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Darted mountain lion. Photo by California Department of Fish and Game, Round Valley Predator-Prey Study.

Effects of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California

John D. Wehausen

Abstract Mountain lion (*Puma concolor*) predation caused populations of bighorn sheep (*Ovis canadensis*) in 2 mountain ranges in California to decline to low densities. In the Granite Mountains in the eastern Mojave Desert, lion predation reduced the sheep population to 8 ewes and held it at that level for 3 years, after which the predation abated and the population has increased at 15%/year for 3 years. Annual survivorship of radiocollared ewes was 62.5% for the first 3 years of study and all mortalities were from lion predation. Mountain lion activity increased in the southern Sierra Nevada on winter ranges between 1976–1988. During this period, 49 sheep killed by lions were found on the winter ranges of the Mount Baxter population. Beginning in 1987, the larger subpopulation of this herd abandoned use of its low-elevation winter range. Increasing mountain lion predation is the best explanation for these habitat shifts. The Mount Baxter sheep that remained at high elevations missed a growing season on the winter range, which was reflected in lower fecal nitrogen levels. The population has declined to <20% of earlier census totals as a result. Mountain lions effectively halted a previously successful restoration program for bighorn sheep in the Sierra Nevada and reversed the overall population trend.

Key words bighorn sheep, Mojave Desert, mountain lion, *Ovis canadensis*, population dynamics, predator–prey dynamics, *Puma concolor*, Sierra Nevada

The role of predation in ungulate population dynamics has interested wildlife ecologists because it can have critical relevance to conservation strategies. Regulation of hunting and control of predators were the first major tools of wildlife management in North America (Connolly 1978), and each was based on some form of hypothesis about how animal and human predators determine wildlife population densities. Eruptions of some wild ungulate populations were documented in North America following predator control (Leopold et al. 1947) and elsewhere following introductions of ungulates to environments that lacked predators (Caughley 1970). This shifted attention to the large effects of intraspecific competition for limited forage resources and ushered in the theory of density-dependent population regulation based on landmark studies in situations lacking large native predators (Caughley 1970, McCullough 1979). Caughley (1976) extended this theory to predators, suggesting that they were not capable of stopping ungulate population eruptions. McCullough (1979) similarly hypothesized that wolves (*Canis lupus*) could not drive white-tailed deer (*Odocoileus virginianus*) to low population densities because density-dependent effects on deer condition influenced vulnerability to predation. While studies of wolf predation by Gasaway et al. (1983, 1992), Messier and Crête (1985), and Van Ballenberghe (1987) have questioned the generality of such theory with wolves, Hornocker's (1970) findings for mountain lion (*Puma concolor*) predation on mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and bighorn sheep (*Ovis canadensis*) corroborated it. Hornocker (1970) found that few bighorn sheep were taken by lions despite considerable spatial overlap and suggested that group behavior of bighorn sheep greatly reduced their vulnerability. Buechner (1960) arrived at a similar conclusion and cited another example of a large bighorn population coexisting with a high density of lions. I present data from bighorn sheep populations for 2 different habitats in California to test the hypothesis that mountain lions cannot cause bighorn sheep populations to decline to low densities.

Study populations and methods

Granite Mountains population

The Granite Mountains lie immediately northwest of the junction of Interstate 40 and Kelbaker Road in the eastern Mojave Desert of California about 70 km south of Baker. Elevations available to bighorn sheep

in these mountains range from 725 to 2,040 m. Upper elevations support pinyon (*Pinus* spp.)-juniper (*Juniperus* spp.) woodland, while most of the range supports various open desert shrub communities depending on elevation. Steep, rocky escape terrain and surface water for bighorn sheep are widely available. The eastern portion of the Granite Mountains supports a sparse mule deer population that spread there from introductions in the New York Mountains in 1948 (Cronin and Bleich 1995). The Granite Mountains are the farthest south and west that these deer have spread and represent the end of a finger of Great Basin habitat that extends into the Mojave Desert in this region. Local residents knew of no mountain lions in this region of the Mojave Desert until the late 1970's (M. Blair, Essex, Calif., pers. commun.), nor did Johnson et al. (1948) list deer or mountain lions in their survey of mammals in this area.

The Granite Mountains study began in summer 1988. In August and October of that year, 5 ewes were caught via net gun from a helicopter (Krausman et al. 1985) and fitted with radiocollars containing mortality sensors (Telonics, Inc., Mesa, Ariz). The California Department of Fish and Game made monthly, fixed-wing flights to determine if any collared sheep had died. Dead sheep were located as quickly as possible to determine cause of death. As mortalities occurred, other ewes were collared in an effort to keep 4 ewes collared. Nine different ewes received radiocollars between 1988-1993, 3 of which were recollared. Survivorship rates of collared ewes were calculated using Heisey and Fuller (1985).

Field efforts to determine the minimum number of ewes in the Granite Mountains took place in 1988, 1990, 1991, 1993, and 1995. Additionally, a mark-resight population estimate was developed for 1989 using a cumulative sampling-with-replacement approach, Bailey's (1951) nearly unbiased estimator, and reciprocal confidence limits (Jensen 1989). This random sampling effort required 43 person-days on the ground and 1 helicopter flight due to the low density of this population. Because of the time required to develop this sample, the number of collars in the population changed during the sampling. Consequently, the average number of collars present weighted by sample sizes was used. The inefficiency of such sampling necessitated the minimum population approach for other years.

Mount Baxter population

The Mount Baxter population is located along the crest and steep eastern slope of the southern Sierra

Nevada north of Independence in Owens Valley. Elevations used by this population ranged from 1,460 m in the winter range at the base of the eastern escarpment to 4,050 m at the crest of the mountains. Plant communities change with elevation from Great Basin sagebrush (*Artemisia tridentata*) scrub to alpine habitats along the mountain crest, with a band of mostly sparse timber at mid-elevations. In early winter, mule deer were in the winter range of these sheep, but in late winter and early spring when bighorn sheep densities commonly peaked on the winter range, the mule deer occupied alluvial fans immediately below the sheep. When bighorn descended to their winter ranges, they entered the range of mountain lions.

Demographic variables were measured most years through samplings carried out in summer at high elevations beginning in 1975 and in winter at the base of the eastern escarpment beginning in 1976. These included multiple direct counts of sheep each year when they were most concentrated on the winter range in late winter and early spring. During these censuses, evidence of mountain lion presence was recorded, as were their kills. Dead sheep were considered lion kills only if they had large tooth holes in the skull consistent with the size of lion canines, or showed other clear characteristics of lion kills, such as being dragged and cached, lion tracks or scats at the site. Coyotes are present in the Sierra Nevada and in Owens Valley immediately below this winter range, but I never observed a coyote on this winter range in >200 field days there; coyotes were unlikely predators or scavengers on bighorn sheep. Older carcasses were generally more difficult to assign a cause of death. Consequently, my kill results represent the minimum numbers of lion kills.

Demographic variables measured in the summer range were early summer lamb:ewe ratios shortly after the completion of lambing, coupled with estimated birth dates by half months in some years, and yearling: adult ewe ratios as estimates of recruitment rates. During most years, summer censuses to develop a meaningful minimum population size were not possible because the population was large and spread out through complex rugged topography. However, the population had declined to <20 ewes in 1994 and 1995 and I was able to develop a minimum population size in summer using individual recognition of ewes by color variation, molt patterns, sizes of lambs, and other distinguishing features. Summer ewe density was also tracked by a catch/unit effort (CPUE) index of number of ewes observed/field

day along the crest (half-day units). I increased my off-trail effort to sample sheep as the population began declining in the late 1980's, and I present only the final 6 years of this index when field efforts were greatest and consistent. I present similar indices of rates at which I recorded lion tracks and kills while hiking through the winter range. These indices are presented in units of paired consecutive winters to maximize the number of days for each index value, which varied from 18 to 55 days.

The Mount Baxter population was composed of 2 herds that wintered on Sand Mountain and in Sawmill Canyon. A dense riparian thicket along Sawmill Creek limited sheep from crossing it at lower elevations. A small data set from radiocollared (Sawmill Canyon herd only) and naturally marked ewes indicated that these represented separate herds in summer also. Demographic data presented here concern only the Sand Mountain herd, which at its peak density constituted approximately 70% of the total population. Data presented on mountain lion kills and tracks represent the entire winter range of both sub-populations.

I used percent fecal nitrogen (FN) to index diet quality. Annual FN curves were developed from approximately monthly winter and summer range samples for most years between 1976 and 1988 (Wehausen 1992). In 1990, I sampled sheep wintering at high elevations during winter and spring. Fecal N data are expressed as lnFN on an organic matter basis (Wehausen 1995).

Results

Granite Mountains

Five collared ewes in the Granite Mountains were killed by lions between March 1989 and

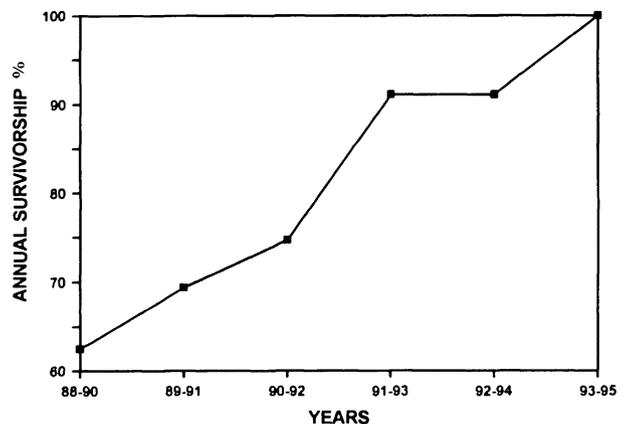


Fig. 1. Overlapping 3-year average survivorships for radiocollared bighorn ewes in the Granite Mountains, California, 1988-1995.

March 1992. Annual survivorship of collared ewes averaged 62.5% for the first 3 years of the study, with all mortality due to lions. However, losses to predation ceased after March 1992, and the rate of losses declined prior to that, resulting in rising 3-year-average survivorship levels, ending at 100% (Fig. 1). A decline in lion predation correlated with a change in the rate that I recorded lion tracks, from 17.1% of 41 hiking days prior to May 1992 to none of 27 days since that time ($\chi^2 = 5.14$; $P = 0.023$).

During the period of lion predation in the Granite Mountains, the sheep population declined from ≥ 11 ewes in 1988 to 8 ewes between 1989 and 1991. The 1989 mark-resight estimate corroborated this low density. One helicopter survey and 43 person days of searching for sheep without the aid of telemetry yielded a sample of only 13 ewes. Seven of these were collared, producing an estimate of only 7.4 ewes (95% CL = 5.1 - 13.1). The helicopter survey yielded a sighting rate of only 0.95 sheep/hour of search time. Following the cessation of lion predation, the population increased at 15%/year from 9 ewes in 1992 to 14 ewes in 1995 (Fig. 2).

Mount Baxter

Minimum winter population sizes for the Sand Mountain herd averaged 127 (range = 106-150) sheep for 1977-1986. This was followed by a steep decline during 1987-1991 as the population abandoned use of its winter range, after which counts averaged only 4.4 for 1991-1995 (Fig. 3). During 1976-1988, I recorded lion tracks on a steeply increasing percentage of hiking days on the winter range ($P = 0.001$, $r^2 = 0.944$), averaging

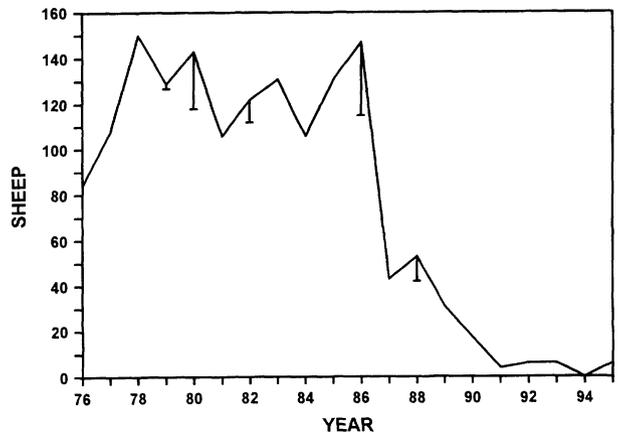


Fig. 3. Bighorn sheep census results for the Sand Mountain winter range on the east slope of the Sierra Nevada Mountains, California, 1976-1994. Vertical lines represent sheep removed for reintroductions.

4.4% more days/year. The rate at which I found lion kills also increased during that same period ($P = 0.05$, $r^2 = 0.657$; Fig. 4). Between 1976-1988 I documented 49 bighorn killed by lions on the Mount Baxter winter ranges. These kills represented 80% of all mortalities documented on the winter range and 71% for all ranges used. During 1979-1988, an additional 103 sheep were removed from this winter range for reintroductions (Bleich et al. 1990).

Prior to winter range abandonment, this population benefited from 2 annual forage growing seasons, one in late winter and spring on the winter range and one in summer in alpine habitats (Wehausen and Hansen 1988; Fig. 5). In contrast, the FN curve for sheep wintering at high elevations lacked any in-

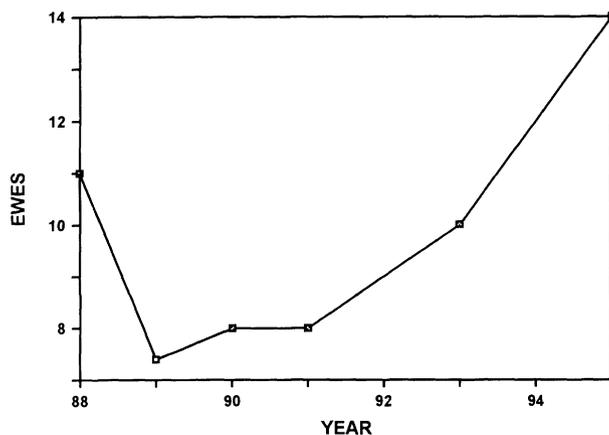


Fig. 2. Numbers of bighorn ewes in the Granite Mountains, California, 1988-1995. All values are minimum numbers except 1989, which is a mark-resight estimate.

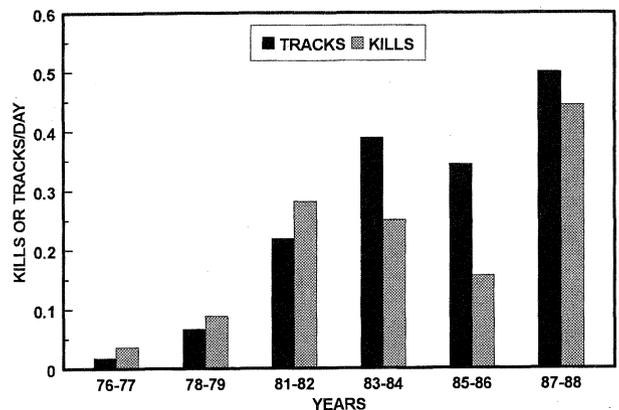


Fig. 4. Proportions of hiking days in which mountain lion tracks were recorded and the rate at which lion kills of bighorn sheep were found on the Mount Baxter winter ranges on the eastern slope of the Sierra Nevada Mountains, California, 1976-1988.

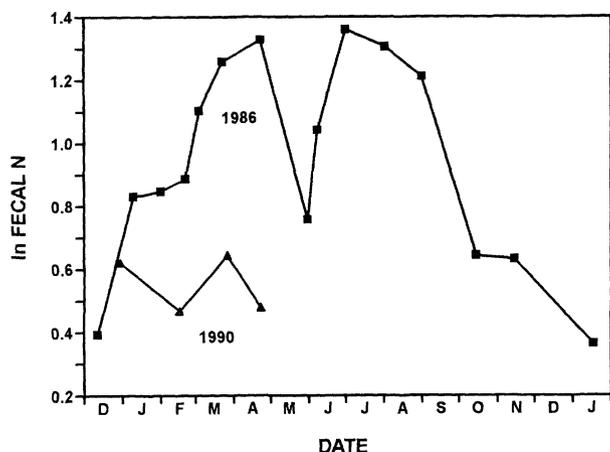


Fig. 5. Fecal nitrogen curves for bighorn sheep of the Mount Baxter population in the Sierra Nevada Mountains, California, December 1985–January 1988 and December 1989–April 1990. Samples in winter and early spring for 1986 came from low elevation winter ranges, while those for 1990 were from high elevations. Data are on an organic matter basis.

crease in winter and early spring. The area between curves in this season indexes the nutritional tradeoff made by sheep remaining at high elevations (Fig. 5), but it varies among years depending largely on the timing of the first major winter storm (Wehausen 1992).

Summer lamb:ewe ratios were not different following change in winter habitat use ($F = 0.223$; 1, 18 df; $P = 0.642$), but the timing of births shifted later by about a month over a 3 year period (Fig. 6). With lambs born later and wintering under extreme climatic conditions of high elevations, their survivorship to summer yearlings dropped significantly ($F = 6.76$; 1, 15 df; $P = 0.02$) from averages of 34.4 year-

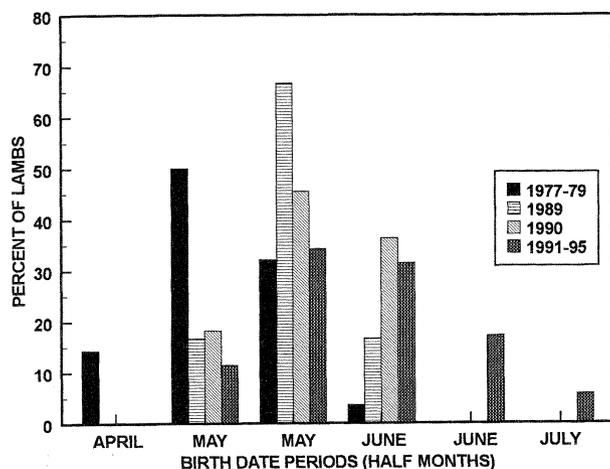


Fig. 6. Percent of bighorn lambs born in different half-month periods for the Mount Baxter sheep in the Sierra Nevada Mountains, California, 1977–1979, 1989, 1990, and 1991–1995.

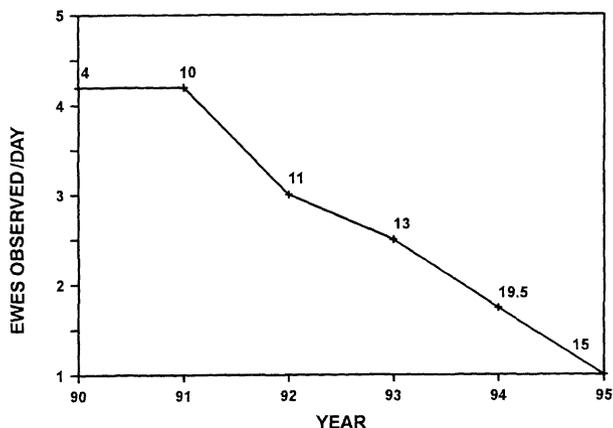


Fig. 7. Rates at which bighorn ewes could be found in summer along the crest of the Sierra Nevada between Kearsarge Pass and Mount Baxter, California, 1990–1995. Sample sizes (days) are beside points.

lings:100 ewes ($N = 9$) to 15.7:100 ($N = 8$) in summer. The resulting population decline since 1991 has been dramatic (Fig. 7), with the summer CPUE index in 1995 only 24% of its 1991 value. In 1995, the Sand Mountain herd consisted of approximately 10 ewes, while 15–20 ewes remained in the entire Mount Baxter population. In contrast, previous peak winter range counts were 76 and 108 ewes, respectively.

Discussion

Granite Mountains

The 1989 mark–resight estimate corroborated the very low population density suggested by minimum population values. Difficulty of finding sheep on the ground and from a helicopter provided further corroboration. Five hours of helicopter time were needed to install the first 2 collars, requiring a second effort to collar the first 5 ewes. Additionally, in 2 attempts to add collars we failed to catch any sheep. The sighting rate of the 1989 helicopter survey was only 6% of the rate recorded that year for a neighboring dense population to the north at Old Dad Peak and is a similar small percentage of helicopter sighting rates for many bighorn sheep populations in deserts (Lee and Lopez-Saavedra 1994).

Populations change due to differences between adult survival and recruitment. Fall lamb:ewe ratios for the Granite Mountains population during the period of lion predation averaged 25:100, which was at least 50:100 less than what would be necessary to balance the annual ewe mortality of 37.5%. In addition to poor adult survivorship, poor recruitment related to inadequate precipita-

tion (Wehausen et al. 1987) was a possible factor in the observed population dynamics in the Granite Mountains. However, data collected simultaneously on the neighboring Old Dad Peak population did not support this idea. While 1989 and 1990 were both dry years, high recruitment from the 1988 and 1991 cohorts resulted in an overall population gain of almost 18% for these 4 years (J. D. Wehausen, Demographic studies of mountain sheep in the Mojave Desert, Calif. Dep. Fish and Game, Sacramento, unpubl. rep., 1992). Furthermore, in the apparent absence of lion predation, the Granite Mountains population exhibited a high recruitment rate and population gain for lambs born in 1994, which was a particularly dry year. The large elevational range available to sheep in the Granite Mountains may have provided some buffer against such environmental variation. Lion predation may have been the major factor depressing lamb survivorship in the Granite Mountains during 1988-1991.

The data from the Granite Mountains show that lion predation is capable of being a very significant mortality factor even at very low prey density. However, lack of data prior to 1988 leaves questions unanswered about the level of the sheep population when predation began and what other factors might have been involved in reaching the low population size when this study began.

Mount Baxter and other Sierra Nevada populations

Abandonment of the Sand Mountain winter range beginning in 1987 was just one event in a series of winter range desertions by bighorn populations in the Sierra Nevada during the 1980's. Three other populations and the Sawmill Canyon herd preceded the Sand Mountain herd in this change; the third and last reintroduced population established in 1986 made this change later. The larger size of the Sand Mountain herd may have been a factor in the delay. An explanation for change in winter range use by the Sand Mountain herd should address the winter range desertion by all bighorn populations in the Sierra Nevada during the 1980's. In addition to increasing mountain lion activity, I consider 2 possible explanations.

The beginning of winter range abandonment by the Sand Mountain herd occurred the year following a capture in which 32 sheep on that winter range were caught in a single day by helicopter herding into drive nets. As an explanation for winter range desertion, this harassment fails because it does not account for: (1) why this did not

occur following previous captures (Fig. 3); (2) 109 sheep I counted on Sand Mountain 2 weeks post capture in 1986; and (3) winter range desertion by all other bighorn sheep populations in the Sierra Nevada, where no such capture events occurred.

The beginning of winter range desertion by the Sand Mountain herd also coincided with the beginning of 6 consecutive years of winter drought in 1987. Drought also fails as an explanation because: (1) it does not explain earlier abandonment by other populations; (2) 1976-1977 were also consecutive years of extreme drought, yet I accounted for many sheep on the Sand Mountain winter range (Fig. 3), despite just learning how to census this population; and (3) these sheep did not reoccupy the winter range in the heavy winters of 1993 and 1995.

These sheep were apparently drawn rather than forced to occupy the winter range in most cases prior to 1987. Except for particularly heavy snow years, best census data were not obtained until at least February, because many sheep remained high in the mountains until forage growth and nutrient levels were increasing rapidly on the winter range. Also, total counts were lower in years of lighter snowfall, indicating that a portion of the population was remaining at high elevations all winter and spring. Thus, while nutritionally and demographically the desertion of winter ranges was a discontinuity, behaviorally it was a more extreme expression of an existing behavior pattern.

Increasing mountain lion activity is the best explanation for the cessation of use of low elevations in winter by bighorn throughout the southern and central Sierra Nevada. For the Mount Baxter population, this involved the tradeoff of an entire forage growing season (Fig. 5), the effects of which were ultimately a major population decline due to inadequate recruitment. Thus, while the population appeared able to withstand direct losses from predation on the winter range, as well as periodic removals for reintroductions (Fig. 3), it declined as a result of indirect effects of mountain lions, mediated through habitat selection by the sheep. Seasonal migration is considered an important influence on the carrying capacity of wild ungulate populations, of which altitudinal migration is 1 type (McCullough 1985). Avoidance of predation is one hypothesis regarding advantages of migration (Fryxell et al. 1988) and high elevation summer ranges are commonly thought of as an extra nutritional input that can boost carrying capacity (Hebert 1973). Both con-

cepts appear reversed in the case of Sierra Nevada bighorn; a decline in migration may have occurred to avoid predation, and the winter range was the extra nutrient input for the population that greatly boosted its carrying capacity. Bighorn sheep are also known to winter at high elevations in some situations in the Rocky Mountains (Wishart 1969), and abandonment of a low elevation winter range has been similarly documented (Bauman and Stevens 1978).

Recent analysis of mtDNA data has allied Sierra Nevada bighorn with sheep from the adjacent southwestern desert region, but found them to be the most unique group within that entire region (Ramey 1993). This distinction also has morphometric support (Wehausen and Ramey 1993), and they are listed as threatened by the State of California. A restoration program used the Mount Baxter herd as reintroduction stock from 1979 to 1988 to successfully reestablish 3 bighorn populations in the Sierra Nevada to augment the 2 surviving native ones. All reintroduced populations suffered lion predation shortly after translocations. The last of these translocations went to Lee Vining Canyon immediately east of Yosemite National Park, where losses to lion predation soon threatened the success of the reintroduction effort (Chow 1991). A small supplementation 2 years later and the removal of 1 lion in each of 3 consecutive winters reversed this trend (Bleich et al. 1991, Chow 1991), a pattern similar to that exhibited by the Granite Mountains population. However, the large decline of the Mount Baxter population following winter habitat shifts has resulted in the loss of the one source of reintroduction stock, and total population size of bighorn sheep within the Sierra Nevada has now dropped well below what existed when the restoration program began. Furthermore, in a 1996 survey of the other native Sierra Nevada population on Mount Williamson, I found that it was on the verge of extinction, with possibly only 1 sheep remaining and no evidence of any groups of sheep. This population was the last one found to be using its low-elevation winter range in 1985, but was then much smaller than the Mount Baxter population. In short, native mountain lions have not only reversed a successful restoration program for Sierra Nevada bighorn, but have caused the virtual extirpation of 1 of the last 2 native populations. If the recent population trend of the Mount Baxter population continues, it too will soon approach extinction.

The increasing trend in mountain lion activity that I recorded is corroborated by a steep increase



Mountain lion with bighorn sheep kill. Photo by California Department of Fish and Game, Round Valley Predator-Prey Study.

during the 1980's in lion depredation problems in Inyo and Mono counties, where all current Sierra Nevada bighorn sheep populations occur. Analyses by Torres et al. (1996) of livestock depredation trends in rural counties relative to trends in number of livestock numbers suggested that increasing size of the lion population was a probable cause for lion depredation trends in California. This increase may reflect recovery in mountain lion populations following the 1963 termination of bounties in California and a moratorium on all lion sport hunting which began in 1972 (Torres et al. 1996). In the final decade of bounties, bounties were collected for 111 lions in Inyo and Mono counties, an indication of abundance of lions at that time.

How bighorn sheep and mountain lions coexisted historically in the Sierra Nevada is open to speculation. Evidence indicates that deer and mountain lions were both rare in the Great Basin prior to the appearance of Europeans (Berger and Wehausen 1991). However, this may not have been the case in the eastern Sierra Nevada at the western edge of the Great Basin. Deer were part of the diet of Owens Valley Indians (Wilke and Lawton 1976), but this does not necessarily imply abundance. Early in this century, the Mount Baxter population occurred in large numbers on its winter range (Ober 1914). These sheep used low-elevation winter range before predator control programs, suggesting that there was less lion predation at that time than in the 1980's. Given the rapid recent population declines and one potential extinc-

tion due to changed wintering habits, it remains uncertain whether populations in the Sierra Nevada can persist under current lion predation rates. Minimally, it appears that Sierra Nevada bighorn may be capable of occupying only a portion of their historic range if mountain lion predation remains high.

Group behavior of bighorn sheep may not be sufficient to prevent high rates of mountain lion predation in all situations, as Buechner (1960) and Hornocker (1970) imply. Lion predation can cause large population reductions by influencing habitat selection by bighorn sheep, and this may lead to extirpation of some populations.

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