COOPERATIVE NATIONAL PARK RESOURCES STUDIES UNIT

University of California at Davis

Institute of Ecology

Davis, California 95616-8576

Stephen D. Veirs, Jr. -- Unit Leader

Charles R. Goldman -- UC Unit Coordinator

Roberta L. Anderson -- Administrative Assistant

Technical Report No. NPS/WRUC/NRTR 92/48

Population Dynamics and Movement Patterns of Bighorn Sheep Reintroduced in the Sierra Nevada, California. By Leslie Stephen Chow.

(A thesis submitted in partial satisfaction of the requirements for the degree of Master of Science in Wildland Resource Science in the Graduate Division of the University of California at Berkeley 1991.)

1992

ACKNOWLEDGEMENTS

To my parents, Jennie and Archie Chow, for their encouragement and support throughout my long tenure as a graduate student.

My sincerest appreciation to Reginald H. Barrett for his patient guidance and advice on not only academic and professional matters, but life as well. Dale R. McCullough and William Z. Lidicker greatly improved this thesis with their insightful comments and editorial skills. I am deeply grateful to Jan van Wagtendonk and David Graber for being project administrators, mentors, and friends.

I owe a special debt of gratitude to my field assistants Kathy Erwin, Larry Ford, Denise Fruitt, Susanne Grube, Bruce Handley, Mead Hargis, Nancy Kehoe, Terry Moore, Richard Perloff, and Michael Smith. This thesis is a testament to their talent, dedication, and hard work. Don Banta's keen eyesight and boundless patience provided valuable data on winter survival and lambing dates. Tina Loo assisted with the tedious task of data entry. Lisa Hanson and Laura Laird produced the Yosemite map. A very special thank you to Peggy Moore, whose suggestions, perseverance, and skill in the field improved every aspect of this study. Her support and encouragement throughout the interminable process of data analysis and writing can never be repaid.

John Wehausen and Lee Anne Ayres generously shared their reprint files and knowledge of mountain sheep ecology. Bob Crabtree provided program PDF-XYZ and answers to my endless questions about home range. Irene Tomasi schooled me in computers and programming. My fellow graduate students, Dave Sterner and Marty Berbach served as sounding boards and sources of ideas. Lois Frisch and Lori Merkle steered me through the maze of University regulations and paperwork.

Members of the Sierra Bighorn Interagency Advisory Group lent their expertise and encouragement from the project's inception. Tina Hargis provided contagious enthusiasm, especially early on when sheep were dying daily. Loren Goehring piloted telemetry flights with reassuring calm and skill.

The generosity of the Richard and Rhoda Goldman Fund and the Sacramento Safari Club set the stage for returning bighorn sheep to Yosemite. This project was funded by the National Park Service, the Yosemite Association, the Yosemite Fund, and McIntyre Stennis Project 4326 of the California Agricultural Experiment Station. The California Department of Fish and Game underwrote the considerable costs of

transplanting sheep, telemetry reconnaissance flights, and predator control. The Student Conservation Association supplied volunteer field assistants for 3 summers. The Inyo National Forest, Mono Ranger District provided an office and a warm, friendly place to hang my hat.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Bighorn sheep (*Ovis canadensis*) were once abundant and widely distributed throughout the western United States. Major dieoffs that coincided with frontier settlement have been attributed to excessive hunting, forage competition, and diseases contracted from domestic sheep. By 1960, it was estimated that population numbers had declined nearly 90% and only 15,000 to 18,200 wild sheep remained (Buechner 1960).

Bighorn numbers have doubled in the past 30 years. Much of this increase has resulted from aggressive reintroduction programs undertaken by wildlife management agencies. Current population estimates for California (*O. c. californiana*) and Rocky Mountain (*O. c. canadensis*) bighorn total 21,800 sheep (Thorne et al. 1985) while desert (*O. c. nelsoni*) bighorn number 16,000 (Weaver 1985). Despite population gains of over 100%, wild sheep have recolonized only a fraction of their original range and many bighorn reintroductions have failed or achieved only moderate success (Coggins 1980, Johnson 1983, Rowland and Schmidt 1981, Smith et al. 1988).

Reintroduction has gained widespread acceptance as a method of establishing, reestablishing or augmenting populations of rare and endangered species. Nearly 700 reintroductions involving a variety of species are conducted annually in North America alone (Griffith et al. 1989). Thriving populations of once threatened pronghorn antelope (Antilocapra americana), white-tailed deer (Odocoileus virginianus), and wild turkey (Meleagris gallopavo) attest to the utility of reintroduction as a wildlife management tool (U.S. Fish and Wildl. Serv. 1987).

Not all reintroductions are successful, however. Failures are subject to intense public scrutiny because significant expenditures and media attention are often associated with a reintroduction. As a result, recent efforts have focused on identifying strategies that maximize a reintroduction's potential for success (Griffith et al. 1989, Kleiman 1989).

Griffith et al. (1989) analyzed the results of 198 recent reintroductions using stepwise logistic regression. They found habitat quality, life history patterns, and initial population size to be the most accurate predictors of a reintroduction's outcome. Reintroductions achieving the greatest success involved wild-caught, native game species translocated into the core of historic ranges. Herbivore reintroductions were more likely to succeed than those of carnivores or omnivores. Griffith et al. (1989) emphasized that a reintroduction's success ultimately depends on identifying and controlling limiting factors.

Studies of bighorn reintroductions have been numerous. Unfortunately, most have been 1) of short duration; usually <2 years, 2) monitored only intermittently or 3) involved few radio collared sheep (Andaloro and Ramey 1981, Berbach 1984, Elenowitz 1983, Hanson 1984). Subsequent information has often been limited to annual censuses. As a result, little is known about the relative affects of various limiting factors on long-term population trends or how transplanted bighorn sheep explore and adapt in a new location.

Because reintroduction is the primary means of reestablishing bighorn populations (Geist 1975, Hansen et al. 1980, Rowland and Schmidt 1981), detailed information on how these populations establish themselves and grow is vital if managers are to refine reintroduction strategies. The translocation of native Sierra Nevada bighorn sheep (O. c. californiana) into Lee Vining Canyon presented the opportunity to initiate a study of factors influencing the outcome of a bighorn reintroduction and assess their relative impacts on the long-term population dynamics of a reintroduced herd.

History and management of Sierra Nevada bighorn sheep

Bighorn sheep originally occupied the Sierra Nevada mountains of California from the Sonora Pass region in the north to Jawbone Canyon on Olancha Peak in the south (Wehausen 1980). They generally summered along the Sierra Nevada crest and wintered at lower elevations on the range's steep eastern scarp (Muir 1894, Riegelhuth 1965, McCullough and Schneegas 1966, Wehausen 1980). Herds in the northern and central Sierra Nevada may have departed the range and wintered in suitable mountainous habitat to the east (Jones 1950, Wehausen 1980).

The decline in Sierra Nevada bighorn sheep numbers began with the influx of gold miners into the range (Wehausen 1988). Wehausen (1980) traced the history of decline and concluded that extirpation had occurred in 2 stages. A period of rapid decline began about 1850 and extended for 3 decades. During that time, many populations were reduced to the status of remnant herds. Overhunting (Grinnell and Storer 1924:243) forage competition with domestic sheep (Dixon 1936), and especially diseases contracted from domestic stock (Jones 1950, Wehausen 1988) have been cited as the major causes of the decline. Subsequently, there was a long period of attrition in which remnant herds gradually dwindled until finally disappearing altogether.

The rapid disappearance of bighorn and other big game throughout the state led the California legislature to institute seasonal hunting restrictions in 1876. This was followed by full protection for bighorn in 1882. Bighorn numbers continued to fall, however, in the absence of sufficient data about factors contributing to their disappearance. Nearly 100 years elapsed between the passage of legislation to protect California's bighorn and the advent of a program to actively manipulate bighorn populations (Wehausen 1987).

In 1971, prompted by Dunaway's (1971) hypothesis citing human disturbance as a limiting factor, the National Forest Service designated 41,000 acres in Inyo National Forest as a bighorn zoological area (Hicks and Elder 1979, Wehausen 1979). The Zoological Area encompassed ranges of the 2 largest remnant herds (Figure 1) and was established to ensure the protection and maintenance of bighorn habitat. Regulations restricting human activities in the Zoological Area also were promulgated in an effort to reduce disturbance (Wehausen 1979). Shortly after the Zoological Area was established, the National Park Service and USDA Forest Service jointly contracted for a study to assess the status of bighorn in the Sierra Nevada.

After conducting an extensive literature review and surveys throughout likely bighorn habitat, Wehausen (1979, 1980) determined that only 2 populations of Sierra Nevada bighorn had survived. He suggested that the existence of 3

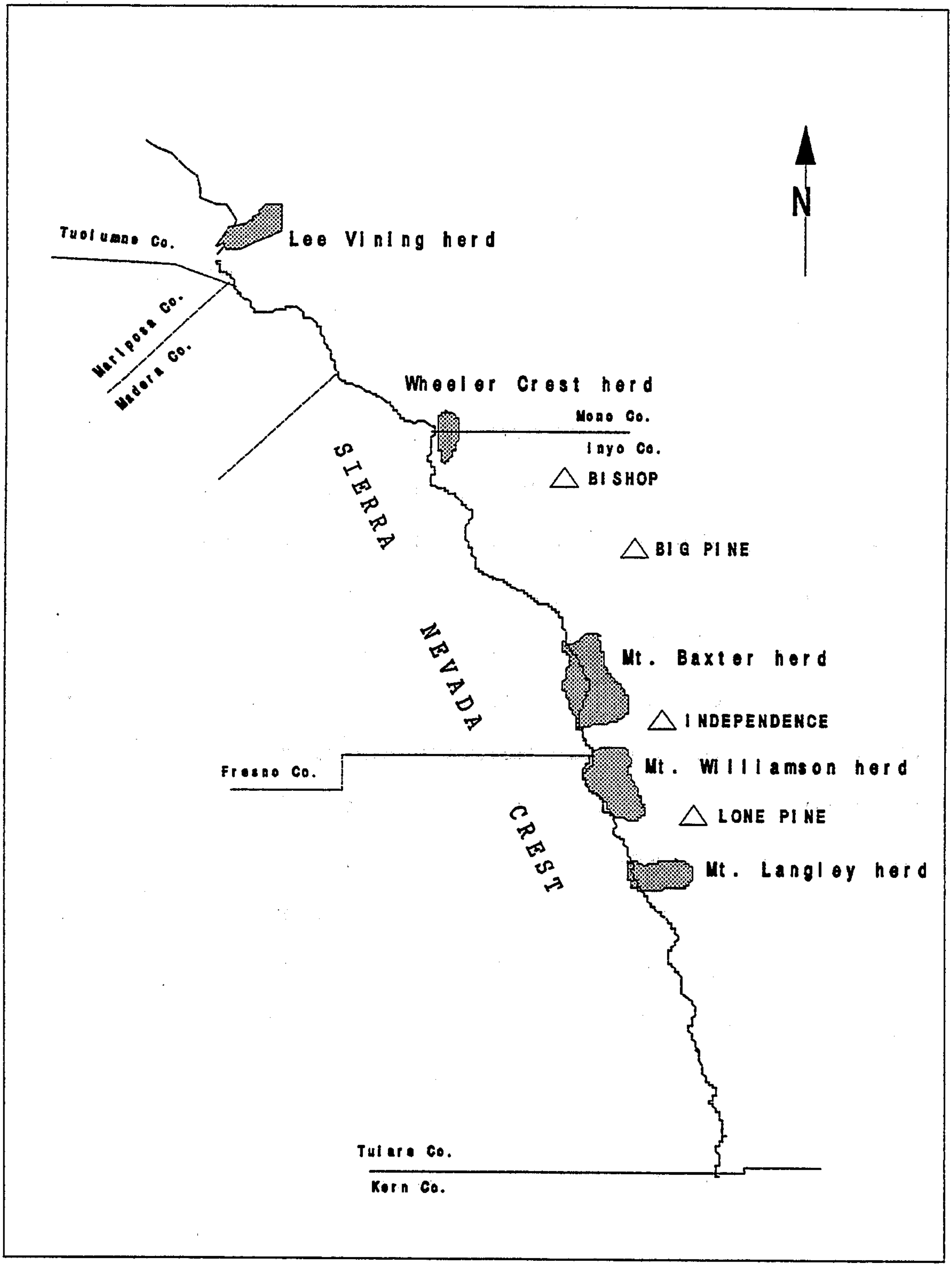


Figure 1. Distribution of Sierra Nevada bighorn sheep in January 1990

additional herds identified in an earlier study conducted by Jones (1950) had been based on questionable evidence and that only the Mt. Baxter and Mt. Williamson herds remained (Figure 1). Wehausen's (1980) analysis of population trends in the surviving herds revealed that the Williamson herd was stable at approximately 30 animals while the herd at Mt. Baxter contained approximately 220 sheep and had been growing for nearly a decade.

Based on the results of his study, Wehausen (1979) developed a series of management alternatives for Sierra Nevada bighorn. Among them was a recommendation that the Mt. Baxter herd serve as a source of transplant stock for restoring bighorn to historic ranges in the Sierra Nevada. In response to Wehausen's recommendations, the California Department of Fish and Game (CDFG) embarked on a reintroduction program in 1979. Another recommendation by Wehausen (1979) stimulated the formation of the Sierra Bighorn Interagency Advisory Group (SBIAG) in 1981 (Keay et al. 1987).

The SBIAG fosters cooperation between federal and state agencies involved with Sierra Nevada bighorn management. Participants include representatives from the CDFG, National Park Service (NPS), USDA Forest Service (USDAFS), Bureau of

Land Management (BLM), and John Wehausen, acting as a private consultant.

In 1984, the Advisory Group produced a management plan subsequently approved by the affected cooperating agencies (Keay et al. 1987). The Sierra Nevada Bighorn Sheep Recovery and Conservation Plan (SBIAG 1984) identified the following management objectives.

- Ensure the future of bighorn sheep in the Sierra Nevada by maintaining the health and viability of all existing populations, and by promoting the establishment of at least 3 populations that are both large (exceeding 100 animals) and geographically distant from one another.

- Restore bighorn sheep to all former ranges within the Sierra Nevada where it is ecologically and politically feasible, and where conditions could be made favorable to their success.

- Ensure genetic integrity of the Sierra Nevada subspecies by using only bighorn from existing Sierra Nevada populations to restock historic ranges.

To achieve these objectives, a program consisting of 4 elements would be implemented. These are: 1) population management, 2) reintroductions, 3) habitat management, and 4) monitoring and research (SBIAG 1984).

As of June 1989, fewer than 350 bighorn remained in the Sierra Nevada. The increase of 100 sheep since 1980 has resulted largely from growth of 2 reintroduced herds. The Sand Mountain and Sawmill Creek herds (formerly considered a single population, the Mt. Baxter herd) are estimated to contain 150 and 40 animals respectively (C. D. Hargis, June 19, 1986 memo to SBIAG, Inyo Natl. For., Lee Vining). The herd at Mt. Williamson is thought to have remained stable at approximately 30 sheep (J. Wehausen, White Mtn. Res. Stn., pers. commun. 1989) while the reintroduced herds at Wheeler Crest and Mt. Langley have grown to nearly 40 sheep each (R. Ramey and L. Brown, unpub. rep. to CDFG, Bishop, 1986, P. Moore and L. Chow, unpub. rep. to Inyo Natl. For., Lone Pine, 1990).

History of bighorn sheep reintroductions in the Sierra Nevada

The Sierra Nevada bighorn sheep reintroduction program was initiated with the translocation of 9 native Sierra Nevada bighorn from Mt. Baxter to Wheeler Crest in 1979 (Andaloro and Ramey 1981). The Wheeler Crest herd was augmented with 10 more animals from Mt. Baxter the following year while 11 sheep were reintroduced to Mt. Langley. During the next 10 years, the Wheeler Crest and Mt. Langley herds (Figure 1) were supplemented with additional sheep at irregular intervals. By April 1988, 27 sheep had been transplanted to Wheeler Crest in 4 separate reintroductions. During the same period, 28 sheep were transplanted to Mt. Langley (Figure 2).

The Wheeler Crest and Mt. Langley reintroductions were monitored from spring 1979 through winter 1980-1981 (Andaloro and Ramey 1981). Information on numbers, range use, and bighorn behavior was collected using radio telemetry, direct observation, reported sightings, and interpretation of sign. Radio telemetry revealed that individual movement patterns of the reintroduced sheep were highly variable and ranged from sedentary to long distance dispersal.

During the first winter, 5 sheep died at Wheeler Crest. Deaths were attributed to avalanches and severe winter weather (Andaloro and Ramey 1981). Two weeks after the 1980 reintroduction, 1 of the newly reintroduced rams at Wheeler was killed by a mountain lion (Felis concolor). During the same period, mountain lion predation also claimed an adult ewe at Mt. Langley. Shortly thereafter, a second ewe in the Langley herd died of unknown causes. All 4 adult ewes reintroduced to Wheeler Crest in 1979 bore lambs. Only 1 of

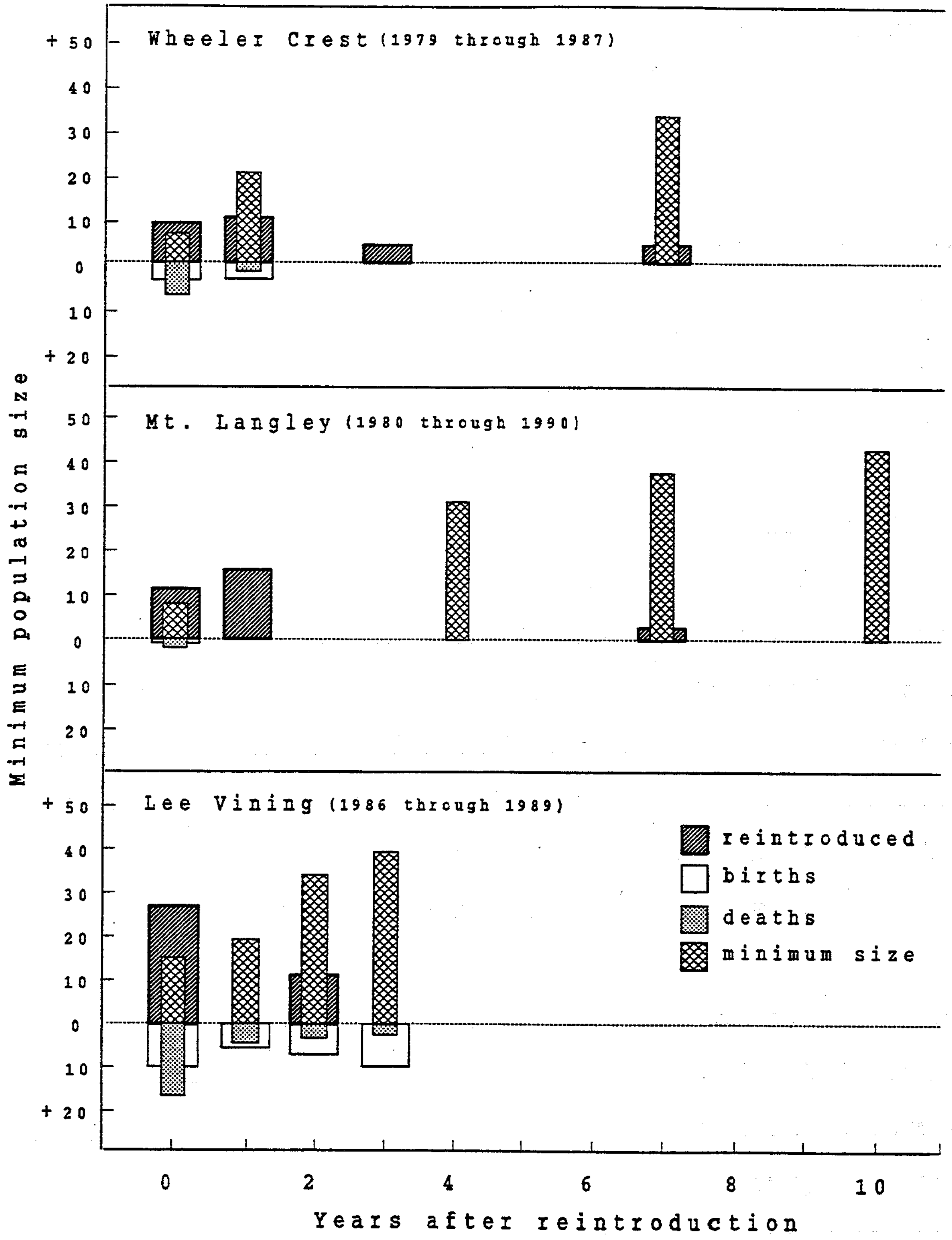


Figure 2. Population growth of Sierra Nevada bighorn sheep herds in the years following reintroduction (note that the scales above and below 0 are both positive)

these survived to the following year. In 1980, 2 of the 3 surviving ewes at Wheeler Crest bore lambs and at least 1 lamb was born at Mt. Langley.

All subsequent information about the status of these herds has been limited to sporadic sightings and infrequent censuses. In the 10 years since reintroduction, the Wheeler Crest herd has been censused once while the Mt. Langley herd has been censused twice.

The Lee Vining Reintroduction

Jones (1950) reported that bighorn were last seen in Yosemite National Park in 1914. However, Wehausen (1980) concluded that Grinnell and Storer (1924) were more likely correct in their belief that most bighorn had disappeared from the area by the early 1880s. Grinnell and Storer (1924:243) attributed the disappearance of Yosemite's bighorn to overhunting by miners and sheep herders.

Historic accounts and the locations of recovered skulls led Jones (1950) to surmise that bighorn in Yosemite had occurred chiefly along the main crest and in the Cathedral Range (Figure 3). It is likely that rams ranged even further west. The location of winter range is unknown. However, Wehausen (1979) speculated that bighorn may have wintered in suitable habitat east of the Sierra Nevada.

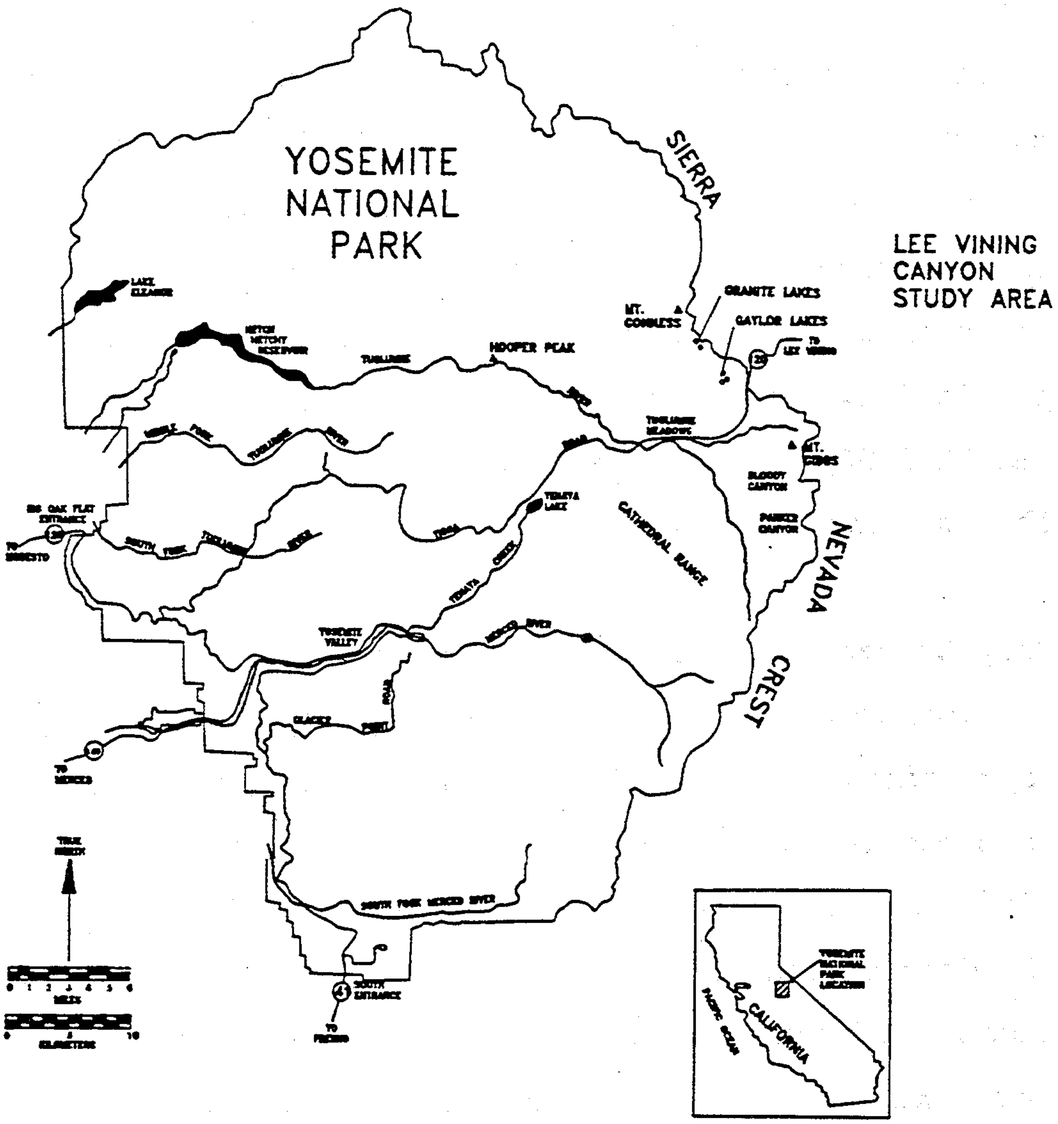


Figure 3. Map of Yosemite National Park showing significant topographic features.

The idea of restoring bighorn to Yosemite gained early support (Blake 1941, 1949). However, biologists believed that natural recolonization was preferable to reintroduction (Wright et al. 1932, Grinnell 1935). A combination of the bighorn's failure to recolonize Yosemite, recognition that bighorn dispersal is limited by their tendency to restrict use to traditional home ranges (Geist 1971:99), and improved capture techniques, set the stage for reintroducing bighorn to Yosemite. The need to establish an another large population, geographically distant from the Mt. Baxter herd (SBIAG 1984), also provided impetus for a reintroduction in the Yosemite region.

Despite occasional reports of bighorn sightings from hikers in Yosemite, Wehausen (1979) found no evidence of any population. He identified Lee Vining Canyon as the best possible reintroduction site in the northern portion of the Sierra Nevada bighorn's original range. Direct access to abundant summer habitat was considered Lee Vining's chief asset. Wehausen cautioned, however, that an assessment of snow conditions was necessary to evaluate Lee Vining Canyon's suitability as winter range.

After winter surveys indicated that Lee Vining Canyon's extensive south facing slopes would remain relatively snow-free (C. D. Hargis, Inyo Nat. For., Lee Vining, unpub.

data), it was selected as the site of the third bighorn reintroduction in the Sierra Nevada. In 1986, the Yosemite Association, with donations from the Richard and Rhoda Goldman Foundation and Sacramento Safari Club, negotiated the abandonment of a domestic sheep grazing allotment in Lee Vining Canyon. This presented an opportunity to restore bighorn to the Yosemite region (Keay et al. 1987).

On 5 and 6 March 1986, CDFG translocated 27 Sierra Nevada bighorn sheep from the Mt. Baxter herd to Lee Vining Canyon, Mono Co., California. The Lee Vining herd was supplemented with 11 more sheep from the Mt. Baxter herd in March 1988 (Table 1).

OBJECTIVES

The goal of this study was to evaluate the outcome of the Lee Vining reintroduction and determine what factors contributed to its success or failure. Specific objectives included: 1) monitoring natality and mortality, 2) investigating exploration and settlement by transplanted bighorn as they established home ranges in an unfamiliar location, and 3) documenting home range and seasonal movement patterns to maximize the efficiency of population censuses once intensive monitoring was terminated.

Table 1. Sex and age distribution of bighorn sheep reintroduced to Lee Vining Canyon in 1986 and 1988.

	Age class (years)										
	0	1	2	3	4	5	6	7	8	9	Total
Rams											
1986	5	4	1			1				1	12
1988			2				1				3
Ewes											
1986	2		2	4	4		1	2			15
1988		1	3		1	1	1		1		8
Total	7	5	8	4	5	2	3	2	1	1	38

STUDY AREA

Topography

The 46-km^2 study area lies in the central Sierra Nevada. It abuts the eastern edge of Yosemite National Park along the Sierra Nevada crest and is bounded on the north by Mill Creek in Lundy Canyon and on the south by Lee Vining Creek (Figure 4). Elevation ranges from 2,188 m at the eastern end of Lee Vining Canyon to 3,758 m atop the summit of Mt. Warren. Extensive topographic relief results from 5 tributary drainages that deeply dissect a central plateau.

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 5 glacial sequences, the last ending 10,000 to 15,000 years ago (Blackwelder 1931, Sharp and Birman 1963). Substrates on the eastern half of the study area are primarily granitic while those to the west, along Tioga Crest, are metasedimentary of Paleozoic origin (Kistler 1966, Bateman et al. 1983). With few exceptions, soils are shallow and poorly developed.

The most distinctive topographic features of the study area are 2 broad, parallel ridges known locally as Warren Bench and Tioga Crest. Each extends 8 km, north to south. Between them lie Warren Fork and Lake Canyons, both

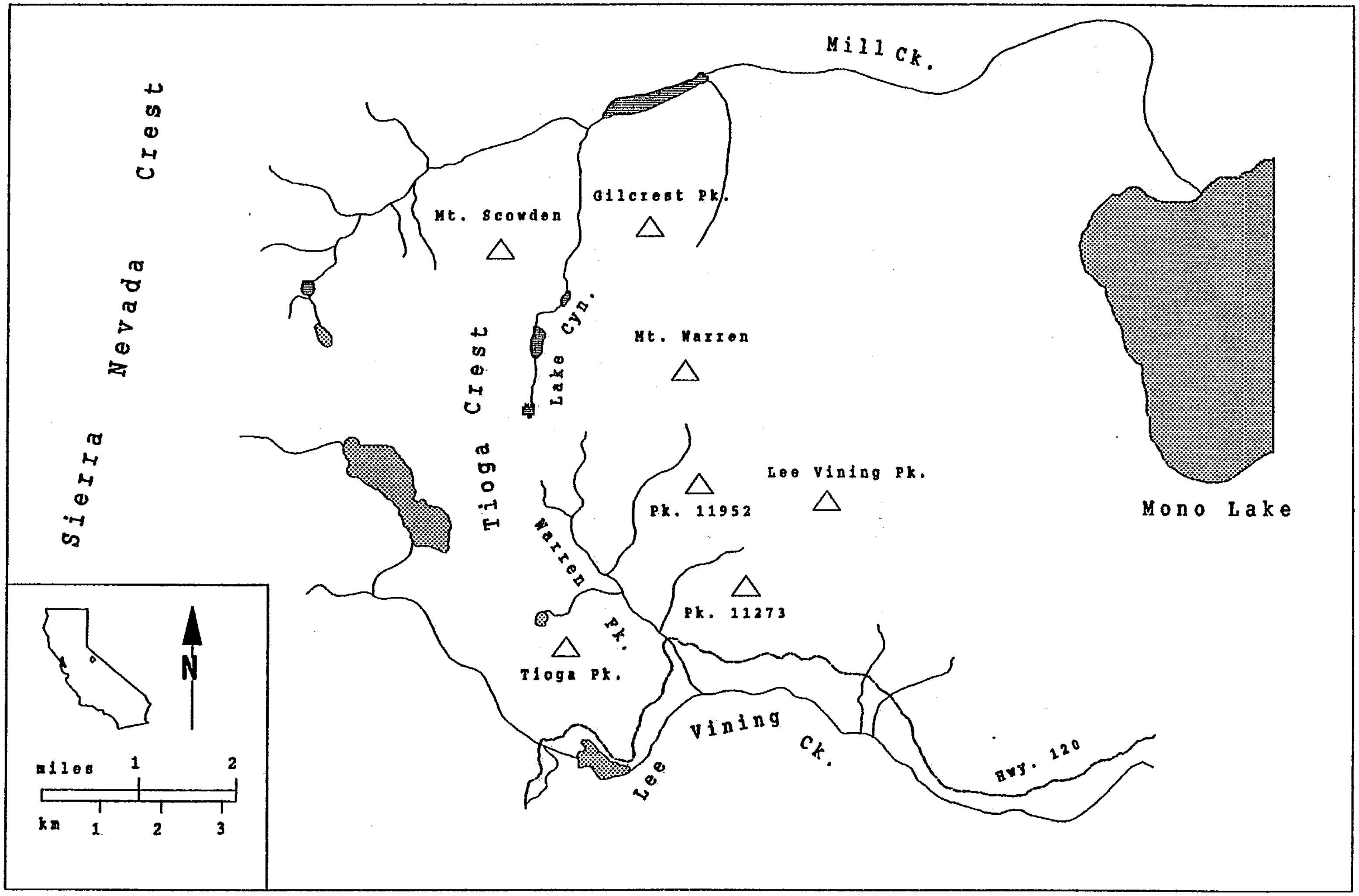


Figure 4. Map of Lee Vining bighorn sheep reintroduction study area showing significant topographic features

approximately 0.75 km wide. Warren Bench and Tioga Crest are joined by a narrow, rocky ridge, hereafter called Lake Warren divide, which separates the heads of Warren Fork and Lake Canyons.

Lands in the study area are managed by the USDAFS as parts of the Inyo National Forest, Hoover Wilderness, and the Harvey Monroe Hall Natural Area. Lands west of the Sierra Nevada crest fall under the jurisdiction of Yosemite National Park. The only significant human development in Lee Vining Canyon is the Tioga Road (State Highway 120). Tioga Road winds along the north side of Lee Vining Canyon and is a major corridor across the Sierra Nevada. The 2-lane highway is usually open to traffic from early June to late November.

Climate

The study area 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 at Ellery Lake (2902 m), the nearest source of long-term weather data, range between 20 C and 1 C in summer ($\bar{X}$ = 13 C) and 2 C and -12 C ($\bar{X}$ = -5 C) during winter. Annual precipitation averages 76 cm per year and is deposited primarily as snow falling between November and April. Additional moisture from occasional summer thundershowers is generally scant (Major 1977) but may be important in prolonging the growing season.

Distribution of snowfall on the study area is highly variable due to the proximity of the lofty Sierra Nevada crest. High winds accompanying winter storms combine with local topography to create a mosaic of deep drifts and snow free patches. Even more significant is the rainshadow produced by the Sierra Nevada crest as it wrings moisture from passing storms (Major 1977). The result is a steep precipitation gradient in which storms can deposit 50 cm of snow at the upper end of Lee Vining Canyon and leave only 5 cm at its mouth.

Vegetation

Low elevations (2,180-2,590 m) used by bighorn 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) dominated by *Pinus monophylla*, *Artemisia tridentata*, *Purshia tridentata*, *Chrysothamnus nauseosus*, *Ceanothus cordulatus*, and *Tetradymia canescens*. Understory dominants include *Eriogonum wrightii*, *E. umbellatum*, *Penstemon bridgesii*, and several native and introduced grasses. Adjacent rock outcrops and talus slopes are dominated by an overstory of

Cercocarpus ledifolius. Understory vegetation in these areas is generally sparse owing to the impenetrable canopy.

Summer ranges include 2 distinct plant communities, subalpine forest and alpine (Major and Taylor 1977, Benson 1988). These areas extend in elevation from 3,232 m to 3,437 m. Forested areas are dominated by *Pinus albicaulis* in both tree and krummholz forms. Understory dominants include *Phyllodoce breweri*, *Carex spp*., and perennial grasses. Adjacent alpine (Major and Taylor 1977) areas display localized, patchy vegetation distributions that include *Calamagrostis breweri*, *Carex breweri*, *C. exserta*, *Potentilla breweri*, *Eriogonum incanum*, and *Chrysothamnus monocephalus*.

METHODS

Fieldwork was conducted between 5 March 1986 and 6 September 1989 with help from seasonal field assistants. The California Department of Fish and Game marked all reintroduced sheep with uniquely numbered metal and vinyl ear tags at the time of capture. Standard physical measurements were collected and ages estimated using horn segment counts (Geist 1966). Radio transmitter collars (Telonics Inc., Mesa, AZ) equipped with mortality sensors were installed on 36 of the 38 transplanted sheep.

Home range and movements

A Telonics TR2/TS1-receiver/scanner (164-165 Mhz) and a 2-element, H-type, hand held, directional antenna were used to obtain locations for each radio-collared sheep. During the first 2 years of the study, sheep were located 5 to 7 times weekly during summer and 4 days a week in winter. Thereafter, sheep were located 4 to 5 times a week. At approximately semi-monthly intervals, aerial telemetry flights in a Cessna 185 equipped with strut-mounted antennas allowed location of sheep whose signals could not be received from the ground. Sheep locations were plotted on 15-min USGS topographic maps and recorded as Universal Transverse Mercator grid coordinates (UTMs) to the nearest 100 m.

I attempted to stratify sampling by time of day to avoid bias resulting from periodicity in sheep movements (Garshelis 1983). On several occasions I monitored movements at night. In the absence of location changes discernable by triangulation, movement was inferred from strong fluctuations in signal strength. Nocturnal monitoring indicated that movements were infrequent or inconsequential: thus I subsequently restricted telemetry to daylight hours.

Several authors have stressed the necessity for independence between locations when using telemetry data to estimate home range size (Dunn and Gipson 1977, Swihart and Slade 1985a, b). I considered locations separated by 8 hours to be independent based on my observations of a sheep's ability to move between any 2 points on the study area within this time period.

Whenever possible, radio telemetry locations were confirmed by visual observations. In addition to noting location, I recorded information on behavior, social status and characteristics of the habitat used. The majority of telemetry locations were determined by triangulation from several points around the study area. However, access and sheep location occasionally combined to render triangulation infeasible. In those cases, location estimates were based on signal characteristics and familiarity with signal behavior in the topography of the study area. Although I was unable to quantify my margin of error, high concordance between locations obtained by this method and subsequent sightings provided evidence for reliability within the conclusions reached in this study. Locations that were ambiguous or unclear because of inability to triangulate were excluded from home range calculations and used only to detect movements between widely separated areas.

Laundré and Keller (1984) warned of possible bias resulting from failure to consider seasonal distribution patterns in home range analyses. Bighorn sheep typically migrate between spatially separated summer and winter ranges and may occupy as many as 7 seasonal ranges annually (Geist 1971). However, the constraint of maintaining a sample size adequate for analysis necessitated dividing the year into only 2 periods corresponding to the occupation of low and high elevation ranges.

I designated 16 November to 26 June as Winter-Spring. This period coincided with sheep movement to lower elevations used as winter range, the departure for lambing areas, and subsequent occupation of mid-elevation spring range. Summer-Autumn extended from 27 June to 15 November when sheep resided at high elevations (≥3200 m). Because the designation of these periods is subjective, some overlap between seasons is possible, especially if distributional shifts are gradual (Geist 1971, Hanson 1984).

I analyzed telemetry data by season and year for all individuals using the computer program HOMERANGE (Ackerman et al. 1989). The 100% minimum convex polygon (MCP) method (Hayne 1949) was used to delineate home range (Burt 1943) boundaries and estimate home range area. Although the MCP method has shortcomings (Van Winkle 1975, Schoener 1981, Worton 1987), it was deemed suitable for documenting the extent of movements around the study area and providing a means of comparison with other studies using the same method.

Because MCP estimates of home range size are highly inflated by outliers (Van Winkle 1975, Schoener 1981), I excluded exploratory movements from analysis. Movements were interpreted as exploratory if they extended outside previously established home range boundaries by >5 km and either were used less than 1 week or were not revisited.

When sample sizes were adequate (≥80), I also examined location data using the home range program PDF-XYZ 1.0 (Appendix A). The PDF-XYZ program is used in conjunction with a graphics program, SURFER (Golden Software, Inc., Golden, CO), to describe the extent and intensity of an animal's space use.

Program PDF-XYZ calculates a utilization distribution (UD) (Van Winkle 1975) based on a set of animal relocations. The UD is defined as a probability density function with an underlying probability of 1.0 (Crabtree 1988). Values for the UD are determined using a modified grid cell method (Rongstad and Tester 1969). Grid cell probabilities or "z" values are calculated by dividing the number of relocations in a cell by the total number of relocations. The magnitude of a given "z" point is the probability of locating an animal at the corresponding x,y coordinates.

SURFER smooths the UD grid cell values using a nearest neighbor routine that weights values of the nearest 16 cells by the inverse of their distances. Other modules in the program generate maps showing probability contours. Probability contours on home range maps correspond to elevation contours on a topographic map and indicate the likelihood of finding an animal along that contour line. Successive interior contours indicate increased probabilities. Home range area in km^2 was estimated by calculating the area within the 0.001 probability contour.

Because the distribution of individual home range sizes did not meet the assumptions of normality and equal variance, I used nonparametric tests for statistical analyses. I compared within-year differences in home range size using sign tests. Differences in home range size between years were compared using Dunn's test for multiple comparisons (Zar 1984:201).

Estimates of group size were based primarily on visual observations although I also used radio telemetry observations when signal characteristics clearly indicated that sheep were in close proximity to one another.

Population dynamics

I monitored recruitment and survival by conducting complete censuses approximately every 10 days in summer and semi-monthly during winter. Censuses entailed visiting areas of use and counting the sheep. I attempted to see all collared sheep at least once during each census period. I secured visual observations of collared sheep by initially using radio telemetry to delimit a search area. That area was then examined using 10x25 binoculars or a 15-45x spotting scope until sheep were visually located.

After locating the sheep, I recorded the identities of all tagged animals present and attempted to classify all uncollared individuals in the group by sex and age. Sex of uncollared sheep was determined by physical attributes (Geist 1971:277) or urination posture in the case of lambs. Ages of uncollared sheep were determined by either obvious size differences between age classes or horn segment counts (Geist 1966). Birth dates of sheep were standardized to 1 May, the approximate midpoint of the lambing period for Sierra Nevada bighorn (Wehausen 1980). Sheep <1-year-old were considered lambs. Sheep between 1 and 2-years-old were classified as yearlings while those between 2 and 3 years of age were considered subadults. Adults were all sheep ≥3 years old.

Reproduction was documented by intensively monitoring ewe locations from the second week in April through the third week in July. During this time, I concentrated on repeatedly obtaining visual observations of all adult ewes in the herd. When a ewe was first seen accompanied by a lamb, I estimated the lamb's age based on physical and behavioral characteristics (Hansen 1965). Individual lambing dates were calculated by subtracting the lamb's estimated age from the date when it was first observed. Lamb:ewe ratios were expressed as the number of lambs per 100 adult ewes (≥2 years old).

Lambs and yearlings generally remain with natal bands until dispersal as 2-year-olds (Blood 1963, Geist 1971, Wehausen 1980). The dispersal of subadults from natal bands largely results from a tendency to follow other adults (Geist 1971:108-110). Thus I was able to document the survival of uncollared sheep by visually censusing all collared sheep. I considered dispersal to be a minor factor in the disappearance of uncollared sheep and assumed that an uncollared sheep had died if it was not seen for a 6-month period.

The absence of definitive markings on sheep born in Lee Vining Canyon and the dynamic nature of band membership made recognition of individual untagged sheep unreliable. Therefore, I calculated the survivorship of uncollared sheep on a cohort basis.

Besides providing information about sheep locations, telemetry also enabled me to detect mortalities of collared animals. Mortality sensors activated after a radio collar remained stationary for 6 hours. When a mortality signal was detected, the collar and its associated animal were normally located within 24 hours. Once the carcass was found, a necropsy was performed to determine cause of death. Cause of death could not be determined for uncollared animals due to the unlikelihood of finding those carcasses.

Most necropsies were conducted in the field and entailed examining a carcass for evidence of nutritional stress, disease, and parasites. I assessed nutritional status by visually estimating the amount of subcutaneous and visceral fat present and by examining femur bone marrow (Kirkpatrick 1980). Internal and external organs were inspected for lesions, swelling, discoloration, parasites, or other abnormalities. I examined muscle tissue in animals that died shortly after being reintroduced for evidence of capture myopathy (Spraker 1976).

I attributed cause of death to mountain lion predation in cases where the carcass had been buried and lion sign was found nearby or if marks on the carcass were diagnostic of lion kills. Diagnostic marks included punctures in the skull, crushed cervical or thoracic vertebrae, and lacerations in the pelage (Shaw 1983:12).

The annual increase by the herd was calculated using the formula

$$(N_{t+1} - N_t) \ / \ N_t \qquad (1)$$

where N_t was the number of individuals at time t and N_{t+1} was the number of individuals at time t+1 in increments of years. The annual mortality rate was calculated by dividing the number of sheep dying (N_d) in time period t by the sum of N_t and N_b, the number of births during time t. The rate of increase (r) by the herd was calculated using the formula

$$N_t = N_o e^{rt} \qquad (2)$$

where N_o was the number of sheep present at the beginning of time t (Caughley 1977). I constructed a composite life table (Downing 1980) based on 3 years of observed annual mortality. Due to the low number of individuals in some age classes, I grouped ages into 4 categories consisting of lambs, 1 and 2 year olds, 3 and 4 year olds, and sheep ≥5 years old.

Population Modeling

I modeled the Lee Vining herd's growth over a 50-year period using the computer program, RAMAS/a (Appendix C). My primary purpose was to evaluate RAMAS/a's utility for modeling bighorn sheep population dynamics. I also used modeling to explore the relationships between population growth and varying rates of predation, fecundity, and survival.

RAMAS/a allowed me to specify adult sex ratios and age-specific fecundity and survival. I derived these values from a survey of the literature (Woodgerd 1964, Bradley and Baker 1967, Hansen 1967, Murphy and Whitten 1976, Simmons et al. 1984, Festa-Bianchet 1988a, b) and compared them to those observed in this study. RAMAS/a also permitted me to designate other mortality. I used this feature to incorporate increases in the predation rate.

I compared population growth over 50 years for 9 different combinations of varying predation, fecundity, and survival rates with 250 replications for each combination. RAMAS/a output included estimates of minimum, maximum, and mean population size for each year of the simulation. Initial population size and age distribution were those of the Lee Vining herd at the end of this study (Table 2). Predation rates used in modeling were the observed mean value and 5%

Table 2. Sex and age distribution of bighorn sheep in Lee Vining Canyon on 6 September 1989.

	Age class (years)												
	0	1	2	3	4	5	6	7	8	9	10	11	Total
Lee Vining Canyon													
Males				3	2	3	1		1				10
Females		3	3	2	3		1	4	2	1			19
Unknown	7	1											8
Bloody Canyon													
Females				1					1			1	3
Unknown		1											1
Total	7	5	3	6	5	3	2	4	4	1		1	41

and 10% increases above that. I altered fecundity and survival rates by specifying coefficients of variation for these parameters at 0.5 and 2 times the observed levels. Specifying coefficients of variation provided stochasticity in the model. Density effects were incorporated using a reverse logistic function (Spanier and Oldham 1987) of the form:

$$y = a - \frac{a}{1 + b^{-cx}} \qquad (3)$$

where Y was the number of lambs surviving in a herd of X number of sheep. The values 1.060, 16.0, and 0.070 replaced function parameters a, b, and c, which specified the origin, slope, and shape, respectively, of the curve. I established a hypothetical carrying capacity of 100 animals.

RESULTS

HOME RANGE

Home range analysis was based on 17,076 sheep relocations. Of these, 72% were telemetry locations (n = 12,351). The remainder were visual observations (n = 4,725). Individual ewes from the 1986 reintroduction, that remained in Lee Vining Canyon and survived to the end of the study (n = 5), were relocated an average of 628 times (SD = 67.7). Individual rams averaged 515 (SD = 29.5) relocations. The average number of relocations for all sheep was almost evenly divided between the summer-autumn (n = 289) and winter-spring (n = 287) seasons for both sexes.

In 1986 and 1987, individual sheep were relocated between 155 and 230 ($\bar{X} = 189$; SD = 24.2) times a year. The number of individual relocations decreased in subsequent years as radio telemetry collars installed in 1986 ceased functioning and the study's emphasis shifted to habitat analysis. Thus, only relocation data from summer-autumn 1986 through winter-spring 1988 provided sample sizes adequate for home range analysis using program PDF-XYZ.

Home range and movement patterns 1986

Sheep in the 1986 reintroduction were released in two groups (n = 14, 13) on successive days (5, 6 March). Members of the first group immediately sought refuge in cliffs directly north of the release site (Figure 5). Those released on the second day fled west along Tioga Road for 3 km before entering cliffs in upper Lee Vining Canyon.

For the first 3 weeks following the reintroduction, a series of severe winter storms swept the area. Between storms, bands of 2 to 4 sheep descended to lower elevations (2285 m). By 1 April, the bands had coalesced to form a loosely knit herd that established a 1986 winter-spring range at the mouth of Lee Vining Canyon, approximately 1.2

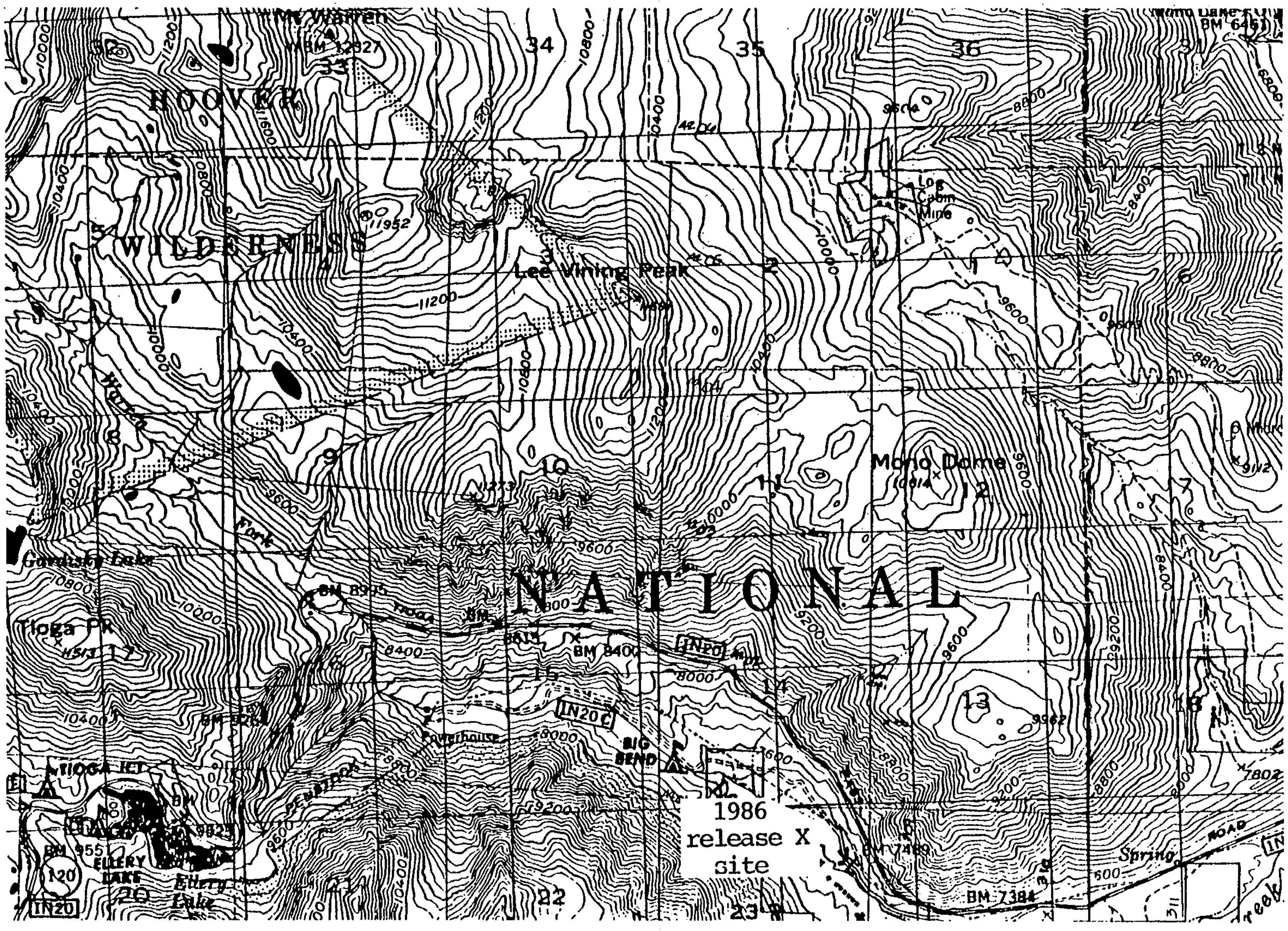


Figure 5. Topographic map of Lee Vining Canyon showing significant features and location of 1986 release site.

km east of the release site (Figure 5) . Individual winter-spring home range sizes for ewes and rams varied from 1.4 km^2 to 15.7 km^2 and 2.9 km^2 to 50.4 km^2, respectively (Table 3).

During early spring, herd movements largely consisted of short sallies between cliffs used for bedding and the adjacent sagebrush covered hillsides where they foraged. In mid-April, individual ewes moved to lambing areas at higher elevations but rejoined the main herd on winter-spring range after parturition. The conclusion of lambing in mid-May was followed by gradual westward expansion of winter-spring range. Soon after range expansion ceased in early June, a minor distributional shift occurred as lamb-ewe bands gathered along the western edge of winter-spring range.

Ewe migration to summer range was abrupt. On the morning of 25 June 1986, ewes 4361 and 4451 departed spring range and walked 2 km west, to upper Lee Vining Canyon. They rejoined the main herd on spring range at 1400 hr that afternoon and after 10 minutes of milling about, returned to upper Lee Vining Canyon followed by 7 ewes, a yearling ram, and 7 lambs. Their route closely paralleled Tioga Road and by nightfall, the band had reached cliffs at the base of Peak 11273 (Figure 5). During the next week, the bighorn ascended the peak's south face following a complex gully

Table 3. Estimates of bighorn home range size (km^2) in Lee Vining Canyon using the minimum convex polygon method.

	Winter-spring						Summer-autumn					
	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*	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

* denote significant differences between years in home range size at $P < 0.05$ level using Dunn's test (Sokal and Rholf 1981).

system to subalpine meadows that served as summer-autumn range.

Rams departed winter-spring range in mid-May. They quickly moved up Lee Vining Canyon to Peak 11273 before continuing west. By mid-June, 2 of them had reached Hooper Peak in Yosemite National Park (Figure 3). On 14 July, both rams returned to Peak 11273 where they rejoined the main herd.

The Lee Vining herd's 1986 summer-autumn range (Figure 6) was utilized from early July through late October and lay within 2.5 km of the release site. Individual home ranges centered around 2 sites. I designated these core areas. Distance between the core areas was 1.5 km and entailed a 640 m elevation difference. The lower site (2620 m) was a 200 m stretch of road embankment along the Tioga Road. Sheep came here to eat soil. The upper site (3260 m) extended from the summit of Peak 11273 to subalpine meadows fringing its north and east slopes and was primarily used for bedding and foraging. Movements between the 2 sites resulted in the establishment of regularly used travel corridors.

A series of mild storms in September and October produced repeated movements between the core areas. As autumn progressed, sheep gradually abandoned subalpine meadows for

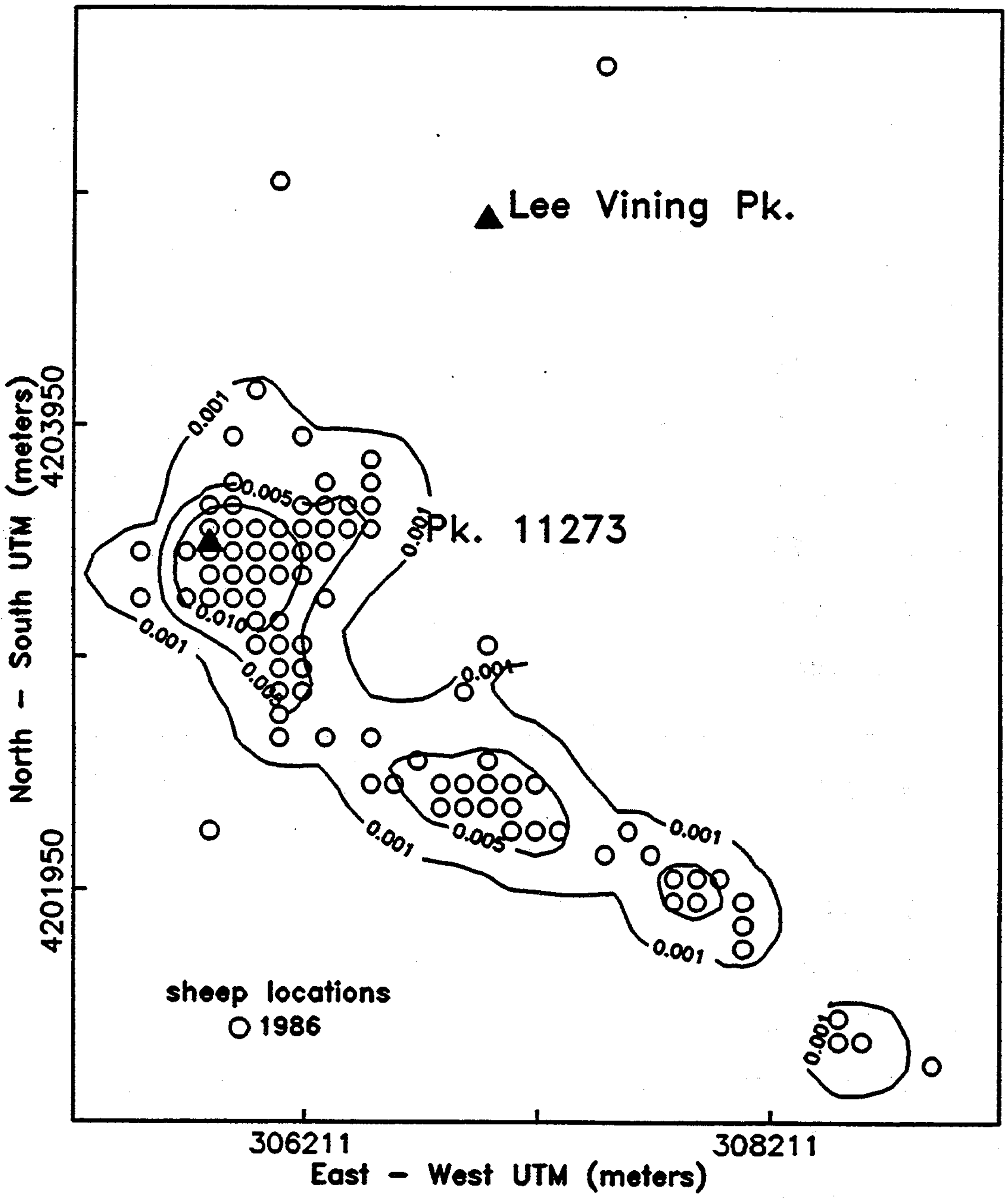


Figure 6. 1986 summer-fall home range used by bighorn ewe 4411 in Lee Vining Canyon, Mono Co., Calif.

talus slopes on the southwest side of Peak 11273. Autumn movements also included forays to previously unvisited areas. On 2 occasions, the herd suddenly moved 6 km north to the vicinity of Mt. Warren (Figure 4) but returned to the summer-autumn range after only 2 or 3 days.

The sizes of individual, summer-autumn home ranges derived from the minimum convex polygon method varied from 5.7 km^2 to 16.6 km^2 for ewes and 8.8 km^2 to 19.5 km^2 for rams. Home range size calculated by PDF-XYZ varied from 1.9 km^2 to 8.2 km^2 ($\bar{X} = 3.6$, SD = 1.72, n = 12) and 2.2 km^2 to 4.2 km^2 ($\bar{X} = 3.4$, SD = 0.76, n = 5) for ewes and rams, respectively. Average home range size did not differ between sexes for either method. The average 1986 summer-autumn home range size calculated by either method was significantly smaller ($P < 0.05$) than those used in subsequent years (Table 3).

Although the movements described above represent the general pattern followed by most herd members, there was also considerable variation among individuals. Ram 4841 and ewe 4451 never moved to lower elevations after being released on the second day. Ram 4841 wintered high on Peak 11273 while ewe 4451 stayed midway up Lee Vining Canyon. In another case, ewe 4411 did not return to winter range after lambing and remained in upper Lee Vining Canyon instead. Other exceptions were ewes 4381, 4371, and 4371's lamb, all of whom, failed to migrate to summer range. The 3 sheep confined their movements to the 1986 winter-spring range (Figure 7) until early September when 4371 was killed by a mountain lion. Within a week, 4381, accompanied by 4371's lamb, had joined the main herd atop Peak 11273.

A more notable variation was the previously mentioned excursion to Yosemite National Park by rams 4421 and 4851 in early June. On 11 May, these sheep departed winter range with ram 4791 and moved 3.5 km up Lee Vining Canyon to Peak 11273. On 27 May, I observed 4421 and 4851 crossing Warren Fork Canyon (4791 returned to Peak 11273 when I accidentally interrupted his progress). I followed them on 29 May as they traversed the length of Tioga Crest. By mid-June, 4421 and 4851 had moved to Hooper Peak (Figure 3), 19 km west of the release site.

The most radical deviation from the general pattern of movement was the dispersal by ewes 4351, 4391, 4781, and 2 lambs to Bloody Canyon (Figure 3), 13 km south of Lee Vining Canyon, in October 1986. This band established residence there and has remained isolated from the main herd. They wintered on the south side of Mt. Gibbs, where telemetry flights invariably located them at elevations exceeding 3,100 m.

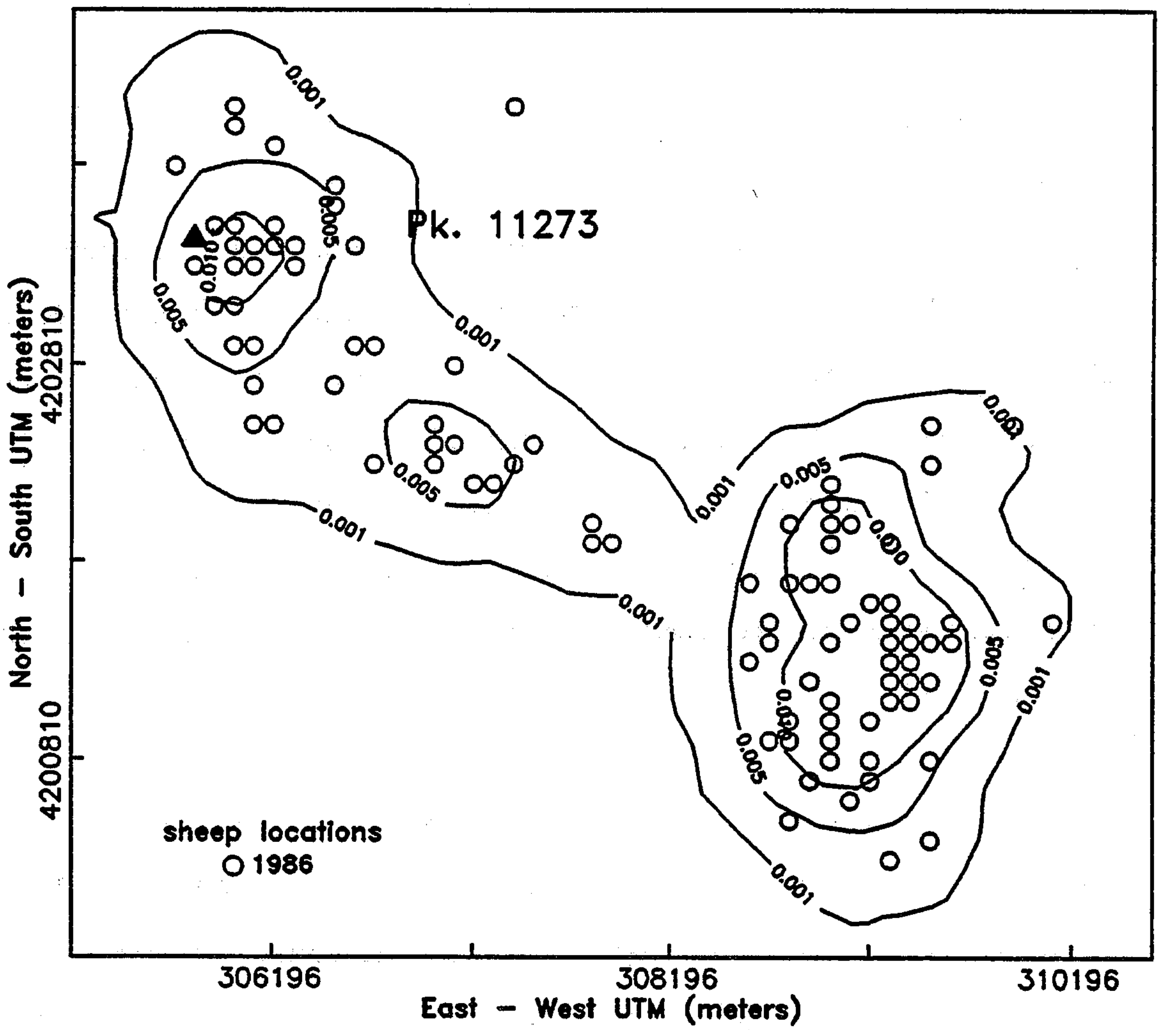


Figure 7. 1986 summer–fall home range of bighorn ewe 4381 in Lee Vining Canyon, Mono Co., Calif.

Home range and movement patterns 1987

Members of the Lee Vining herd began moving to lower elevations following the first major storm in late November 1986. They established a 1987 winter range on the brushy hillsides bordering embankments along Tioga Road (Figure 8). Although some individuals occasionally returned to the 1986 winter range near the mouth of Lee Vining Canyon, the majority of activities in winter of 1987 were concentrated approximately 2 km further west. Ram winter ranges during 1987 appeared to be larger than those of ewes although an inadequate sample size prevented statistical comparisons. During winter 1987, bands were significantly smaller ($P \leq 0.05$) than those of the previous year.

Departure from winter range in mid-April 1987, was initiated by ewes as they moved to lambing areas on the south face of Peak 11273. The remainder of the herd, 5 rams, a ewe, and 4 yearlings, gradually joined them during the next month. Soon after lambing, ewes formed nursery bands and confined their movements to the immediate vicinity of Peak 11273 until late June.

As in 1986, ewe migration to summer ranges was sudden and swift. On 30 June 1987, ewes 4411 and 4601 and their lambs departed spring range heading north. By 7 July they had moved to the vicinity of Gilcrest Peak, 6 km north of Lee

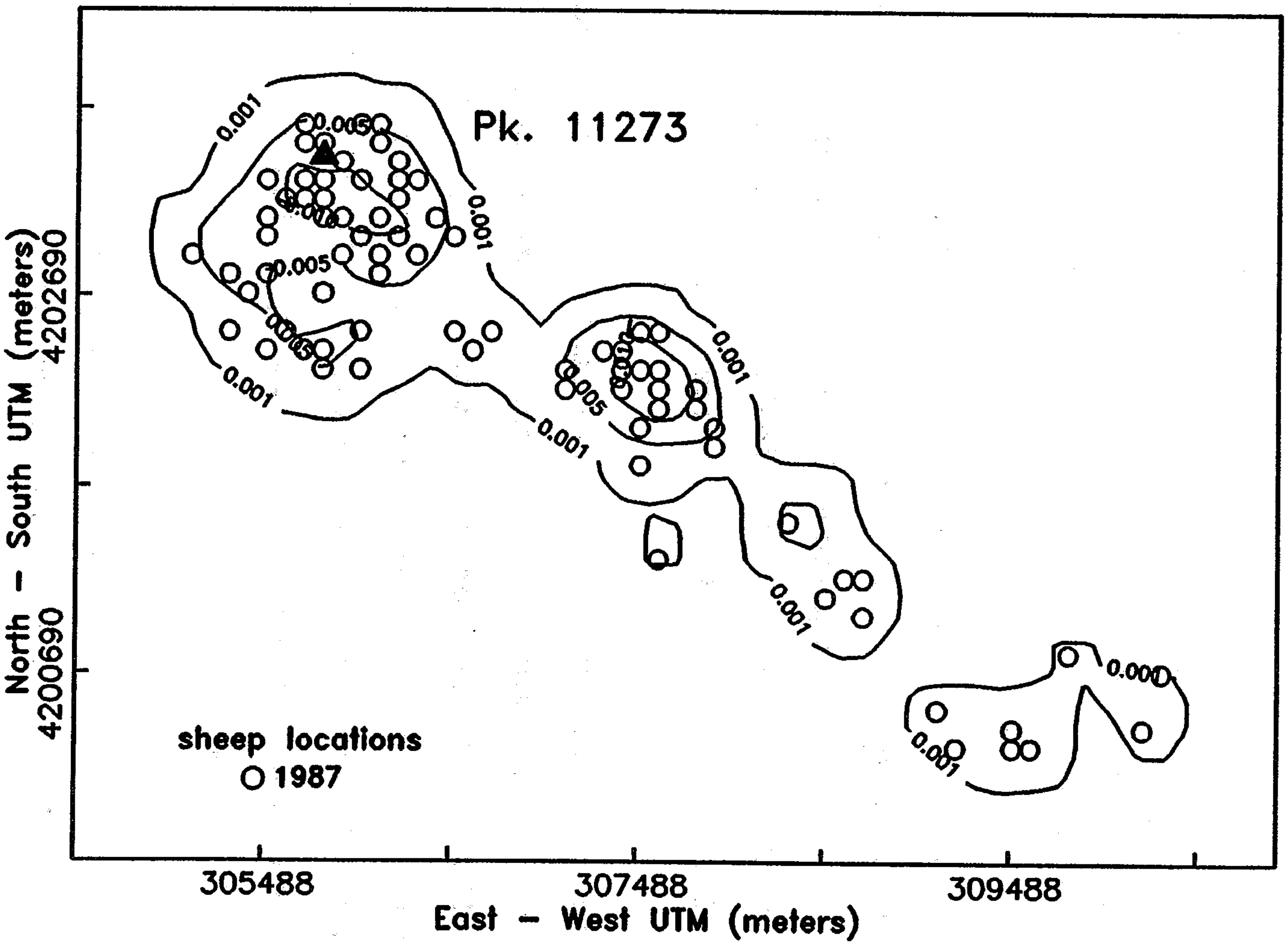


Figure 8. 1987 winter–spring home range used by bighorn ewe 4411 in Lee Vining Canyon, Mono Co., Calif.

Vining Canyon. During the next 7 weeks, the band utilized the steep gullies and shattered ridges on the north and west sides of the peak (Figure 9).

On 6 July 1987, rams 4421 and 4851, accompanied by ewe 4381 and her lamb, also departed spring range and moved northwest, across Warren Fork Canyon, to Tioga Crest. The band meandered north for 3 days until reaching Mt. Scowden, 8 km northwest of Lee Vining Canyon. Telemetry indicated that the band moved around Mt. Scowden before fragmenting in mid-July. Ewe 4381 and her lamb remained on Mt. Scowden until late August, confining their movements to the convoluted northwest side of the peak (Figure 10). The rams traveled more extensively until late July when they joined rams (4791, 4841) who had moved from Peak 11273 to Tioga Crest in late May.

Not all ewes established new summer ranges. Ewes 4451, 4731, 4801, and 2 lambs remained near Peak 11273 which had served as the herd's summer range in 1986. The center of their activities shifted, however, from the east side of Peak 11273 to the labyrinthine gully system on the peak's south face (Figure 11). The mineral lick along Tioga Road again received repeated use as the sheep frequently moved between the 2 areas.

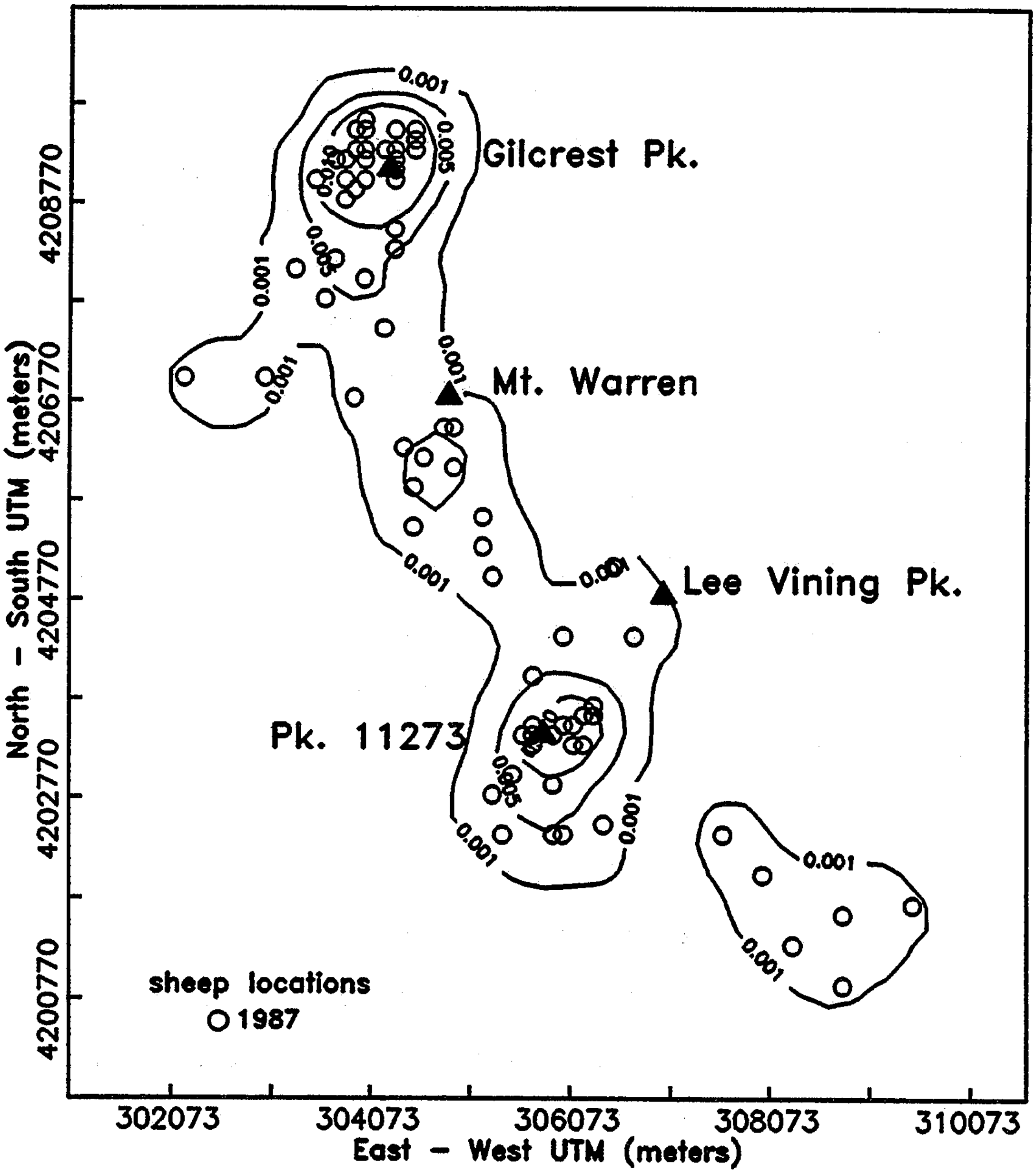


Figure 9. 1987 summer-fall home range used by bighorn ewe 4411 in Lee Vining Canyon, Mono, Co., Calif.

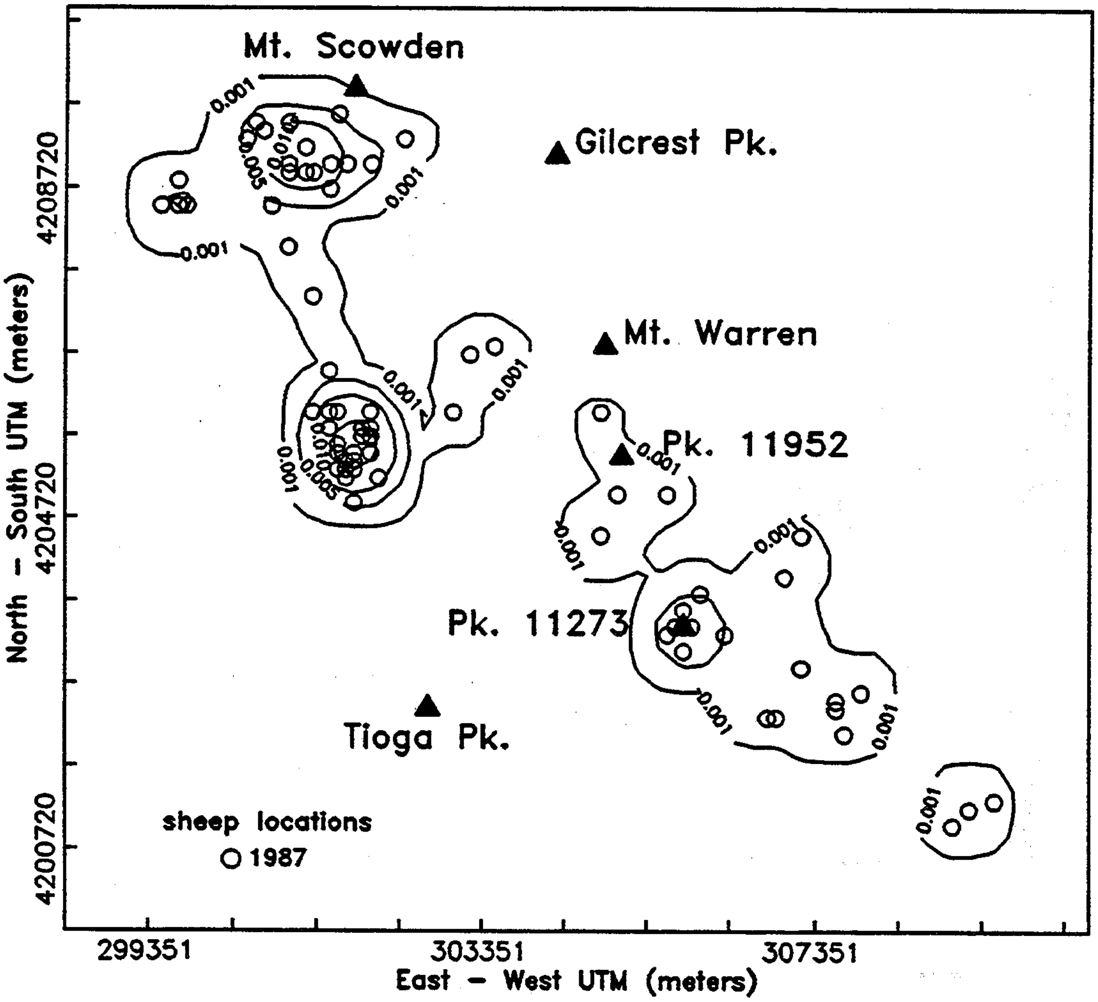


Figure 10. 1987 summer-fall home range used by bighorn ewe 4381 in Lee Vining Canyon, Mono Co., Calif.

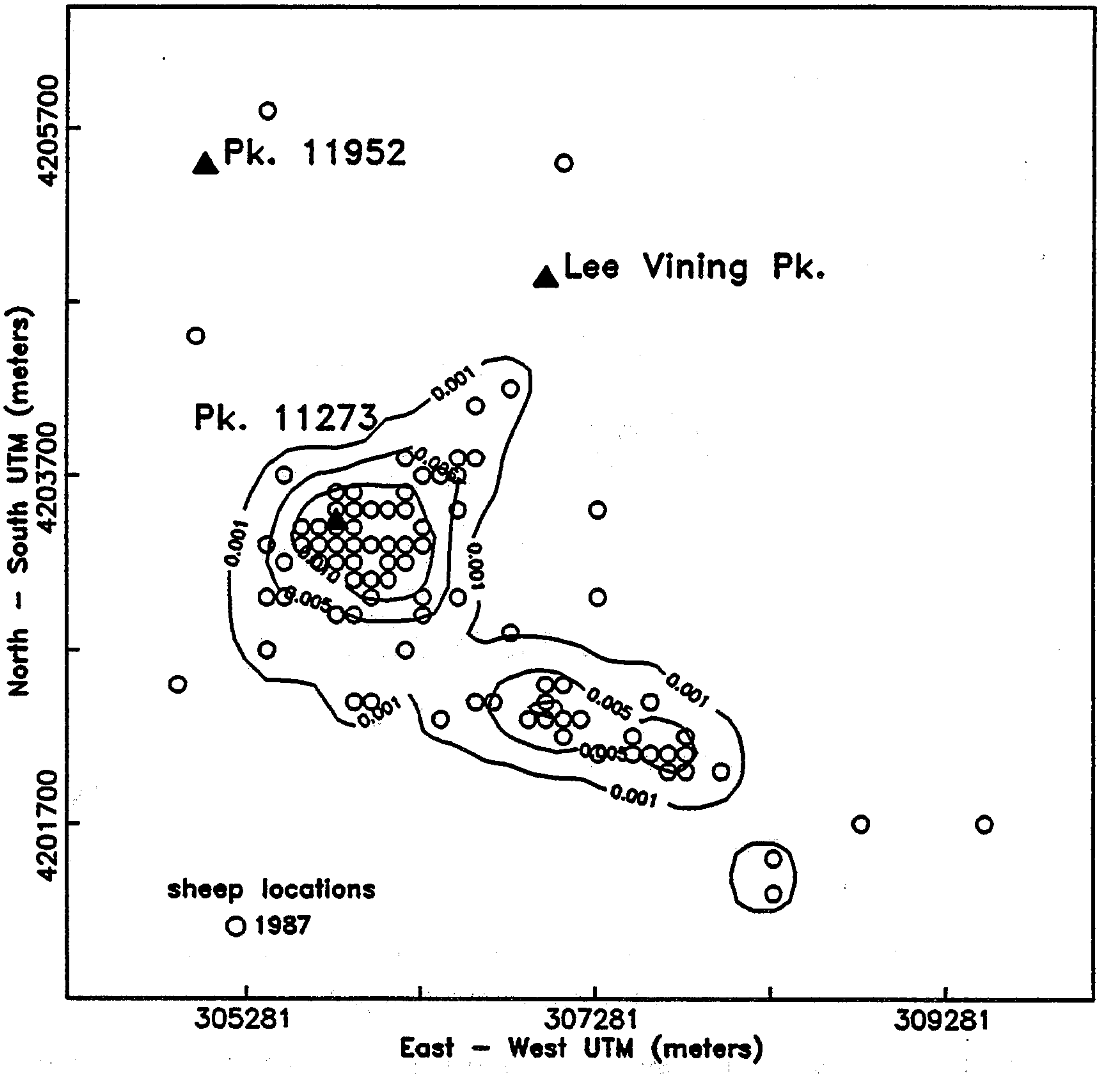


Figure 11. 1987 summer-fall home range used by bighorn ewe 4451 in Lee Vining Canyon, Mono Co., Calif.

In mid-October, ewes 4411, 4601, and 4731 traversed the ridge connecting Warren Bench to Tioga Crest (Lake Warren divide), and spent the remainder of autumn moving between Mt. Scowden and Tioga Crest with ewe 4381. During this time, these sheep were repeatedly observed on the east side of Tioga Crest where it meets Lake Warren divide. A series of storms in early November precipitated their movement to winter range in Lee Vining Canyon.

Ram migration to summer range in 1987 began prior to the first week of June when rams 4791 and 4841 moved from Peak 11273 to the junction of Tioga Crest and Lake Warren divide. In late July, they were joined by rams 4421 and 4851 who had been exploring Mt. Scowden. All 4 rams formed a loosely knit band that circulated among areas occupied by the widely scattered ewe bands. In mid-October, all 4 rams reunited atop Peak 11952 (Figure 4). I frequently observed them foraging on the south side of the peak until mid-November when they joined the ewes on winter range.

Changes in the location of summer ranges did not preclude occasional returns to Peak 11273 or use of the mineral lick along Tioga Road. During the course of summer and autumn, all of the sheep were eventually observed using both locations.

Spring and Summer 1987 also saw the Bloody Canyon band expand its range to an area of 8 km^2 with the winter range at its core. Summer range extended from the summit of Mt. Gibbs to Parker Pass, 5 km south of Bloody Canyon (Figure 3).

Home range and movement patterns 1988

The Lee Vining herd occupied 1988 winter range from late November 1987 through early April 1988. Most ewes increased the size of their winter ranges but retained the same core areas used the previous year. Ram winter ranges also appeared to expand, however, sample size constraints again prevented meaningful comparisons.

The Lee Vining herd was augmented with 11 more sheep from Mt. Baxter on 28 and 29 March 1988. The additional sheep were released at the mouth of Lee Vining Canyon in 2 groups on successive days. The first group of 2 rams and 4 ewes moved to Peak 11273 within 2 days. The 2 rams and a ewe continued west to Tioga Peak but returned to Peak 11273 10 days later.

A ram and 4 ewes were released on the second day. The ram proceeded to Peak 11273 where he joined the sheep released the first day. The 4 ewes remained near the release site and established a winter-spring range which they occupied until mid-July.

The oldest supplement ram, 4640, wandered extensively after his release. His initial foray to Tioga Peak was followed by an early May visit to Tuolumne Meadows in Yosemite National Park. Aerial telemetry monitored his progress on the weeklong, 40-km round trip. Just 3 days after his return to Lee Vining Canyon, he was found at the head of Post Office Creek, 10 km east of the release site.

Supplemental ewes on Peak 11273 confined early spring movements to the summit and immediately adjacent areas. Two supplemental rams joined them during that time. The band also was briefly accompanied by ewe 4451 and ram 4791 from the 1986 reintroduction. The supplemental sheep left Peak 11273 in the first week of May and drifted north along the west side of Warren Bench. By month's end, they had traversed Lake Warren divide and established summer range on Tioga Crest.

Two of the 5 ewes from the 1986 reintroduction, 4411 and 4601, departed lambing range on Peak 11273 and moved to Gilcrest Peak in mid-June. The remaining ewes, 4451, 4731, and 4801, followed 3 weeks later. On Gilcrest Peak they formed loosely knit nursery bands whose movements revolved around the plateau on the west side of Mt. Warren. Weeklong visits to this site were interspersed with short trips to more distant areas. Eating soil along Tioga Road became less frequent as the ewes found alternate mineral licks on Gilcrest Peak.

The 4 supplemental ewes, 4361, 4514, 4564, and 4688, who had settled near the release site, began migrating to summer range on 11 July 1988. They arrived at Peak 11273 5 days later. Ewes 4514, 4564, and 4688 continued north to Gilcrest Peak where they joined ewes from the 1986 reintroduction. Ewe 4361 remained on Peak 11273 until her death in the last week of August.

In late July, ewes 4411 and 4601 moved from Gilcrest Peak, traversed Lake Warren divide, and joined the supplemental sheep summering on Tioga Crest. Other ewes from Gilcrest Peak followed a month later. For the remainder of the summer-autumn season, bands containing sheep from both reintroductions routinely moved between Tioga Crest and Mt. Warren. With the first significant snowfall in mid-November, sheep from the 2 reintroductions separated. Ewes from the 1986 reintroduction left Tioga Crest and descended to winter range in Lee Vining Canyon. Sheep from the 1988 supplement moved to the summit of Tioga Peak where they spent the winter.

The 1988 summer-autumn home ranges of rams from the original reintroduction were nearly identical to those seen the previous year. Summer movements were characterized by constant travel between core sites along a circuit that encompassed most of the study area. These rams again congregated on the south slope of Peak 11952 in late autumn. The 2 oldest supplemental rams, 4371 and 4640, adopted similar summer movement patterns. However, telemetry flights in the autumn consistently found them on the Sierra Nevada crest in the Granite Lakes and Gaylor Lakes basins (Figure 3). Although summer ranges of rams from both reintroductions overlapped considerably, the 2 groups rarely associated. Rams rejoined ewes in early November, just prior to the start of the rut.

Home range and movement patterns 1989

Shrub covered slopes above Tioga Road again served as the core of winter range. Most members of the 1986 reintroduction also expanded their winter ranges to include the upper slopes of Peak 11952. With the exception of 2 ewes that wintered on Gilcrest Peak, all members of the 1988 supplement established a winter range on the summit of Tioga Peak.

Summer distribution patterns in 1989 resembled those of the 2 previous years. The only noteworthy difference was a higher degree of association between adult rams from both reintroductions and their concentration of activities on the Sierra Nevada crest. Although the rams spent the majority of summer and autumn in the Granite Lakes, Gaylor Lakes, and Skelton Lakes basins, they often visited ewe groups in distant corners of the study area.

POPULATION DYNAMICS

Nine (33%) of the 27 sheep reintroduced to Lee Vining Canyon in 1986 died within 3 weeks of their release. The causes of these deaths are discussed in the section on mortality. Although these deaths ultimately must be considered when evaluating the reintroduction's outcome, their timing obviated any meaningful influence on subsequent reproduction and mortality. Consequently, these individuals have been omitted from all birth and death rate calculations.

In September 1989, 3.5 years after the initial transplant, the Lee Vining herd numbered 41 sheep (Table 2). Eleven were from the original reintroduction, 10 were members of the 1988 supplement, and 20 were born at Lee Vining. The 37 sheep that remained in Lee Vining Canyon included 13 adult ewes, 10 adult rams, and 14 subadults. Four sheep, 3 adult ewes, and a yearling of unknown sex, established residence in Bloody Canyon, 13 km south of the main herd. Annual increase by the herd during the first 2 years of the study averaged 7.0% (SE = 2.0) and the rate of increase (r) was 0.100. The annual increase following the 1988 supplement averaged 8.5% (n = 3, SE = 1.8).

Reproduction

During the study, 31 lambs were born (Table 4), and spring lamb:ewe ratios over the 4-year period averaged 64:100 (SD = 18.1) for Lee Vining Canyon and 52:100 overall (SD = 11.9). Of the 31 lambs born during the study, 8 were females, 4 were males and I was unable to determine the sex of 19 individuals. Between 20 April and 20 May 1986, 9 of 12 ewes from the initial transplant to Lee Vining bore lambs, yielding a spring lamb:ewe ratio of 75:100.

In 1987, 5 of 6 ewes remaining in Lee Vining Canyon bore lambs. The 3 ewes that dispersed to Bloody Canyon in October 1986 failed to produce lambs in 1987, most likely because no adult rams visited Bloody Canyon during the breeding season. Thus, the spring 1987 lamb:ewe ratio was 83:100 for Lee Vining Canyon and 56:100 overall.

Eight lambs were born in 1988. Two were produced by members of the 1986 reintroduction and 4 were born to ewes from the 1988 supplement. Two of the 4 ewes (≥ 2 years old) in Bloody Canyon, apparently bred by the lone yearling ram that accompanied them as a lamb in 1986, also produced lambs.

Table 4. Lamb production and recruitment by cohort from 1 May 1986 to 6 September 1989.

Cohort	Initial number	Lee Vining lamb:ewe ratio	Overall lamb:ewe ratio[1]	% surviving to next age class					
				0	(n)	1	(n)	2	(n)
1986	9	75:100		67	(6)	100	(6)	83	(5)
1987	5	83:100	66:100[2]	60	(3)	100	(3)		
1988	8	43:100	44:100	63	(5)				
1989	9	56:100	47:100[2]						
Total	31	64:100	52:100	63	(14)	100	(9)	83	(5)

[1] includes ewes in Bloody Canyon.

[2] no rams were present in Bloody Canyon during the previous breeding season

The 1988 spring lamb:ewe ratio in Lee Vining Canyon was thus 43:100 while the overall ratio was 44:100.

Nine of 16 ewes (≥2 years old) in Lee Vining Canyon produced lambs in 1989. No lambs were born in Bloody Canyon because the only ram there died prior to the breeding season. The Lee Vining Canyon spring lamb:ewe ratio for 1989 was 56:100 while the overall ratio was 47:100.

During the study, there was an increase in the length of the lambing season. In 1986, lambing extended from 20 April to approximately 20 May. The following year, lambing began in late April but extended through mid-June. Duration of the 1988 and 1989 lambing seasons was similar to that observed in 1987 with a 1-week-old lamb observed in early July both years.

Lamb survival and recruitment

Six of the 9 lambs born in 1986 survived to 1 year (Table 4). Of these, 4 (3 male, 1 female) remained in Lee Vining Canyon. The other 2 surviving 1986 lambs, a male and a female, migrated with their ewes to Bloody Canyon in autumn 1986. Three of 5 lambs born in 1987 survived to become yearlings. Of the 8 lambs born in 1988, 5 survived to 1 year. Lamb survival to 1 year of age in 1986, 1987, and 1988 cohorts was 67%, 60%, and 63%, respectively ($\bar{X}$ =

63%). Survival from 1 to 2 years of age was 100% both years for which there were data. Survival between 2 and 3 years of age was 83% for the 1986 lamb cohort. Recruitment, traditionally represented by winter lamb:ewe ratios, was 67:100 in 1986, 60:100 in 1987, and 45:100 in 1988.

Mortality

Twenty-eight sheep died during the study (Table 5). A third of the mortality (n = 9) occurred within 3 weeks of the 1986 reintroduction. Subsequent losses included 12 confirmed deaths and 7 presumed mortalities. Mountain lion predation accounted for 66.6% (n = 8) of the confirmed mortalities. Cause of death for the remainder of the confirmed mortalities (n = 4) could not be determined. The 7 presumed mortalities were uncollared sheep that disappeared.

The 9 members of the 1986 reintroduction that died shortly after their release included 2 adult rams and an adult ewe. Four of 5 radio-collared lambs also perished while 2 uncollared lambs released with the initial transplant were never seen again and are presumed dead. The carcasses of all 7 radio-collared sheep were recovered to determine the causes of death.

It snowed daily for 2 weeks following the transplant and average daytime temperatures were -8 C. Two sheep died when

Table 5. Cumulative sources of mortality by cohort in the Lee Vining herd (including Bloody Canyon) between 5 March 1986 and 15 September 1989.

	Sources of mortality																				
Cohort	Initial number			Exposure			Accident			Mt. lion predation			Unknown			Presumed dead			Current number		
	M	F	U	M	F	U	M	F	U	M	F	U	M	F	U	M	F	U	M	F	U
1986 transplant	12	15		4	1		2			1	5					1	2		4	7	
1986 lambs	4	2	3							1					1			2	3	2	
1987 lambs		4	1								1							1		3	
1988 transplant	3	8												1					3	7	
1988 lambs		2	6												1			2		2	3
1989 lambs			9															2			7
Total	19	31	19	4	1		2			2	6			1	2	1	2	7	10	21	10

M = male, F = female, U = unknown sex

they fell into snow-covered crevices and were unable to extricate themselves. Necropsies of the 5 remaining carcasses found evidence of nutritional stress. Fat reserves were severely depleted in 4 cases and weight loss was as high as 28% in lambs. Rumen contents included undigested twigs and pine needles. Examinations of muscle tissue yielded no evidence of capture myopathy for any of the dead sheep. These findings suggest that the majority of post-release mortality (n = 4) resulted from malnutrition and exposure (D. Jessup, Wildl. Invest. Lab., pers. commun. 1986).

There were no mortalities during the spring and summer 1986. Between 1 September 1986 and 31 March 1987, 3 ewes and 1 ram were lost to mountain lion predation. Three 1986 lambs died during the winter. One was found dead at the base of a cliff and 2 others disappeared. The cause of these deaths could not be determined.

Confirmed mortality for the first year (ignoring the 9 initial mortalities) was 18.5% (n = 5) although actual mortality was probably 25.9% (n = 7). Of the known causes of mortality, predation accounted for 80% (n = 4).

At a December 1986 meeting (C. D. Hargis, 1986 memo to SBIAG, Lee Vining), members of the SBIAG agreed that mountain lion predation posed a serious threat to the continued existence of the Lee Vining herd. They accordingly instituted a predator control program in Lee Vining Canyon. The program authorized the destruction of mountain lions found in the study area. During the study, CDFG hunters tracked and killed 3 mountain lions known to have preyed on sheep in the Lee Vining herd.

Four of the 20 sheep present in Lee Vining Canyon on 1 May 1987 had died by 31 March 1988 while none died in Bloody Canyon. Two of the mortalities, an adult ewe and a female lamb, were due to mountain lion predation. A lamb and a 2-year-old ram were last seen on 2 November 1987 and 30 January 1988, respectively, and were presumed dead. Thus, confirmed mortality in 1987 was 8.0% (n = 2) although actual mortality was more likely 16.0% (n = 4).

The mortality rate in 1988 was 10.0% with 4 confirmed deaths. I recovered the collar worn by ewe 4361 from the 1988 supplement in late August 1988. Although her carcass was never found, I assumed she had died. The skull of a 1988 lamb was later found nearby. Two members of the Bloody Canyon band, adult ewe 4391 and the uncollared 3-year-old ram, were victims of mountain lion predation. The 1988 lamb of ewe 4391 also disappeared and was presumed dead. Thus actual mortality may have been 12.5% (n = 5).

Three uncollared sheep disappeared in 1989. One was a 1988 lamb and 2 were 1989 lambs. The 1988 lamb disappeared between late autumn 1988 and spring 1989. Both 1989 lambs disappeared during summer 1989. The cause of death could not be determined in any of these cases.

Of the 11 confirmed mortalities over the study period, 7 (63.6%) occurred between 1 November and 31 March while the sheep were on winter range. The remaining 4 confirmed mortalities occurred during the summer and autumn. Among presumed mortalities, 62.5% (n = 5) also occurred while sheep were on the winter range. Seven of 11 confirmed mortalities occurred during the first 2 years.

During the study, 5 of 23 (21.7%) ewes and 3 of 13 rams (21.4%) died. These totals do not include lambs. The low number of dead rams did not permit statistical examination of sex related mortality. All of the ewes that died were accompanied by lambs of the year.

An examination of mortality by age class (Table 6) revealed that lambs had the highest incidence of death among all age classes in the Lee Vining herd. Mortality among sheep ≥1 years old was lower and averaged 0.128 (SD = 0.025). Because confounding effects are likely to be involved in the

Table 6. Composite mortality rate for the Lee Vining bighorn sheep herd between 1 May 1986 and 30 April 1989.

Age interval	Begin 1986-1988	End 1987-1989	Mortality rate (q_x)
0 - 1	22 (9+5+8)[1]	15 (6+3+6)	0.318
1 - 3	22 (5+7+10)	19 (4+6+9)	0.136
3 - 5	20 (7+5+8)	18 (5+5+8)	0.100
≥5	27 (6+7+14)	23 (5+6+12)	0.148

[1] numbers in parentheses are actual data for each year

growth of a recently reintroduced herd, no inferences can be drawn from these data.

DISCUSSION

Home Range and movement patterns

The Lee Vining herd established stable home range patterns in 2 stages. The first stage commenced with the initial reintroduction and extended through the summer-autumn season in 1986. Stage I was characterized by small home range sizes, the absence of long-distance migration, large group sizes, and the failure of rams and ewes to segregate. The herd's move to winter range in late November 1986 marked the beginning of Stage II. During Stage II, the sheep developed long-distance migration patterns and distinct seasonal home ranges that were retained in subsequent years. The 2-stage process appears typical of reintroduced bighorn sheep and has been observed in reintroductions of the Rocky Mountain (Kopec 1982), desert (Elenowitz 1983, Berbach 1984, Shaw 1986), and California (Andaloro and Ramey 1981, Hanson 1984) subspecies.

The Lee Vining herd's failure to disperse from the release site during the first year contrasts with the pattern of long-distance migration normally seen in native bighorn herds (Murie 1940, Packard 1949, Geist 1971) and observed by Wehausen (1980) at Mt. Baxter. Migration enables an organism to maintain itself in a patchy or seasonal environment (McCullough 1985, Begon et al. 1986). Hebert's (1973) study of captive bighorn found correlations between altitudinal migration and body condition. Altitudinal migration allows bighorn to maintain a high level of diet quality by permitting them to remain in a zone of active plant growth where forage species are at peak nutritional content (Geist 1971, Hebert 1973, Wehausen 1980).

Visual assessments of condition (McCutchen 1985) indicated that Lee Vining Canyon ewes residing on winter range all year were in poorer condition than migrating conspecifics. Furthermore, 3 of 6 ewes that remained on the winter range for part or all of the summer became victims of predation. Poor condition probably resulted from the lack of moisture and associated decline in forage quality at lower elevations during summer. Because poor condition is likely to reduce alertness and a sheep's ability to escape predators, the transition from sedentary to migratory status may be important for a reintroduction's success.

Geist (1971) proposed that movement and distribution patterns of native bighorn are determined by traditions perpetuated when younger sheep follow older sheep and acquire knowledge about the location of resources. This also appears to be true of other mountain ungulates inhabiting patchy or seasonal habitats (McCullough 1985). Based on his survey of agencies conducting bighorn reintroductions in western North America, Geist (1971:121) concluded 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 a new location and an evolutionary history in which dispersal and exploratory behavior were penalized.

Questions about the importance of tradition arise, however, in light of range extensions by the Lee Vining herd and other reintroduced bighorn. Geist (1971:128) speculated that in the absence of tradition, range extensions were possible where habitat was continuous or visibility was unobscured by forest. He went on to describe a scenario strikingly similar to the exploration and settlement of Mt. Scowden by the ram and ewe band in the summer of 1987.

Between-year differences in snow depth offer an alternate explanation for the Lee Vining herd's shift from sedentary to migratory status. In 1986, Lee Vining Canyon snowfall was nearly twice the annual average. This was followed by 3 consecutive years of drought. Most snow had melted before the herd moved to summer ranges and thus did not impede movements in any year of the study. However, snowbanks that persisted throughout the year in 1986 may have exerted an indirect influence on movements.

Plant growth in the Sierra Nevada is generally limited by available moisture (Major 1977) and 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 snowbanks in 1986 may have allowed the herd to obtain adequate forage in one location while drought conditions in subsequent years necessitated long-distance movements in search of food. By not migrating, sheep also may have avoided expending the energy required to move and decreased their vulnerability to predation while exploring an unfamiliar area.

Predation pressure may also have provoked shifts in distribution. In one instance, the herd moved to a new core area after being chased by a coyote (_Canis latrans_). In another case, a nursery band moved 2 km following the loss of a lamb to a mountain lion. J. Wehausen (Univ. California, White Mtn. Res. Stn., pers. commun.) observed the Mt. Baxter herd abandon a wintering area in response to mountain lion predation. The Lee Vining herd's relocation of its winter range to the upper slopes of Peak 11952, may have been a similar response to mountain lion predation. The sparse shrub cover on the upper slopes of Peak 11952 may have increased visibility and the sheep's ability to detect predators.

Additional benefits derived from wintering at higher elevations may include prolonged exposure to direct sunlight. On mid-winter afternoons, lower elevations in Lee Vining Canyon are shadowed by 1400 hrs while the summits of surrounding peaks receive direct sun until much later in the day. Increased insolation could decrease the metabolic cost of maintaining body temperature (Hansen 1982, 1984a, Gionfriddo and Kraussman 1986). Benefits from reduced predation and lowered metabolic costs may offset the slight decrease in air temperature at higher elevations.

The absence of sexual segregation during the first year may have been attributable to disorientation and unfamiliarity with the area. It is also possible that rams failed to segregate because they were all <2-years-old when reintroduced in 1986. Geist (1971) observed that rams in British Columbia began dispersing from natal bands between 2 and 3 years of age.

Although several factors may have influenced the pattern of home range establishment, the most likely explanation for the Lee Vining herd's failure to use a larger area during the first year was the absence of traditional movement patterns and disorientation in a new location. I suspect that range expansion in succeeding years resulted from the herd's increased familiarity with their surroundings during the second year of residence. Establishment of summer ranges in areas visited previously provides the strongest support for this interpretation. Further evidence is provided by the decrease in group size and increased sexual segregation, behaviors representative of native bighorn herds. Range expansion may have been further encouraged by the continuous nature of the habitat and accompanying absence of visual obstructions as proposed by Geist (1971).

Geist (1971) hypothesized that movement and distribution patterns in native bighorn herds are dictated by tradition. Traditions evolve as younger sheep follow older sheep and acquire knowledge about the location of suitable habitat and resources. However, I was forced to explain the herd's range expansion during the second year and the rapid migration of supplemental ewes to Tioga Crest and Gilcrest Peak following their release in Lower Lee Vining Canyon in 1988 in the absence of tradition. Contrasts in the patterns of home range settlement by sheep reintroduced in 1986 and those from the 1988 supplement as well as the high degree of overlap between summer ranges used by sheep from both reintroductions suggest that additional mechanisms may exist.

Olfactory clues could provide an additional means of disseminating information about the location of resources. Scent is recognized as a widely used means of communication among mammals (Müller-Schwarze 1971, Johnson 1973, Eisenberg and Kleiman 1982). Eisenberg and Kleiman (1982) and Johnson (1973) noted that unfamiliar odors encountered while exploring a new environment often elicit an increase in the frequency of scent marking. Members of the genus Ovis possess interdigital (pedal) glands on all 4 feet (Geist 1971). Pedal glands could provide an ideal means of transmitting information about the location of use areas (Johnson 1973). In the absence of tradition, olfactory clues from beds and scats may provide evidence of previous use. Areas frequented by bighorn soon developed a distinctive odor detectable even by humans. My observation of a Lee Vining ram marking twigs with his preorbital gland and sniffing objects along his route also lend support to this idea. Visual cues such as the distinct trails produced by the repeated passage of sheep hooves could also supplement olfactory clues.

The establishment of stable home range patterns by the end of the second year indicates that traditions can develop rapidly. It also suggests that bighorn behavior may be more flexible than previously recognized. Fears that human disturbance may limit herd growth would appear to be dispelled by the herd's frequent use of the mineral lick along the Tioga Road.

Although most members of the Lee Vining herd adhered to the pattern of exploration and settlement previously described, there was considerable variation among individuals. The exploration of Yosemite National Park by rams, ewe dispersal to Bloody Canyon, and the high coefficient of variation for individual home range size all illustrate this. Individual variability in movements by transplanted sheep has been reported for desert bighorn sheep (McQuivey and Pulliam 1981, Elenowitz 1983, Shaw 1986), Rocky Mountain bighorn (Bear 1979) and California bighorn (Andaloro and Ramey 1981, Hanson 1984). In a study of reintroduced pronghorn antelope, Goldsmith (1988) attributed the high degree of variability in behavior to increased expression of individual variation in the absence of social structure normally found in established herds. This hypothesis may also be true for reintroduced bighorn sheep.

Population dynamics

Geist (1971) believed reintroduced bighorn populations should increase rapidly when transplanted into suitable, unoccupied habitat. His hypothesis has been supported by results from previous reintroductions. A herd of 8 bighorn reintroduced to historic range at Lava Beds National

Monument, California grew to 28 animals in 4 years (Blaisdell 1976). Bighorn sheep reintroduced to Wildhorse Island, Montana (Woodgerd 1964) and Hart Mountain, Nevada (Hansen 1984b) also multiplied rapidly, achieving r values of 0.305 and 0.246, respectively.

In contrast, the Lee Vining herd's rates of increase were 0.100 during the first 2 years and 0.090 following the 1988 supplement. Recent censuses of other reintroduced herds in the Sierra Nevada indicate that population growth at those locations has also been slow. My attempts to explain disparities between the observed patterns of population growth prompted an examination of limiting factors.

Reproductive data from bighorn reintroduced to Wildhorse Island recorded annual lamb:ewe ratios between 67:100 and 100:100 with an 8 year mean of 80:100 (Woodgerd 1964). Hansen (1984b) examined 2 sequences of reproductive data from bighorn reintroduced to Hart Mountain and calculated mean lamb:ewe ratios of 94:100 and 83:100. Lamb:ewe ratios in the Lee Vining herd were 75:100 and 83:100 during 1986 and 1987 respectively. These estimates are comparable to those observed by Woodgerd (1964) and Hansen (1984b) but are slightly biased by the method of calculating lamb:ewe ratios.

Age of first lambing in North American wild sheep is generally 3 years (Streeter 1970). This is also true for Sierra Nevada bighorn (Wehausen 1980). Ewes are difficult to age in the field, however, and most studies include all females ≥2 years old when reporting lamb:ewe ratios (Murie 1940, Blood 1963, Geist 1971, Murphy and Whitten 1976, Elenowitz 1983, Wehausen 1980). Because no 2-year-old females were present in the Lee Vining herd during 1986 and 1987, lamb:ewe ratios for that period were based on ewes ≥3 years old. Consequently, lamb:ewe ratios for those years were inflated relative to other estimates.

The apparent decline in lamb production during 1988 and 1989 probably reflects the entry of 2-year-old females into the population. Although no 2-year-olds bore lambs, I included them when calculating lamb:ewe ratios to maintain comparability with other studies. If 2-year-olds are excluded from calculations, lamb:ewe ratios in Lee Vining Canyon during 1988 and 1989 increase to 53:100 and 69:100, respectively.

Annual lamb survival in the Lee Vining herd ($\bar{X} = 63\%$) fell within the wide range of values observed in native bighorn herds (Geist 1971, Murphy and Whitten 1976, Simmons et al. 1978, Wehausen 1980, Hoefs and Bayer 1983, Douglas and Leslie 1986). Furthermore, recruitment rates, generally expressed as the winter lamb:ewe ratio, were twice the figure McQuivey (1978) deemed necessary for maintaining a stable bighorn population in Nevada and 1.5 times greater than the ratio of 40:100 that Wehausen (1980) felt was indicative of population increase in the Mt. Baxter herd. On the basis of natality and recruitment rates in the Lee Vining herd, I concluded that habitat and forage resources are adequate for bighorn reproduction and survival.

With the exception of those sheep that died immediately after the transplant, predation accounted for 8 of 11 (73%) mortalities for which I was able to determine the cause of death (Table 5). The high loss of collared sheep to mountain lions suggests that predation also contributed to some of the presumed mortality.

The primary predator in Lee Vining Canyon appeared to be the mountain lion. Although golden eagles (_Aquila chrysaëtos_) are present and known to prey on young lambs (Kelly 1980) the low number of eagles inhabiting Lee Vining Canyon likely makes their impact negligible. Coyotes and bobcats (_Lynx rufus_), because of their small size, are also likely to pose a threat only to lambs.

Three-fourths (75%) of the predation during the first 2 years occurred while the sheep were on winter-spring range.

One exception was ewe 4371. She remained at lower elevations following the 1986 reintroduction and was subsequently killed by a mountain lion in September 1986. Predation rates may have been elevated during winter months because dense brush and broken terrain characterizing habitat in lower Lee Vining Canyon probably impair predator detection. Increased predation during winter may also have been related to the migration of mule deer (<u>Odocoileus hemionus</u>) from summer range in Lee Vining Canyon to winter range, 15 km away. In the absence of deer, bighorn may represent alternate prey for resident and transient mountain lions.

Predation is generally thought to play only a minor role in regulating bighorn population numbers (Buechner 1960, Kelly 1980, Berger 1990). Although this may be true for a large, established herd, it is not necessarily applicable to small, reintroduced populations. Because carcasses are quickly consumed by predators and scavengers, evidence of predation is scant. As a result, predation is likely to be underestimated as a source of mortality. Predation's effects are likely to be magnified in a small population because each individual represents a larger proportion of the total numbers. In such cases, the loss of only a few individuals is capable of offsetting reproductive gains. Observations of 6 interactions between coyotes and sheep during this study suggest that bighorn may encounter predators frequently.

An examination of the circumstances under which reintroduced bighorn herds grew rapidly is particularly revealing. Predators were absent from Wildhorse Island (Woodgerd 1964), and bighorn reintroduced to Hart Mountain and Lava Beds were released into fenced enclosures that excluded predators. Data from Hart Mountain included only one incident of predation (Hansen 1984b) and although predators were seen in the enclosure at Lava Beds, no deaths resulted from predation (Blaisdell 1976).

The high proportion of predation related mortality during the first 3 years of this study suggest that predation was the primary factor limiting growth of the Lee Vining herd. Additional factors contributing to the slow growth of the population included high post-release mortality and dispersal of ewes to Bloody Canyon. These events were responsible for half of the population decline during the first year and resulted in the loss of 7 females, 4 of which were of reproductive age.

An additional factor with the potential for even greater impact on future herd growth appears to be a lowered recruitment resulting from prolonged drought. Although drought had little effect on birth rates, prolonged drought may lower the recruitment rate.

Wehausen (1980) observed that wet winters produced larger snowbanks which persisted throughout the year. Persistent snowbanks extend the growing season by providing moisture to plants during dry summer months (Billings and Bliss 1959). Wehausen (1980) found winter precipitation to be positively correlated with recruitment the following spring and hypothesized that prolonged availability of high quality forage following wet winters allowed lambs to attain greater size thus increasing their chances of survival. This hypothesis is supported by my observations which clearly indicated that lambs born in 1986 grew more rapidly and were larger at the onset of winter than lambs born in subsequent years.

Attaining large size is advantageous because it increases the ability to store reserves necessary for survival during periods of inclement weather. A small lamb's higher surface to volume ratio also increases its radiant heat loss and the risk of death from exposure. Small lambs that can survive mild winters may have difficulty surviving severe winters or long periods of limited forage availability. This appeared to be the case in 1986 when 6 of the 7 newly reintroduced lambs died during 3 weeks of severe winter weather.

Lamb survival and recruitment have been shown to be highly correlated with birth date (Bunnell 1980, 1982, Thompson and Turner 1982, Festa-Bianchet 1988b). Drought may further inhibit population growth by indirectly determining a lamb's birth date. Visual comparisons of lambs in late autumn indicated that those born after June 15 were much smaller than those born earlier, and I observed late born lambs still suckling in November.

Studies of other ungulates (Mitchell and Lincoln 1973, McCullough 1979, Hamilton and Blaxter 1980) found reproductive timing to be influenced by prior nutrition. Ewes lambing after June 15 may subsequently have ovulated later in autumn because nutrition had been directed towards lactation instead of accumulating reserves necessary for reproduction and survival the following year. Consequently, their lamb was again born late the following year. Ewes bearing late lambs completed molt later and appeared in worse condition than those that weaned their lambs earlier. The problem is likely to be exacerbated in dry years when rapid declines in forage quality increase the difficulty of acquiring adequate reserves. Late lambing and autumn lactation may also increase a ewe's risk of overwinter mortality because she is unable to direct her nutritional intake into fat stores that would enable her to survive the winter.

Population modeling

Using RAMAS/a to model the population dynamics of the Lee Vining herd revealed shortcomings in the program that reduce its applicability to bighorn sheep and other ungulates species. The program's major weaknesses stem from stated and unstated assumptions that are unrealistic for certain large mammals, including bighorn sheep. The most serious problems are: 1) density dependence does not directly affect the survival of older age classes and 2) there is no difference in survival rates between males and females.

Although increasing density is likely to have the greatest impact on lamb survival, it is improbable that older age classes of a "K" selected species would escape its effects (Fowler 1981). The model's failure to include density dependent effects on older age classes will cause predation's impact to be overestimated because mortality designated in the "other" category becomes almost entirely additive (Conroy and Krementz 1990), regardless of population size. The inclusion of unrealistic assumptions in the RAMAS/a population model renders its accuracy suspect for making precise predictions about the dynamics of bighorn sheep populations.

The inability to specify different survival rates for males and females is also likely to produce erroneous results.

Especially when dealing with a species such as bighorn sheep, for which differential survival rates have been widely documented (Welles and Welles 1961, Hansen 1967, Wishart 1978, Wehausen 1980).

Another problem encountered while modeling the population dynamics of the Lee Vining bighorn sheep herd was the inability to vary the rate of additional mortality during simulations. Because I used this feature to incorporate predation, the predation rate remained constant throughout simulations regardless of population size. However, it is more likely that territorial behavior among mountain lions would preclude a constant rate of predation and result instead in a constant number of sheep being taken (Hornocker 1970). Thus, the predation rate would probably decrease as the sheep population grew. The predation rate is also likely to vary with population size because of differences in search times and changes in the probability of encountering a sheep. Thus, although RAMAS/a may provide a general model of population dynamics, results may lack the precision necessary for properly managing bighorn sheep and other large mammal populations.

Although using RAMAS/a to model the population dynamics of certain large mammals may be inappropriate, it can serve as a pedagogical tool or be used to assess the relative importance of various population parameters. In this instance, results from RAMAS/a consistently supported Goodman's (1987) contention that the persistence of small populations, which typify transplants, depends on minimizing environmentally driven variance (Figure 12).

The highest rate of herd growth predicted by the RAMAS/a model was achieved under the combined conditions of observed predation rate and 0.5 times the observed coefficients of variation for fecundity and survival (Figure 12). At these levels, the hypothetical carrying capacity of 100 animals was reached in 23 years, and the herd fluctuated between 100 and 102 sheep thereafter. The same coefficients of variation for fecundity and survival combined with a 5% increase in the annual predation rate produced a slow but steady increase by the herd. The most notable change induced by increasing predation was that the herd had not reached hypothetical carrying capacity by the end of 50 years and contained only 58 sheep under the conditions of observed CV for fecundity and survival. A 10% increase in the annual predation rate produced a steady population decline and the herd was always extinct at the end of 45 years.

Increased variation in fecundity and survival rates also suppressed population growth but to a lesser degree than

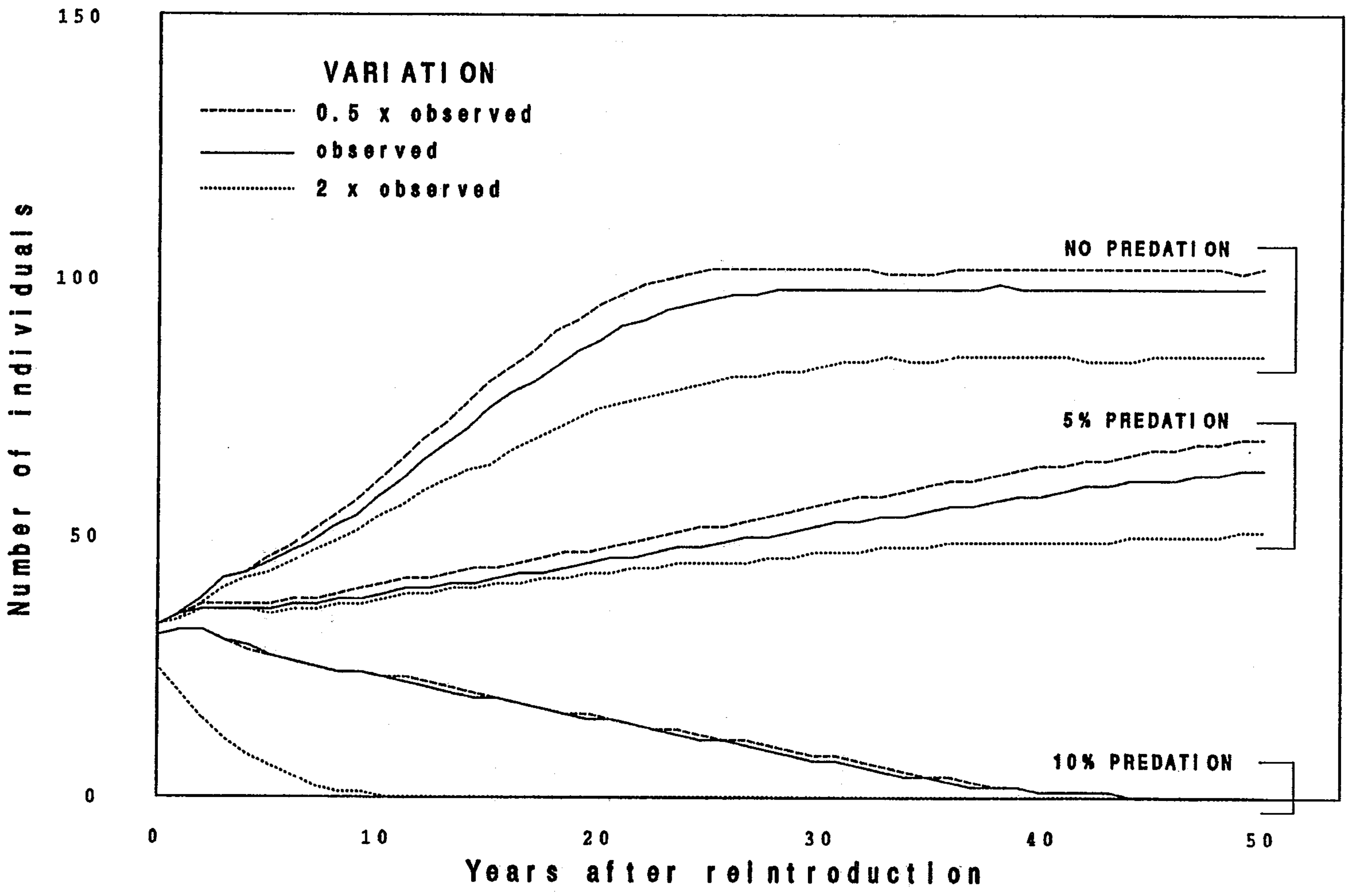


Figure 12. Results of simulation modeling using RAMAS/a to project growth of the Lee Vining bighorn sheep herd over a 50 year period at different levels of variation and predation

predation. The herd's growth rate and final population size were always greater at lower levels of variation (Figure 12). Although coefficients of variation for fecundity and survival at twice the observed levels occasionally produced the greatest number of sheep during the 250 simulations of that combination, they always resulted in a lower mean number of sheep than lesser levels of variation. In addition, twice the observed CV in combination with a 10% increase in the observed rate of predation consistently resulted in herd extinction 8 to 10 years after reintroduction.

MANAGEMENT IMPLICATIONS

Herd persistence

The primary objective of Sierra Nevada bighorn sheep management is to ensure their continued existence. This objective is to be achieved by maintaining the health and viability of all existing populations, and by promoting the establishment of at least 3 populations that are both large (exceeding 100 animals) and geographically distant from one another (SBIAG 1984). The results of this study have several implications for the successful establishment of additional herds.

Although the Lee Vining herd increased to 53 animals with the birth of 16 lambs in spring 1990 (L. Chow, unpublished data), uncertainty remains about the herd's long-term survival. Berger (1990) examined 121 bighorn populations and found that all herds containing fewer than 50 animals went extinct within 50 years. Without intervention, a similar fate could befall the Lee Vining herd. Goodman (1987) modeled the demography of small populations and concluded that the key to their long-term persistence lay in reducing environmentally driven variance associated with population growth rate. The effects of environmentally driven variance can be ameliorated through either habitat manipulation or steps to reduce mortality (Goodman 1987).

At present, the high rate of lamb production in Lee Vining Canyon suggests that forage resources there are sufficient for reproduction and survival. Thus, habitat manipulation to increase forage productivity appears unnecessary. However, removing shrubs and trees on the winter range may increase visibility and facilitate predator detection.

Because habitat manipulation to enhance forage productivity appears unnecessary, ensuring the persistence of the Lee Vining herd will require a reduction in mortality. Reducing mortality would increase the numbers and growth rate of the Lee Vining herd. Increased herd size would reduce the risk of extinction by increasing the probability of herd survival in the event of a major dieoff due to disease (Foreyt 1989, Foreyt and Jessup 1982). Increased herd size would also dilute the effects of predation, create a larger effective breeding population that is less susceptible to the effects of inbreeding depression (Berger 1990, Ralls et al. 1986, Schwartz et al. 1986, Skiba and Schmidt 1982), and provide a buffer against extinction due to stochastic events. An increase in the herd's growth rate would reduce the period during which the herd is vulnerable to loss from disease, predation, and inbreeding.

During this study, the major source of known mortality in the Lee Vining herd was predation by mountain lions. Although the accuracy of population estimates and growth rates predicted by RAMAS/a may be questionable, consistent trends in the results of modeling indicate that predation can significantly influence the growth rate of a small population such as the Lee Vining herd. If a higher rate of increase in the Lee Vining herd is desired, managers should consider the continued removal of mountain lions from Lee Vining Canyon for several more years. Those making the decision must weigh the costs and effectiveness of short-term predator control against the long-term objectives of Sierra Nevada bighorn sheep management.

Although no deaths were known to have been caused by disease, and domestic sheep grazing has been discontinued in

Lee Vining Canyon, the potential for disease transmission still exists. In July 1988, a domestic sheep strayed onto the Lee Vining herd's winter range from one of the neighboring grazing allotments. Luckily, the ewes inhabiting that area had departed 3 weeks before and there was no contact. However, the incident underscores the continued concern over catastrophic loss due to disease.

Monitoring

The Sierra Bighorn Recovery and Conservation Plan (SBIAG 1984) states that a reintroduction will be judged a success if the herd increases to 100 animals and appears to be capable of sustaining itself. Due to the slow rate of population growth, the determination of whether the Lee Vining reintroduction is ultimately a success or failure will require long-term monitoring to evaluate population trends.

A minimum of 2 censuses should be conducted annually. Because juveniles remain with ewe groups until they are 2-year-olds (Geist 1971), the maintenance of functioning radio telemetry collars on adults would permit the most complete censuses to be conducted in the shortest period of time. Non-functioning collars should be replaced and uncollared sheep should be equipped with radio telemetry collars if feasible. Although capturing bighorn and installing radio collars is expensive, each additional collared animal dramatically increases the efficiency of censuses.

The first census should concentrate on evaluating lamb production. It would require 1 month and be scheduled for late July after ewes and lambs have left the safety of lambing areas where they are extremely difficult to see. Lamb mortality is negligible between the onset of lambing and the end of July (L. Chow and P. Moore, Unpub. Rep. to the Natl. Park Serv., Yosemite Natl. Park. 1987). Thus July censuses should accurately reflect lamb production. Using radio telemetry and distribution maps of seasonal use areas (Appendix B), the census could be conducted by a team of 2 individuals.

The second census should be scheduled for winter, when most of the mountain lion predation has occurred. This census would have the dual purpose of detecting mortalities and the presence of mountain lions in Lee Vining Canyon. The winter census would entail a series of counts conducted at monthly intervals from January through April. Each count can generally be completed within a week. The counts will be most successful if conducted 2 to 3 days after a significant snowfall when the sheep are concentrated on their winter range and mountain lion tracks are most visible. While the sheep are on lower elevation winter range, access presents less of a problem and only a single individual should be needed to conduct the census. However, if sheep remain at high elevations during winter, safety would require that 2 people conduct censuses following the procedures used during summer.

Intensive monitoring of the Lee Vining herd since reintroduction has provided accurate estimates of natality and mortality within the herd. Monitoring also enabled me to identify limiting factors, a necessary step toward increasing the reintroduction's chances for success (Griffith et al. 1989). Intensive monitoring incurred significant expenditures, however, and its continued role in establishing a viable, self sustaining Sierra Nevada bighorn sheep herd in Lee Vining Canyon must be weighed against costs.

LITERATURE CITED

Ackerman, B. B., F. A. Leban, E. O. Garton, and M. D. Samuel. 1989. User's manual for program Home Range. second ed. For., Wildl., Range Exp. Stn., Univ. Idaho, Moscow, Tech. Rep. 15. 81pp.

Andaloro, L. and R. R. Ramey II. 1981. The relocation of bighorn sheep in the Sierra Nevada of California. Univ. California, Santa Cruz, Environ. Field Pub. No. 7. 60pp.

Bateman, P. C. and C. Wahrhaftig. 1966. Geology of the Sierra Nevada. Pages 107-172 in E. H. Bailey, ed. Geology of Northern California. Calif. Div. Mines Geol., Sacramento, Bull. 190.

_____ , R. W. Kistler, D. L. Peck, and A. Busacca. 1983. Geologic map of the Tuolumne Meadows quadrangle, Yosemite National Park, California, GQ-1570. U.S. Geol. Surv., Washington, D.C.

Bear, G. D. 1979. Evaluation of bighorn transplants in two Colorado localities. Colorado Div. Wildl., Fort Collins, Spec. Rep. No. 45. 11pp.

Begon, M., Harper, J. L. and Townsend, C. R. 1986. Ecology: individuals, populations and communities. Sinauer Assoc. Inc., Sunderland, Mass. 876pp.

Benson, G. L. 1988. Alpine dwarf-shrub. Pages 94-95 in Mayer, K. E. and W. F. Laudenslayer, eds. A guide to wildlife habitats of California. Calif. Dept. For. Fire Protection, Sacramento.

Berbach, M. W. 1987. The behavior, nutrition, and ecology of a population of reintroduced desert mountain sheep in the Whipple Mountains, San Bernardino County, California. M.S. Thesis, California State Poly. Univ., Pomona. 135pp.

Berger, J. 1990. Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. Conserv. Biol. 4:91-98.

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.

Blackwelder, E. 1931. Pleistocene glaciation in the Sierra Nevada and Basin ranges. Geol. Soc. Am. Bull. 42:865-922.

Blaisdell, J. A. 1976. Bighorn transplant in Lava Beds National Monument, California. Trans. North Am. Wild Sheep Conf. 2:89-90

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

_____ . 1949. Will the Sierra bighorn survive? Sierra Club Bull. 34:119-122.

Blood, D. A. 1963. Some aspects of behavior of a bighorn herd. Can. Field-Nat. 77:78-94.

Bradley, W. G. and D. P. Baker. 1967. Life tables for Nelson bighorn sheep on the desert game range. Desert Bighorn Counc. Transactions 11:142-170

Bunnell, F. L. 1980. Factors controlling lambing period of Dall's sheep. Can. J. Zool. 58:1027-1031.

_____ . 1982. The lambing period of mountain sheep: synthesis, hypothesis, and tests. Can. J. Zool. 60:1-14.

Buechner, H. K. 1960. The bighorn sheep in the United States, its past, present, and future. Wildl. Monogr. 4:1-74.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24:346-352.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley and Sons Ltd., New York, N.Y. 234pp.

Coggins, V. L. 1980. Present status of Rocky Mountain bighorn sheep in northeast Oregon. Bienn. Symposium North. Wild Sheep and Goat Counc. 2:90-104.

Conroy, M. J. and D. G. Krementz. 1990. A review of the evidence for the effects of hunting on American black duck populations. North Am. Wildl. Nat. Resour. Conf. 55:501-517

Crabtree, R. L. 1988. Sociodemography of an unexploited coyote population. Ph.D. Thesis, Univ. Idaho, Moscow. 79pp.

Dixon, J. S. 1936. The status of the Sierra bighorn sheep. Trans. North Am. Wildl. Conf. 1:631-643.

Douglas, C. L. and D. M. Leslie Jr. 1986. Influence of weather and density on lamb survival of desert bighorn sheep. J. Wildl. Manage. 50:153-156.

Downing, R. L. 1980. Vital statistics of animal populations. Pages 247-268 _in_ S. D. Schemnitz, ed. Wildlife management techniques manual. Fourth ed. The Wildl. Soc., Washington, D.C.

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

Dunn, J. E. and P. S. Gipson. 1977. Analysis of radio telemetry data in studies of home range. Biometrics 33:85-101.

Eisenberg, J. F. and D. G. Kleiman. 1972. Olfactory communication in mammals. Ann. Rev. Ecol. Syst. 3:1-32.

Elenowitz, A. S. 1983. Habitat use and population dynamics of transplanted desert bighorn sheep in the Peloncillo Mountains, New Mexico. M.S. Thesis, New Mexico State Univ., Las Cruces. 158pp.

Festa-Bianchet, M. 1988a. Age-specific reproduction of bighorn ewes in Alberta, Canada. J. Mammal. 69:157-160.

_____. 1988b. Birthdate and survival in bighorn lambs (Ovis canadensis). J. Zool., Lond. 214:653-661.

_____. 1989. Survival of male bighorn sheep in southwestern Alberta. J. Wildl. Manage. 53:259-263.

Ferson, S., F. J. Rohlf, L. Ginsburg, and G. Jacquez. 1988. RAMAS/a: modeling fluctuations in age-structured populations. Exeter Publ., Ltd., Setauket, N.Y. 117pp.

Foreyt, W. J. 1989. Fatal Pasteurella haemolytica pneumonia in bighorn sheep after direct contact with clinically normal domestic sheep. Am. J. Vet. Res. 50:341-344.

_____. and D. A. Jessup. 1982. Fatal pneumonia of bighorn sheep following association with domestic sheep. J. Wildl. Dis. 18:163-168.

Fowler, C. W. 1981. Density dependence as related to life history strategy. Ecology 62:602-610.

Garshelis, D. L. 1983. The role of sampling intensity in the selection of a home range model. Proc. Int. Conf. Wildl. Biotelem. 4:270-275.

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

_____ . 1971. Mountain Sheep: a study in behavior and evolution. Univ. Chicago Press, Chicago, Ill. 383pp.

_____ . 1975. On the management of mountain sheep: theoretical considerations. Pages 77-99 <u>in</u> J. B. Trefethen, ed. The wild sheep in modern North America. The Winchester Press, New York, N.Y.

Goldsmith, A. E. 1988. The behavior and ecology of pronghorn after reintroduction to Adobe Valley, California. Ph.D. Thesis, Univ. California, Berkeley. 112pp.

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

_____ , and T. I. Storer. 1924. Animal life of the Yosemite. Univ. California Press, Berkeley. 752pp.

Gionfriddo, J. P. and P. R. Kraussman. 1986. Summer habitat use by mountain sheep. J. Wildl. Manage. 50:331-336.

Goodman, D. 1987. How do any species persist? Lessons for conservation biology. Conserv. Biol. 1:59-62.

Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. Science 245:477-480.

Hamilton, W. J. and K. L. Blaxter. 1980. Reproduction in farmed red deer. J. Agric. Sci. Camb. 95:261-273.

Hansen, C. G. 1965. Growth and development of desert bighorn sheep. J. Wildl. Manage. 29:387-391.

_____ . 1967. Bighorn sheep populations of the Desert Game Range. J. Wildl. Manage. 31:693-706.

_____ , T. L. Hailey, and G. I. Day. 1980. Capturing, handling, and transplanting. Pages 273-287 <u>in</u> G. Monson and L. Sumner, eds. The desert bighorn: its life history, ecology, and management. Univ. Arizona Press, Tucson.

Hansen, M. C. 1982. Status and habitat preference of California bighorn sheep on Sheldon National Wildlife Refuge, Nevada. M.S. Thesis, Oregon State Univ., Corvallis. 75pp.

_____ . 1984a. Activity patterns of California bighorn sheep on Sheldon National Wildlife Refuge. Desert Bighorn Counc. Transactions 28:14-17.

_____ . 1984b. Population growth and dispersal of reintroduced California bighorn in northwestern Nevada. Trans. West. Sec. Wildl. Soc. 20:43-49.

Hanson, R. B. 1984. Grouping tendencies and home range development in an introduced herd of bighorn sheep (*Ovis canadensis californiana*). M.S. Thesis, California State Univ., Sacramento. 93pp.

Hayne, D. W. 1949. Calculation of size of home range. J. Mammal. 30:1-18.

Hebert, D. M. 1973. Altitudinal migration as a factor in the nutrition of bighorn sheep. Ph.D. Thesis, Univ. British Columbia, Vancouver. 346pp.

Heimer, W. E., S. M. Watson, and T. C. Smith. 1984. Excess ram mortality in a heavily hunted Dall sheep population. Bienn. Symposium North. Wild Sheep and Goat Counc. 4:425-432.

Hicks, L. L. and J. M. Elder. 1979. Human disturbance of Sierra Nevada bighorn sheep. J. Wildl. Manage. 43:909-915.

Hoefs, M. and M. Bayer. 1983. Demographic characteristics of an unhunted Dall sheep (_Ovis dalli dalli_) population in southwest Yukon, Canada. Can. J. Zool. 61:1346-1357.

_____ . and I. M. Cowan. 1979. Ecological investigation of a population of Dall sheep (_Ovis dalli dalli_). Syesis 12:1-83.

Hornocker, M. E. 1970. An analysis of mountain lion predation upon mule deer and elk in the Idaho Primitive Area. Wildl. Monogr. 21:1-39.

Johnson, R. L. 1983. Mountain goats and mountain sheep of Washington. Wash. Dept. Game, Olympia, Biol. Bull. No. 18. 196pp.

Johnson, R. P. 1973. Scent marking in mammals. Anim. Behav. 21:521-535.

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

Jorgensen, J. T. and W. D. Wishart. 1986. Ram Mountain bighorn project. Progress report--1984 and 1985. Alta. Energy Nat. Resour., Fish and Wildl. Div., Edmonton. 72pp.

Keay, J. A., J. D. Wehausen, C. D. Hargis, R. A. Weaver, and T. E. Blankinship. 1987. Mountain sheep reintroduction in the central Sierra: a cooperative effort. Trans. West. Sec. Wildl. Soc. 23:60-64

Kelly, W. E. 1980. Predator relationships. Pages 186-196 <u>in</u> G. Monson and L. Sumner, eds. The desert bighorn: its life history, ecology, and management. Univ. Arizona Press, Tucson.

Kenward, R. E. 1987. Wildlife radio tagging: equipment, field techniques, and data analysis. Academic Press, London. 222pp.

Kirkpatrick, R. L. 1980. Physiological indices in wildlife management. Pages 99-127 <u>in</u> S. D. Schemnitz, ed. Wildlife management techniques manual. Fourth ed. The Wildl. Soc., Washington, D.C.

Kistler, R. W. 1966. Geologic map of the Mono Craters, Mono and Tuolumne Counties, California, GC-462. U.S. Geol. Surv., Washington, D.C.

Kleiman, D. G. 1989. Reintroduction of captive mammals for conservation. Bioscience 39:152-161.

Kopec, L. L. 1982. Cutoff bighorn transplant: the first two years. Bienn. Symposium North. Wild Sheep and Goat Counc. 3:92-105.

Laudenslayer, W. F. and J. R. Boggs. 1988. Pinyon-juniper. Pages 62-63 <u>in</u> K. E. Mayer and W. F. Laudenslayer, eds. A guide to wildlife habitats of California. Calif. Dept. For. and Fire Protection, Sacramento.

Laundré, J. W. and B. L. Keller. 1984. Home-range of coyotes: a critical review. J. Wildl. Manage. 48:127-129.

Leslie, D. M. Jr. and C. L. Douglas. 1986. Modeling demographics of bighorn sheep: current abilities and missing links. North Am. Wildl. Nat. Resour. Conf. 51:62-73.

Major, J. L. 1977. California climate in relation to vegetation. Pages 11-74 in M. G. Barbour and J. Major, eds. Terrestrial vegetation of California. John Wiley and Sons, New York, N.Y.

_____ , and D. W. Taylor. 1977. Alpine. Pages 601-675 in M. G. Barbour and J. Major, eds. Terrestrial vegetation of California. John Wiley and Sons, New York, N.Y.

Macdonald, D. W., F. G. Ball, and N. G. Hough. 1979. The evaluation of home range size and configuration using tracking data. Pages 405-424 in C. J. Amlaner and D. W. Macdonald, eds. A handbook on biotelemetry and radio tracking. Pergamon Press, Oxford.

McCullough, D. R. 1979. The George Reserve Deer Herd. Univ. Michigan Press, Ann Arbor. 271pp.

_____ . 1985. Long range movements of large terrestrial mammals. Pages 444-465. in M. A. Rankin, ed. Migration: mechanisms and adaptive significance. Contrib. Marine Science, Suppl. vol. 27.

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

McCutchen, H. E. 1985. A technique to visually assess physical condition of bighorn sheep. Desert Bighorn Counc. Transactions 29:27-28.

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

_____ , and D. Pulliam. 1981. Results of a direct release desert bighorn sheep transplant in the Virgin Mountains of Nevada. Desert Bighorn Counc. Transactions 25:55-57.

Mitchell, B. and G. A. Lincoln. 1973. Conception dates in relation to age and condition in 2 populations of red deer in Scotland. J. Zool. Lond. 171:141-152.

Muir, J. 1894. The mountains of California. The Century Co., New York, N.Y. 381pp.

Müller-Schwarze, D. 1971. Phermones in black-tailed deer. Anim. Behav. 19:141-152.

Munz, P. A. and D. D. Keck. 1973. A California flora. Univ. California Press, Berkeley. 1681pp.

Murie, A. 1940. Ecology of the coyote in the Yellowstone. Fauna of the national parks of the United States. Contrib. Wildl. Surv. Fauna Ser. No. 4. 206pp.

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.

Packard, F. M. 1946. An ecological study of the bighorn sheep in Rocky Mountain National Park, Colorado. J. Mammal. 27:3-28.

Ralls, K., P. H. Harvey, and A. M. Lyles. 1986. Inbreeding in natural populations of birds and mammals. Pages 35-56 in M. Soulé, ed. Conservation biology: the science of scarcity and diversity. Sinauer Assoc., Inc. Sunderland, Mass.

Ricker, W. E. 1975. Computation and interpretation of biological statistics for fish populations. Fish. Res. Board Canada, Ottawa, Bull. 191. 382pp.

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

Rongstad, O. J. and J. R. Tester. 1969. Movement and habitat use of white-tailed deer in Minnesota. J. Wildl. Manage. 33:366-379.

Rowland, M. M. and J. L. Schmidt. 1981. Transplanting desert bighorn sheep, a review. Desert Bighorn Counc. Transactions 25:25-28.

Schoener, T. W. 1981. An empirically based estimate of home range. Theor. Pop. Biol. 20:281-325.

Schwartz, O. A., V. C. Bleich, and S. A. Holl. 1986. Genetics and the conservation of mountain sheep _Ovis canadensis nelsoni_. Biol. Conserv. 37:179-190.

Sharp, R. P. and J. H. Birman. 1963. Additions to classical sequence of Pleistocene glaciations, Sierra Nevada, California. Geol. Soc. Am. Bull. 74:1079-1086.

Shaw, H. G. 1983. Mountain lion field guide. Arizona Game and Fish Dept., Phoenix, Spec. Rep. No. 9. 38pp.

_____ . 1986. Evaluation of desert bighorn reintroductions. Arizona Game and Fish Dept., Phoenix, Fed. Aid Wildl. Restor. Proj. W-78-R. Final Rep. 13pp.

Sierra Nevada Bighorn Sheep Interagency Advisory Group. 1984. Sierra Nevada bighorn sheep recovery and conservation plan. Inyo Natl. For., Bishop, Calif. 17pp.

Simmons, N. M., M. B. Bayer, and L. O. Sinkey. 1984. Demography of Dall's sheep in the Mackenzie Mountains, Northwest Territories. J. Wildl. Manage. 48:156-162.

Skiba, G. T. and J. L. Schmidt. 1982. Inbreeding in bighorn sheep. Bienn. Symposium North. Wild Sheep and Goat Counc. 3:43-53.

Smith, T. S., Flinders, J. T., and Olsen, D. W. 1988. Status and distribution of Rocky Mountain bighorn sheep in Utah. Bienn. Symposium North. Wild Sheep and Goat Counc. 6:5-12.

Spanier, J. and K. B. Oldham. 1987. An atlas of functions. Hemisphere Pub. Corp. Washington, D.C. 700pp.

Spencer, W. D. and R. H. Barrett. 1984. An evaluation of the harmonic mean measure for defining carnivore activity areas. Acta Zool. Fennica 171:255-259.

Spraker, T. 1976. Capture myopathy in bighorn sheep. Pages 113-116 in E. T. Thorne, ed. Bienn. Symposium North. Wild Sheep Counc. Jackson, Wyo.

Streeter, R. G. 1970. A literature review on bighorn sheep population dynamics. Colorado Div. Game, Fish, Parks, Denver, Spec. Rep. No. 24. 11pp.

Swihart, R. K. and Slade, N. A. 1985a. Influence of sampling interval on estimates of home-range size. J. Wildl. Manage. 49:1019-1024.

_____ , and _____ . 1985b. Testing for independence of observations on animal movements. Ecology 66:1176-1184.

Thorne, E. T., Hickey, W. O., and Stewart, S. T. 1985. Status of California and Rocky Mountain bighorn sheep in the United States. Pages 56-81 in M. Hoefs, ed. Wild sheep: distribution, abundance, management, and conservation of the sheep of the world and closely related mountain ungulates. North. Wild Sheep and Goat Counc. Whitehorse, Yukon, Canada.

Thompson, R. W. and J. C. Turner. 1982. Temporal geographic variation in the lambing season of bighorn sheep. Can. J. Zool. 60:1781-1793.

U.S. Fish and Wildlife Service. 1987. Restoring America's wildlife. U.S. Gov. Printing Off., Washington, D.C. 394pp.

Van Winkle, W. 1975. Comparison of several probablistic home range models. J. Wildl. Manage. 39:118-123.

Weaver, R. A. 1985. The status of desert bighorn in the United States. Pages 82-85 in M. Hoefs, ed. Wild sheep: distribution, abundance, management, and conservation of the sheep of the world and closely related mountain ungulates. North. Wild Sheep and Goat Counc. Whitehorse, Yukon, Canada.

Wehausen, J. D. 1979. Sierra Nevada bighorn sheep: An analysis of management alternatives. Inyo Nat. For. and Sequoia and Kings Canyon Nat. Parks, Coop. Admin. Rep. 92pp.

_____ . 1980. Sierra Nevada bighorn sheep: history and population ecology. Ph. D. Thesis, Univ. of Michigan, Ann Arbor. 240pp.

_____ . 1987. Mountain sheep in California: a historical perspective on 108 years of full protection. Trans. West. Sec. Wildl. Soc. 23:65-74.

_____ . 1988. The historical distribution of mountain sheep in the Owens Valley region. Pages 97-105 in Mountains to Desert: selected Inyo readings. Friends East. Calif. Museum, Independence.

Welles, R. E. and F. B. Welles. 1961. The bighorn of Death Valley. Contrib. Wildl. Surv. Fauna Ser. No. 6. U.S. Gov. Printing Off., Washington, D.C. 242pp.

Wishart, W. D. 1978. Bighorn sheep. Pages 161-171 in J. L. Schmidt and D. L. Gilbert eds. Big game of North America: ecology and management. Stackpole Books. Harrisburg, Pa.

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

Worton, B. J. 1987. A review of models of home range for animal movement. Ecol. Modeling 38:277-298.

_____ . 1989. Kernel methods for estimating the utilization distribution in home range studies. Ecology 70:164-168.

Wright, G. M., J. S. Dixon, and B. H. Thompson. 1932. Fauna of the national parks of the United States. Contrib. Wildl. Surv. Fauna Ser. No. 1. U.S. Gov. Printing Off., Washington, D.C. 157pp.

Young, J. A., R. A. Evans, and J. Major. 1977. Sagebrush steppe. Pages 763-796 <u>in</u> Barbour, M. G. and J. Major, eds. Terrestrial vegetation of California. John Wiley and Sons, New York, N.Y.

Zar, J. 1984. Biostatistical analysis. Prentice Hall, Inc. Englewood Cliffs, N.J. 718pp.

APPENDIX A

PROGRAM INFORMATION FOR HOME RANGE PROGRAM PDF-XYZ.

The program PDF-XYZ 1.0 (Copyright (c) 1988, by Bob Crabtree and Fred Leban) is used in conjunction with the graphics program SURFER (Copyright (c) 1989 Golden Software Inc.) to describe the extent and intensity of an animal's space use. Program PDF-XYZ calculates a utilization distribution (UD) (Van Winkle 1975) based on a series of animal relocations. SURFER smooths the UD and generates probability contours which indicate the likelihood of finding an animal at a given location.

The UD is technically defined as a probability density function (PDF) with an underlying probability of 1.0 (Crabtree 1988). Program PDF-XYZ determines UD values using a modified grid cell method (Rongstad and Tester 1969) that assumes no underlying distribution. Grid cell probabilities or "z" values are calculated by dividing the number of relocations in a cell by the total number of relocations. The height of a given "z" point on the variable surface of the UD is the probability of locating an animal at the corresponding x,y coordinates (Crabtree 1988).

Grid size has a substantial influence the estimated UD (Ackerman et al. 1989, Macdonald et al. 1979, Spencer and

Barrett 1984). To reduce the subjectivity of selecting a grid size, PDF-XYZ analyzes location data using 32 iterations to calculate the appropriate grid size. Each iteration is the average of 9 nested iterations that place a grid of specified cell size over relocation data. Subsequent iterations steadily increase the grid size and calculate a dispersion coefficient that measures the distribution of relocations among the cells of the UD. PDF-XYZ calculates the percent change between dispersion coefficients from successive iterations and suggests a grid size based on the asymptote where percent change stabilizes.

Grid cell values of the UD are smoothed by SURFER using a nearest neighbor routine which weights values for the nearest 16 cells by the inverse of their distances. SURFER's nearest neighbor search originates from grid nodes so that the nearest 16 cells are those comprising a shell 2 cells deep. PDF-XYZ adds 2 lines to the end of each <filename>.XYZ file to offset the UD grid and the grid used by SURFER to establish probability contours. This centers UD values in grid cells and avoids the bias produced when values close to grid nodes are disproportionately weighted (Spencer and Barrett 1984).

Because UD methods are nonparametric, the distribution must be estimated from the sample itself. In addition, smoothing interpolates values to intermediate cells. Thus, a large number of relocations is necessary to obtain reliable results (Worton 1987, 1989). A minimum sample size of 80 relocations is recommended.

Input data format

Input files must be formatted as an ASCII text file with the filename extension .DAT. Data must be in 7 space-delimited columns, each representing a data field. Columns cannot contain embedded blanks. Columns 1-5 can be any length and may contain dummy variables since they are not used for processing. Columns 6 and 7 must contain the x and y grid coordinates for animal locations and consist of 8 and 9 spaces with 1.0 decimal place, respectively. The east-west and north-south UTM (universal transverse mercator) grid coordinate system is the most convenient to use although other grid systems are acceptable if they conform to the aforementioned requirements.

In the example below, columns 1 - 5 are observation number, date, observer, activity, and accuracy codes, respectively. Columns 6 and 7 are the east-west and north-south UTM coordinates. PDF-XYZ cannot distinguish between missing data values such as 9999999.9 and actual data in the UTM fields. Extreme values like these will produce error messages and cause the program to crash. Remove them before running the program.

```
880909 880830 TM 0 4 305800.0 4203300.0
880932 880903 LC 0 4 305800.0 4203500.0
880949 880908 LC 0 4 304100.0 4207400.0
880960 880910 LC 0 4 303600.0 4207000.0
880965 880911 LC 0 4 304000.0 4208000.0
870604 870626 lc 0 4 306300.0 4203300.0
870138 870627 lc 0 1 305900.0 4203400.0
......
 ......
  ......
```

Running PDF-XYZ

To start the program, type XYZ and press enter. You will be presented with the following list of questions/statements:

```
ENTER FILENAME WITHOUT ('.DAT') EXTENSION?
ENTER DRIVE/PATH OF OUTPUT .XYZ FILE?
ENTER THE PROPORTION OF OUTLIERS FLAGGED?
ENTER THE DETAIL FACTOR?
PLEASE WAIT - READING <filename>.DAT AND WRITING
<filename>.OUT
SUGGESTED GRID SIZE IS <filename> ##
DO YOU WANT TO ENTER YOUR OWN GRID SIZE (Y/N)?
ENTER GRID SIZE? (depending on your answer to the
previous question)
ENTER NUMBER OF ROWS AND COLUMNS ADDED TO THE
PERIPHERY?
PLEASE WAIT - WRITING <filename>.XYZ
DO YOU WANT TO RUN THE PROGRAM AGAIN (Y/N)?
```

In response to the prompt "ENTER FILENAME WITHOUT ('.DAT') EXTENSION?" enter the file to be processed. Default is the current drive and path. If the file resides in another directory, enter the full path. XYZ will next prompt you to "ENTER DRIVE/PATH OF OUTPUT .XYZ FILE?". The default is the current directory and filename.

The program will then prompt "ENTER THE PROPORTION OF OUTLIERS FLAGGED?". To minimize bias produced by extreme locations, XYZ allows the user to specify a percentage of outliers to be omitted in the calculation of grid cell size. Thus, given a sample size of 100, a response of 0.1 to the query "ENTER THE PROPORTION OF OUTLIERS FLAGGED?" would cause the 10 points farthest from the arithmetic mean of locations to be ignored. The default is 0.1.

Note that outliers are not physically removed from the data. They are only omitted from the calculation of grid cell size and the original data remains unchanged. If you decides to eliminate outliers they must be removed from the data manually.

The program will display "PLEASE WAIT - READING <filename>.DAT AND WRITING <filename>.OUT". After completing this task, it will display "SUGGESTED GRID SIZE IS <filename>" followed by a value. The value represents the length in data units of one side of the grid cell. Thus a suggested grid size of 100 represents a cell measuring 100 data units (meters if you are using UTM data) on a side. The program will also ask "DO YOU WANT TO INPUT YOUR OWN GRID SIZE?". At this point you can enter a grid size that XYZ will use to calculate grid cell values. Remember the grid size you select. You will be required to use it again later in SURFER.

In selecting your own grid cell size, keep in mind the precision of your data (Ackerman et al 1988, Kenward 1987, Macdonald et al. 1980) and that grid cell size will influence home range estimates by determining the number of relocations in a given cell. For a discussion of appropriate grid cell size, see Ackerman et al. (1988).

After a grid cell size has been entered, XYZ will ask "ENTER THE NUMBER OF ROWS AND COLUMNS TO ADD TO THE PERIPHERY?" The default is 2. These have no effect on grid cell size and their primarily purpose is to prevent contours from extending beyond the boundaries of the grid.

At this point, the program will display "PLEASE WAIT - WRITING <filename>.XYZ followed by "DO YOU WANT TO RUN THE PROGRAM AGAIN (Y/N)?" Enter the appropriate response.

XYZ output files, <filename>.OUT and <filename>.XYZ can be viewed using the DOS Type command or an ASCII text editor. Doing so may help the user to understand the workings of the program.

Processing PDF-XYZ output in SURFER

SURFER uses <filename>.XYZ to produce maps displaying probability contours for the smoothed UD. To start SURFER type SURFER and enter. Follow directions in the SURFER manual to input the <filename>.XYZ data file (remember that the input filename extension is .XYZ not .DAT). From the SURFER menu select the following options changing program defaults as necessary. Use program defaults in instances where no change is specified.

Type GRID to enter the SURFER GRID module. Once in GRID select the following menu options:

> DUPLICATE: select Ignore (program PDF-XYZ will generally not produce duplicate data points)
> GRIDSIZE: change Distance in Data Units Between x and y Grid Lines to the value entered at the prompt "SUGGESTED GRID SIZE IS?" or "DO YOU WANT TO INPUT YOUR OWN GRID SIZE?" in Program PDF-XYZ.
> SEARCH: select Normal; change Number of Nearest Points to 16
> METHOD: select InvDist; change InvDist Weighting Power to 1
> BEGIN

Once GRID has produced the output file <filename>.GRD, use TOPO to generate a contour map of the UD. For output, follow instructions detailed in the SURFER manual to produce contour maps and surface plots.

APPENDIX B

HOME RANGE MAPS FOR BIGHORN SHEEP REINTRODUCED TO LEE VINING CANYON IN 1986 AND 1987 PRODUCED BY PROGRAM PDF-XYZ.

Interior contours on home range maps were left unlabeled to improve legibility. When shown, interior contours indicate probabilities of 0.005, 0.01, 0.02, 0.03, 0.04, and 0.05.

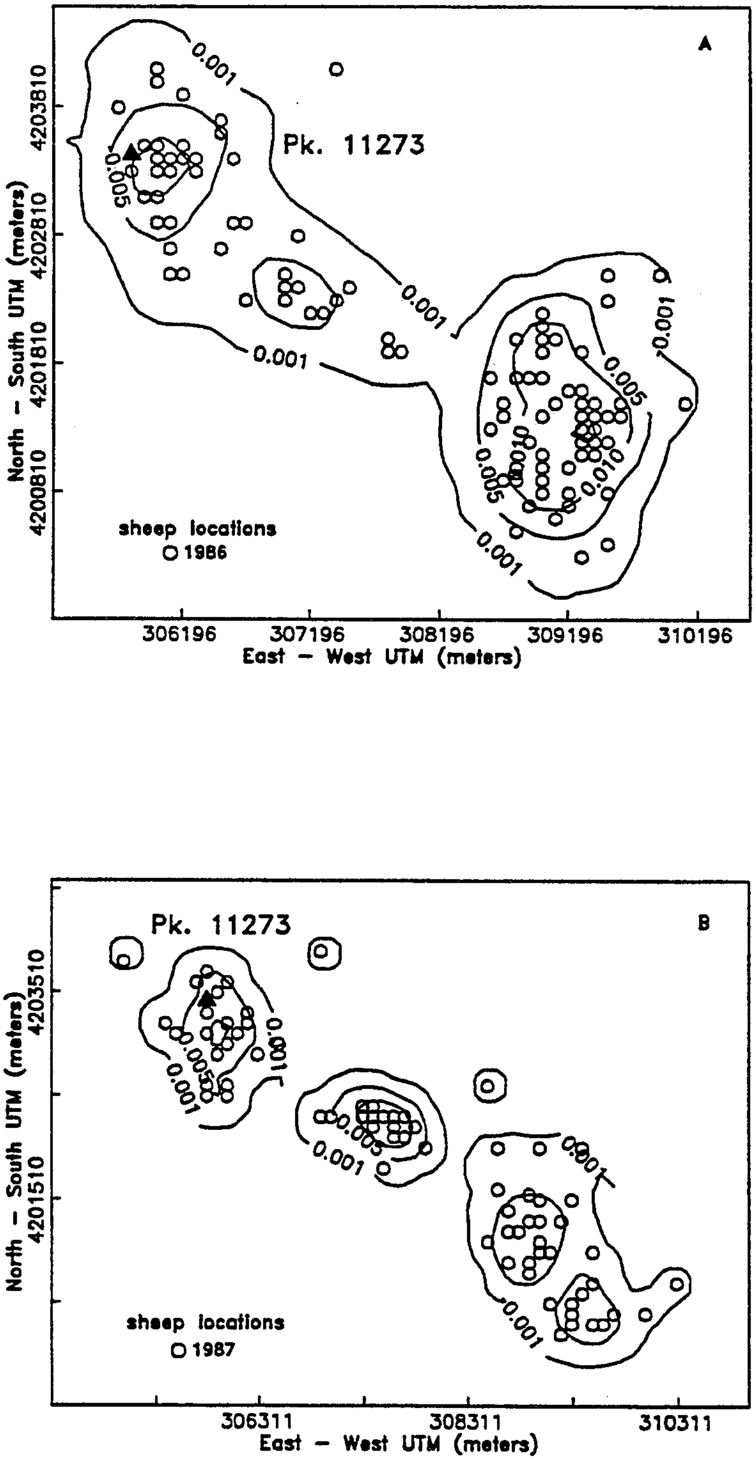


Figure 1. summer/fall 1986 (A) and winter/spring 1987 (B) ranges used by bighorn ewe 4381 in Lee Vining Canyon, Mono Co., Calif.

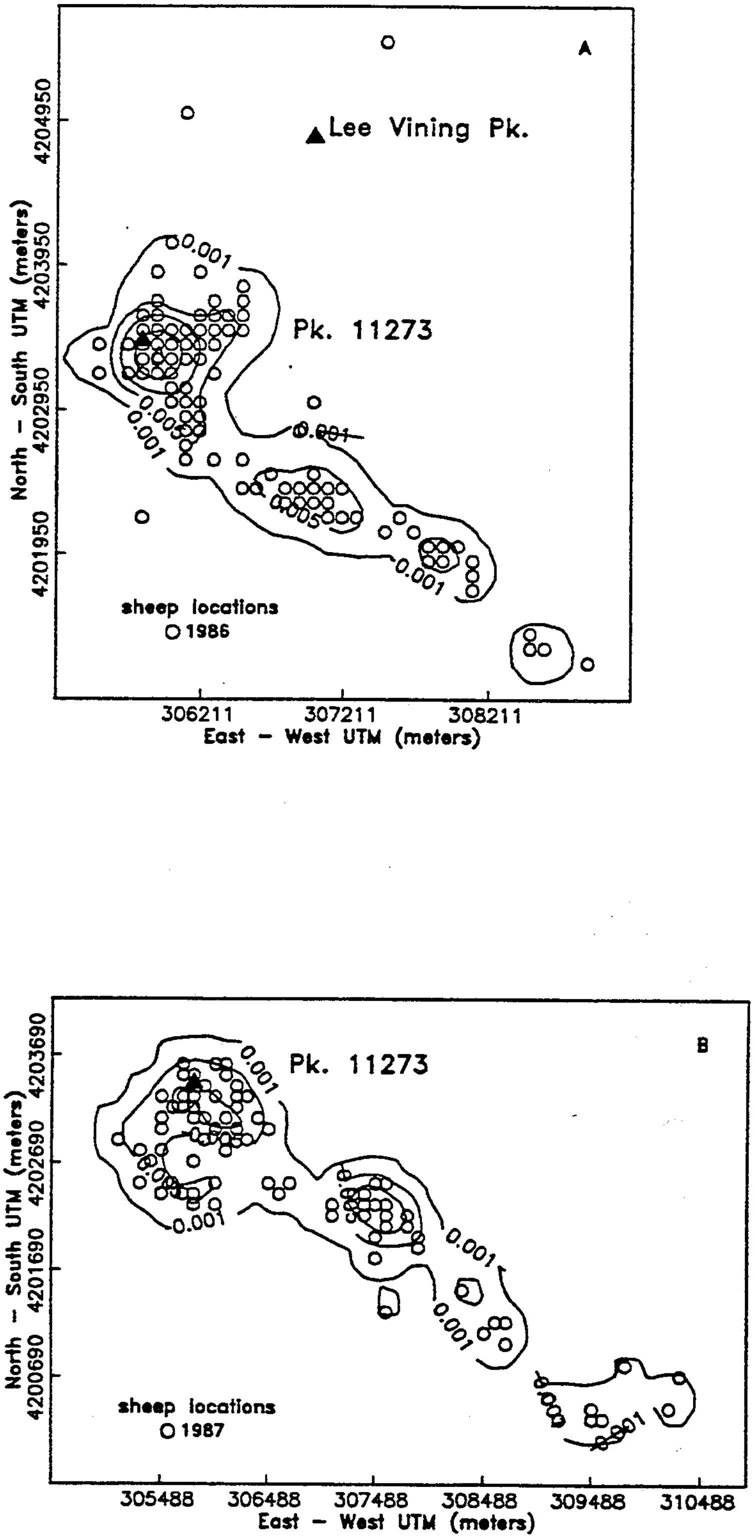


Figure 2. summer/fall 1986 (A) and winter/spring 1987 (B) ranges used by bighorn ewe 4411 in Lee Vining Canyon, Mono Co., Calif.

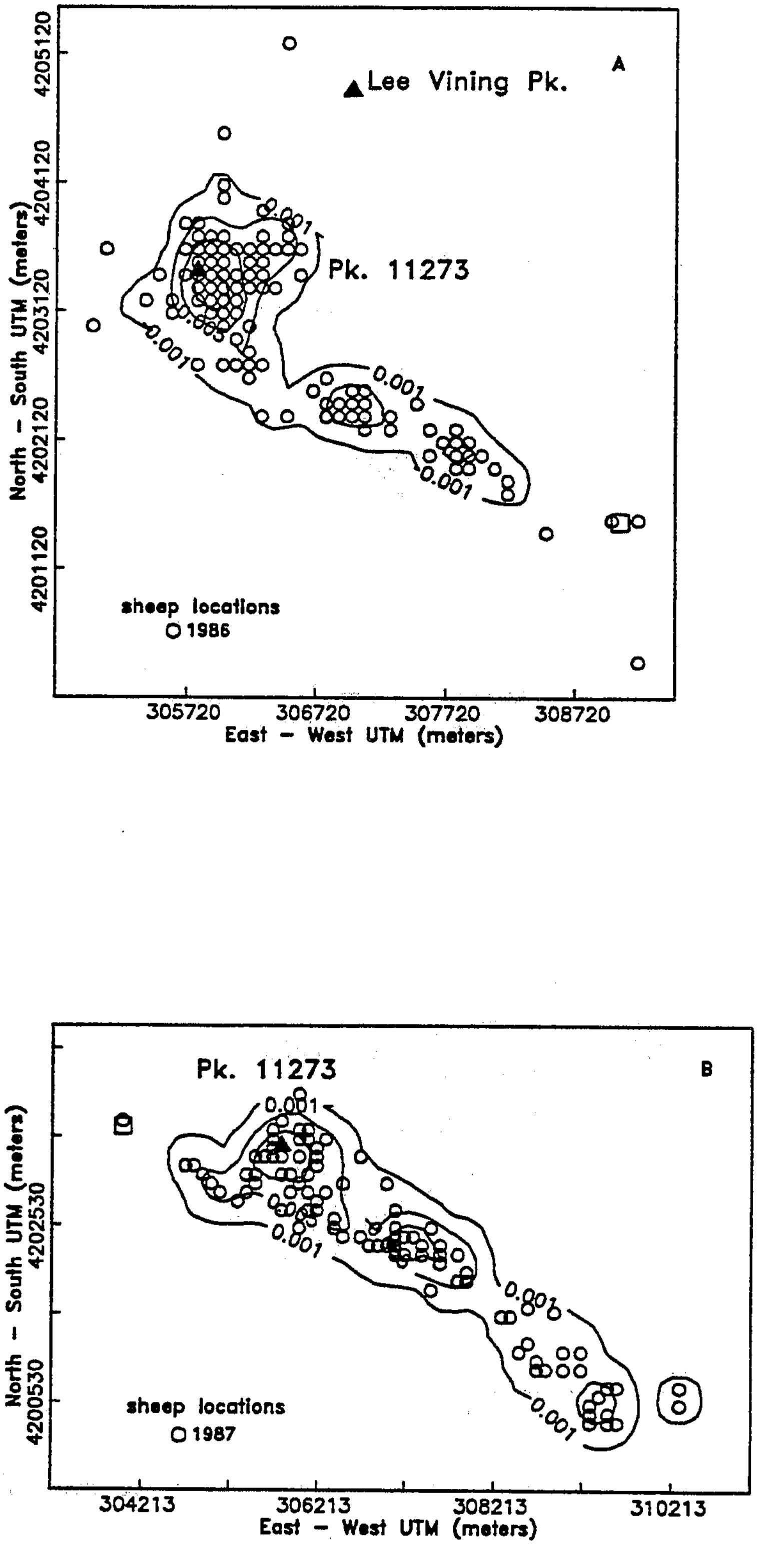


Figure 3. summer/fall 1986 (A) and winter/spring 1987 (B) ranges used by bighorn ewe 4451 in Lee Vining Canyon, Mono Co., Calif.

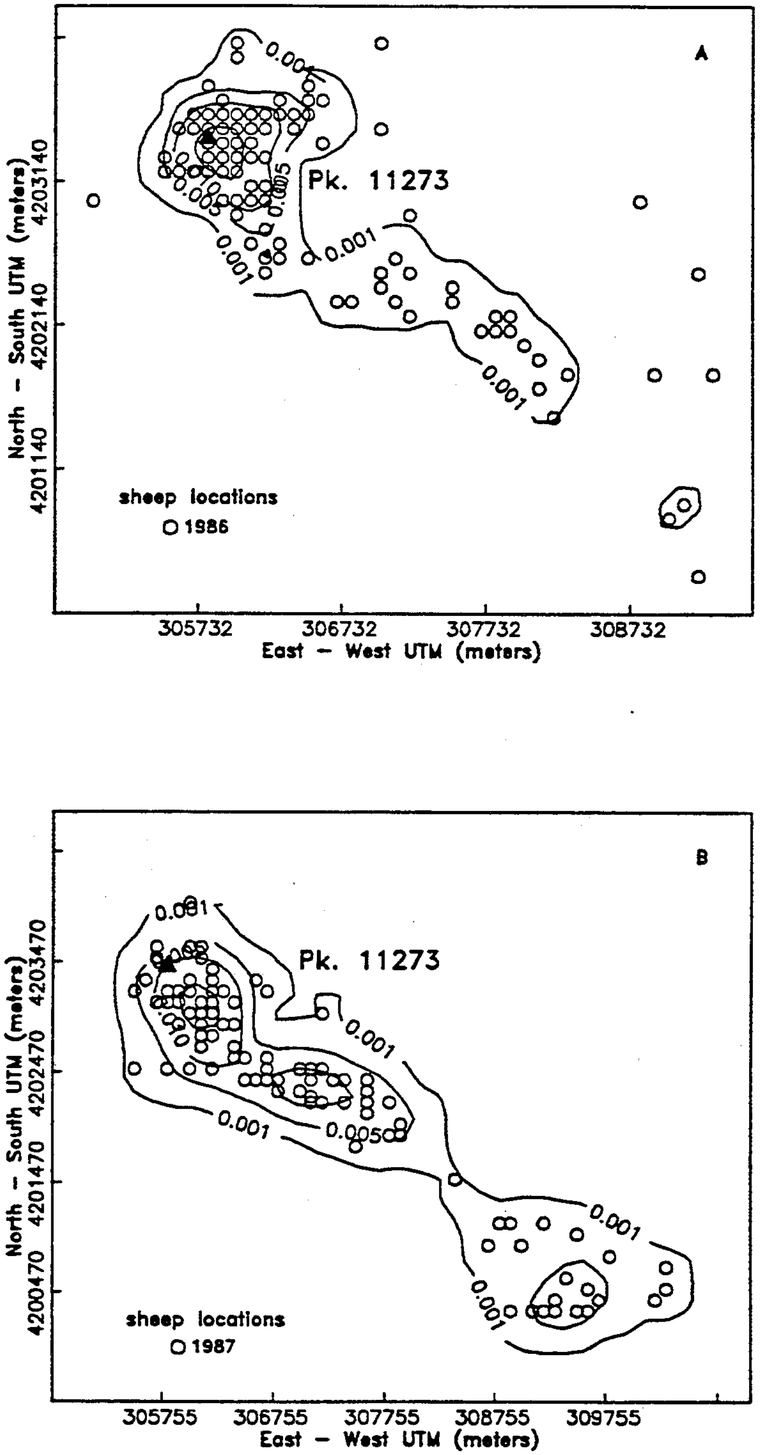
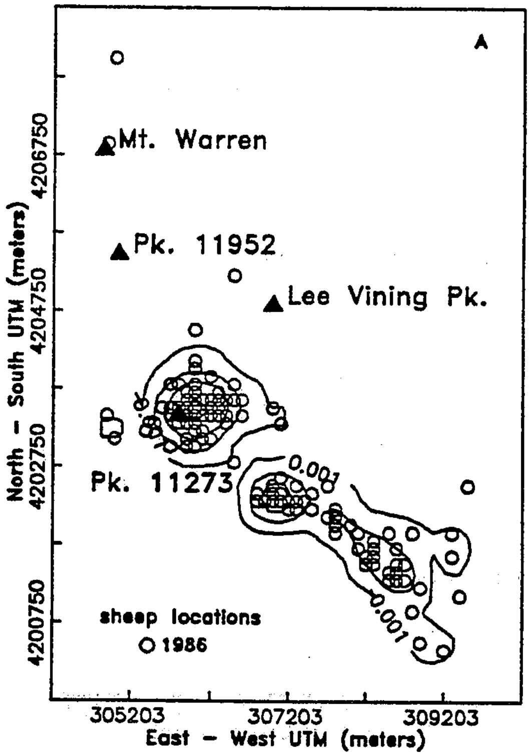


Figure 4. summer/fall 1986 (A) and winter/spring 1987 (B) ranges used by bighorn ewe 4601 in Lee Vining Canyon, Mono Co., Calif.



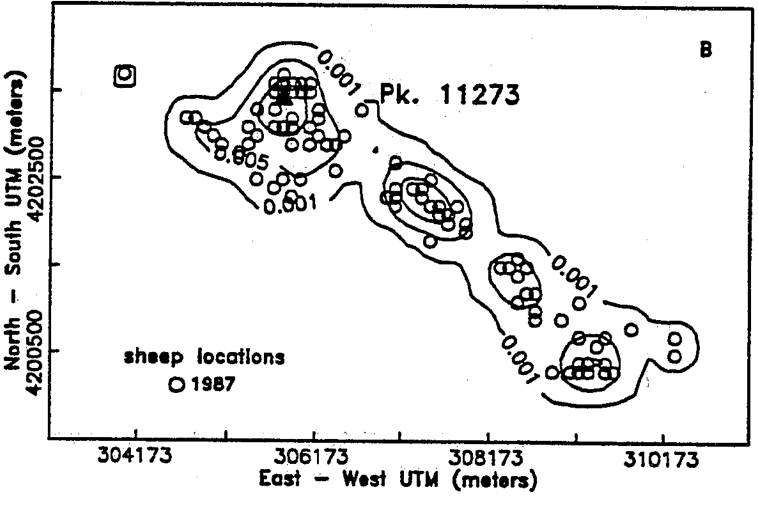
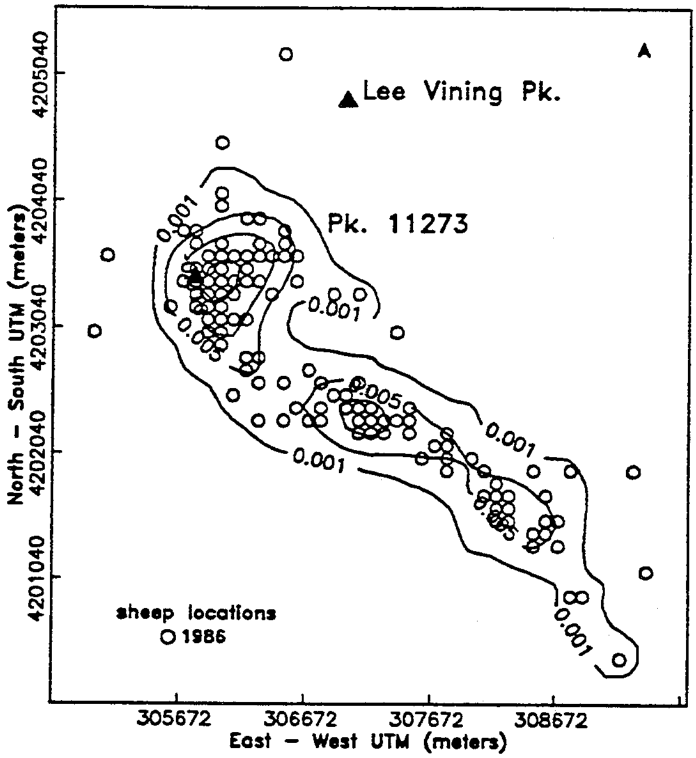


Figure 5. summer/fall 1986 (A) and winter/spring 1987 (B) ranges used by bighorn ewe 4731 in Lee Vining Canyon, Mono Co., Calif.



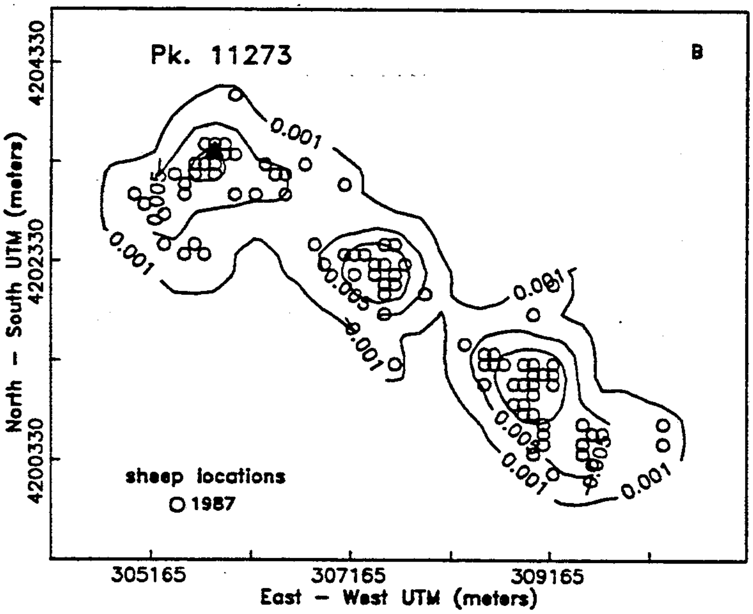


Figure 6. summer/fall 1986 (A) and winter/spring 1987 (B) ranges used by bighorn ewe 4801 in Lee Vining Canyon, Mono Co., Calif.

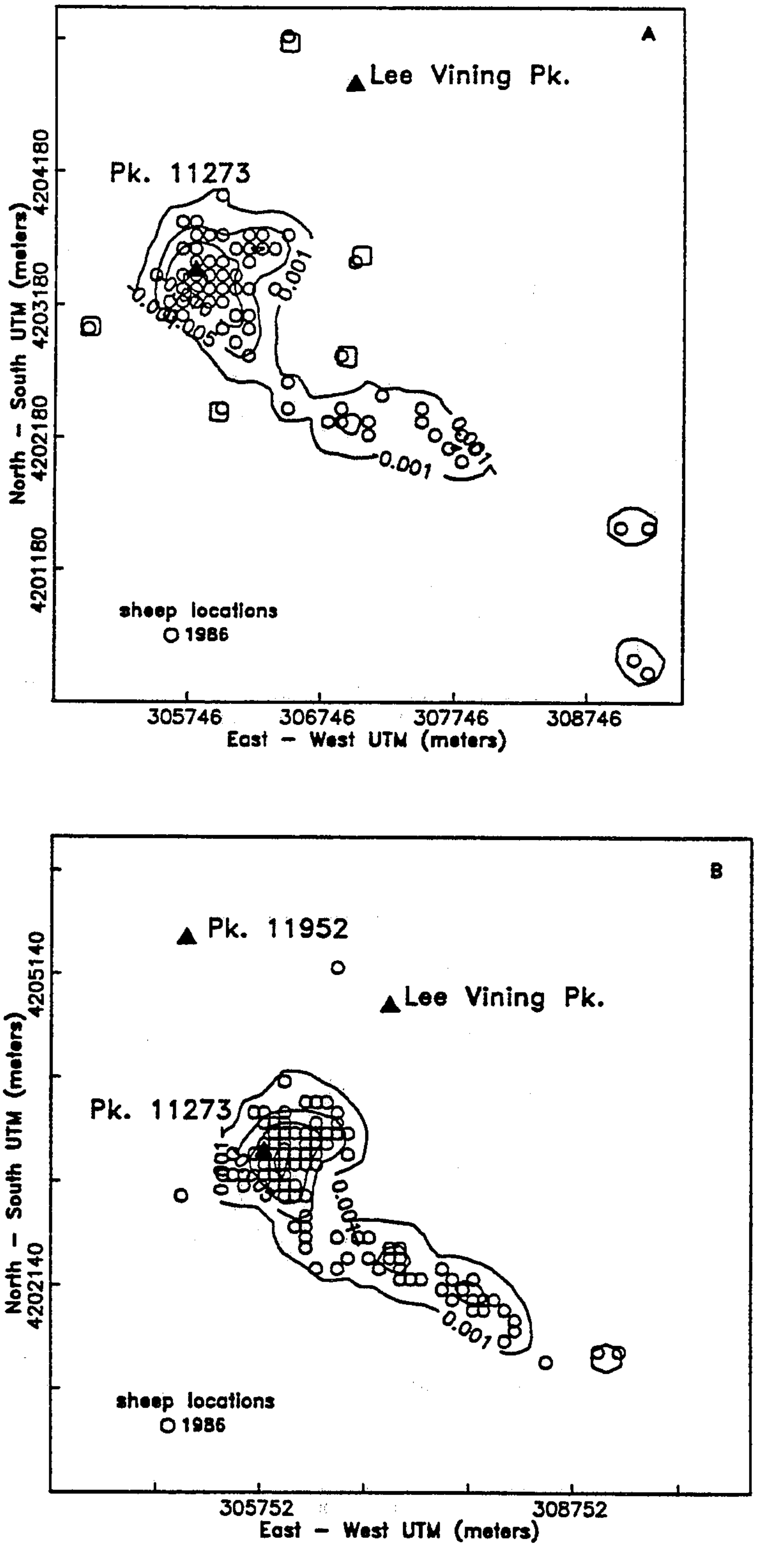


Figure 7. 1986 summer/fall ranges used by bighorn ewes 4351 (A) and 4361 (B) in Lee Vining Canyon, Mono Co., Calif.

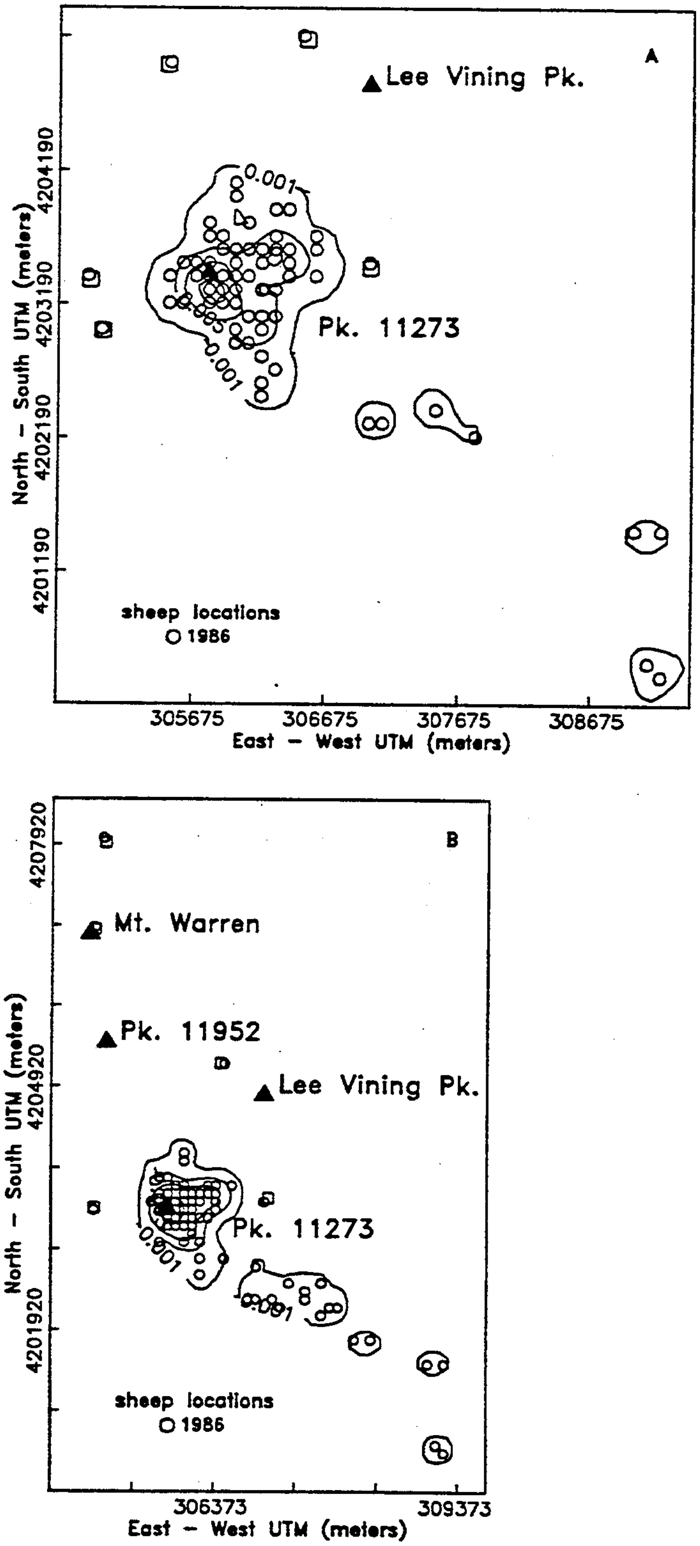


Figure 8. 1986 summer/fall ranges used by bighorn ewes 4391 (A) and 4781 (B) in Lee Vining Canyon, Mono Co., Calif.

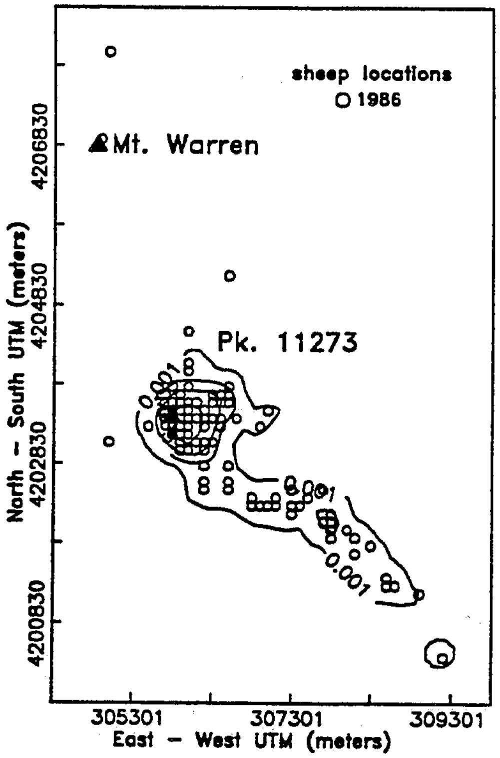


Figure 9. 1986 summer/fall range used by bighorn ewe 4651 in Lee Vining Canyon, Mono Co., Calif.

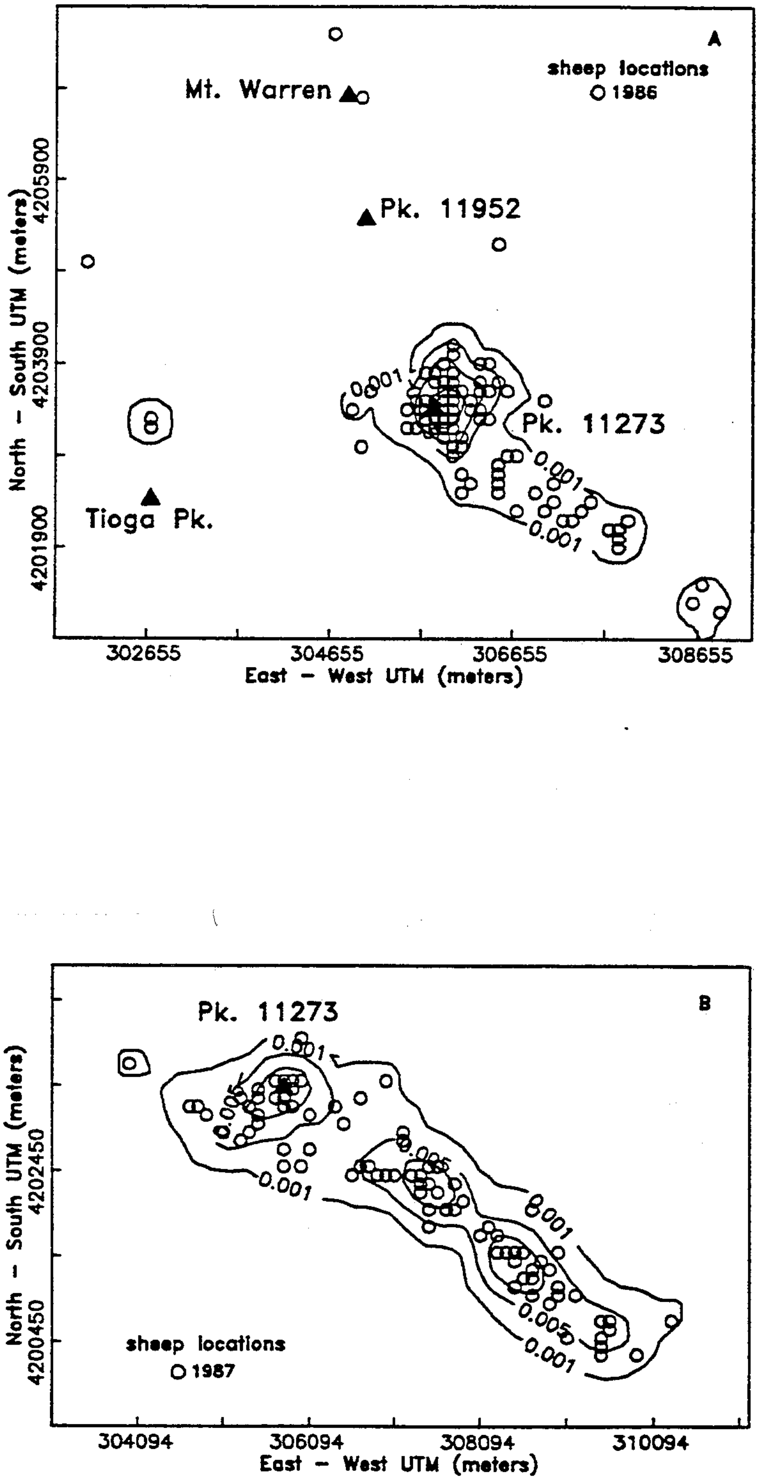


Figure 10. summer/fall 1986 (A) and winter/spring 1987 (B) ranges used by bighorn ram 4421 in Lee Vining Canyon, Mono Co., Calif.

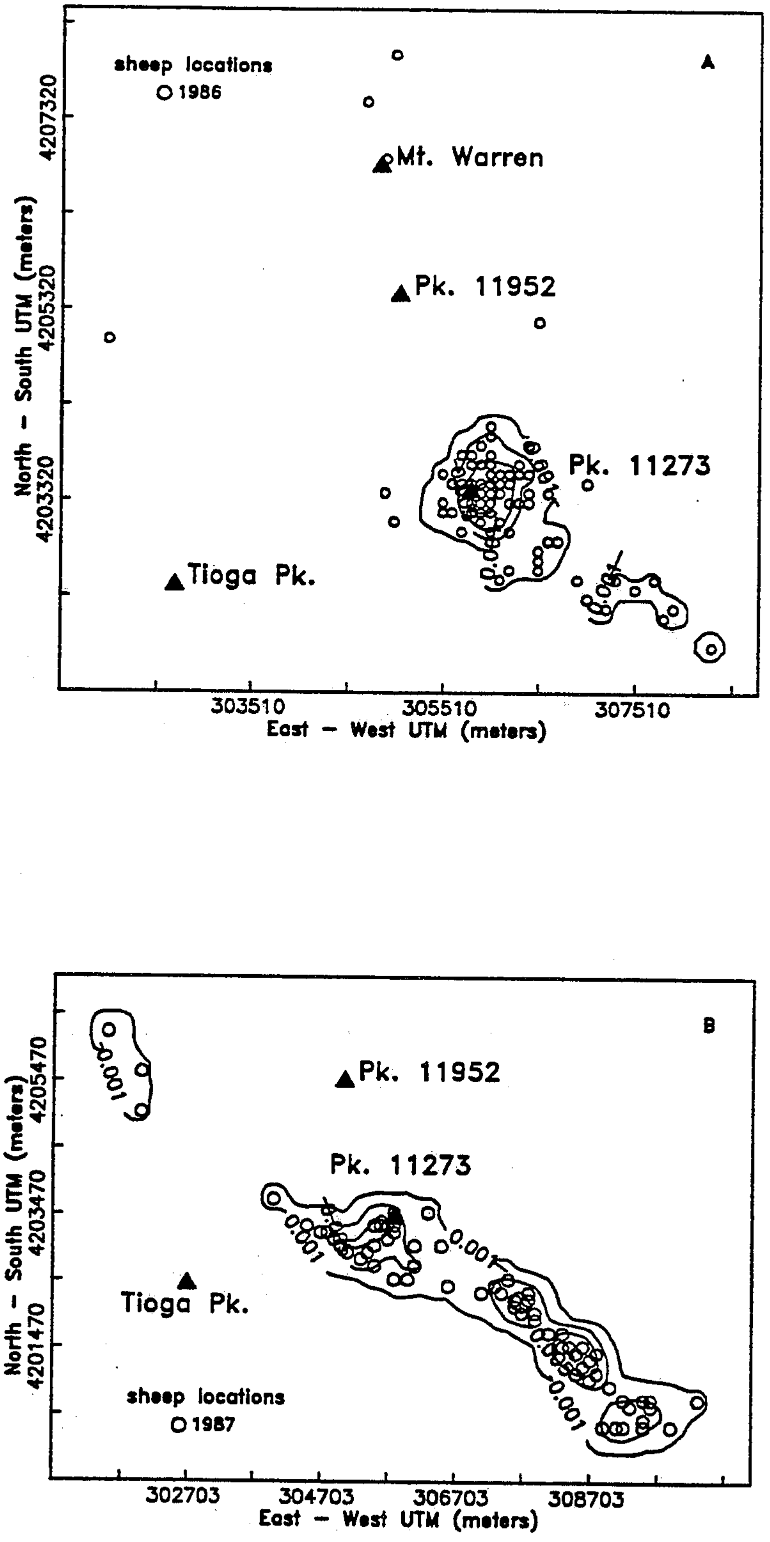


Figure 11. summer/fall 1986 (A) and winter/spring 1987 (B) ranges used by bighorn ram 4791 in Lee Vining Canyon, Mono Co., Calif.

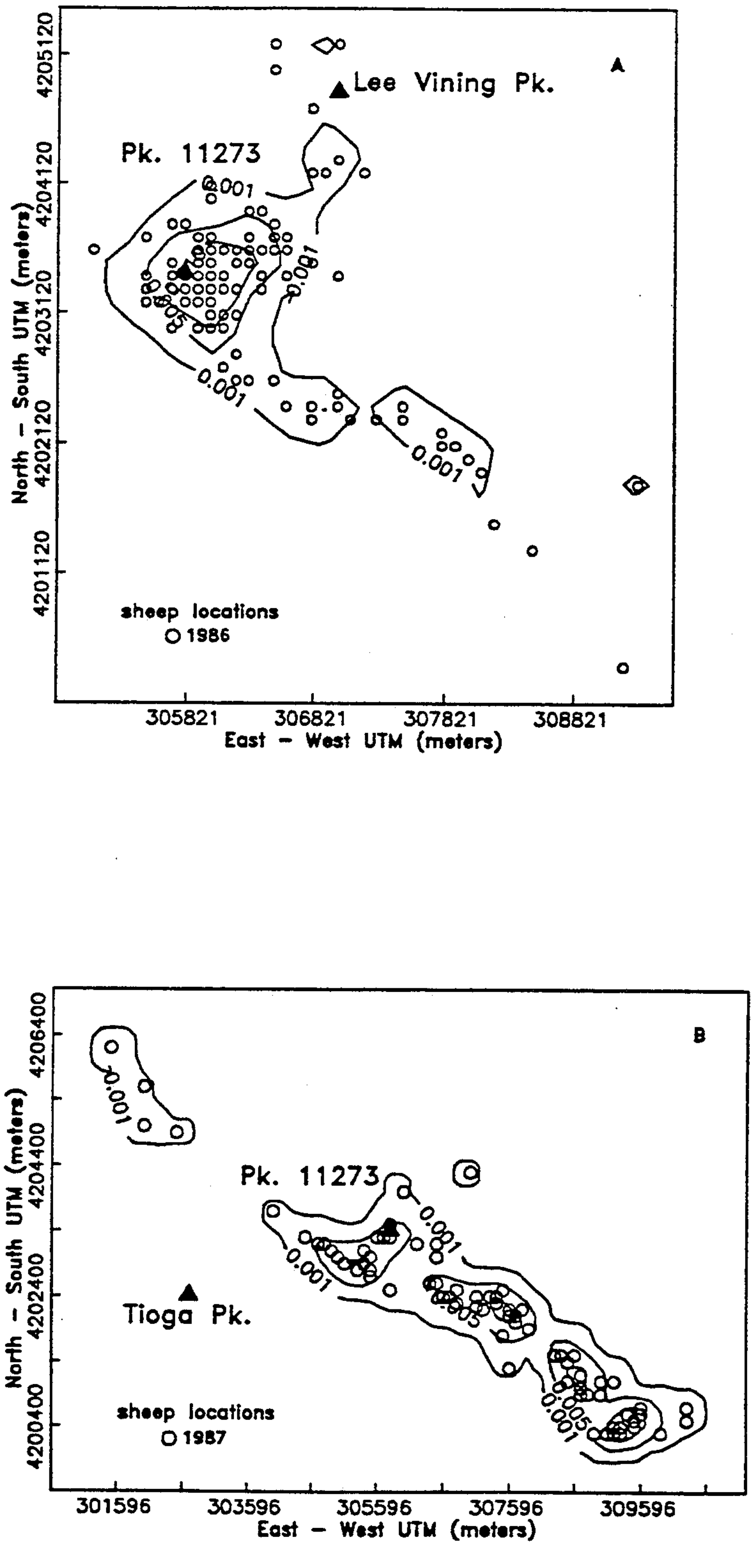
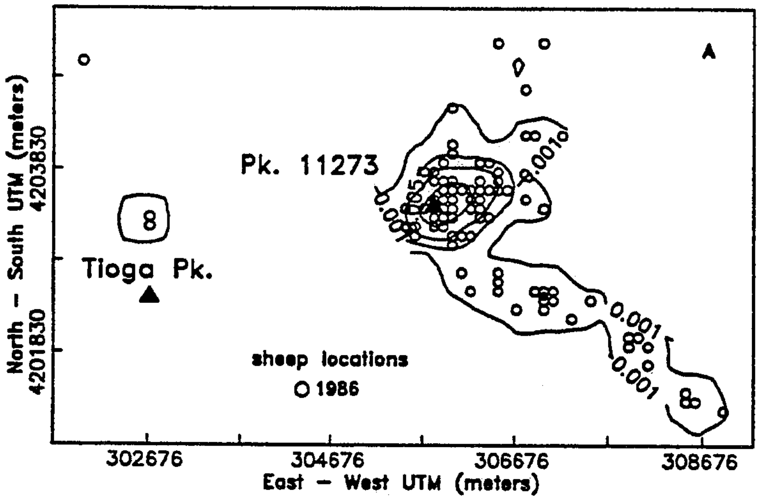


Figure 12. summer/fall 1986 (A) and winter/spring 1987 (B) ranges used by bighorn ram 4811 in Lee Vining Canyon, Mono Co., Calif.



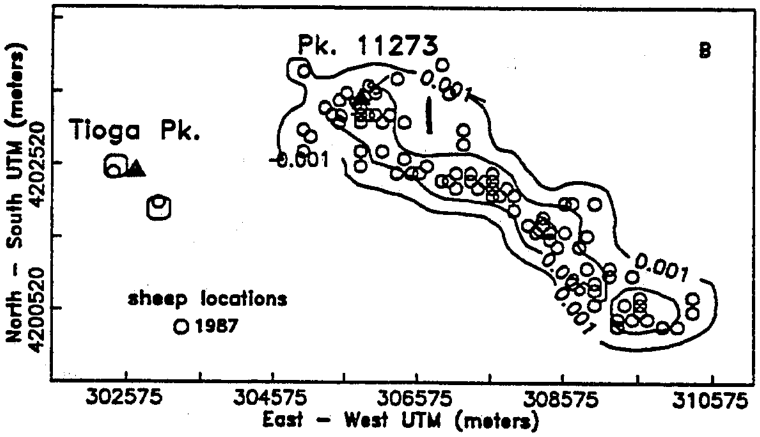


Figure 13. summer/fall 1986 (A) and winter/spring 1987 (B) ranges used by bighorn ram 4851 in Lee Vining Canyon, Mono Co., Calif.

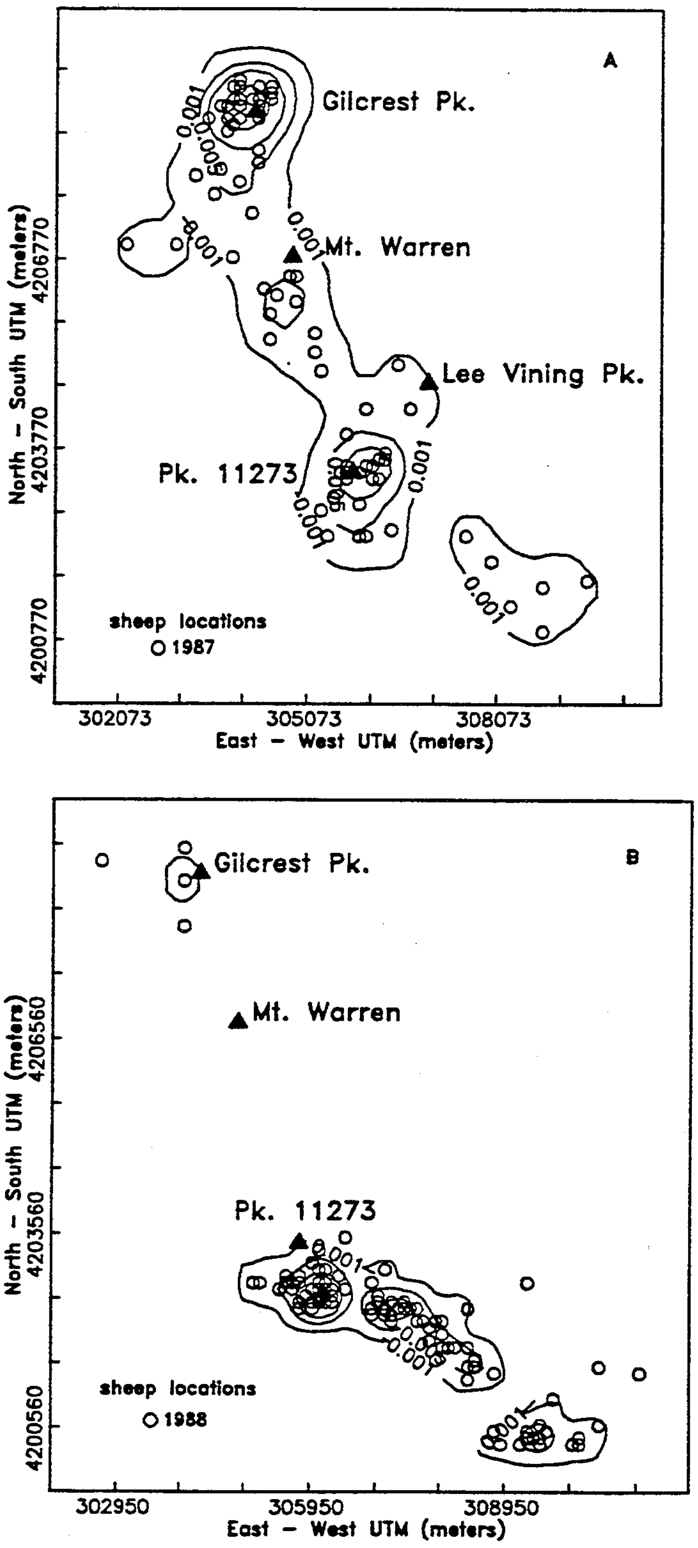


Figure 14. summer/fall 1987 (A) and winter/spring 1988 (B) ranges used by bighorn ewe 4411 in Lee Vining Canyon, Mono Co., Calif.

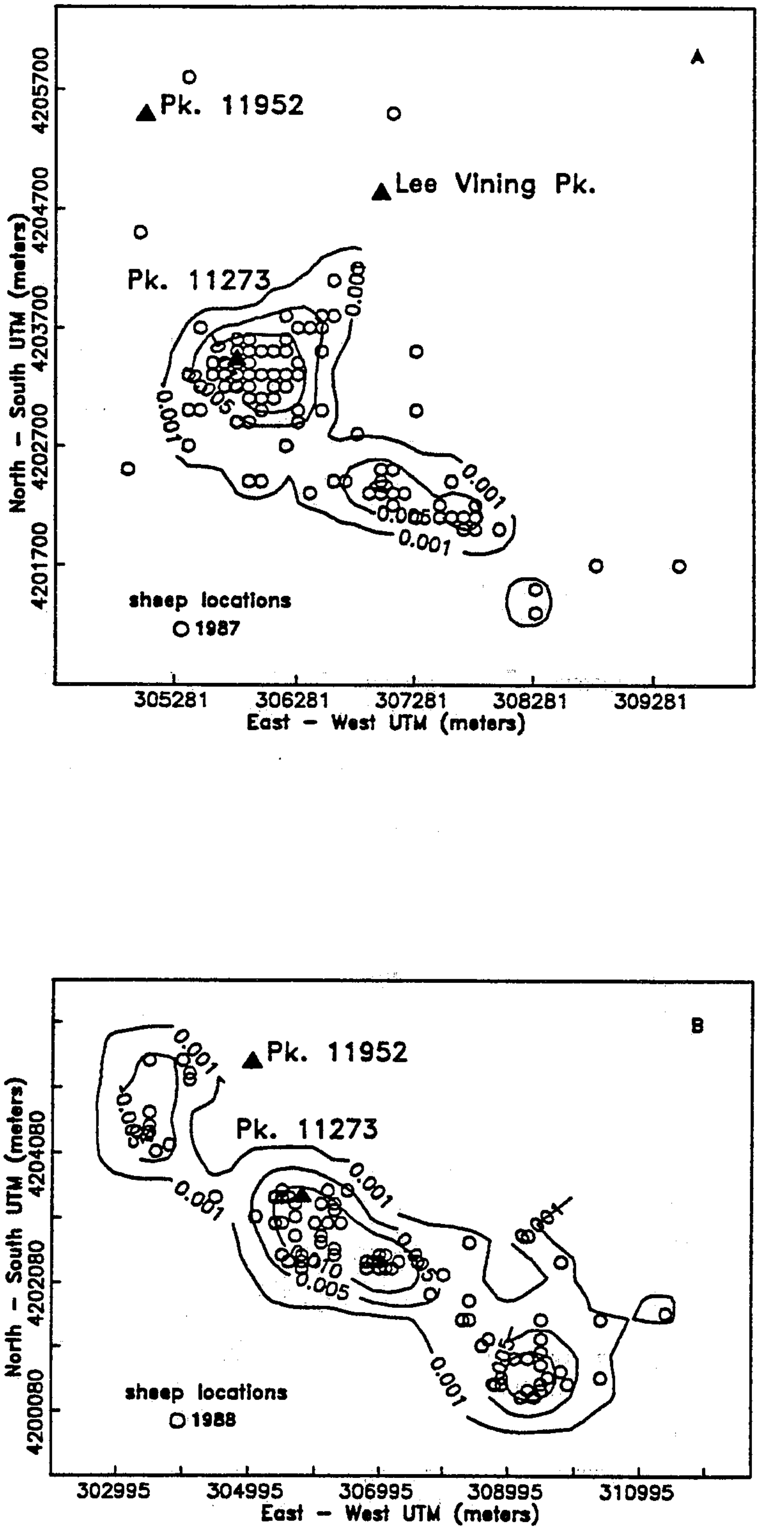


Figure 15. summer/fall 1987 (A) and winter/spring 1988 (B) ranges used by bighorn ewe 4451 in Lee Vining Canyon, Mono Co., Calif.

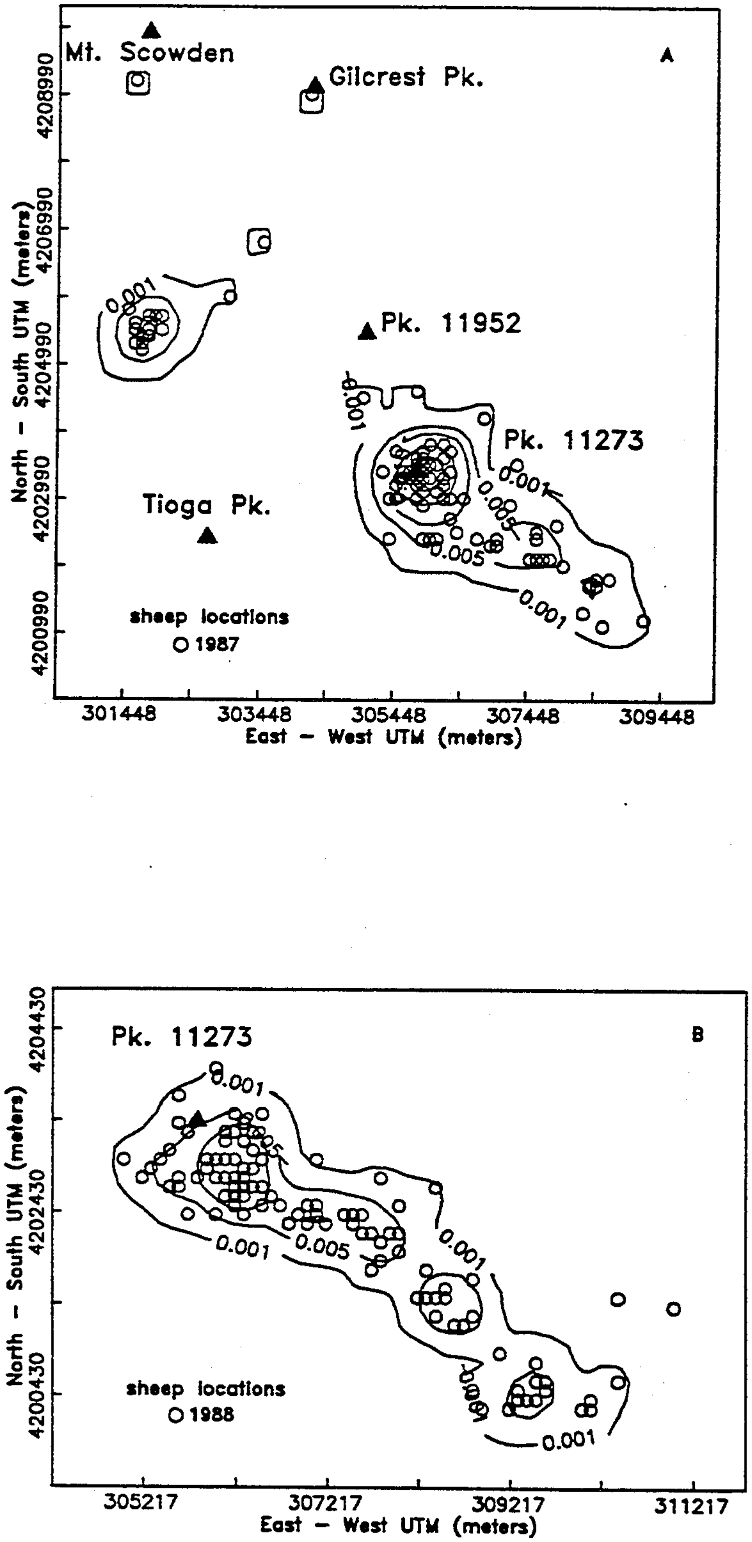


Figure 16. summer/fall 1987 (A) and winter/spring 1988 (B) ranges used by bighorn ewe 4731 in Lee Vining Canyon, Mono Co., Calif.

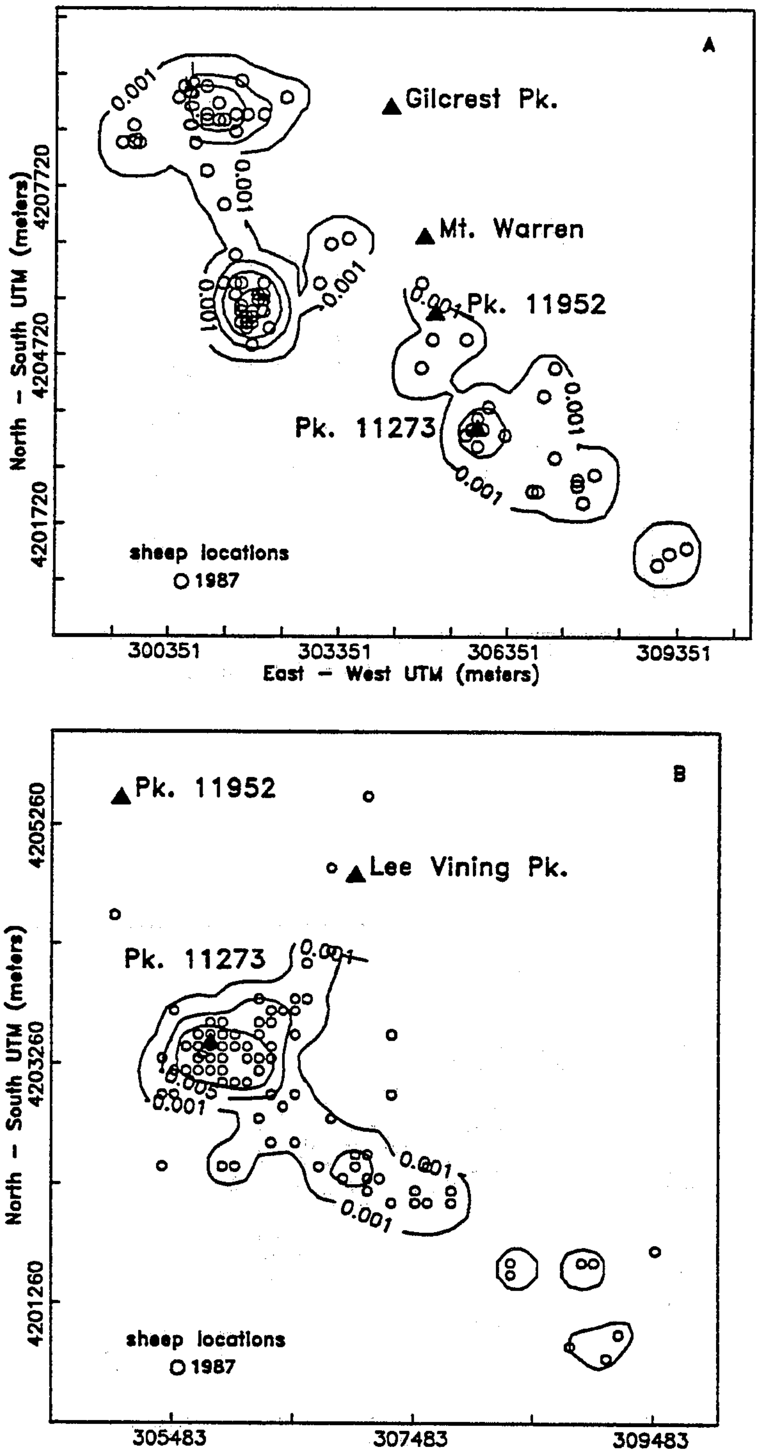


Figure 17. 1987 summer/fall ranges used by bighorn ewes 4381 (A) and 4801 (B) in Lee Vining Canyon, Mono Co., Calif.

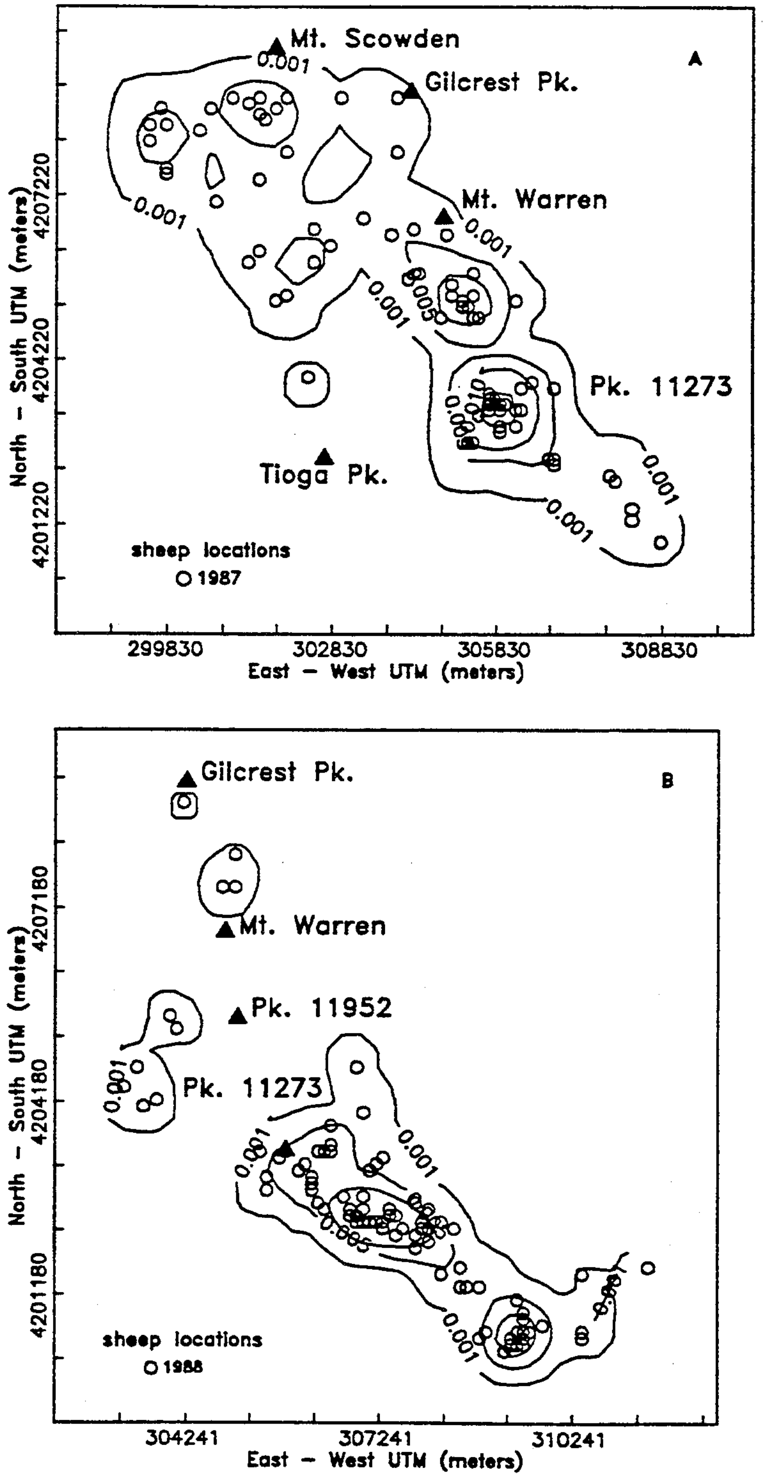
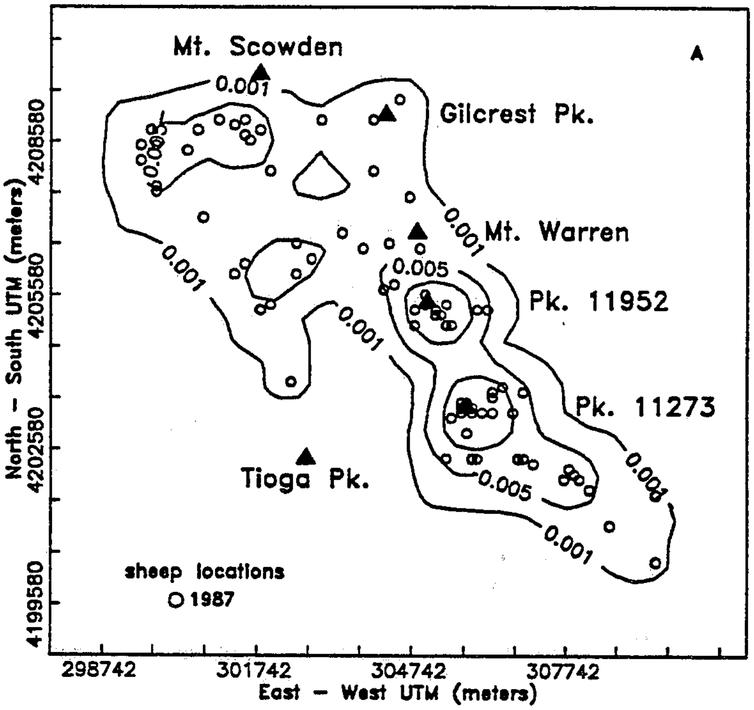


Figure 18. summer/fall 1987 (A) and winter/spring 1988 (B) ranges used by bighorn ram 4421 in Lee Vining Canyon, Mono Co., Calif.



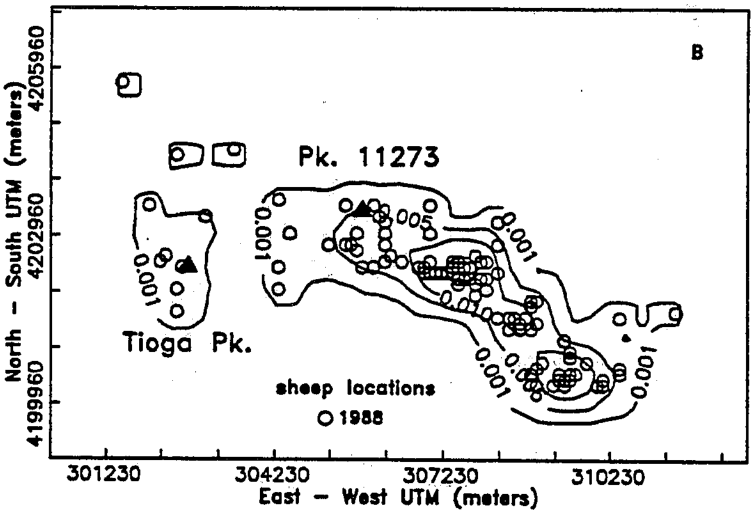


Figure 19. summer/fall 1987 (A) and winter/spring 1988 (B) ranges used by bighorn ram 4851 in Lee Vining Canyon, Mono Co., Calif.

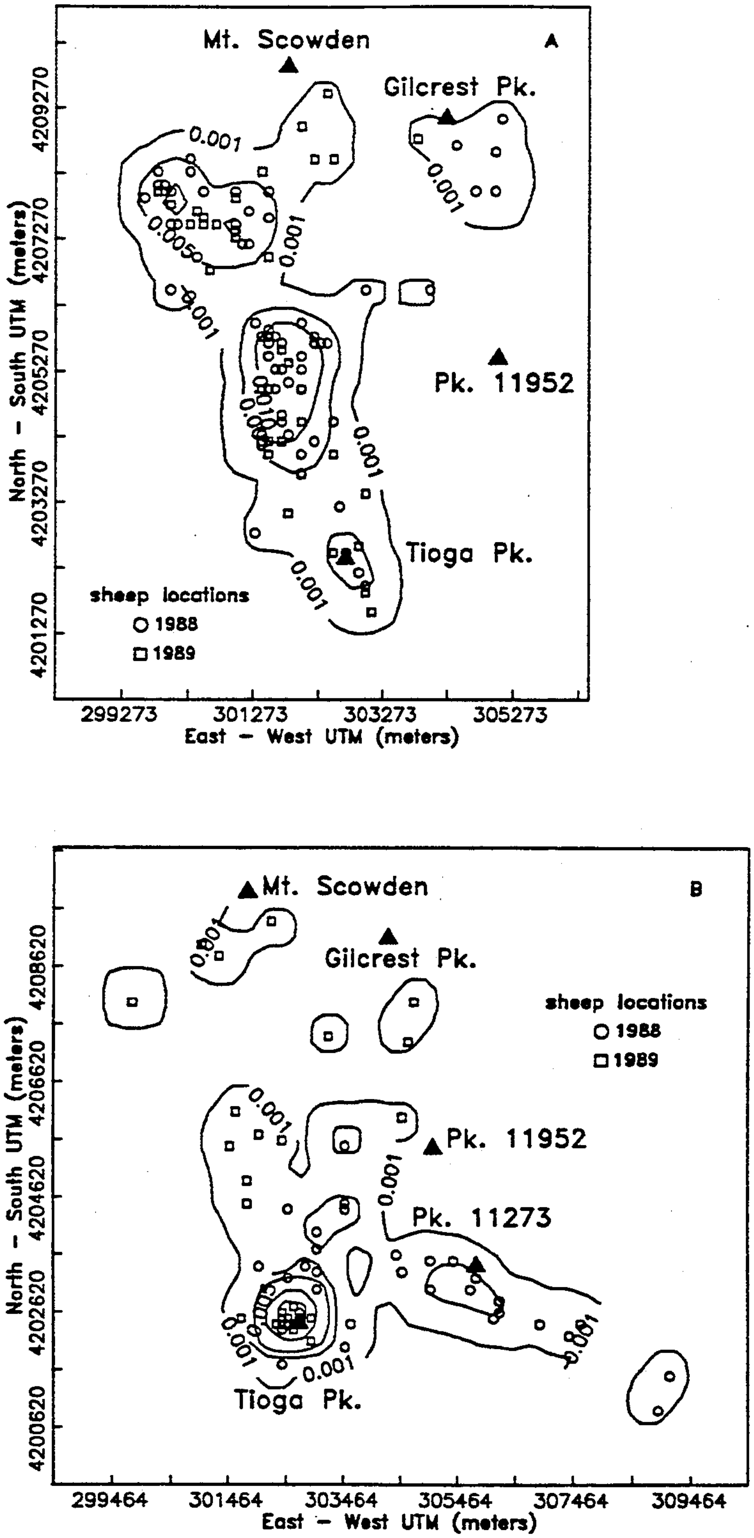


Figure 20. 1988-1989 summer/fall (A) and winter/spring (B) ranges used by bighorn ewe 4381 in Lee Vining Canyon, Mono Co., Calif.

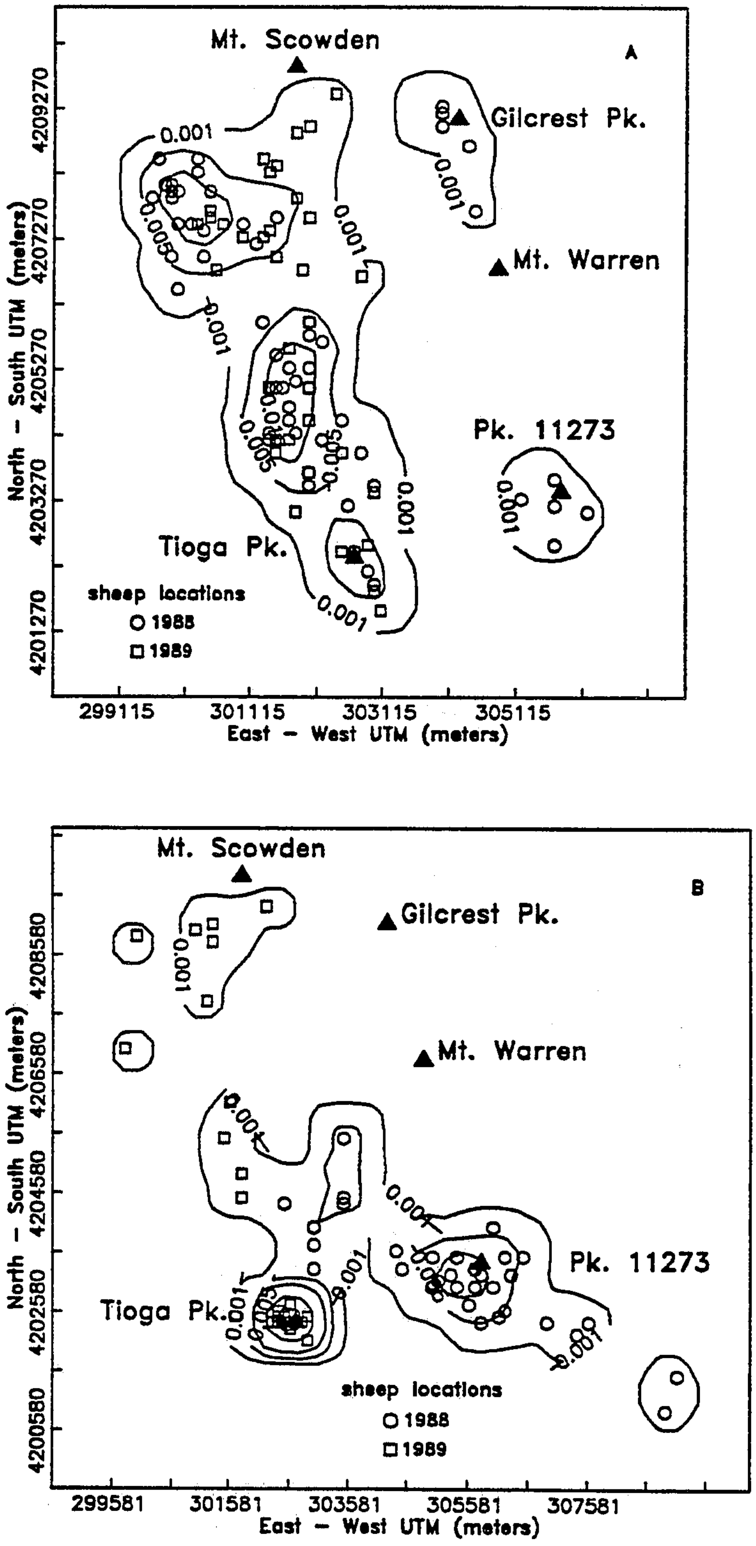


Figure 21. 1988–1989 summer/fall (A) and winter/spring (B) ranges used by bighorn ewe 4464 in Lee Vining Canyon, Mono Co., Calif.

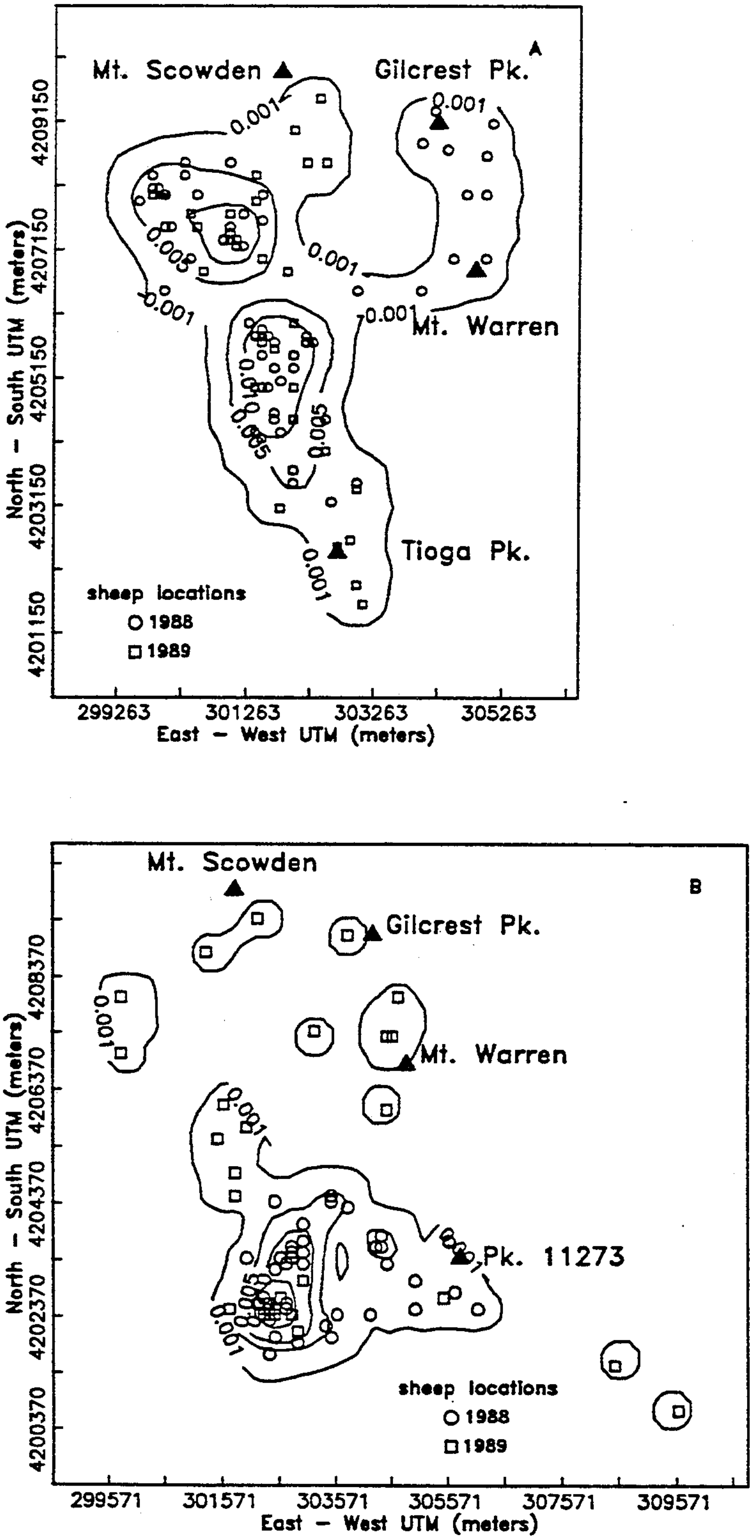


Figure 22. 1988–1989 summer/fall (A) and winter/spring (B) ranges used by bighorn ewe 4651 in Lee Vining Canyon, Mono Co., Calif.

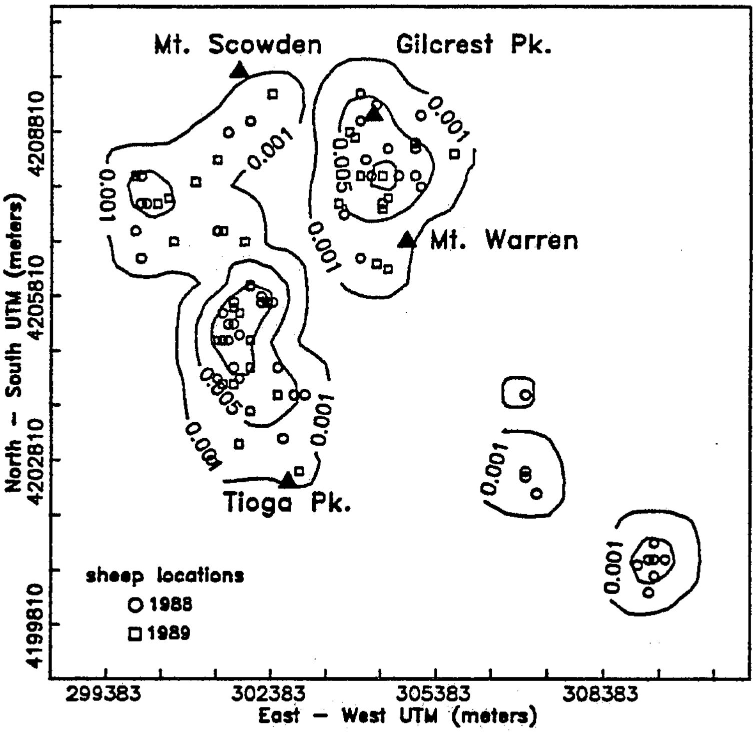


Figure 23. 1988–1989 summer/fall range used by bighorn ewe 4688 in Lee Vining Canyon, Mono Co., Calif

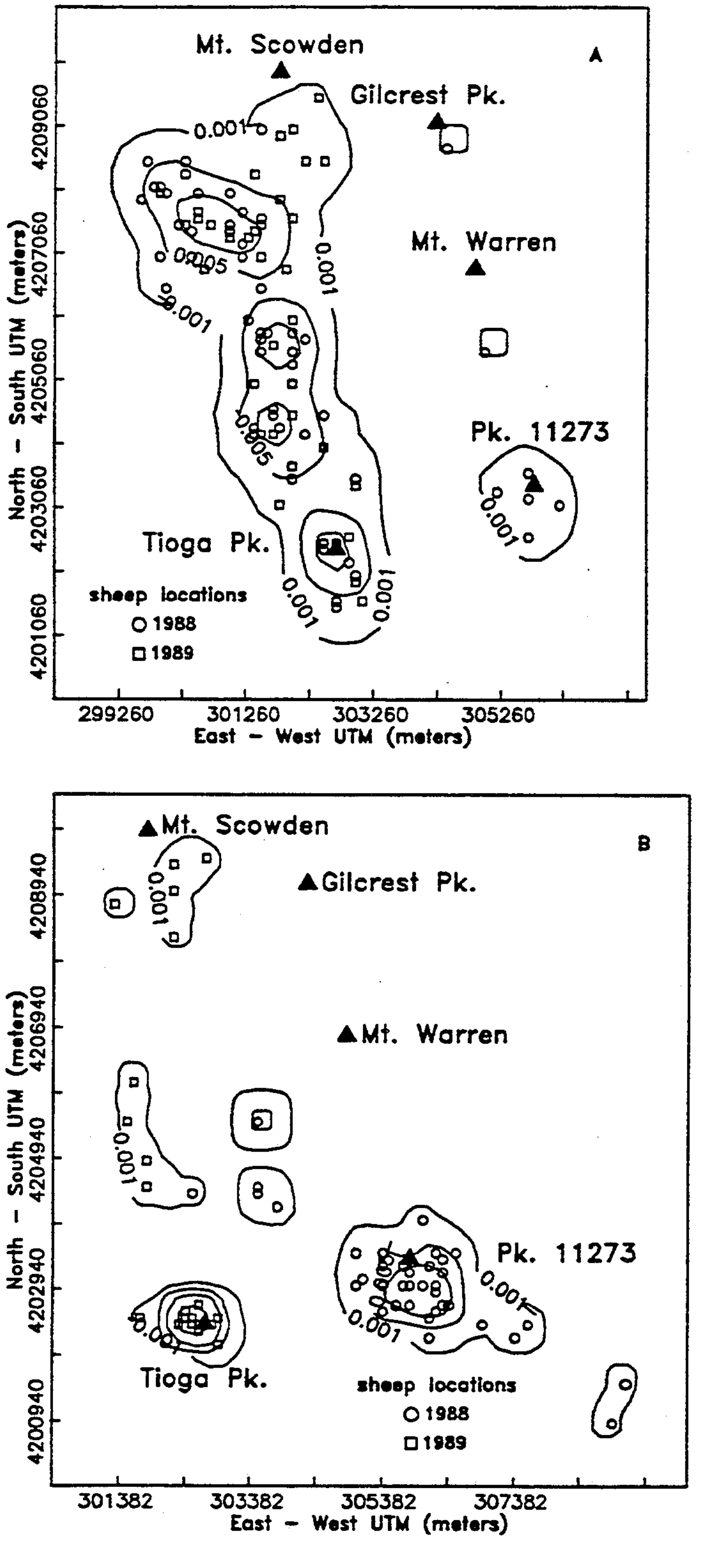


Figure 24. 1988–1989 summer/fall (A) and winter/spring (B) ranges used by bighorn ewe 4841 in Lee Vining Canyon, Mono Co., Calif.

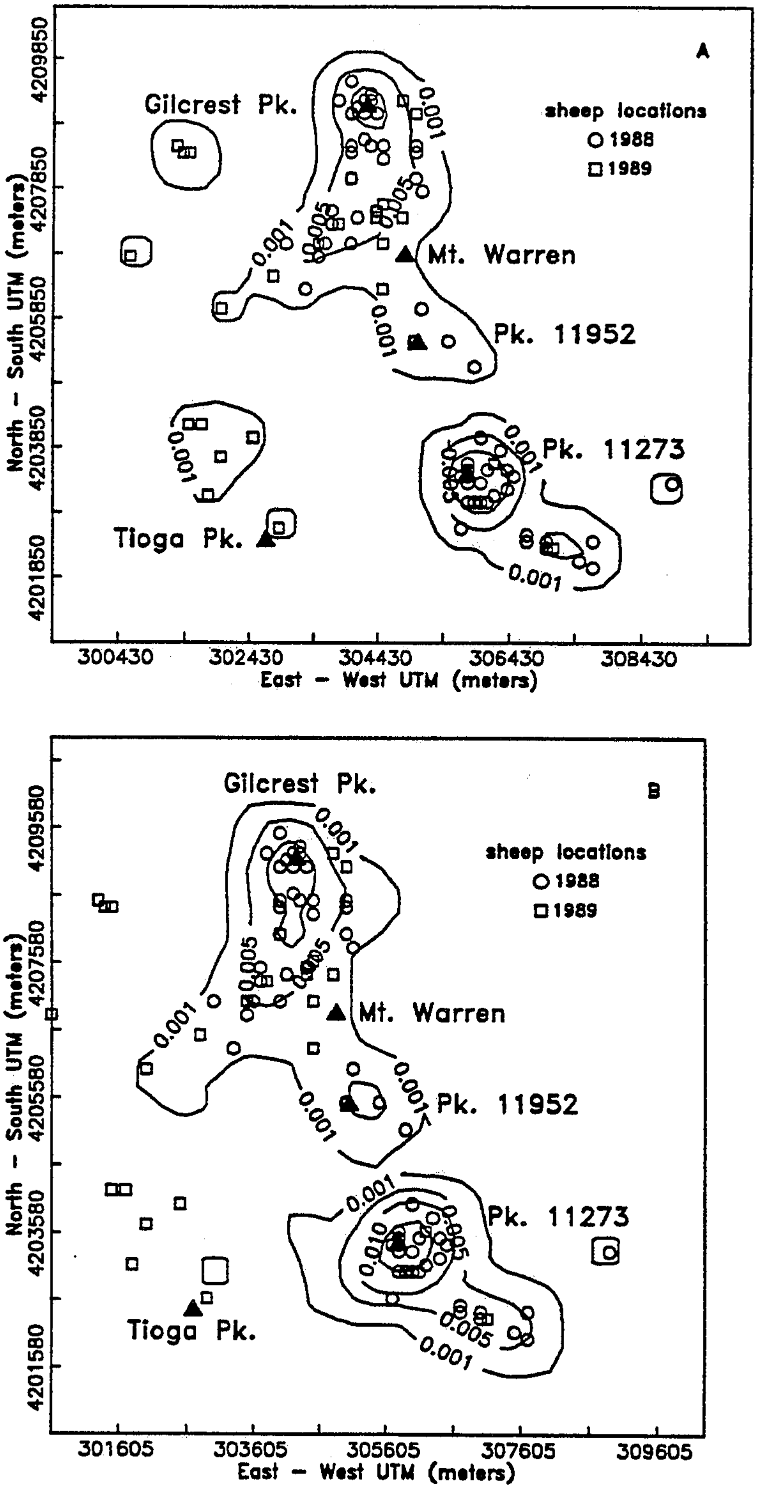


Figure 25. 1988–1989 summer/fall ranges used by bighorn ewes 4451 (A) and 4731 (B) in Lee Vining Canyon, Mono Co., Calif.

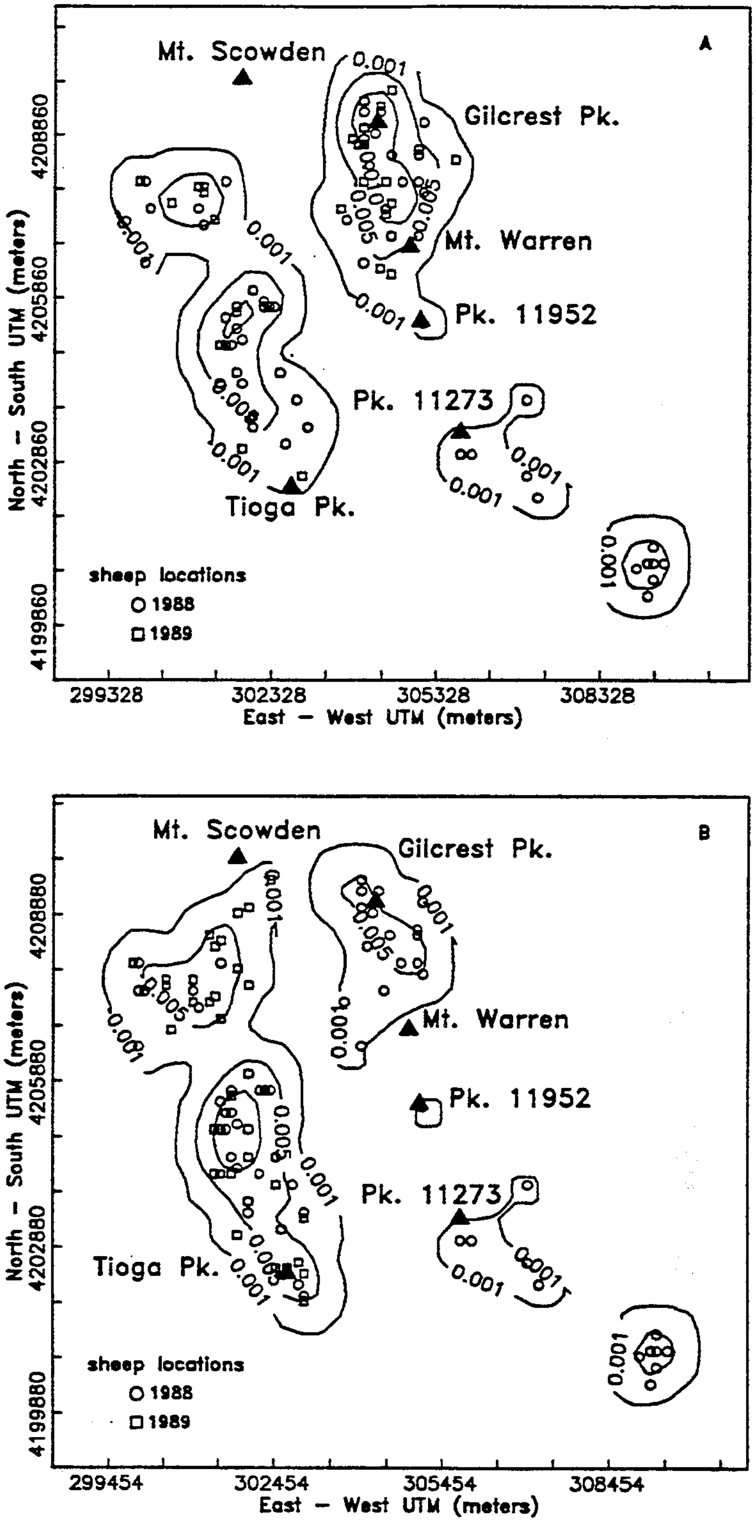


Figure 26. 1988–1989 summer/fall ranges used by bighorn ewes 4514 (A) and 4564 (B) in Lee Vining Canyon, Mono Co., Calif.

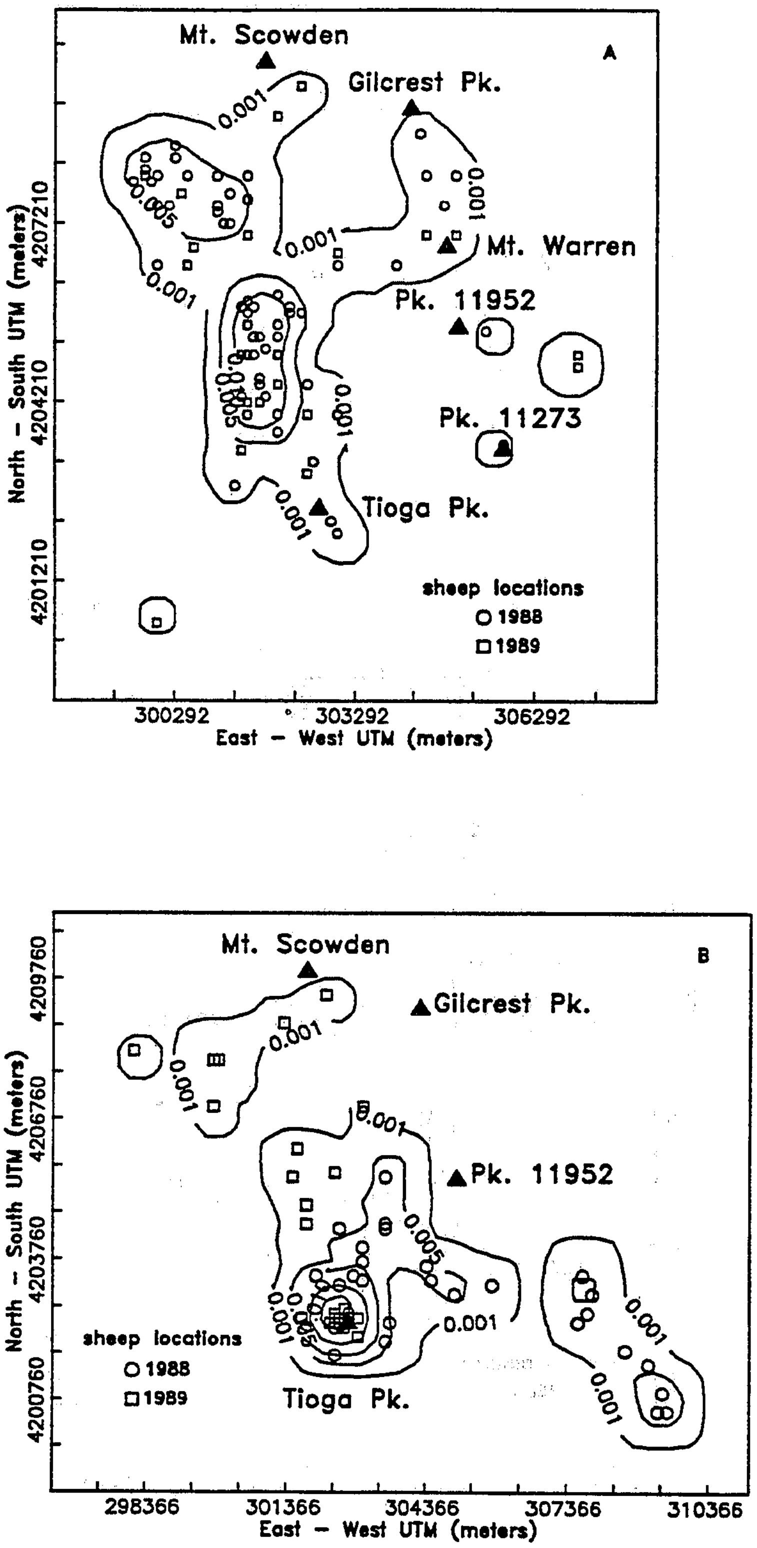


Figure 27. 1988–1989 summer/fall (A) and winter/spring (B) ranges used by bighorn ram 4438 in Lee Vining Canyon, Mono Co., Calif.

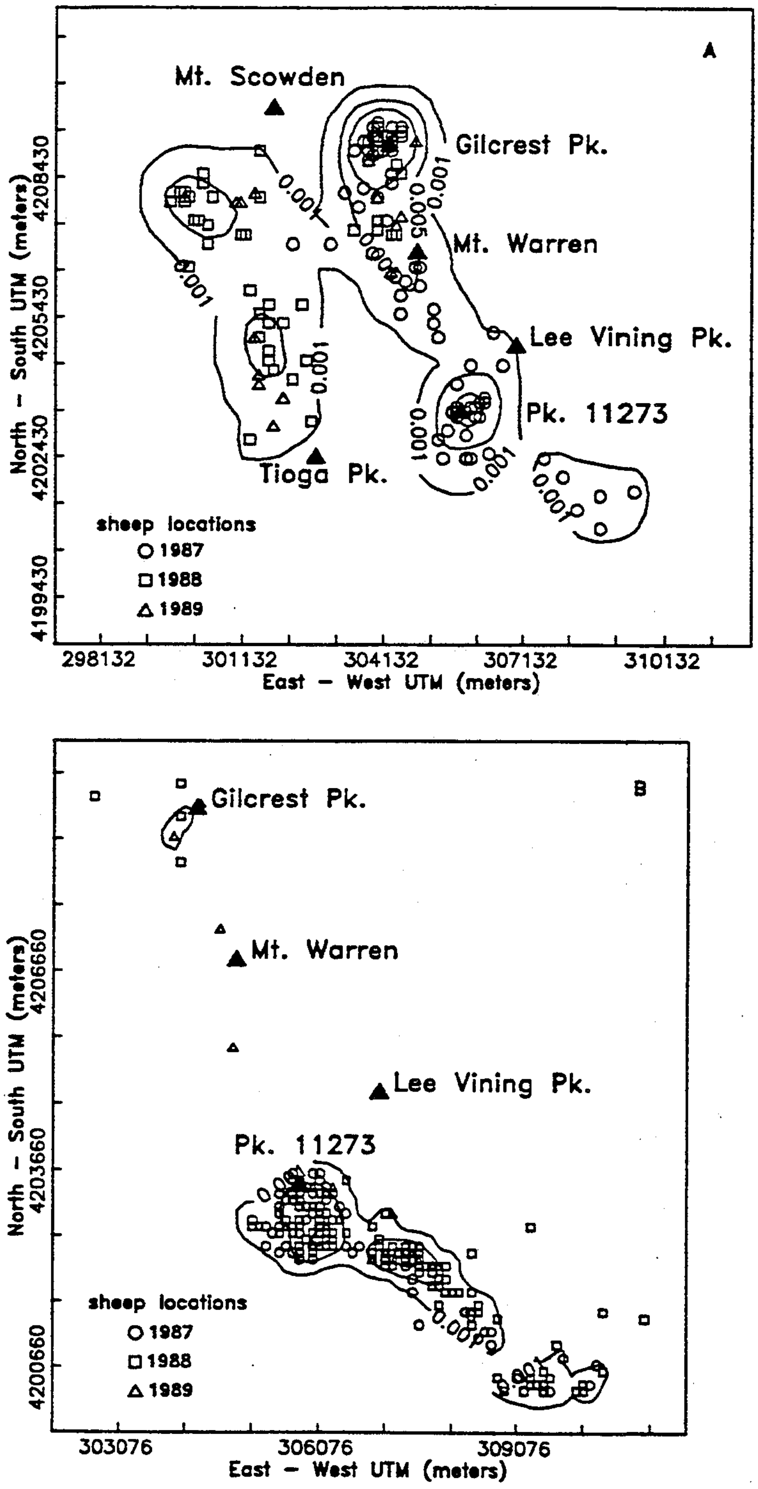


Figure 28. 1987–1989 summer/fall (A) and winter/spring (B) ranges used by bighorn ewe 4411 in Lee Vining Canyon, Mono Co., Calif.

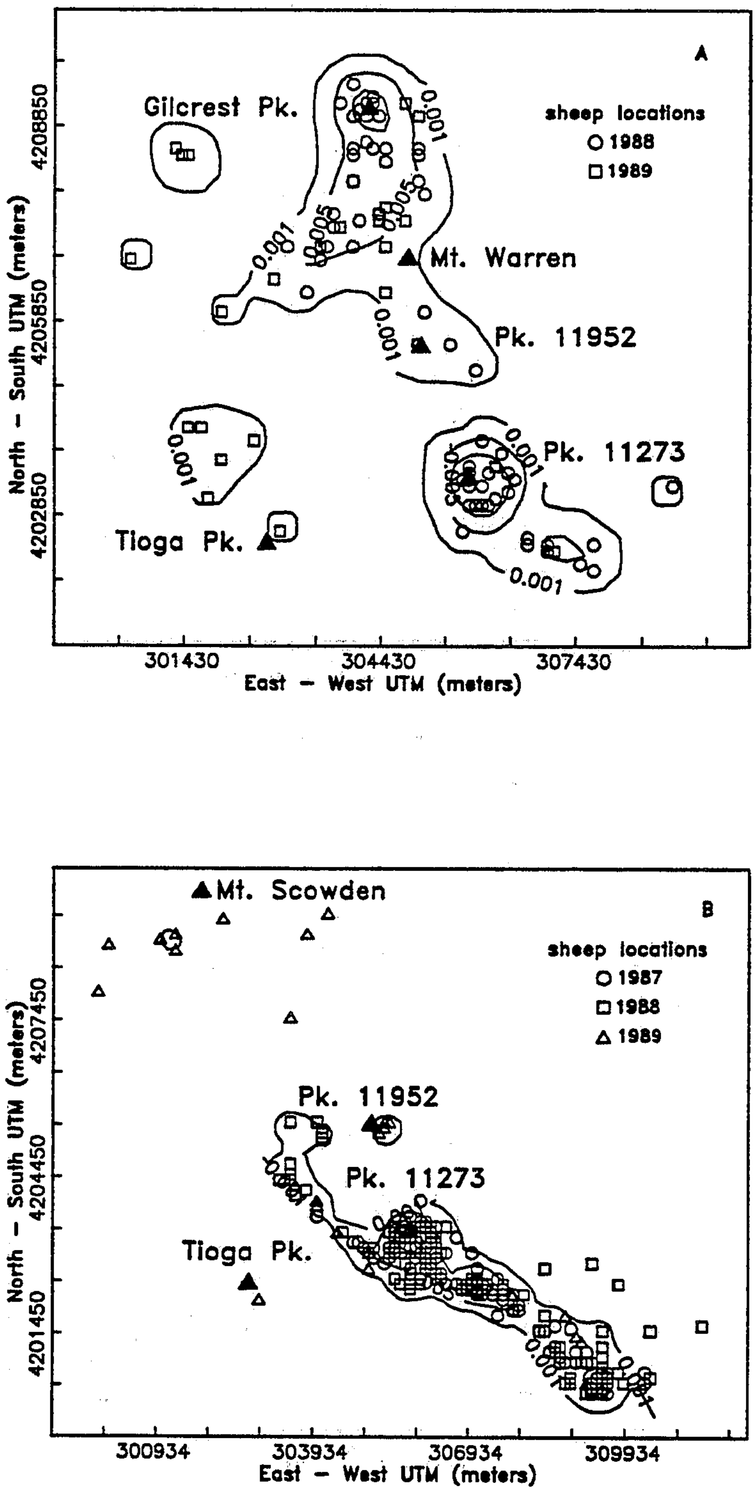


Figure 29. 1987–1989 summer/fall (A) and winter/spring (B) ranges used by bighorn ewe 4451 in Lee Vining Canyon, Mono Co., Calif.

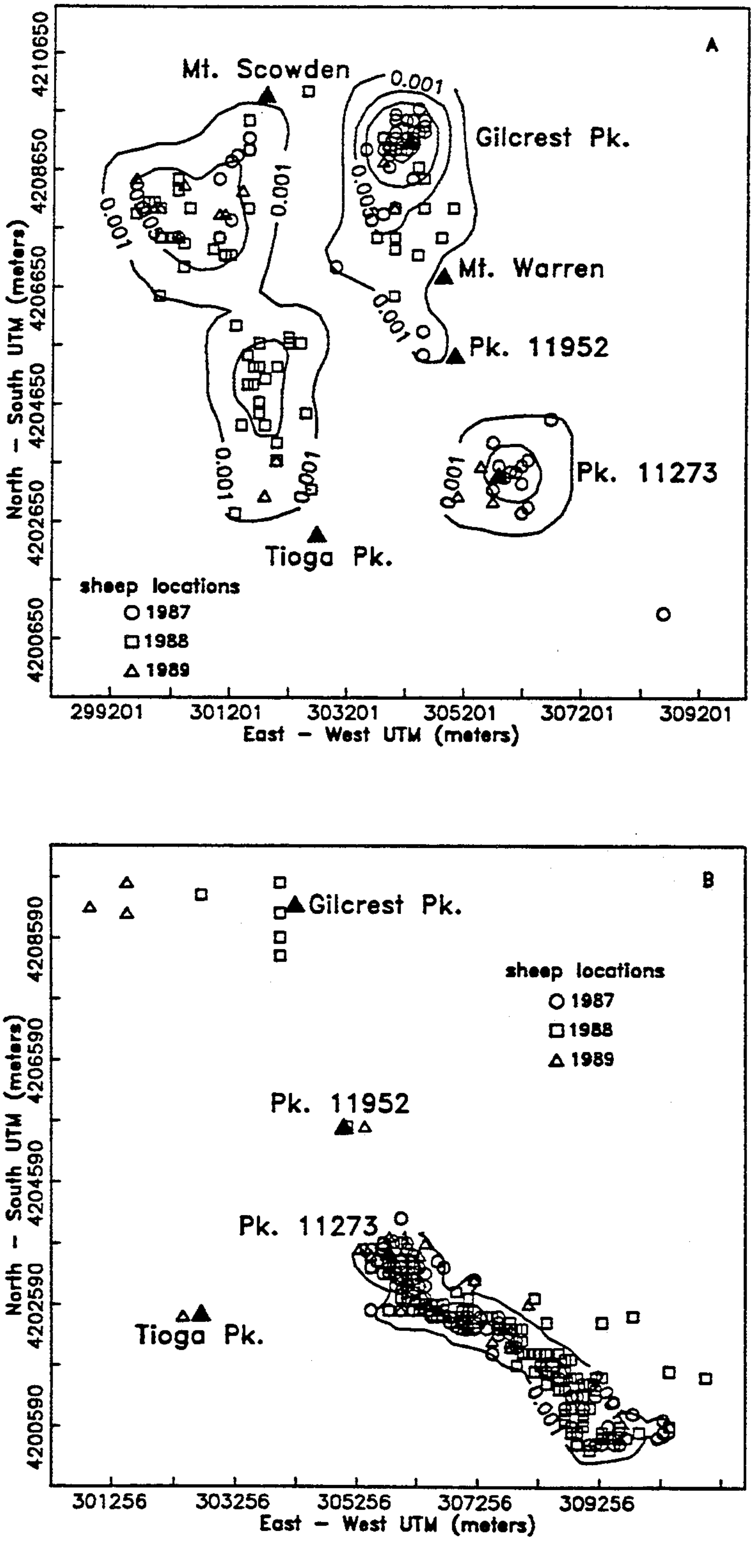


Figure 30. 1987–1989 summer/fall (A) and winter/spring (B) ranges used by bighorn ewe 4601 in Lee Vining Canyon, Mono Co., Calif.

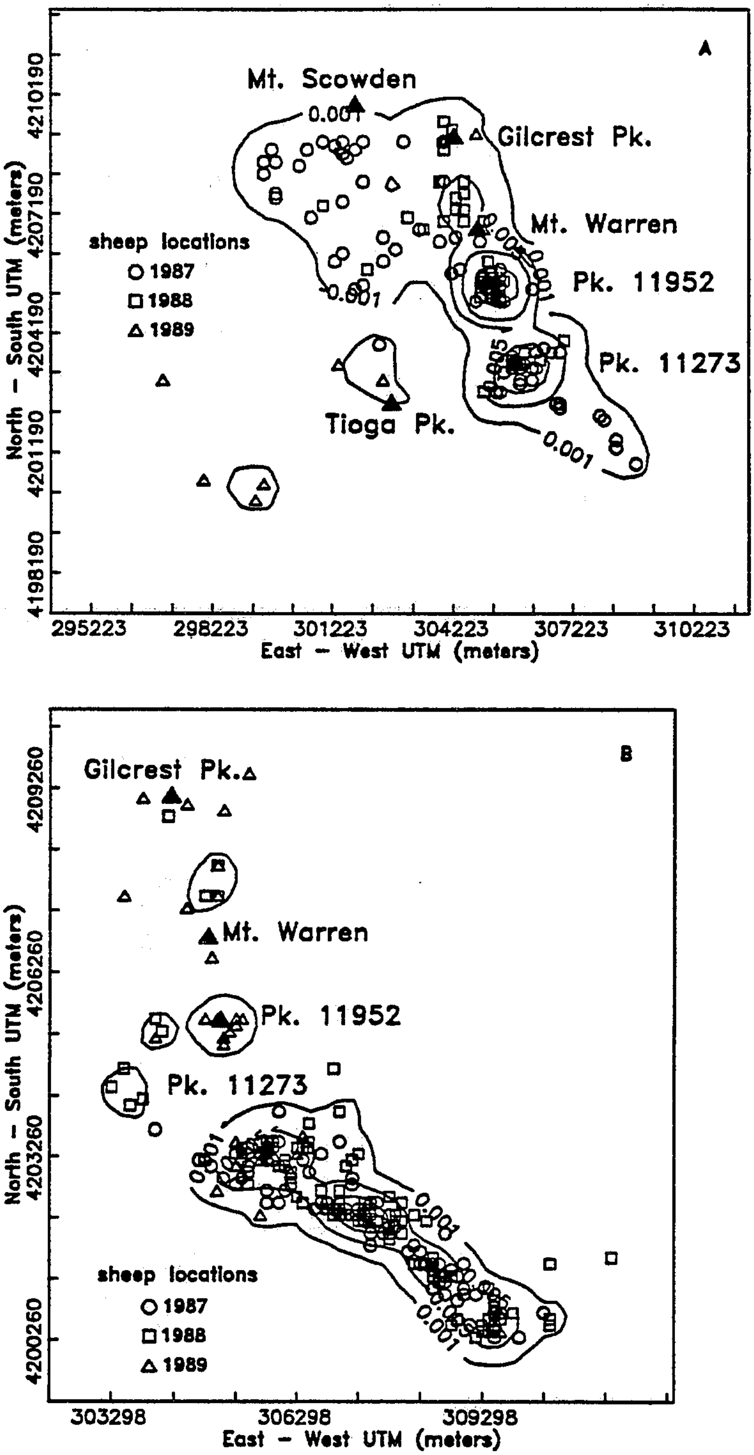
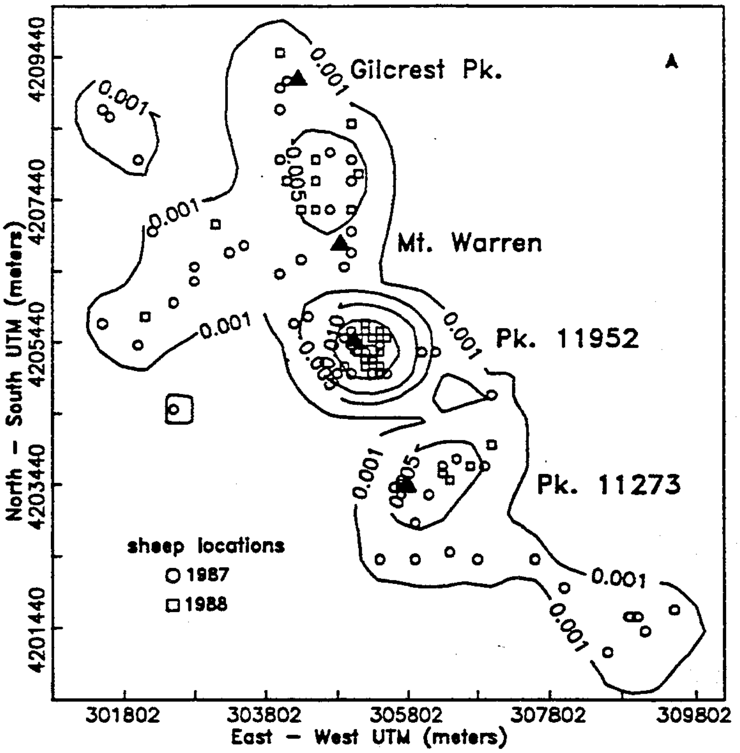


Figure 31. 1987-1989 summer/fall (A) and winter/spring (B) ranges used by bighorn ram 4421 in Lee Vining Canyon, Mono Co., Calif.



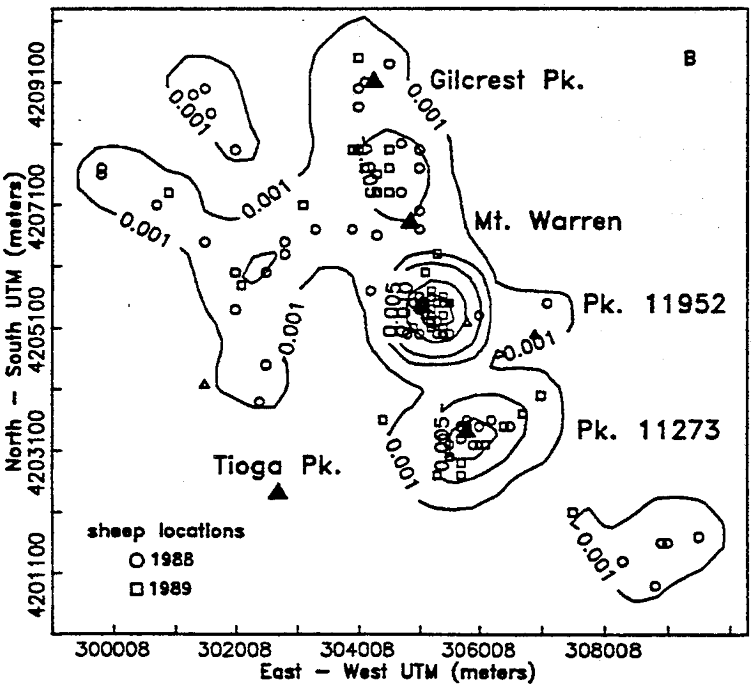


Figure 32. summer/fall ranges used by bighorn rams 4791 (A), 1987–1988 and 4811 (B), 1988–1989 in Lee Vining Canyon, Mono Co., Calif.

APPENDIX C

PROGRAM INFORMATION FOR POPULATION MODELING USING RAMAS/A.

The program, RAMAS/a (Ferson et al. 1988), was used to model the population dynamics of the Lee Vining herd. RAMAS/a models changes in an age structured population for periods as long as 50 years using a combination of Monte Carlo simulation and user-specified population parameters. Utilizing 4 interactive, menu-driven, data entry screens and a text editor, RAMAS/a places population parameters under user control. Variables under user control include:

maximum age
sex ratio
age specific natural survival
human induced or other age specific mortality
age specific fecundity
initial abundance
density dependence factors
sampling distributions of survival and fecundity
correlations between survival and fecundity
years to run
number of replications.

Data used to model the population dynamics of the Lee Vining herd are shown in Appendix C, Figure 1. Age-specific natural survival was based on a survey of the literature and results from this study (Appendix C, Table 1)

Density dependence factors are included in RAMAS/a by varying the birth rate (fecundity) as population size increases (Ferson et al. 1988). Although RAMAS/a supplies the Ricker and Beverton-Holt functions (Ricker 1975) to

```
Maximum age = 11
Sex ratio = 0.588

        Natural     Other                  Initial
Age     survival    mortality   Fecundity  abundance

 0        0.66        0.00        0.00        7
 1        0.85        0.00        0.00        5
 2        0.95        0.00        0.00        3
 3        0.95        0.00        0.78        5
 4        0.95        0.00        0.87        4
 5        0.95        0.00        0.98        4
 6        0.90        0.00        0.99        4
 7        0.89        0.00        0.99        3
 8        0.88        0.00        0.99        4
 9        0.87        0.00        0.98        0
10        0.85        0.00        0.90        1
11        0.75        0.00        0.75        1


Stochastic model parameters

Coefficients of variation:
  CV natural survival for age 0 (yoy)        = 0.11700
  CV natural survival for ages ≥ 1           = 0.06866
  CV fecundity                               = 0.44800

Probability distributions
  Natural survival for age zero is normally distributed.
  Natural survival for ages ≥ 1 is normally distributed.
  Fecundity is normally distributed.

The number of iterations in the simulation = 250

Years to run = 50
```

Figure 1. Input data used to model the population dynamics of the Lee Vining bighorn sheep herd using RAMAS/a.

Table 1. Age specific survival for various populations and subspecies of mountain sheep in North America.

	Age in years												
Sex	0	1	2	3	4	5	6	7	8	9	10	11	Investigators
rams		88.2	93.3	92.8	92.3	91.6	87.1	44.3	24.8				Woodgerd 1964[a]
rams	50.0	42.8	98.6	98.1	98.0	98.0	93.4	89.1	87.1	87.1	70.4	72.0	Hansen 1967[b]
ewes	50.0	42.8	94.8	97.5	94.4	90.9	93.5	86.8	76.8	80.1	50.6	67.4	Hansen 1967[b]
rams		100.0	97.0	96.0	92.0	87.0	87.0	79.0	72.0	61.0			Geist 1971[a]
rams		96.0	96.0	96.0	94.0	95.0	89.0	86.0	76.0	61.0			Hoefs and Cowan 1979[c]
rams	58.1	92.9	96.9	96.0	95.0	93.9	90.7	85.7	77.4	66.2	46.5	30.0	Hoefs and Bayer 1983[c]
rams		97.0	99.0	88.0	72.0	77.0	61.0	55.0	25.0				Heimer et al. 1984[c]
ewes	48.9	93.0	92.0	90.9	88.9	87.0	84.7	79.0	75.9	72.4	69.7	66.1	Simmons et al. 1984c[c]
rams		72.0	72.6	46.5	63.4	91.6	77.3	41.3	42.2	31.6			Leslie and Douglas 1986[b]
rams		81.0	97.0	86.0	90.0	87.0	76.0	70.0	83.0	59.0			Jorgensen and Wishart 1986[a]
rams		67.0	82.0	94.0	91.0	94.0	82.0	83.0	88.0	0.0			Festa-Bianchet 1989[a]
both	66.6	90.0	81.8	83.3	100.0	81.8	77.7	100.0	100.0	86.4			This study[d]
	54.7	80.2	91.8	88.8	89.3	89.6	83.3	74.9	69.0	60.5	59.3	58.9	mean values

[a] *Ovis canadensis canadensis*
[b] *O. c. nelsoni*
[c] *O. c. dalli*
[d] *O. c. californiana*

introduce density dependent effects into the model, I deemed these inappropriate for modeling the population dynamics of bighorn sheep. Fortunately, RAMAS/s also provides the ability to manually input an ASCII text file consisting of 50 data pairs. This feature enabled me to specify a relationship between density and the number of lambs recruited. I related recruitment to density using the reverse logistic function (Spanier and Oldham 1987).

The reverse logistic function produced a nonlinear decrease in fecundity as the population approached carrying capacity (Fowler 1981). I created the function in a Lotus 1-2-3 (copyright (c) 1989 Lotus Development Corp.) spreadsheet. Doing so allowed me to simultaneously compare the effects of substituting various function parameters in different combinations (Appendix C, Figure 2). I used a reverse logistic function of the form:

$$y = a - \frac{a}{1 + b^{-cx}}$$

where Y was the number of lambs surviving in a herd of X number of sheep. I set carrying capacity at 100 sheep and ultimately selected the values, 1.060, 16.0, and 0.070 to replace function parameters a, b, and c, respectively. These values specified the origin, slope, and shape of a curve which I interpreted as best representing the

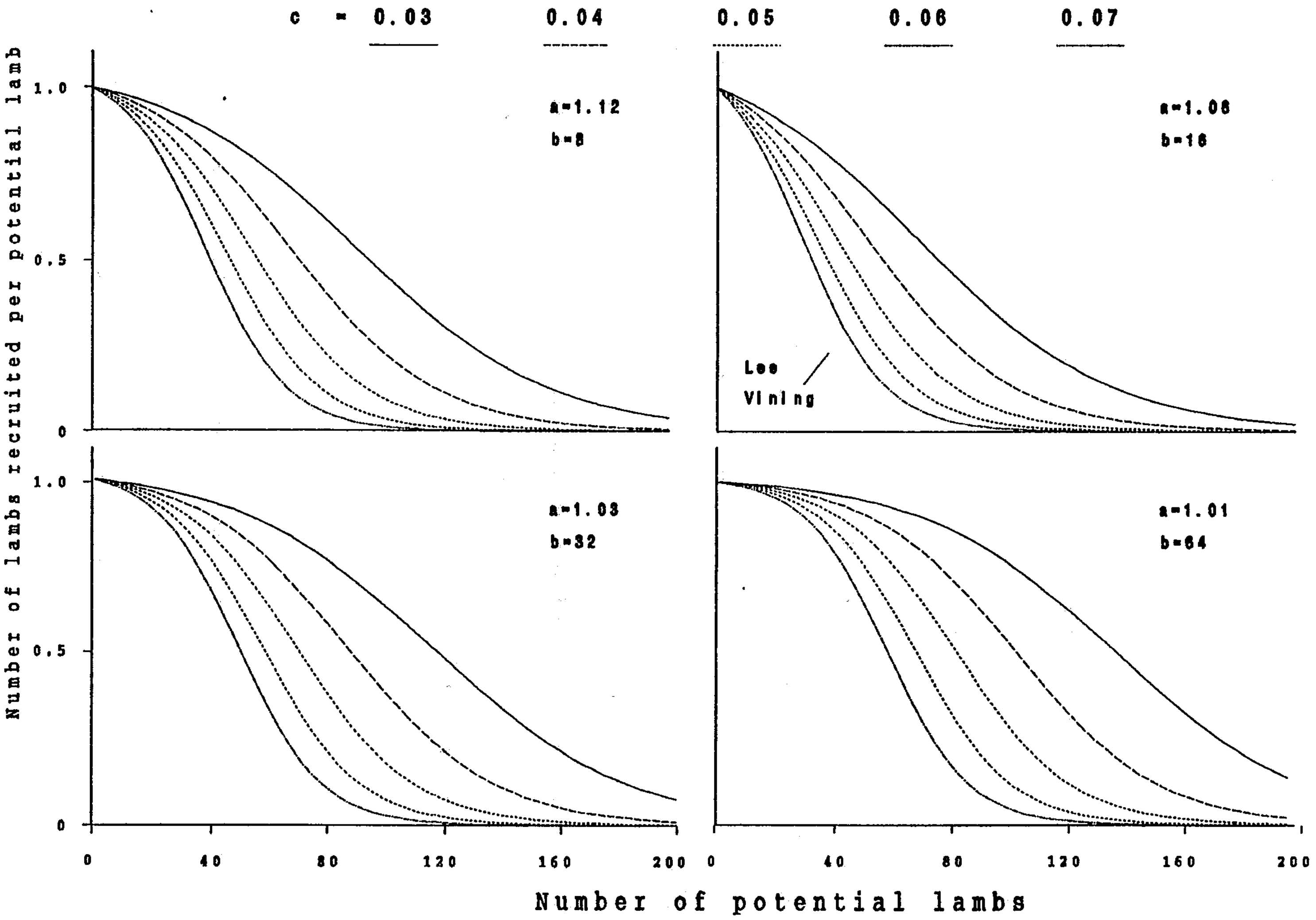


Figure 2. Comparison of curves produced by various combinations of replacement values for model parameters a, b, and c in the reverse logistic function.

relationship between density and bighorn lamb recruitment (Appendix C, Figure 3).

Stochasticity was incorporated into the model by including coefficients of variation for age specific fecundity and survival (Appendix C, Figure 1). These were based on 4 years of data gathered from the Lee Vining herd. I specified that adult survival, lamb survival and fecundity were all normally distributed.

RAMAS/a computed population structure during a given year using the following procedures and assumptions: (Ferson et al. 1988).

1. No individuals live beyond the maximum age class.

2. The number of individuals surviving to a given age class greater than 1 year, $n_{(t+1)}$, is derived using the formula:

   $$n_t * m_{other} * m_{natsurv}$$

   where n^t is the number of individuals in the previous age class at time t, m_{other} is the mortality rate in excess of natural mortality, and $m_{natsurv}$ is the natural survival rate. The natural survival rate for adults

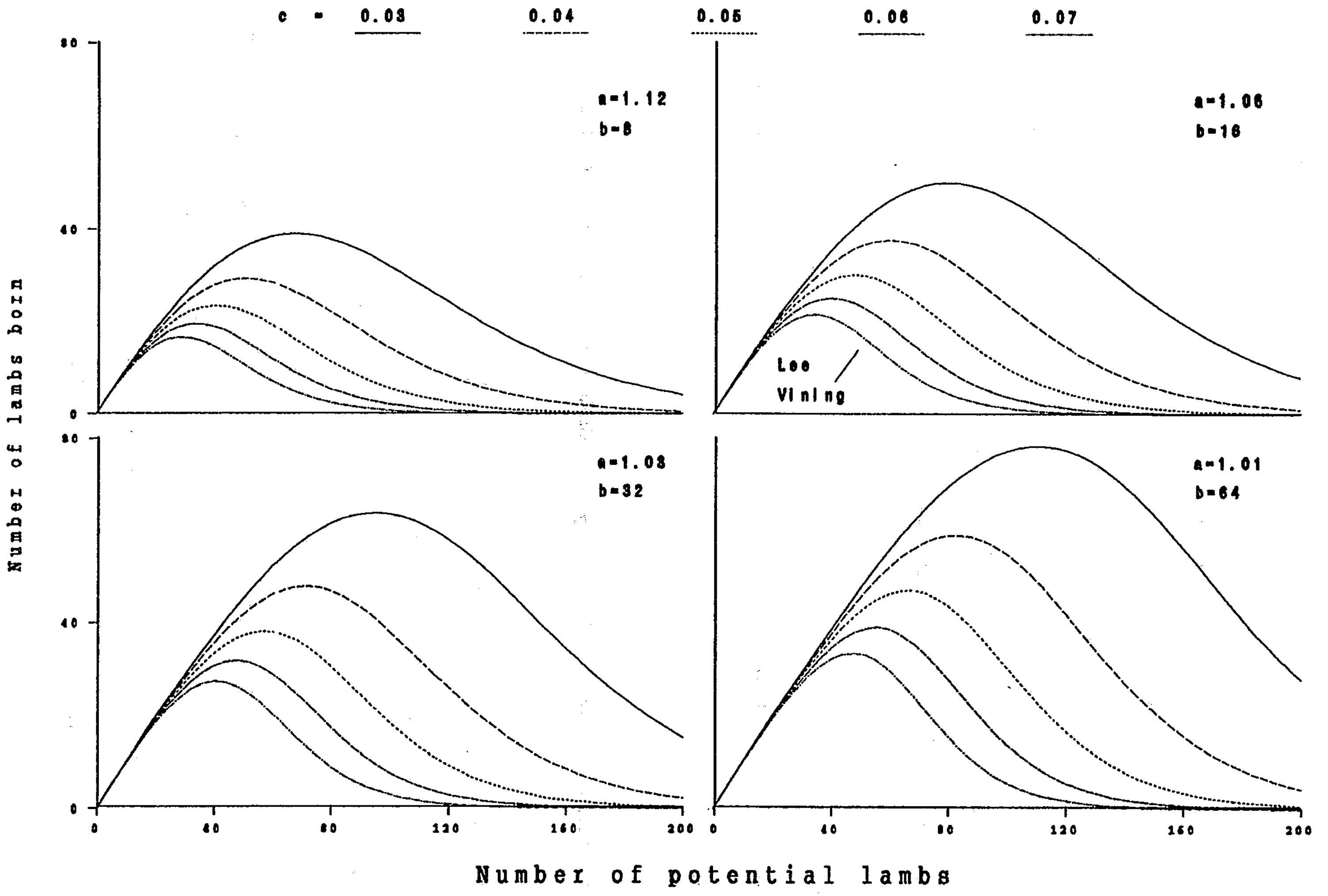


Figure 3. Density dependent recruitment curves for bighorn sheep produced by various model parameters a, b, and c in the reverse logistic function

was the mean of the normally distributed variable, natsurv with the coefficient of variation, CV natural survival for ages ≥ 1 year old.

3. The number of 1-year-olds is calculated by multiplying the number of lambs born the previous year by m_{other} and $m_{natsurv}$ for lambs. The natural survival rate for lambs was the mean of the normally distributed variable, natsurv with the coefficient of variation, CV natural survival for age 0 (yoy).

4. The number of potential lambs is the sum of the products of mean age-specific fecundity and the number of ewes in each age class. Mean fecundity is normally distributed with a coefficient of variation, CV fecundity. The number of ewes in an age class was the product of the sex ratio and the number of sheep in that age class (Appendix C, Figure 1).

5. The number of lambs actually recruited is a function of herd size as specified in the lookup table shown in Figure 3.

The program answers 3 kinds of questions:

the expected number of individuals in the population or in a specified age class a certain number of years from now;

the variance associated with each estimate;

> the probability that the population size will exceed or fall below a specified threshold at least once during or at the end of a specified time period?

RAMAS/a produces both graphical and text results. Graphics include histograms showing the distribution of ages during a specified year or the number of individuals in a given age class for each year of the simulation. Line graphs show population trajectory with minimum, maximum, and mean population sizes with ± 1 standard deviation confidence limits around each estimate. All of this information is also presented in tabular form. Text information includes probabilities associated with the population exceeding or falling below some threshold during the simulation.