).

Fecal crude protein (6.25 × nitrogen values) levels were used as indices of diet quality (Wehausen 1980; Leslie and Starkey 1985). We tracked fecal crude protein levels throughout the year by collecting fecal pellets at weekly intervals and analyzing them using the micro-Kjeldahl technique. Results were expressed on a percent-organic matter basis (Seip and Bunnell 1985). We indirectly assessed habitat suitability using rates of reproduction and lamb recruitment.

Results

Movement and Distribution

Distribution patterns during the first year consisted of seasonal movements between summer range on the upper slopes of Peak 11,273 (Fig. 3a) and winter range in lower Lee Vining Canyon (Fig. 3b). Movements rarely extended more than 3 km from the release site, and the boundary between winter and summer ranges was indistinct. Rams associated with ewes throughout the year. Home range sizes averaged 9.5 km^2 for ewes and 15.8 km^2 for rams during the first summer (Table 1). A series of mild storms in September and October produced repeated movements between summer and winter ranges. Movements during this period also included forays to previously unvisited areas. On two occasions, the herd abruptly moved 6 km north to the vicinity of Mount Warren (Fig. 2) but returned to summer range within 2 or 3 days.

Members of the Lee Vining Canyon herd moved to lower elevations following the first major storm in late November 1986. They established their 1987 winter range on the brushy hillsides bordering embankments along Tioga Road (Fig. 4a). A notable exception was the emigration in October 1986 of three ewes and two lambs to Bloody Canyon, 8 km south of Lee Vining Canyon. These sheep established residence in Bloody Canyon and remained isolated from the main herd for the duration of the study.

During the second year, distances between summer and winter ranges increased as some herd members extended movements into new areas. The average female summer range increased ($P < 0.05$) to 22.4 km^2 (Table 1) with the migration of ewes to Gilcrest Peak and Mount Scowden (Fig. 4b). Most rams shifted summer activities to areas along the Sierra Nevada crest in Yosemite National Park (Fig. 2). These changes increased sexual segregation. By late November, most herd members had returned to winter range used the previous year (Fig. 4a).

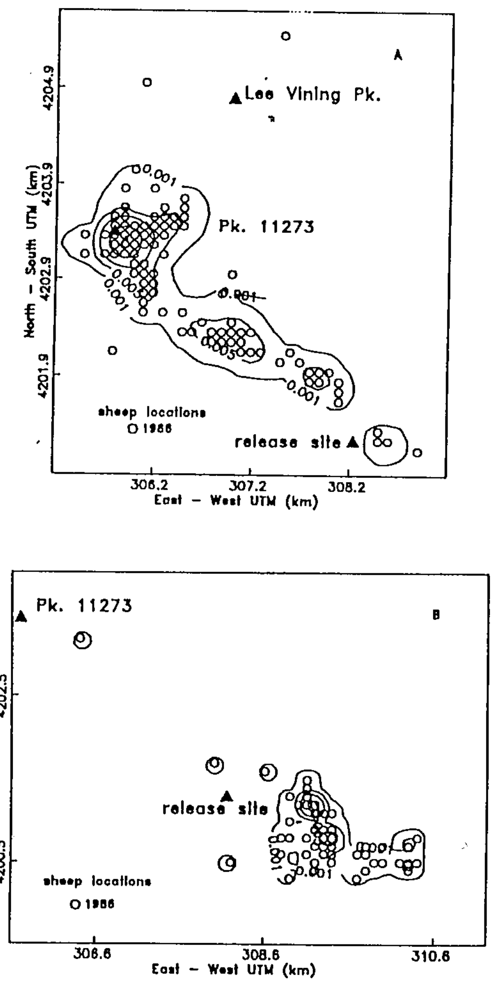

Fig. 3. Summer (*A*) and winter (*B*) home ranges used by bighorn ewe 4411 in 1986 in Lee Vining Canyon, Mono County, California.

Table 1. Estimates of individual home range size (km^2) in the Lee Vining Canyon mountain sheep (*Ovis canadensis californiana*) herd determined using the minimum convex polygon method.

	Winter–Spring						Summer–Fall					
	Ewes			Rams			Ewes			Rams		
Year	$\bar{x}$ area	SD	*n*	$\bar{x}$ area	SD	*n*	$\bar{x}$ area	SD	*n*	$\bar{x}$ area	SD	*n*
1986	4.2	4.3	12	18.1	22.0	4	9.5[a]	2.9	12	15.8	4.4	5
1987	7.3	0.9	7	11.9	3.8	4	22.4	8.3	6	35.4	5.1	4
1988	18.1	9.1	5	28.0	1.2	4	22.0	3.9	5	23.7	11.4	4
1989	17.4	17.0	5	17.7	7.8	4	18.0	10.2	5	14.7	16.9	3

[a]Denotes significant differences between years at $P < 0.05$ level using Dunn's test (Zar 1984:201).

The general pattern of movements exhibited during the second year remained relatively constant in subsequent years. An exception occurred when a few individuals from the 1986 reintroduction delayed returning to lower elevations until midwinter 1988. This change persisted through the remainder of the study.

Members of the 1988 supplement generally adopted the movement patterns of their predecessors with one significant exception. While most sheep from the 1986 reintroduction descended to lower elevations by mid-March 1988, members of the 1988 supplement remained on the summit (3,509 m) of Tioga Peak (Fig. 2).

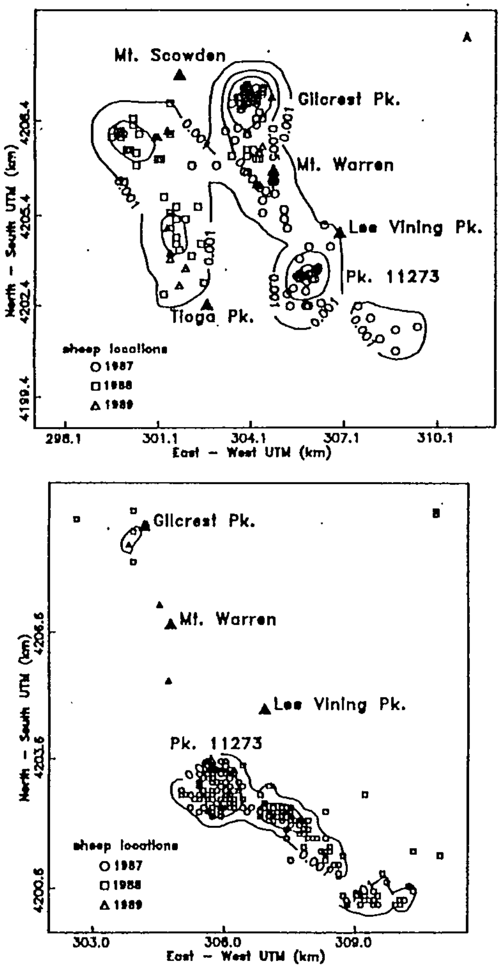

Fig. 4. Winter (*A*) and summer (*B*) home ranges used by bighorn ewe 4411 in 1987, 1988, and 1989 in Lee Vining Canyon, Mono County, California.

Population Dynamics

Natality

A minimum of 56 lambs was born during the study, and the annual ratio of lambs to ewes averaged 65:100 (Table 2). Lamb survival averaged 72% annually for the first 5 years. The mean recruitment rate during that period, expressed as the ratio of yearlings per 100 ewes ($\geq$2 years of age), was 47:100.

Mortality

Twenty-two confirmed deaths and 10 presumed deaths (Table 3) occurred between March 1986 and September 1991. Seven of 22 confirmed deaths occurred within 3 weeks of the 1986 reintroduction and resulted from accidents and exposure (Chow 1991). Ten of the remaining 15 confirmed deaths were from mountain lion (*Felis concolor*) predation. At least seven of nine radio-collared sheep that died were killed by mountain lions. Thus, it is likely that some of the presumed deaths also resulted from mountain lion predation.

Population Size

The Lee Vining Canyon herd increased from 38 sheep (Table 4) to an estimated maximum of 62 sheep in 6 years (Table 5). If the sheep in Bloody Canyon are discounted, and lamb survival in 1990 and 1991 is recalculated using the mean survival rate observed during the first 4 years of the study, estimated herd size is 51 animals. A minimum of 49 sheep was recorded during a census conducted in July 1991. Discrepancies between the minimum number and the totals projected in Table 5 are probably attributable to unconfirmed lamb deaths in 1990 and 1991.

Despite the birth of nine lambs in 1986, the Lee Vining Canyon herd declined from 27 to 20 sheep. The annual growth rate that year was −25.9% (Table 6). Annual growth rates during the next 2 years were only 5.0 and 6.3%, respectively. The 1988 supplement of 11 more sheep from Mount Baxter increased the total herd size to 32. In 1989, the annual growth rate rose to 17.6% and reached 25% in 1990. Because monitoring ended in September 1991, the 24% growth rate for 1991 does not account for probable overwinter mortality, and the actual figure is probably slightly lower.

Habitat

Analysis by TWINSPAN divided vegetation at forage and random sites into seven communities (Fig. 5). The primary dichotomy was between dry and wet sites. Dry site communities fell along an elevation gradient, indicating temperature may be the second most important factor affecting species composition on summer range.

Of the classified forage sites, 43% were located on high, exposed alpine slopes and ridges with sparse cover (< 25%) of low perennial herbs and graminoids. Indicator species of this dry *Podistera–Phlox* community included *Podistera nevadensis*, *Phlox covillei*, *Eriogonum ovalifolium*, and *Festuca ovina*. *Astragalus kentrophyta* and *Chrysothamnus parryi monocephalus*

Table 2. Lamb production and recruitment by cohort in the Lee Vining Canyon mountain sheep (*Ovis canadensis californiana*) herd between 1 May 1986 and 6 September 1991.

		Lee Vining		Overall[a]		
Year	Number of lambs born	Lamb:ewe ratio	Yearling:ewe ratio	Lamb:ewe ratio	Surviving to 1 year (%)	*n*
1986	9	75:100		75:100	67	6
1987	5	83:100	67:100	55:100[b]	60	3
1988	8	43:100	50:100	44:100	63	5
1989	9	56:100	25:100	47:100[b]	78	7
1990	13	68:100	37:100	59:100	92	12
1991	12	57:100	57:100	50:100[b]		

[a]Includes ewes in Bloody Canyon.
[b]No rams were present in Bloody Canyon during the previous breeding season.

Table 3. Sources of mortality in the Lee Vining Canyon mountain sheep (*Ovis canadensis californiana*) herd between March 1986 and September 1991.

		Sources of mortality					
Cohort	Initial number	Exposure	Accident	Mountain lion[a] predation	Unknown	Presumed dead	Current number
1986 transplant	27	5	2	6		3	11
1986 lambs	9			1	1	2	5
1987 lambs	5			1	1		3
1988 transplant	11			2	2		7
1988 lambs	8				1	2	5
1989 lambs	9					2	7
1990 lambs	13					1	12
1991 lambs	12						12
Total	94	5	2	10	5	10	62

[a]*Felis concolor*.

commonly occurred as well. Ewe groups used this community throughout summer, once it was free of snow.

A second alpine xeric community, which included 10 (20%) of the forage sites, was characterized by *Ribes cereum*. Mean elevation of the *Ribes* community was 245 m lower than the *Podistera–Phlox* community. The xerophytic species *Leptodactylon pungens* and *Sitanion hystrix* were common in both of these communities.

The *Carex–Juncus* community was used throughout the growing season, but the *Artemisia tridentata–Monardella odoratissima* community received minimal use.

Samples from mesic sites were grouped into three plant communities (Fig. 5). Sheep visited these in mid- to late August in both years. *Trisetum spicatum* and *Trifolium monanthum* were indicators for sites located on, or adjacent to, metasedimentary rock outcrops or cliffs. These were steep, moderately high elevation ($\bar{x}$ = 3,224 m) sites with surface or subsurface water. The other two mesic communities were dominated by sedge (*Carex* sp.) and grass species. Forage sites in these communities were less common but those present were used repeatedly.

Five variables were used in the final discriminant model to explain differences between forage sites (FS) and random sites (RS). They were presence of water (H_2O), herbaceous dicot cover (FORBCOV), distance to escape terrain (ETD), vegetation height (VEGHT), and visibility (VIS). Surface water was present on 19% of forage sites and none of the random sites. Forage sites averaged more than twice as much herbaceous cover ($\bar{x}_{FS}$ = 9.8%; $\bar{x}_{RS}$ = 3.9%), and mean vegetation height was 32% taller than on random sites ($\bar{x}_{FS}$ = 11.0 cm; $\bar{x}_{RS}$ = 8.3 cm). Steep, rocky terrain averaged 68.6 m from forage sites ($\bar{x}_{RS}$ = 150.0 m), and mean visibility on forage sites was 51.4% ($\bar{x}_{RS}$ = 43.1%). The resulting linear discriminant function was

$$\text{Discriminant score} = 1.309(H_2O) + 4.188(\text{FORBCOV}) - 0.097(\text{ETD}) + 0.609(\text{VEGHT}) + 0.984(\text{VIS}) - 2.180.$$

Table 4. Sex and age distribution of mountain sheep (*Ovis canadensis californiana*) reintroduced to Lee Vining Canyon, Mono County, California, in 1986 and 1988.

Sample	Age class										Total
	L[a]	1	2	3	4	5	6	7	8	9	
1986											
Male	5	4	1			1				1	12
Female	2		2	4	4		1	2			15
1988											
Male			2				1				3
Female		1	3		1	1	1		1		8
Total	7	5	8	4	5	2	3	2	1	1	38

[a]Lamb.

Table 5. Sex and age distribution of mountain sheep (*Ovis canadensis californiana*) in Lee Vining and Bloody canyons on 1 September 1991.

Sample	Age class														Total
	L[a]	1	2	3	4	5	6	7	8	9	10	11	12	13	
Lee Vining Canyon															
Male		3	2	1		3	1	3	1		1				15
Female		3	2	3	3	2	3		1	3	2				22
Unknown	12	6	3												21
Subtotal	12	12	7	4	3	5	4	3	2	3	3				58
Bloody Canyon															
Male				1											1
Female						1					1			1	3
Total	12	12	7	5	3	6	4	3	2	3	4			1	62

[a]Lamb.

Of the 51 sites used by sheep, 36 (70.6%) were correctly classified. Of the 54 randomly placed sites, 40 (74.1%) were assigned accurately (Table 7).

Fecal crude protein values ranged from a high of 41.90% in summer to a low of 4.46% in winter. Monthly mean levels of crude protein plotted annually increased with the onset of new growth in spring, then gradually declined from July to December each year (Fig. 6).

Table 6. Annual natality, mortality, and growth rate in the Lee Vining and Bloody canyon mountain sheep (*Ovis canadensis californiana*) herds between March 1986 and October 1991.

Year	Initial number	Number born	Natality	Number dying	Mortality	Final number	Growth rate
1986	27	9	75.0	16	44.4	20	−25.9
1987	20	5	55.5	4	16.0	21	5.0
1988	32[a]	8	44.4	6	15.0	34	6.3
1989	34	9	47.4	3	7.0	40	17.6
1990	40	13	59.1	3	5.7	50	25.0
1991	50	12	50.0			62	24.0

[a]Includes 11 sheep reintroduced in the 1988 supplement.

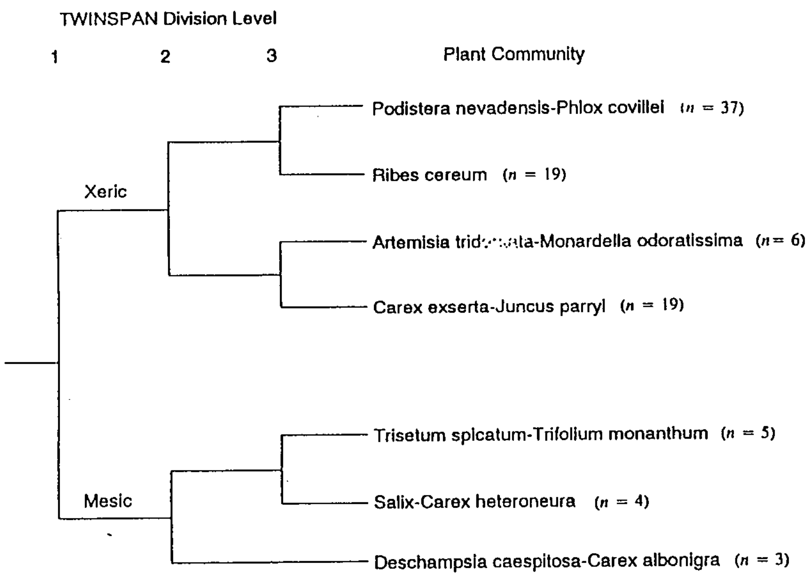

Fig. 5. Plant communities identified by two-way indicator species analysis (TWINSPAN) from mountain sheep summer ranges in Lee Vining Canyon, Mono County, California.

Seasonal means of fecal crude protein were significantly different between seasons in the Lee Vining Canyon herd ($\chi^2 = 147.04$, $P < 0.0001$). Spring and summer values were similar but were significantly higher than fall and winter values in all years. There were no differences in seasonal fecal protein levels from year to year.

Discussion

Movement and Distribution Patterns

The Lee Vining Canyon herd colonized their new location in two stages. The two-stage process seems typical of reintroduced mountain sheep and has

Table 7. Number of sites classified as forage sites or as randomly located sites by discriminant analysis for mountain sheep (*Ovis canadensis californiana*) ewes in Lee Vining Canyon, summer 1988 and 1989.

Sampled group	n	Predicted group membership: Random	Predicted group membership: Forage
Random	54	40 (74.1%)	14 (25.9%)
Forage	51	15 (29.4%)	36 (70.6%)

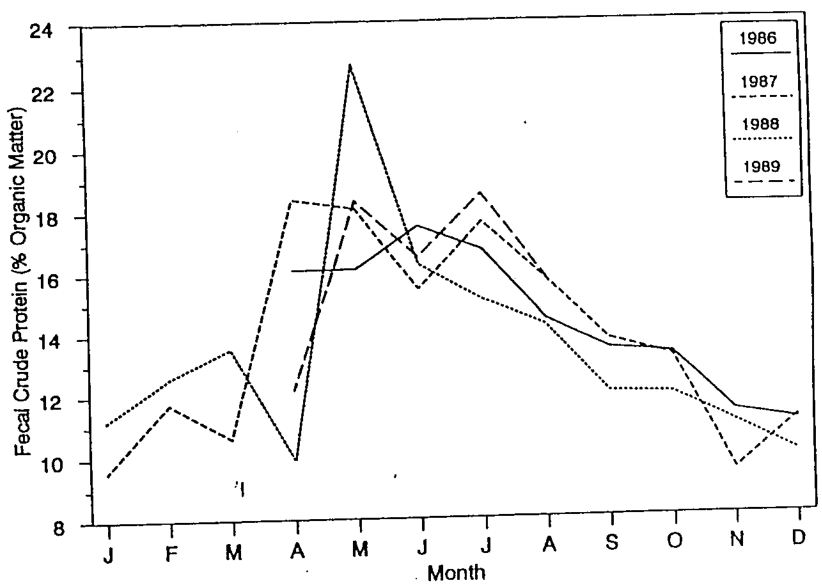

Fig. 6. Mean monthly percent fecal crude protein by year for mountain sheep at Lee Vining Canyon, Mono County, California, 1986–89.

been observed in the Rocky Mountain (Kopec 1982), desert (Elenowitz 1983; Shaw 1986; Berbach 1987), and California (Andaloro and Ramey 1981; Hanson 1984) subspecies.

The first stage commenced with the initial reintroduction and extended through the summer of 1986. This stage was characterized by small home range sizes ($\overline{x}_{ewes}$ = 9.5 km^2; $\overline{x}_{rams}$ = 15.8 km^2) and the absence of long-distance (> 5 km) migration between seasonal ranges. The move to winter range in late November 1986 marked the beginning of the second stage. During the second stage, the sheep began migrating long distances between summer and winter ranges and developed distribution patterns retained in subsequent years.

The herd's restricted movements during the first year contrasted sharply with patterns of long distance migration seen in native mountain sheep herds (Murie 1940; Packard 1946; Geist 1971) and observed by Wehausen (1980) at Mount Baxter. Failure to segregate by sex was also atypical of native herds (Blood 1963; Geist 1971).

Migration enables mountain sheep to remain in a zone of active plant growth where forage species are at peak nutritional content (Geist 1971; Hebert 1973; Wehausen 1980). Hebert (1973) studied captive mountain sheep and found a strong correlation between altitudinal migration and body condition. Thus, the transition from sedentary to migratory status may be important for a reintroduction to succeed.

Geist (1971) suggested that movement and distribution patterns in native mountain sheep herds are determined by tradition. Traditions arise when younger sheep follow older sheep, learn the location of resources, and subsequently maintain fidelity to those sites.

Geist (1971) surveyed agencies conducting mountain sheep reintroductions in western North America and found that transplanted sheep frequently remain near the release site and fail to expand into new areas. He attributed the sedentary nature of reintroduced herds to the absence of existing traditions in their new location. He proposed that, in the absence of tradition, range extensions were possible where habitat is continuous and visibility unobscured by forest. The absence of trees on the high elevation summer range and the Lee Vining Canyon herd's establishment of migration routes through areas lacking trees support this idea.

Differences in snow depth between years offers an alternate explanation for the shift from sedentary to migratory status. In 1986, snowfall was nearly twice the annual average. This was followed by 5 consecutive years of drought. Most snow melted before sheep moved to summer ranges and did not impede movements. In 1986, however, movements may have been indirectly influenced by snow banks that persisted throughout the year.

Plant growth in the Sierra Nevada is generally limited by available moisture (Major 1977). Winter snowpack has a major influence on the length of the growing season by providing water to plants during dry summer months (Billings and Bliss 1959). Persistent snow banks at higher elevations in 1986 may have allowed the herd to obtain adequate forage in one location while drought conditions in subsequent years necessitated long-distance movements.

Restricted movements by the sheep also may have reduced energy expenditures and decreased their vulnerability to predation in an unfamiliar area.

Predation also may have provoked shifts in distribution. In one instance, the herd moved to a new area after being chased by a coyote (*Canis latrans*). On another occasion, a nursery band moved 2 km after a mountain lion took a lamb. J. Wehausen (University of California, White Mountain Research Station, personal communication) observed the Mount Baxter herd abandon a wintering area in response to increased mountain lion predation.

The failure of rams and ewes to segregate during the first year may have been due to disorientation in their new location. The absence of a strict social hierarchy typically found in established herds (Goldsmith 1988) also may have curtailed sexual segregation. Finally, Geist (1971) observed that rams in British Columbia remained with natal bands until they were 2 or 3 years old. Thus, the rams may have failed to disperse because they were less than 2 years old when reintroduced in 1986.

Although a combination of factors is likely to have been involved, the most significant influences on the Lee Vining Canyon herd's pattern of home range establishment during the first year were the absence of traditional movement patterns and disorientation in a new location. Increased knowledge of their new surroundings fostered range expansion in the second year. Establishment of summer ranges in areas visited previously provides the strongest support for this interpretation. The rapidity with which members of the 1988 supplement adopted the movement and distribution patterns of their predecessors also strengthens this idea. The presence of continuous habitat and accompanying absence of visual obstructions may have promoted further range expansion (Geist 1971).

The development of stable migration patterns after only 2 years suggests traditions can arise rapidly. Further evidence is provided by increased sexual segregation, which may indicate that the Lee Vining Canyon herd began functioning more like an established mountain sheep population.

Population Dynamics

The Lee Vining Canyon herd grew slowly during the first 3 years of the study. Annual growth rates during this period were well below those reported by previous studies of reintroduced mountain sheep (Woodgerd 1964; Hansen 1984) and contrasted sharply with annual growth rates recorded later in the study. The low rate of growth is attributed to heavy predation on a small population. The problems of small population size were further exacerbated by unexpectedly high postrelease mortality and the emigration of three ewes and two lambs to Bloody Canyon.

From 1989 to 1991, annual growth rates rose dramatically (Fig. 7), nearly attaining the theoretical maximum (Buechner 1960; Woodgerd 1964; Streeter 1970). The sudden rise in growth rates seemed to result from increased lamb production while the number of deaths remained relatively constant.

Two events contributed to the increase in lamb production. The most significant was the 1988 supplement, which increased the number of reproductive aged ewes in the Lee Vining Canyon herd from 5 to 12. Although the natality rate in 1987 was high, only five lambs were born. Recruitment the next year barely offset deaths (Fig. 7). Despite a lower natality rate and a higher number of deaths in 1988, the addition of seven adult ewes boosted total lamb production so that the absolute number of recruits was greater.

Lamb production rose again in 1989 when ewes born at Lee Vining Canyon first entered the breeding population. The loss of both female lambs to post-release deaths in 1986 precluded recruitment of any females into the 3-year-old age class until 1989. Sierra Nevada mountain sheep ewes typically have their first lamb at 3 years (Wehausen 1980). Thus, adult females lost to emigration and death between 1986 and 1988 were not replaced. Steady erosion of the herd's reproductive potential during those years was finally arrested when ewes born at Lee Vining Canyon began lambing in 1989.

The number of deaths in the Lee Vining Canyon herd remained relatively constant after the second year (Fig. 7). This was due, in part, to the reduced probability of detecting deaths as the proportion of radio-collared sheep in the herd declined. It may also have been a consequence of territorial behavior among mountain lions (Hornocker 1970), resulting in a constant density of lions in Lee Vining Canyon. Because each mountain lion could only take a certain number of sheep, the number of lion kills would remain relatively constant.

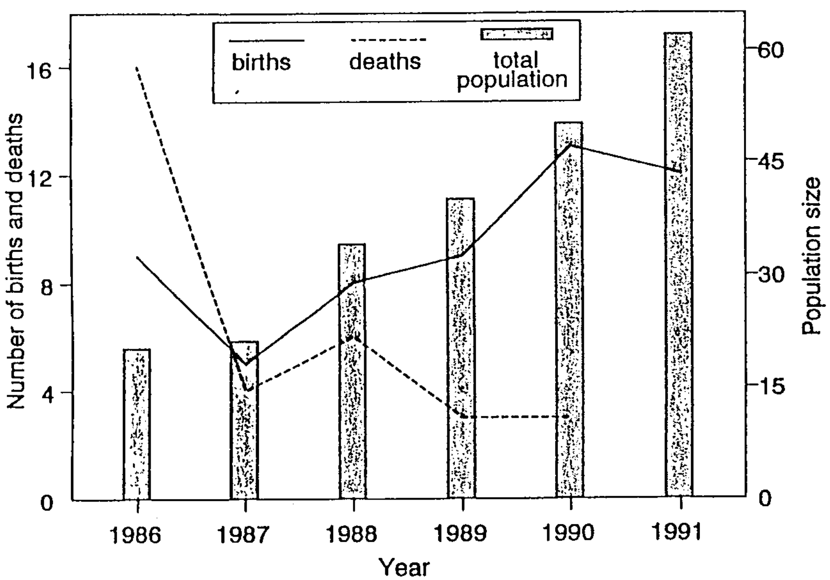

Fig. 7. Population dynamics of 27 bighorn sheep reintroduced to Lee Vining Canyon, Mono County, California, in March 1986. Population sizes represent end-of-year totals. Total population size shown for 1988 includes 11 additional sheep added in March 1988.

The adult sex ratio of 68 rams per 100 ewes was within the range seen in established mountain sheep herds (Streeter 1970; Geist 1971) and was virtually identical to the 67.7:100 observed by Wehausen (1980) at Mount Baxter. The adult sex ratio, however, was largely the product of random selection during the two reintroductions and, thus, is not particularly meaningful.

The mean ratio of yearlings to ewes of 47:100 was 1.5 times greater than the figure McQuivey (1978) deemed necessary for maintaining a stable mountain sheep population in Nevada and exceeded the ratio of 40:100 that Wehausen (1980) felt was indicative of population increase in the Mount Baxter herd. However, age ratios are difficult to interpret or may be misleading (Murphy and Whitten 1976; Caughley 1977) if changes in ratio result from increased adult mortality. Because adult mortality remained relatively constant, we interpreted the shift towards younger age classes in 1990 and 1991 as an increasing trend.

Habitat Suitability

Results of vegetation classification are consistent with previous work on alpine vegetation in the Sierra Nevada. Taylor (1984) described communities corresponding to the *Podistera–Phlox*, *Ribes*, *Artemisia–Monardella*, *Carex–Juncus*, *Trisetum–Trifolium*, and *Deschampsia–Carex* communities found on summer range. He reported the *Podistera–Phlox* community from stable, metamorphic substrates where snow cover was sparse in winter and moisture availability was low during the growing season. Pemble (1970) described a similar association but did not find it limited to metamorphic substrates. He regarded it as the most common association in the Sierra alpine (Pemble 1970:135). This association seemed to be the most common vegetation type within home ranges of ewe–juvenile groups and was used for resting and traveling as well as foraging.

Mesic sites on the Lee Vining Canyon herd summer range varied in species composition and cover. Some mesic sites were misclassified by TWINSPAN as members of the *Podistera–Phlox* community because of the presence of *Festuca ovina*, *Sitanion hystrix*, or *Ribes cereum*, indicator species for xeric communities. Additional sampling, stratified to focus on mesic sites, might provide a more detailed and useful classification of these complex communities. Alternatively, these sites may represent small, poorly developed examples of communities that thrive under more benign conditions and may have been sampled at the extreme of their environmental tolerance. Better developed examples of these communities as described by Pemble (1970) and Taylor (1984) were not observed and may not occur in the study area.

Fifteen of 51 forage sites were misclassified by the linear discriminant function. The forage sites most strongly identified as random sites had sparse vegetative cover, no surface water, and were located far from escape terrain or had low visibility. All forage sites misclassified because of sparse cover, however, contained important forage species.

The *Salix–Carex* and *Deschampsia–Carex* communities were the easiest forage sites to predict (100% correctly classified) because they offered moist conditions, abundant herbaceous cover, and were often near cliffs. Forage sites in the *Ribes* type were correctly classified nearly as often (89% of the time), and forage sites in the *Podistera–Phlox* community were correctly identified 68% of the time. Sites in the *Podistera–Phlox* community probably represent opportunistic foraging strongly influenced by the abundance of that community.

Ewe groups repeatedly visited snowmelt-fed or spring-fed sites. These sites offered the highest vegetative cover and species diversity per unit area. Although these areas were limited in size (typically 10–15 m diameter) and number, repeated use highlights their importance. Higher cover and protracted phenological development at these sites are likely to increase the overall amount of green forage and prolong its availability. Forage moisture content as well as plant nutrient status may be most important during late summer and early fall months when sources of moisture become scarce elsewhere.

Annual patterns of forage quality paralleled those of other California mountain sheep herds (Hebert 1973; Wehausen 1980). The decline in fecal crude protein levels from a high in early summer to lower levels during winter reflects patterns of plant phenology. Pattern alone, however, is insufficient to make conclusions about absolute forage quality. Other considerations necessitate treating apparent fecal protein levels with caution.

Fecal nitrogen concentrations may be elevated when the diet includes a large proportion of species containing phenolic compounds (Mould and Robbins 1981). These species include shrubs and some herbs (Nagy et al. 1964; Swain 1979). These compounds may reduce protein digestibility by complexing with dietary and microbial proteins in the rumen (McLeod 1974). The result is an increased level of fecal protein without a corresponding rise in diet quality. This effect seems to be mitigated when these species contribute less than a third of the diet (Leslie and Starkey 1985). The winter diet of the Lee Vining Canyon herd included up to 60% shrub species. Thus, fecal protein levels during this period may be unreliable and should be interpreted with caution.

Reproductive success is related to body condition in ungulates (Thomas 1982; Saether and Haagenrud 1983). High ratios of lambs to ewes in the herd from 1986 to 1989 indicate forage quality is probably comparable to that available to other rapidly growing populations (Chow 1991). Because of the problems associated with fecal protein as an indirect measure of forage quality, reproduction rate is a more reliable index of overall habitat quality.

Management Implications

Current population size and a steadily increasing growth rate allow the Lee Vining Canyon reintroduction to be labeled a qualified success. However, an analysis of population statistics from 121 herds of mountain sheep showed that those having fewer than 50 animals were extirpated within 50 years (Berger 1990). A similar fate could befall the Lee Vining Canyon herd without some management intervention.

Goodman (1987) modeled the demography of small populations and concluded that long-term persistence required reducing population fluctuations

resulting from environmental variables. Effects of environmental variables can be ameliorated by either manipulating habitat or reducing mortality (Goodman 1987).

At present, habitat analysis and the high rate of lamb production suggest forage resources in Lee Vining Canyon are sufficient for reproduction and survival. Thus, habitat manipulation to increase forage productivity seems unnecessary. Removing shrubs and trees on the winter range, however, would increase visibility and facilitate predator detection by the mountain sheep.

Because forage resources seem adequate, ensuring persistence of the Lee Vining Canyon herd requires lowering mortality to increase its growth rate. A higher growth rate would shorten the herd's period of vulnerability to extirpation from disease, predation, and inbreeding. A larger population would increase the probability of herd survival in the event of a major disease epizootic (Foreyt and Jessup 1982; Foreyt 1989). Greater numbers would also dilute the effects of predation, reduce the potential for inbreeding depression (Skiba and Schmidt 1982; Ralls et al. 1986; Schwartz et al. 1986; Berger 1990), and provide a buffer against extinction from stochastic events.

Predation was the major source of known deaths. Data from the first 3 years of the study indicate that predation can significantly influence the growth rate of a small population. If the goal is to maintain a maximum rate of increase, managers need to consider continuing mountain lion removal from Lee Vining Canyon for several more years. The removal of mountain lions would require monitoring to document its efficacy. Those making the decision must weigh the costs and effectiveness of short-term predator control against the long-term objectives of Sierra Nevada mountain sheep management.

In July 1988, a domestic sheep strayed onto the winter range of the Lee Vining Canyon herd. Luckily, the ewes inhabiting that area had departed 3 weeks earlier. However, the incident underscores the continued concern over catastrophic loss because of disease. The propensity for adult rams to wander long distances (Geist 1971; Wehausen 1980) and presence of grazing allotments within 5 km of Lee Vining Canyon maintain the potential for disease transmission from domestic stock. Disease remains the greatest threat to the long-term survival of the Lee Vining Canyon herd (Foreyt and Jessup 1982; Foreyt 1989), and consideration should be given to reduce or eliminate the threat.

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