MOUNTAIN LION PREDATION OF BIGHORN SHEEP IN THE PENINSULAR RANGES, CALIFORNIA

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Abstract: We investigated survival and cause-specific mortality of 113 radiocollared bighorn sheep (*Ovis canadensis*) in the Peninsular Ranges of southern California from November 1992 through May 1998. Mountain lion (*Puma concolor*) predation was the most frequent cause of mortality, and was the cause of death for 69% (42/61) of all mortalities. Predation was documented during all months of the year except June, and 62% (26/42) of predation events occurred from December through March. Annual adult mortality rates due to predation ranged from 0.08 to 0.25 among 6 subpopulations of bighorn sheep, and the mean annual survival rate (0.79) was low relative to other bighorn sheep populations. Bighorn sheep in the Peninsular Ranges were listed as endangered by the U.S. Fish and Wildlife Service in 1998. We propose that a sustained high level of predation by mountain lions, such as was seen during this study, may impede the recovery of this population.

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Bighorn sheep in the Peninsular Ranges of southern California have declined in numbers since the 1970s (DeForge et al. 1995, Rubin et al. 1998). This population was listed as endangered in 1998, at which time it consisted of about 330 yearling and adult animals (Federal Register 1998, U.S. Fish and Wildlife Service 1999). In the Santa Rosa Mountains, near the northern end of the Peninsular Ranges, high lamb mortality and low recruitment were thought to be responsible for the population decline (DeForge et al. 1982, Wehausen et al. 1987, DeForge et al. 1995). Although mountain lions, or signs of mountain lions, had been observed in the Peninsular Ranges (Jones et al. 1957; Jorgensen and Turner 1973, 1975), predation was not thought to be an important cause of bighorn sheep mortality.

In the early 1990s we initiated a study of bighorn sheep population health in the Peninsular Ranges (Rubin et al. 1998, Boyce et al. 1999, Rubin et al. 2000). One of our goals was to quantify demographic parameters of adult bighorn sheep distributed among subpopulations within the Peninsular Ranges. When it became apparent that mountain lion predation was a frequent cause of mortality, we focused on quantifying adult survivorship and lion specific mortality, and identifying spatial and temporal patterns of mortality.

STUDY AREA

The Peninsular Ranges in the United States extend north from the California–Mexico border for approximately 225 km, and are bounded by the Pacific Coast on the west and the Imperial and Coachella valleys on the east. Bighorn sheep habitat in these ranges is bordered on the west by densely vegetated, chamise (*Adenostoma fasciculatum*)-dominated California chaparral, and on the east by lowland valleys within the lower Colorado desert subdivision of Sonoran desert-scrub community (Brown and Lowe 1980). Typically, bighorn sheep in these ranges are found below elevations of 1,400 m (Jorgensen and Turner 1975). During our study temperatures ranged from below freezing to above 45° C, and precipitation averaged about

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17 cm per year (National Oceanic and Atmospheric Administration 1992–98).

METHODS

We studied bighorn sheep from 6 subpopulations within the Peninsular Ranges, corresponding to 6 of the 8 ewe groups delineated by Rubin et al. (1998). These subpopulations, from south to north, were located in Carrizo Canyon, Vallecito Mountains, south San Ysidro Mountains, north San Ysidro Mountains, Coyote Canyon, and the Santa Rosa Mountains southeast of Highway 74.

We used a net-gun fired from a helicopter (Jessup et al. 1988) in 1992, 1993, and 1997 to capture new animals and to replace old radiocollars. We placed color-coded ear tags and a radiocollar with a mortality sensor (Telonics, Mesa, Arizona, USA) on each animal and estimated age by counting annular horn rings (Geist 1966) and examining patterns of tooth replacement (Hansen and Deming 1980). Age at death was calculated by taking age at capture and adding a year on March 1 of each subsequent year, because most lambs in the Peninsular Ranges were born in March (Rubin et al. 2000).

We began monitoring transmitters immediately following capture. We attempted to visually locate or receive a telemetry signal, by ground or aircraft, from each radiocollared animal ≥1×/month. Transmitters emitting a mortality signal were located as soon as possible. Month of death was estimated by using the date on which the last normal (live) telemetry signal was received, and by examining the stage of decomposition of the remains.

We categorized causes of mortality using field necropsies, field inspections of mortality sites, previous observations of animal condition, and photographic images from remote cameras that were placed on some fresh carcasses. Causes of death were categorized as mountain lion predation, causes other than lion predation (but otherwise undetermined), and unknown. Mortalities were classified as mountain lion kills if ≥2 of the following were observed: bite marks on the sheep's neck, a mountain lion scat, a photographic record of a mountain lion visiting a carcass shortly after the animal's death, a cached pile of remains, a trail where the prey had been dragged or carried, and fresh mountain lion tracks at the site of the carcass. The following additional criteria were used when the carcass was discovered within 48 hr of death: lion scrapes in soil, hair plucked from the carcass, large leg bones crushed or broken, and consumption of skull bones from the nose to the base of the horns. We excluded mortalities with unknown causes of death from subsequent comparisons and presentations of cause-specific mortality rates.

We used analysis of variance and natural log transformations (SPSS, Chicago, Illinois, USA) to test for differences in mean age among subpopulations of bighorn sheep captured in the first 2 years of the study. We tested for differences in ages between causes of death using *t*-tests. We calculated monthly (S_m) and annual survival rates, and cause-specific mortality rates (M_x), using the methods of Trent and Rongstad (1974) and the program MICROMORT (Heisey and Fuller 1985). Annual survival rates are presented for descriptive purposes, but all statistical comparisons were made using values of S_m. Some transmitters failed prior to the conclusion of the study and before radiocollars could be replaced. Therefore, monthly survival rates were calculated using only data from animals that had functional transmitters for the entire month (White 1983). Yearly survival rates were not based on calendar years, nor were years determined a priori. We divided years between the 2 consecutive months with the fewest mortalities (May and Jun), so that periods of elevated mortality were not split between years. We tested for differences in S_m and M_x by year, subpopulation, sex, and age class at time of death (1–4, 5–8, ≥9 yr) using the *t*-test for binomial proportions (Steel and Torrie 1980). We used the Bonferroni procedure to control experimental error rates when simultaneous tests were performed.

RESULTS

We collected 3,167 animal-months of data from 113 radiocollared bighorn sheep (16 M, 97 F) from November 1992 through May 1998. Sixty-one of these animals died during the study. Three animals died from possible capture or survey-related activities and were excluded from the analysis. Overall monthly survival was 0.98, which translated to an annual survival rate of 0.79 (95% CI = 0.74–0.83). Annual survival rates by subpopulation ranged from 0.70 in Coyote Canyon to 0.87 in the southern San Ysidro Mountains (Table 1). Yearly survival rates ranged from 0.72 in 1995–96 to 0.91 in 1992–

Table 1. Survival and cause specific mortality (M_x) rates[a] of adult bighorn sheep by subpopulation within the Peninsular Ranges of California, 1992–98.

Subpopulation	Survival	M_{lion}	M_{nonlion}	n^b
Carrizo Canyon	0.80	0.14*	0.01	755
Vallecito Mountains	0.76	0.14	0.07	303
S. San Ysidro Mountains	0.87	0.09	0.00	261
N. San Ysidro Mountains	0.86	0.12*	0.02	651
Coyote Canyon	0.70	0.26*	0.00	278
Santa Rosa Mountains	0.76	0.14	0.07	919
All subpopulations	0.79	0.14*	0.03	3,167

[a] Overall mean yearly rates are presented. Monthly rates were used for all comparisons. Cause-specific mortality rates exclude mortalities with unknown cause of death.

[b] Number of animal-months.

* $P(M_{\text{lion}} = M_{\text{nonlion}}) < 0.05$.

93 (Table 2). Monthly survival rates (Table 3) were highest in June ($S_m = 0.996$) and lowest in March ($S_m = 0.963$). Most (69%, 42/61) mortalities occurred from November through March. Mean age at capture at the beginning of the study was 5.7 years (SE = 0.3, range = 4.4 in Coyote Canyon to 6.9 in the north San Ysidro Mountains) and varied significantly among subpopulations ($P = 0.02$). Monthly survival rates did not differ among age classes ($P > 0.05$). The overall monthly survival rates for females and males were similar at 0.98 and 0.96, respectively.

Of the 61 mortalities that occurred during the study, 42 (69%) resulted from mountain lion predation, 10 (16%) were from causes other than lion predation, and 9 (15%) were from unknown causes. We located and conducted field necropsies of mortalities a median of 10 (range 1–145, $n = 49$) days after the estimated date of death, including a median of 7 (range 1–27, $n = 33$) days for mortalities that were classified as lion kills. Mountain lion predation accounted for 57–88% of all mortalities (including those with undetermined cause of death) within subpopulations of bighorn sheep, and 50–100% of all mortalities occurring within any given year of the study. The mean annual mortality rate due to lion predation (M_{lion}) was 0.14 (95% CI = 0.10–0.18). The mean annual mortality rate from non-lion predation causes ($M_{nonlion}$) was 0.03 (95% CI = 0.01–0.05, Table 1). Overall M_{lion} was greater than $M_{nonlion}$ ($P < 0.001$). M_{lion} exceeded $M_{nonlion}$, although sometimes non-significantly, within all subpopulations, years, sexes, and age classes. M_{lion} was significantly greater than $M_{nonlion}$ within Carrizo Canyon, the north San Ysidro Mountains, and Coyote Canyon (Table 1), and during years 1994–95, 1995–96, and 1997–98 (Table 2). With regard to age and sex classes, M_{lion} was significantly greater than $M_{nonlion}$ for the 1- to 4-year-old and ≥9-year-old age classes ($P < 0.01$, both cases), and rates of predation by mountain lions were not

Table 2. Survival and cause specific mortality (M_x) rates[a] of adult bighorn sheep by year within the Peninsular Ranges of California, 1992–98.

Year[b]	Survival	M_{lion}	$M_{nonlion}$	n^c
1992–93	0.91	0.09	0.00	244
1993–94	0.79	0.13	0.06	758
1994–95	0.79	0.16*	0.03	808
1995–96	0.72	0.21*	0.05	605
1996–97	0.82	0.09	0.03	368
1997–98	0.83	0.12*	0.00	384

[a] Mean yearly rates are presented. Monthly rates were used for all comparisons. Cause-specific mortality rates exclude mortalities with unknown cause of death.

[b] Years began on 1 June and ended the following 31 May.

[c] Number of animal-months.

* $P(M_{\text{lion}} = M_{\text{nonlion}}) < 0.05$.

Table 3. Monthly survival and mountain lion-caused mortality rates (M_{lion}) for bighorn sheep in the Peninsular Ranges of California, 1992–98.

Month	Survival	M_{lion}	Proportion of mortalities[a]	n^b
Jan	0.984	0.013	1.0	314
Feb	0.971	0.016	0.7	307
Mar	0.963	0.027	0.8	294
Apr	0.986	0.011	0.8	280
May	0.989	0.011	1.0	275
Jun	0.996	0.000	0.0	238
Jul	0.987	0.004	0.3	236
Aug	0.978	0.009	0.5	231
Sep	0.982	0.009	0.7	222
Oct	0.991	0.009	1.0	231
Nov	0.984	0.012	1.0	247
Dec	0.966	0.031	1.0	292
Mean	0.981	0.013	0.69	3,167

[a] Proportion of mortalities attributed to lion predation.

[b] Number of animal-months.

different for ewes and rams ($P = 0.52$). Annual mortality rates due to mountain lion predation ranged from 0.25 in Coyote Canyon to 0.08 in the south San Ysidro Mountains (Table 1). For all years combined, 62% (26/42) of all mountain lion predation events occurred from December through March, and monthly M_{lion} values for these months equaled or exceeded the mean monthly rate ($\bar{x} = 0.013$; Table 3) only during these months. Non-predation mortalities were documented in 4 subpopulations and during 4 years (Tables 1, 2).

DISCUSSION

Our results corroborate and extend the findings of recent studies indicating that mountain lions are an important cause of bighorn sheep mortality in North America (Wehausen 1996, Ross et al. 1997). Bighorn sheep are considered to be an alternate prey to the mountain lion's primary prey, mule deer (*Odocoileus hemionus*; Anderson 1983). The Peninsular Ranges are unique because bighorn sheep occur in arid low-elevation habitats immediately below a dense, shrub-dominated coastal chaparral community inhabited by mule deer (Longhurst et al. 1952). Moreover, mule deer and bighorn sheep occur sympatrically in portions of the Peninsular Ranges (Schaefer 1999). Thus, mountain lions in the Peninsular Ranges can move easily between habitat types and can prey on both bighorn sheep and mule deer. Although predation was documented during all months of the year except June, most lion kills (62%, 26/42) occurred seasonally from December through March (Table 3). This seasonality may represent mountain lion avoidance of extreme summer temperatures, cyclical changes in mule deer or bighorn sheep densities, or other unexplored factors.

Patterns in adult bighorn survival during this study were driven primarily by mountain lion predation. The lowest bighorn sheep survival occurred in the Coyote Canyon subpopulation and during 1995–96 when lion predation rates were highest (Tables 1, 2). The mountain lion predation rate was nearly 4-fold more than the rate for non-predation mortality, and tended to exceed it within each age category. The mean survival rate of 0.79 was low relative to rates reported for desert bighorn sheep in southeastern California (≥0.91; Andrew et al. 1997), Arizona (≥0.86 when highway mortality was excluded; Cunningham and DeVos 1992), and 4 of 5 populations in the Mojave Desert (≥0.85; Wehausen 1992). The 1 exception in the Mojave Desert was a small bighorn sheep population in the Granite Mountains that had a low adult survival rate (0.72) due to a high rate of mountain lion predation (Wehausen 1992, 1996).

Previous studies have demonstrated that recruitment and population trajectories vary among subpopulations in the Peninsular Ranges. For example, Rubin et al. (1998) reported that the number of ewes counted at waterholes in Coyote Canyon decreased during 1971–96, while no changes in this index of abundance were detected in the nearby north or south San Ysidro Mountains. Furthermore, Rubin et al. (2000) found that lamb survival varied among subpopulations within and across years during 1993–96. In our study, differences in mean capture ages among subpopulations indicated that location-specific variability in adult survival or recruitment may have existed prior to capture. Although independent dynamics among subpopulations may increase the persistence of metapopulations (Hanski 1989), a key finding of our study was that overall adult survival of bighorn sheep in the Peninsular Ranges was low compared to survival in other bighorn sheep populations.

Declines in bighorn sheep abundance within the Peninsular Ranges have previously been attributed to periods of low recruitment and infectious disease (Wehausen et al. 1987, DeForge et al. 1995). However, Rubin et al. (2000) demonstrated that lamb production and lamb survival were relatively high in most regions of the Peninsular Ranges during 1993–96 compared to rates reported for other desert populations (Krausman et al. 1989, Hass 1993). During this same period, we observed relatively low adult survival rates and demonstrated that mountain lion predation was the major cause of adult mortality. Predation by even a small number of mountain lions can affect bighorn survival rates (Wehausen 1996, Ross et al. 1997), and population-level effects may be exacerbated if female bighorn sheep are heavily preyed upon. Population impacts may be compounded when mountain lions kill reproductive females and their offspring, as was observed in several instances in our study ($n = 7$).

MANAGEMENT IMPLICATIONS

A sustained high level of adult mortality due to mountain lion predation has the potential to limit population growth in the future. The removal of mountain lions apparently reversed a population decline among Sierra Nevada bighorn sheep (Bleich et al. 1991), and it has been proposed as a management option to enhance the recovery of bighorn sheep in the Peninsular Ranges (U.S. Fish and Wildlife Service 1999). In addition to predator removal, we suggest that careful consideration be given to habitat factors that influence predation levels. For example, visibility is considered an important component of suitable bighorn sheep habitat (Risenhoover and Bailey 1985, Gionfriddo and Krausman 1986), and habitat visibility likely has been altered by fire suppression practices in the Peninsular Ranges (U.S. Fish and Wildlife Service 1999).

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