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Near-Extinction of Porcupines by Mountain Lions and Consequences of Ecosystem Change in the Great Basin Desert

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Abstract: *In North America's Great Basin Desert changes in plant communities that occurred after the introduction of domestic livestock in the late 1800s resulted in the irruption of mule deer (*Odocoileus hemionus*) and expansion of mountain lions (*Felis concolor*). We report on a situation in which mountain lion predation caused the near-extinction of another native species, porcupines (*Erethizon dorsatum*). We used demographic information collected over 8 years on an individually identified population and long term climatic data in a stochastic population model to examine the hypothesis that predation and not weather-induced starvation or random population fluctuations threatened the persistence of a naturally small population of porcupines. Whether drought-related reductions in mule deer densities induced mountain lions to prey on porcupines is unclear, but our results suggest predation and not climatic conditions caused the decline of a once robust population of over 80 to <5 animals in only 3 years. These data represent an unusual case in which predation by a native predator caused the near-extinction of a native prey species, suggesting that one unforeseen consequence of ecosystem change in western North America may be the impending loss of small, native vertebrate populations.*

Cuasi-extinción de Puercoespines por Pumas y Consecuencias del Cambio en el Ecosistema del Desierto Great Basin

Resumen: *Los cambios ocurridos en las comunidades vegetales del Desierto Great Basin en Norteamérica después de la introducción de ganado a fines del siglo pasado resultaron en la irrupción del venado bura (*Odocoileus hemionus*) y en la expansión del puma (*Felis concolor*). Este trabajo reporta un caso en el que la depredación por pumas casi causó la extinción de otra especie nativa, el puercoespín (*Erethizon dorsatum*). Utilizamos información demográfica de una población individual obtenida a lo largo de 8 años así como datos climáticos de varios años en un modelo estocástico de la población para examinar la hipótesis de que la persistencia de poblaciones naturalmente pequeñas de puercoespines estaba amenazada por la depredación y no por hambruna ni por fluctuaciones poblacionales aleatorias. No es claro si la reducción en la densidad de venado bura asociada a períodos de sequía indujo a los pumas a depredar puercoespines, pero nuestros resultados sugieren que la depredación y no las condiciones climáticas, provocó la declinación de una población robusta de más de 80 animales a menos de 5 en solo tres años. Estos datos representan un caso inusual en el que la depredación por una especie nativa casi causó la extinción de una especie-presa nativa, lo que sugiere que una consecuencia no prevista de los cambios en los ecosistemas de Norteamérica occidental puede ser la inminente pérdida de poblaciones pequeñas de vertebrados nativos.*

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Introduction

Humans have indirectly affected the world's non-polar ecosystems by the global dissemination of domestic animals, which has induced changes in plant succession and altered the composition of vertebrate communities by the removal of some large carnivores such as grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*) to protect livestock (Grumbine 1992; Bock et al. 1993; Fleischner 1994; Brown & McDonald 1995). Although humans, livestock, and non-domestic species have associated for millennia in the Middle East and Asia, pastoralist systems are comparatively new in North and South America, having operated for only the last four centuries (Wagner 1978). Other than in the Neotropics, however, the indirect role of the activities of contemporary humans on interspecific interactions has received little attention (Terborgh 1988; Robinson & Redford 1991; Redford 1992).

In the Great Basin Desert large-bodied domestic herbivores brought about ecological change that began in the last century and indirectly resulted in the irruption of populations of mule deer (*Odocoileus nemionus*) (Leopold 1950; Gruell 1986; Berger & Wehausen 1991). Prior to the introduction of livestock, mule deer were rare based on the archeological record and infrequent observations by Native Americans and explorers (Fremont 1844; Fletcher 1980; Grayson 1983). As mule deer populations increased, so did the range of mountain lion (*Felis concolor*), whose Great Basin populations are now at the highest levels ever recorded (Stiver 1988). Although the introduction of non-native predators such as dingoes (*Canis dingo*) in Australia, brown tree snakes (*Boiga irregularis*) on Guam, and Nile perch (*Lates* sp.) in African lakes has caused the extinction of species and whole community assemblages (Savidge 1987; Goldschmidt et al. 1993; Corbett 1995), little is known of the effects of recently overabundant native predators on native species (Garrott et al. 1993).

We report a 94% reduction in the size of a porcupine (*Erethizon dorsatum*) population coincident with the onset of mountain lion predation. In the course of studying an individually identified porcupine population in the Great Basin Desert in Nevada from 1988 to 1995, we witnessed the reduction of the population from 82 to <5 animals after 2 to 3 years of predation by mountain lions. Although weather-induced starvation affected survival during the study, predation appeared to be the primary factor responsible for driving the population to near-extinction. We characterized survival under different levels of predation and winter snow conditions and used a stochastic population model to examine the hypothesis that increased predation and not weather-induced starvation threatened the persistence of this population. Whether a drought-related reduction in mule deer densities induced mountain lions to prey on porcupines remains unclear, but our results suggest that increased pre-

ation and not climatic conditions drove this naturally small population to near-extinction. These results are important because (1) as populations of native species become smaller, predation may increase the probability of local extinction and (2) they offer insights into the cascade of subtle effects that may ensue as a result of ecosystem changes from past pastoral practices.

Methods

We studied porcupines intensively from December 1988 to June 1993 in an approximately 15 km² enclosed basin (Granite Basin, Fig. 1) in the Granite Range of northwestern Nevada. More limited research was conducted in the winters of 1993–1994 and 1994–1995 when we surveyed the study site for porcupines. The study population included all porcupines whose ranges overlapped three riparian areas within Granite Basin (five animals located around the periphery of Granite Basin were not considered part of the population). We searched systematically for porcupines in foraging areas (buffalo-berry [*Shepardia argentia*] and willow [*Salix* spp.] "groves" in riparian areas) and den sites (primarily rock outcroppings but also groves and juniper [*Juniperus osteosperma*] trees). We used trained dogs, radiotelemetry, a spotting telescope, night vision equipment, and tracks when snow was present to locate them. Upon initial sighting, all porcupines were captured, processed, and tagged for subsequent identification (Sweitzer & Berger 1992).

The population size for a given year was the sum of all individuals observed during surveys within the population year (May to April). In each of five population years we conducted intensive surveys for porcupines from September to March. Surveys were conducted on 37, 65,



Figure 1. Overview of the Granite Basin study area showing foraging habitats of buffalo-berry and willow groves (A), rock outcroppings used for winter denning by porcupines (B), and juniper-sagebrush habitats (C) around the perimeter of the study site.

36, 50, and 49 days in population years 1988-1989, 1989-1990, 1990-1991, 1991-1992, and 1992-1993, respectively (surveys were conducted on 4 days in 1993-1994 and 5 days in 1994-1995 and 1995-1996 combined). Dead porcupines ($n = 46$) located during surveys were categorized by probable cause of mortality as starvation, predation, or unknown based on examination of remains (Sweitzer 1996).

We assumed the population estimates in each of the 5 years from 1988 to 1993 approached a total enumeration of porcupines in Granite Basin. Two aspects of habitat use by porcupines facilitated conducting comprehensive surveys. First, in winter porcupines used den sites in rock outcroppings and juniper trees for cover and traveled to and from dens to forage on tree bark in three small riparian areas (Fig. 1). Thus, during surveys we inspected all known den sites and riparian foraging areas and searched for tracks in snow to locate animals traveling in and around the study area. Second, it was relatively easy to locate porcupines in the open juniper-shrublands at our Great Basin study site compared to more closed conifer and mixed conifer-hardwood forest habitats occupied by porcupines in other regions. When marked animals not observed in one year were relocated later, the possibility of temporary emigration was ignored, and we included the animals in the population for the year (s) that they were not observed (6, 6, 5, 0, 0, and 0 marked animals that were not located in popula-

tion surveys for 1989-1990, 1990-1991, 1991-1992, 1992-1993, 1993-1994, and 1994-1995 and 1995-1996 combined were subsequently relocated). Although the ages of porcupines were known up to 7 years old, for examining the demography of the population we grouped animals into juveniles or adults (\geq yearlings) (four animals that died during handling were excluded from calculations).

To examine the demography of the population and construct a simulation model, surviving individuals were defined as those that did not permanently disappear from the population. However, the population was not closed because animals both dispersed from and immigrated into the area. We considered all untagged, greater than or equal to yearling-aged animals observed in the population after 1988-1989 to be immigrants (Sweitzer & Berger, in press). Because dispersing animals often survive elsewhere (Van Vuren & Armitage 1994), we assumed the number of animals that dispersed and survived was approximated by the number of immigrants occurring in a cohort (Waser & Lucas 1994) and included immigrants in survival calculations. For example, 5 of the 11 juvenile females from 1988-1989 were observed in the yearling female cohort in 1989-1990, along with 2 additional untagged yearling female immigrants. Thus, the survival rate for juvenile females in 1988-1989 was estimated at 0.64 (0.45 without the immigrants; Table 1).

Table 1. Population structure, survival rates, sources of mortalities, and snow cover information for porcupines in Granite Basin, Nevada.

| Parameter | Population year | | | | | | 1994-1995, 1995-1996 |
|---|-----------------|-------------|-------------|-------------|-----------|-----------|-------------------------|
| | 1988-1989 | 1989-1990 | 1990-1991 | 1991-1992 | 1992-1993 | 1993-1994 | |
| Population structure | | | | | | | |
| unknown | 4 | | | | | | |
| juvenile males | 6 | 8 | 15 | 13 | 5 | | |
| juvenile females | 11 | 2 | 12 | 3 | 8 | | |
| \geq yearling males ^a | 14 | 16 (2) | 26 (2) | 32 | 18 | 9 | 3 |
| \geq yearling females ^a | 25 | 25 (5) | 29 (5) | 26 (3) | 15 (1) | 4 | |
| Survival rate ^b | | | | | | | |
| juvenile males | 1.00 (0.83) | 1.00 | 0.71 | 0.15 | 0.00 | | |
| juvenile females | 0.64 (0.45) | 1.00 (0.50) | 0.08 | 0.33 (0.00) | 0.00 | | |
| \geq yearling males | 0.83 (0.75) | 1.00 (1.00) | 0.85 | 0.50 | 0.50 | | |
| \geq yearling females | 0.72 (0.60) | 1.00 (0.92) | 0.86 (0.76) | 0.54 | 0.27 | | |
| Mortalities ^c | | | | | | | |
| predation | 2 | 1 | 1 | 11 | 11 | | 1 |
| starvation | 8 | | | 1 | 4 | | |
| unknown or research-related | 2 | | 1 | 2 | 1 | | |
| Number of days with >2.5 cm snow cover | | | | | | | |
| | 55 | 24 | 34 | 2 | 59 | | |

^a Values in parentheses are the number of immigrants observed in each sex and age each year. The population data for 1993-1994 were based on animals observed alive after March 1993 and animals observed during 4 days of surveys in winter 1993-1994. Population data for 1994-1995 and 1995-1996 were combined because of limited population surveys those years.

^b Survival rates were calculated by including immigrants that occurred in cohorts after 1988-1989 (values in parentheses are the survival rates calculated without including immigrants in the sex or age class affected. Four research-related mortalities (2, 1, and 1 in 1988-1989, 1990-1991, and 1992-1993, respectively) were not included when calculating survival rates. Also, survival rates were not calculated after 1992-1993 because surveys were limited after 1993-1994.

^c Four animals that died due to research handling were included in population numbers but excluded from survival calculations.

The assumption of immigration equaling emigration requires that adjacent populations have the same demographics as our study population. Although this assumption will probably be false in a most precise measure, we have no way of assessing the extent to which the assumption may have biased our calculations of survival. For example, if more animals entered the Granite Basin population than dispersed from it ("sink" scenario), then survival values would have been overestimated; however, if the population was a "source" population and more animals dispersed than emigrated, then survival values would have been underestimated. Nevertheless, because our principle objective when assessing survival was to incorporate the results into a simulation model to test the hypothesis that the near-extinction of the population was more due to predation than starvation, minor violations of the assumption in either direction would not be expected to change the qualitative results of the analyses.

Effects of Predation and Winter Weather on Survival

Predation on porcupines varied among years. Empirical data indicated that predation was low during the first 3 years of the study when mountain lions apparently did not prey on porcupines and high in the last 2 years when mountain lions did prey on porcupines (Table 1, Fig. 2a; Sweitzer 1996). We used data on mule deer populations and mountain lion depredation permits to examine the possibility that drought-related declines in mule deer densities from 1987 to 1993 led to increased predation on porcupines by mountain lions. Specifically, we compiled information on mule deer population estimates for northwestern Nevada (Washoe and Pershing counties) and northeastern California (eastern Lassen County) and mountain lion depredation permits for northeastern California (Lassen and Modoc counties) from Nevada and California wildlife department records (mule deer data were not available for Modoc County; Dick 1995). Washoe and Pershing counties in Nevada and Lassen and Modoc counties in California comprise the area of the northwestern Great Basin that includes the Granite Range. The California Department of Fish and Game (CDF&G) issues depredation permits to landowners following verified attacks by mountain lions on livestock or pets or when lions threaten public safety (Title 14, California Code of Regulations 4801-4808). We used the correlation relationship between the estimated sizes of mule deer populations and the number of mountain lion depredation permits in each year from 1987 to 1993 to examine indirectly the hypothesis that mountain lions switched to alternative prey species as mule deer densities declined in the Northwestern Great Basin from 1987 to 1992.

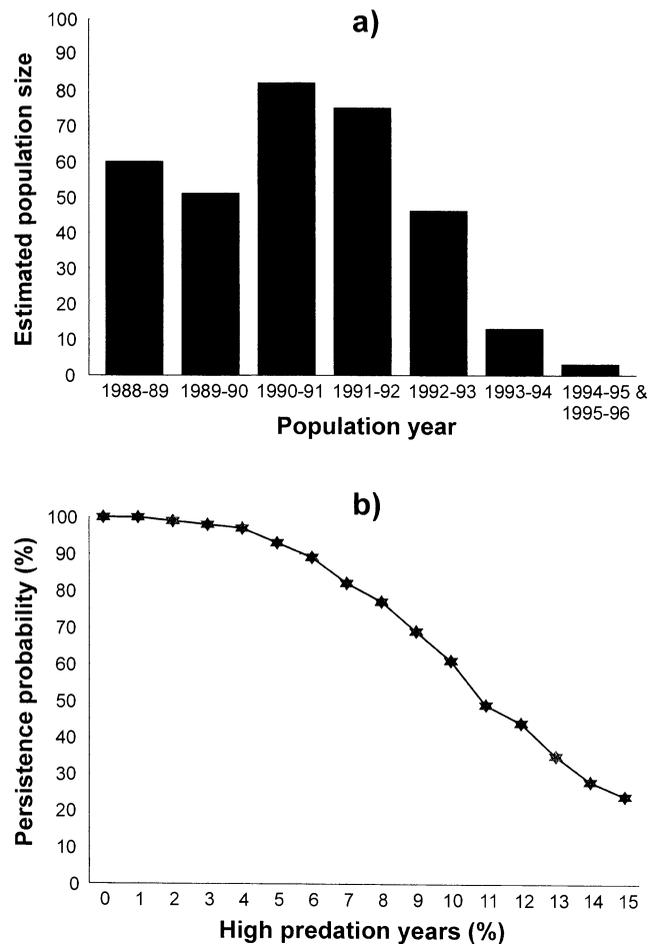


Figure 2. Annual sizes of the porcupine population in the Granite Basin during the study (a) and effects of the frequency of high predation years on the probability of persistence of the porcupine population based on a stochastic population model (b). Population years are based on the porcupine parturition season commencing around early May. The estimated population size for 1993-1994 is the sum of (1) porcupines observed alive subsequent to March 1993 and (2) animals observed during four surveys in 1993-1994. Data for 1994-1995 and 1995-1996 were combined because of relatively low survey effort in those years.

Starvation also varied among years related to the extent to which snow obscured nutrient-rich forage during late winter. Starvation was low in 3 years (1989-1990, 1990-1991, and 1991-1992) with relatively little winter snow (≤ 34 days with >2.5 cm of snow cover at a nearby weather station in Winnemucca, Nevada) and high in 2 years (1988-1989 and 1992-1993) with long periods of snow cover (≥ 55 days with >2.5 cm of snow cover at the Winnemucca weather station; Sweitzer 1996). Thus, we compiled available data for the Winnemucca, Nevada weather station on the number of days with >2.5 cm of snow cover in each year from 1928 to

1993 to examine the effects of weather-induced starvation on the porcupine population using modeling.

Survival Analyses for Modeling

We used logistic regression to estimate survival probability as a function of age, sex, snow conditions, and predation intensity. We treated juveniles and adults separately because variations in survival from year-to-year were markedly different for the two age classes. Snow condition was defined as the number of days with snow cover >2.5 cm at Winnemucca, Nevada. Predation intensity was coded as 0 for 1988–1989, 1989–1990, and 1990–1991 and 1 for 1991–1992 and 1992–1993.

For juveniles the most parsimonious logistic-regression model predicted survival probability as a function of sex and predation intensity. Adding terms for snow conditions or interactions among the predictor variables did not improve the fit of the model. Predicted survival probabilities were 0.412 for females in low-predation years, 0.026 for females in high-predation years, 0.871 for males in low-predation years, and 0.151 for males in high-predation years.

For adults the most parsimonious logistic-regression model predicted survival probability as a function of snow conditions, predation intensity, and a multiplicative interaction between these two variables. There were no differences in survival probabilities between sexes. The logistic-regression equation for adults was maximum survival probability = $\exp(f)/[1 + \exp(f)]$, where $f = 4.52 - 0.06 \times \text{snow} - 4.43 \times \text{pred} + 0.06 \times \text{snow} \times \text{pred}$, with *snow* representing snow conditions (number of days with >2.5 cm snow cover) and *pred* representing predation intensity defined as above.

Computer Simulation Model

We used a computer program written in True BASIC to simulate the effects of weather and predation on population growth using the survival equations. Each run involved 1000 trials, and each trial lasted 100 years. For each run we specified the initial number of juvenile and adult porcupines of each sex, average fecundity, and sex ratio at birth. For most runs, initial numbers equaled those in the Granite Basin in the first year of the study (Table 1). We assumed that the secondary sex ratio in porcupines is equal and used data on pregnancy rates from this population to calculate an average fecundity of 0.45 female offspring per adult female per year (Sweitzer & Holcombe 1993). The model also required a ceiling or carrying capacity on population size. We set the carrying capacity at 164, or twice the largest population size observed during our study. We used the logistic-regres-

sion equations described above to determine expected survival probabilities of both sexes of juveniles and adults; these varied from year-to-year as a function of random variation in weather conditions and predation intensity.

For the 100-year run of the model we specified the proportion of years when predation intensity was high, then whether or not a predation was high during a given year was determined by selecting a random number uniformly distributed in the interval 0 to 1. Year-to-year variation in snow conditions was simulated by randomly selecting one of the values of duration of snow cover from the weather record for the last 65 years. The code for predation intensity and the value for snow cover were used in the logistic-regression equation for adults to determine the actual survival probability of adults for a given year. For juveniles the program determined actual survival probabilities for a given year by picking random numbers from normal distributions with mean equal to the mean for females or males under low or high predation, as appropriate, and standard deviation of 0.10. In the rare instances in which a survival probability computed in this manner was <0 or >1, it was increased to 0 or decreased to 1, respectively.

The first step in simulating population size in year $n+1$ from population size in year n was to determine the number of survivors for each sex/age class. For each individual, the program selected a random number from a uniform distribution over the interval 0 to 1. If this number was less than survival probability for that year then that individual survived, otherwise it died. This procedure simulates demographic stochasticity, whereas the procedure described in the preceding paragraph simulates environmental stochasticity. Once the fates of all individuals were determined, juvenile survivors became adults. Then, reproduction was simulated by choosing a random number from a uniform distribution over the interval 0 to 1 for each adult female, adding a juvenile each time that the random number was less than average fecundity for the population, with sex of that juvenile determined by a similar random process.

If the total population size in any year was greater than the ceiling of 164 animals, then the total was reduced to the ceiling by removing the same proportion of individuals from each sex and age class. The program kept track of the minimum population size and ending population size during each trial. Theoretically, when a population declines below some threshold size (usually ≤ 10 animals) it enters an "extinction vortex" and cannot recover (Gilpin & Soulé 1986; Lacy 1993). We assumed a conservative extinction threshold population size of five and considered the population effectively extinct if ≤ 5 animals remained at the end of a 100-year run. We used a 90% persistence probability as a baseline for evaluating the modeling results, which implies that if the population size was greater than five animals in 900 out of 1000, 100-year runs then the population persisted.

We examined the sensitivity of the population model to the different parameters by systematically reducing each parameter by 10% while holding the others constant (Mills & Shenk 1992). In runs of the model examining sensitivities, we arbitrarily set the frequency of high predation years at 4% and compared changes in persistence probabilities between runs before and after varying each parameter. We used *G*-tests to compare extinction frequencies between runs.

Effects of Predation and Weather on Population Persistence

Predation and weather influenced survival, and we used results from population modeling to evaluate which factor was more likely to cause the population to perish. The model allowed us to vary the frequency of years with high predation to examine how lower survival in those circumstances affected the persistence probability of the population. When the frequency of high predation was zero, the model used survival values calculated from the first 3 years of the study and effects of the number of days with snow cover on survival to determine population trajectories. This allowed for examining how the combined effects of environmental stochasticity in the form of weather-induced starvation and demographic stochasticity might influence population persistence independent of high rates of predation. Model runs with $\geq 1\%$ frequency of high predation years allowed for examining how the added effect of increased rates of predation might affect population persistence.

Results

Survival varied during the study from relatively high survival in 1988–1989, 1989–1990, and 1990–1991 to much lower survival in 1991–1992 and 1992–1993 (Table 1). The low survival among juvenile females in 1990–1991 was unusual and may have reflected increased dispersal when population densities were high because females are the predominant dispersers in porcupines (Sweitzer & Berger 1996). We noted an average of 5.7 immigrants per year ($SD = 2.3$) from 1989 to 1991 but found only one unmarked immigrant in the population from 1991–1992 to 1995–1996 (Table 1).

Population sizes ranged from a maximum of 82 porcupines in 1990–1991 to an estimated 13 animals in 1993–1994 (Fig. 2a). Only 3 male porcupines were located in 1994–1995 and 1995–1996 combined and the carcass of 1 of those animals was found after having been killed by a predator (Table 1). Although relatively few surveys were conducted in 1994–1995 and 1995–1996, the population trajectory has been sharply downward since 1991–

1992, and porcupines in Granite Basin are now nearly extinct (Fig. 2).

Data on known mortalities indicated that both starvation and predation influenced survival and population sizes (Table 1). All but one of the deaths from starvation occurred in 1988–1989 and 1992–1993, which were the 2 years with the longest periods of winter snow cover during the study (Table 1). However, predation appeared to be the primary factor causing the population reduction after 1990–1991 because 82% of the 28 known mortalities from 1991 to 1995 were attributable to predation (Table 1). Although a coyote preyed on at least one porcupine in 1991–1992, mountain lion scats associated with predator-killed animals suggested that mountain lions were primarily responsible for the increased predation in 1991–1992 and 1992–1993 (Table 1; Sweitzer 1996).

Declines in Mule Deer Populations and Predation by Mountain Lions

Mule deer populations in the northwestern Great Basin experienced a gradual decline from 1987 to 1991 and a more pronounced drop from 1992 to 1993 (Fig. 3). The decline in mule deer populations was related to a persistent drought in the northwestern Great Basin from 1988 to 1993. Weather stations in Winnemucca, Nevada, and Cedarville, California reported 78% and 77% of the average annual precipitation from 1988–1993, respectively (National Oceanic and Atmospheric Administration reports). In 1993, however, precipitation was near or above normal (94% and 114% of normal precipitation was recorded at the Winnemucca and Cedarville weather stations, respectively), and deep winter snows exacerbated the mule deer population decline when many deer died of starvation (M. Doble personal communication).

Depredation permits indicated there were relatively few cases of mountain lions preying on livestock in northeastern California from 1972 to 1989. The CDF&G issued only three depredation permits to landowners in Modoc and Lassen counties from 1972 to 1989 (one each in 1986, 1988, and 1989; Fig. 3). In contrast, 29 depredation permits were issued from 1990 to 1993 (Fig. 3). There was a pronounced increase in lion depredations on domestic livestock from 1992 to 1993, concomitant with the period when the decline in mule deer numbers accelerated (Fig. 3). The regional decline in mule deer populations and the increase in mountain lion depredations on domestic livestock in northeastern California were correlated (correlation analyses of data on the combined Nevada and California deer population estimates and lion depredations for Lassen and Modoc counties, California from 1987 to 1993; Pearson correlation = -0.92 , Bartlett's statistic = 8.31, $df = 1$, $p =$

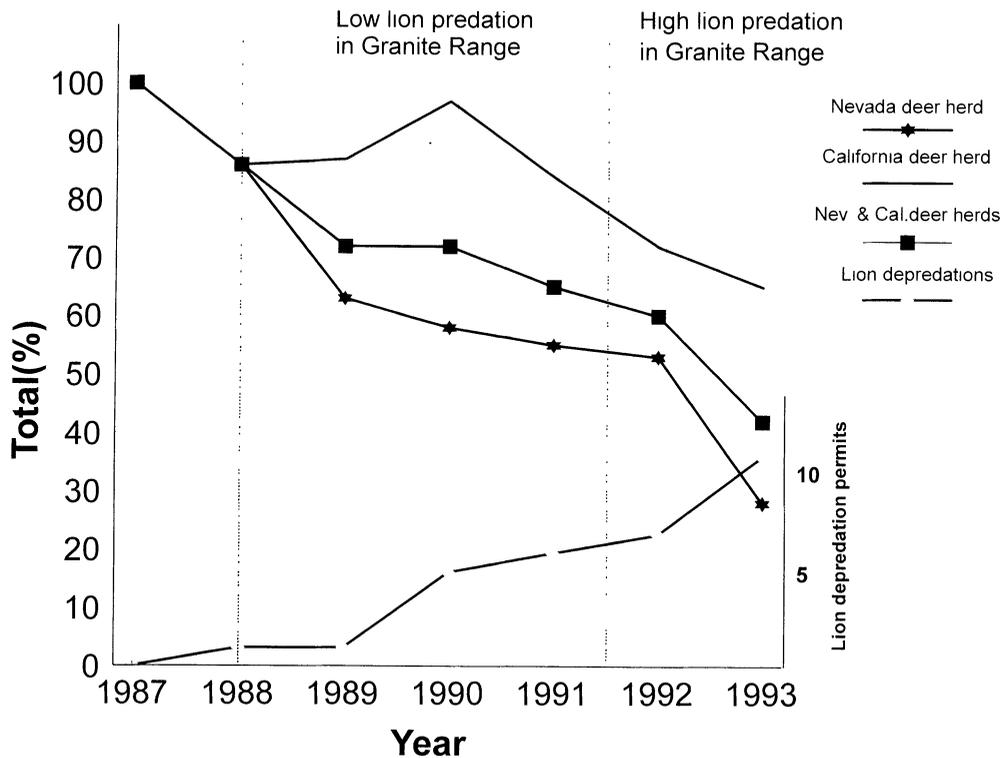


Figure 3. Information on mule deer populations for northwestern Nevada (Wasboe and Pershing counties) and eastern Lassen County in northeastern California and mountain lion depredation permits for Lassen and Modoc counties in northeastern California. Mule deer data were scaled for plotting based on the percent decrease in the yearly mule deer population estimates from the number of deer present in 1987. In 1987 there were an estimated 11,842, 6,900, and 18,742 mule deer in Wasboe and Pershing counties, Nevada; eastern Lassen County, California; and Wasboe, Pershing, and eastern Lassen counties combined, respectively. Mountain lion depredations were scaled for plotting based on the percentage of the total 31 permits issued in the period from 1987 to 1993 that were issued in each year from 1987 to 1993.

0.01). These data and our observation of increased rates of predation by mountain lions on porcupines indirectly support the idea that mountain lions switched to consuming alternative prey species when the density of mule deer declined.

Effects of Weather and Predation on Population Persistence

Population modeling suggested that under long-term patterns of climatic variation and stochastic survival and reproduction the population should persist indefinitely because the persistence probability at 0% high predation years was 100% (Fig. 2b). With the added effect of decreased survival due to high predation, however, the population was at risk. Only those modeling runs with a frequency of high predation of less than 6% had a $\geq 90\%$ probability of persisting (Fig. 2b). These results support our empirical observation that increased predation and not weather-induced starvation was the primary cause of the near-extinction of porcupines in Granite Basin (Ta-

ble 1). Sensitivity analyses indicated that the model was most sensitive to changes in adult survival (measured by the effect of the snow and predation coefficients on adult survival), fecundity, and juvenile female survival (Table 2). The model was relatively insensitive to carrying capacity, the effect of the snow \times predation coefficient on adult survival, and juvenile male survival (Table 2).

Discussion

Our results implicate mountain lion predation as the cause that exacerbated the near-extinction of a small population of porcupines in the Great Basin Desert of North America. Although environmental stochasticity in the form of deep, persistent snow cover was linked to decreased survival and population declines, modeling suggested that unusually snowy winters were insufficient to explain the near-extinction (Fig. 2b). There was a significant interacting effect of snow and predation on adult survival, but sensitivity analyses suggested that the effect of the snow \times predation coefficient was a rela-

Table 2. Summary of analyses examining the sensitivity of the population model to 10% decreases in the various input parameters.^a

| Parameter | Initial value | Initial value -10% | Change in persistence probability (%) ^b |
|------------------------------------|---------------|--------------------|--|
| Juvenile female survival | | | |
| low predation years | 0.412 | 0.371 | 5.0 ^c |
| high predation years | 0.026 | 0.023 | |
| Juvenile male survival | | | |
| low predation years | 0.871 | 0.784 | 0.7 |
| high predation years | 0.151 | 0.136 | |
| Adult survival equation parameters | | | |
| constant | 4.514 | 4.063 | 32.5 ^c |
| snow coefficient | -0.064 | -0.070 | 11.8 ^c |
| predation coefficient | -4.427 | -4.870 | 11.1 ^c |
| snow × predation coefficient | 0.055 | 0.054 | 2.0 ^d |
| Fecundity | 0.90 | 0.81 | 5.8 ^c |
| Carrying capacity | 164 | 148 | 1.9 ^d |

^aFor all model runs (1000 trials of 100 years each) the frequency of high predation was set at 4%. The sensitivity of the model to changes in each parameter was evaluated by the magnitude of decrease in the persistence probability compared to running the model with the parameters listed in the initial values column (the persistence probability for the model run using the initial values was 97.3%).

^bWe used G tests to compare changes in extinction frequencies between runs; however, p-values should be interpreted only as measure of the relative importance of the different parameters in the model because probabilities will change with the number of iterations of the model.

^cp < 0.001.

^dp < 0.05.

tively unimportant determinant of long-term population persistence (Table 2).

Although a vigorous population of porcupines had occupied Granite Basin since at least 1979 when one of us studied wild horses there from 1979 to 1984 (Berger 1986), the population was naturally small, suggesting that it may have been vulnerable to prior extinction. Dendrochronological evidence from elsewhere in North America suggests that porcupine populations fluctuate and may occasionally experience extinctions (Spencer 1964; Harder 1979). Further, several authors have reported on the limiting effect of predation by fishers on populations of porcupines (Earle & Kramm 1982; Powell & Brander 1977). Most notably, Powell (1993) reported that predation by reintroduced fishers (*Martes pennanti*) nearly eliminated porcupines from forests in the Great Lakes Region of North America. He suggested that the removal of secure den sites (hollow trees) by forest managers increased the susceptibility of porcupines to fisher predation (R. Powell, personal communication). At our Great Basin site, however, there have been no direct habitat manipulations that may have rendered porcupines more susceptible to predation.

We noted numerous immigrants in the population in several years and it is possible that immigration from elsewhere in the mountain range may "rescue" the population from total extinction (Brown & Kodric-Brown 1977; Stacey & Taper 1992). But, when conducting extensive surveys of the juniper-sagebrush (*Artemisia* sp.) shrub lands rimming our study area (Fig. 1), we failed to locate other dense populations of porcupines like the one occupying grove habitats in Granite Basin.

Most importantly, we did not observe a single unmarked immigrant or any juveniles in the area from 1992-1993 to 1995-1996 (Table 1), suggesting that porcupine populations elsewhere in the Granite Range may have also been depleted.

The modeling results implicating the frequency of high predation as the most likely determinant of population persistence appear realistic based on empirical observations (Fig. 2). Nevertheless, the model was unrealistic in that the rate of predation in 1 year was independent of predation in the previous year. In natural systems the rate of predation will more likely be correlated between years such as in cases where predators switch to alternative prey when the density of their primary prey decreases; predators may rely on the alternative prey for several successive years until the density of their primary prey increases again (Murdoch 1969; Drost & McCluskey 1992; Powell 1980; Krebs et al. 1995). In our population the 2 years with high predation occurred in sequence (Fig 2), which may have been related to particularly low densities of mule deer in the region after 1991-1992 (Fig. 3). Data on mule deer populations and mountain lion depredations on domestic livestock provided indirect support for the idea that mountain lions switched to preying on porcupines when the density of mule deer populations declined (Fig. 3). It is possible, however, that mountain lions were transient in the Granite Range, and one lion moved into the area and began preying on porcupines independently of mule deer population dynamics. Irrespective of the causal factor driving increased predation by mountain lions on porcupines, historical changes in the composition of Great Ba-

sin plant and animal communities may provide important insight into this near-extinction event.

Ecosystem Change and Predator-Prey Disequilibrium

The advent of livestock grazing in the late 1800s initiated significant changes in Great Basin ecosystems. Historical information compiled by Berger and Wehausen (1991) suggested that grazing by domestic and feral livestock in the Great Basin in the 1800s altered plant communities, which led to an irruption of mule deer populations and the spread of mountain lions. Although the spread of a "native" predator may not seem significant, Berger and Wehausen (1991) cautioned that the previously absent mule deer-mountain lion predator-prey system might affect other native prey species in the region because mountain lions can be a keystone carnivore.

Our observations combined with the disappearance and declines noted among other populations of porcupines in the Great Basin and increased mountain lion predation on bighorn sheep (*Ovis canadensis*) in the adjacent Mohave Desert region (Boyce 1995; Wehausen 1996) suggest that the overabundance of mountain lions may be a regional conservation problem. In 1989 Nevada rancher M. Knudtsen contacted R.A.S. regarding the disappearance of once abundant porcupines from the Grass Valley in the Toiyabe Range in central Nevada (subsequent surveys of the Grass Valley by R.A.S. in 1990 detected no porcupines or evidence of their recent presence). Similarly, a biologist for the Nevada Department of Wildlife (S. Stiver, personal communication) noted that porcupines in Mason Valley in eastern Nevada had also decreased in abundance in recent years. Although we have no direct data linking mountain lions to these disappearances and declines, increased rates of predation on bighorn sheep by mountain lions in the eastern Mohave Desert to the south of the Great Basin have now been documented (Wehausen 1996). Although the numerous, small bighorn sheep populations in the Mohave Desert did not traditionally support lion populations (Berger & Wehausen 1991), mountain lions now prey regularly on bighorn sheep to the extent that some populations may now be at risk of extinction (Boyce 1995; Wehausen 1990, 1996).

Although mountain lions are a native species in western North America, lion populations are increasing or are already at historically high numbers across large parts of this region (Stiver 1988; Torres et al. 1996). Overabundance is an important issue in conservation because overabundant native species can alter the composition of communities, change the relative abundances of interacting species in community assemblages, and prey on small populations of endangered species (Gar-

rott et al. 1993; Goodrich & Buskirk 1995). Other than the Pleistocene extinctions in North America caused by early human hunters (Martin & Klein 1984), there are few reports of predation by native predators causing the extinction of native prey species. In addition to the fisher example, which was at least partially attributable to habitat loss, the only documented case we are aware of where predation by a native species caused the extinction of another native species was for island-dwelling owls. Drost and McCluskey (1992) observed the extinction of Burrowing Owls (*Athene Cunicularia*) on a small island off the coast of western North America when Barn Owls (*Tyto alba*) switched to preying on them subsequent to the decline of small rodent populations. Thus, our data represent one of the few cases in which predation caused the near-extinction of a population of a native mammalian prey species.

Conservation and management issues related to large predators in the remaining natural areas in western North America have recently received significant attention in the scientific literature (see *Conservation Biology* 10[4], *Wildlife Society Bulletin* 24[3]). Mountain lions are a conservation issue in this region not because of declining numbers but because these increasingly abundant large carnivores may be eliminating small populations of other native vertebrates. In the Great Basin region some 99% of the land area available to the public is managed for multiple use, meaning that a small fraction is left available for protection under statutes devised by national park status. Although we do not necessarily advocate the widespread removal of mule deer and mountain lions, if the goals of regional national parks and preserves such as Death Valley National Park, Great Basin National Park, and Mohave National Preserve are to maintain ecosystems in a state somewhat reminiscent of those prior to the advent of European colonization, then control of lions, deer, and other recently colonizing yet native species may be warranted. If, on the other hand, the political pressure is too great to seriously implement such action, then, at the very least, scientists and natural resource managers must recognize the changes that have occurred and take steps in other areas not only to detect such changes but to plan for ways to develop monitoring programs so that the extent of such alterations become known.

Our data suggest that the spread and increasing numbers of mountain lions in large parts of western North America are an important conservation issue because lions have the potential to extirpate small populations of native vertebrates. As conservation scientists we may need to direct research efforts toward understanding how relatively recent ecosystem changes have altered the dynamics of interacting native species in ways that change or threaten regional patterns of biodiversity. It is possible for example, that predation by expanding mountain lions exacerbated losses of mammalian diversity in

mountain ranges in the intermountain west, previously attributed primarily to species relaxation and island biogeography (Brown 1971; Lomolino et al. 1989).

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