THE INFLUENCE OF MOUNTAIN LION PREDATION ON BIGHORN SHEEP TRANSLOCATIONS

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***Abstract*:** We studied the effects of mountain lion (*Puma concolor*) predation on 2 translocated populations of bighorn sheep (*Ovis canadensis*) in New Mexico, USA. During 1993, 32 Rocky Mountain bighorn sheep (*O. c. canadensis)* were translocated to Wheeler Peak Wilderness Area in northern New Mexico, and during 1992–1993, 31 desert bighorn sheep (*O. c. mexicana*) were translocated to Sierra Ladron in central New Mexico. We monitored both populations from release through 2000 using fixed-wing aircraft and ground and/or helicopter surveys. We determined cause of mortality for radiomarked individuals ($n = 26$) and calculated survival rates, cause-specific mortality rates, exponential growth rates, and lamb:ewe ratios. The post-lambing population estimates in 2000 were 180 in Wheeler Peak and 21 in Sierra Ladron. Annual adult survival was higher ($P < 0.005$) in the Wheeler Peak population (0.955) than in the Sierra Ladron population (0.784). Annual lamb:ewe ratios also were higher ($P < 0.001$) in the Wheeler Peak population (66.7 vs. 29.8). Mean annual exponential growth rate (r) in the Wheeler Peak population was 0.25 compared to –0.01 for the Sierra Ladron population. Predation by mountain lions was the primary proximate cause (75%) of 16 known-cause mortalities of radiomarked bighorn sheep in the Sierra Ladron population, while we did not document any predation in Wheeler Peak. The annual cause-specific mortality rates due to mountain lion predation in Sierra Ladron were 0.13 for males, 0.09 for females, and 0.11 for all adult bighorn sheep. Mountain lion predation may have limited the Sierra Ladron bighorn sheep population and could be imposing a destabilizing inverse density-dependent mortality. Mountain lions preyed on domestic cattle in the Sierra Ladron area and throughout desert bighorn sheep habitat in New Mexico; we therefore hypothesize that cattle "subsidized" the diets of mountain lions (i.e., reduced or eliminated natural starvation). The ultimate cause of mortality for these desert bighorn sheep may be related to subsidized mountain lion populations that do not appear to decline following native ungulate population decreases. In addition, the encroachment of woody vegetation may increase the hunting success of ambush predators like mountain lions. High mountain lion predation may require mitigation for the successful restoration of bighorn sheep.

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Although estimates of bighorn sheep numbers in pre-Columbian North America have been debated (Seton 1929, Buechner 1960, Valdez 1988), the low population estimates of the 20th century have met with general consensus (Buechner 1960, Toweill and Geist 1999, Valdez and Krausman 1999). All subspecies of bighorn sheep combined probably declined to <15,000 individuals (Toweill and Geist 1999). Desert bighorn sheep were extirpated from Coahuila, Chihuahua, and Nuevo Leon, Mexico, and Colorado and Texas, USA. Populations in other western states of the United States and Mexico probably declined to <5,000 individuals (Toweill and Geist 1999). Northern subspecies of bighorn sheep were extirpated from Arizona, New Mexico, Nebraska, Nevada, North Dakota, South Dakota, Utah, and Washington, USA (Toweill and Geist 1999). Populations of northern subspecies in other western states and provinces of the United States and Canada probably declined to 10,000 individuals (Toweill and Geist 1999). The decline of bighorn sheep numbers has been attributed to several anthropogenic events related to the arrival of Europeans, including market hunting, direct competition with introduced livestock, and perhaps most importantly, the introduction of diseases from domestic livestock (Buechner 1960).

Because bighorn sheep are poor colonizers (Geist 1971), restoration into most unoccupied habitat has required translocation from wild or captive-raised populations (Demarchi and

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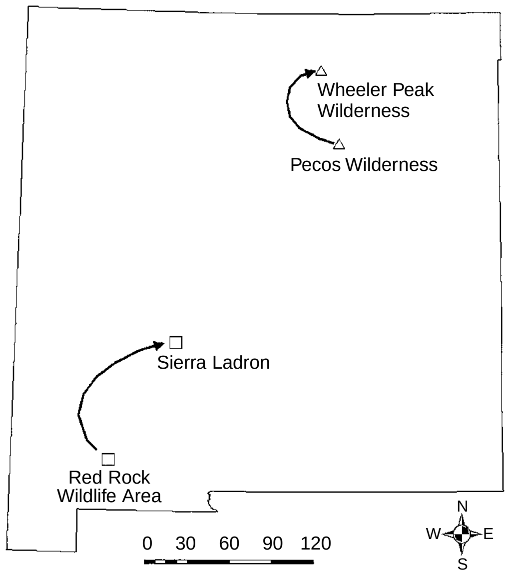

Fig. 1. Locations of source and translocated bighorn sheep herds used in our study in New Mexico, USA, 1992–1993.

Mitchell 1973, Rowland and Schmidt 1981, Cook et al. 1990). With the exception of Nuevo Leon, all states and provinces in Mexico, Canada, and the United States with historical records of bighorn sheep have attempted restoration of this species via translocation. These efforts have resulted in an estimated 65,000 bighorn sheep in North America (Toweill and Geist 1999). However, to fill unoccupied or under-occupied historical habitat will require future translocation of thousands of bighorn sheep.

Despite successes in translocating desert and Rocky Mountain bighorn sheep, translocations continue to fail. The specific causes of failures include predation, disease, and dispersal (Rowland and Schmidt 1981, Bailey 1990, Berger and Wehausen 1991, Singer et al. 1999). Documentation of mountain lion predation as the proximate cause of translocation failures and declines in extant bighorn sheep populations is a recent phenomenon (Wehausen 1996, Ross et al. 1997, Hayes et al. 2000, Rominger and Weisenberger 2000, Kamler et al. 2002).

Predator–prey theory predicts that large populations of ungulates are relatively unaffected by predation, even in ecosystems with a full complement of predators (Mech 1970). However, numerous studies have documented, or modeled, the negative effects of high levels of predation on small or isolated populations of ungulates (Bergerud and Elliot 1986, Wehausen 1996, Harrington et al. 1999, Rominger and Weisenberger 2000). Increases in ungulate populations following release into predator-free environments (Klein 1968, Caughley 1970, Leader-Williams 1988) or following control of predators (Gassaway et al. 1983, Smith et al. 1986, Farnell and McDonald 1988, Boertje et al. 1996) are well documented.

In 1932, New Mexico Department of Game and Fish (NMDGF) personnel initiated restoration of Rocky Mountain bighorn sheep with animals from Alberta, Canada. This effort resulted in >650 Rocky Mountain bighorn sheep in 6 populations in 2001. By the 1940s, only 2 desert bighorn sheep populations remained in New Mexico, and these declined to <80 bighorn sheep by 1979 (NMDGF, unpublished data). No wild desert bighorn sheep populations have been large enough to provide translocation stock. Therefore, in 1972, NMDGF personnel developed a 500-ha captive breeding facility at the Red Rock Wildlife Area (RRWA). Although NMDGF personnel attempt to control predators within the facility, bighorn sheep are subjected to predation from mountain lions, coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and golden eagles (*Aquila chrysaetos*). Bighorn sheep within this facility are behaviorally wary and considered an excellent source for release into the wild. Since 1979, 264 desert bighorn sheep have been translocated from RRWA to establish or augment 6 desert bighorn sheep populations within New Mexico. However, following autumn 2001 surveys, the estimated free-ranging population of desert bighorn sheep was <170 (Goldstein and Rominger 2002). Our objectives were to determine cause-specific mortality rates of radiomarked bighorn sheep translocated to 2 areas in New Mexico, determine the population growth rates of bighorn sheep in both populations, and review proximate causes of mortality in an ecological context.

STUDY AREAS

Sierra Ladron is surrounded by low-elevation desert in central New Mexico (Fig. 1), with elevations ranging from 1,530 to 2,797 m. Flora changed from desert shrub dominated by creosote bush (*Larrea tridentata*) at lower elevations to Douglas-fir (*Pseudotsuga menziesi*) at the highest elevations. Most habitat used by bighorn sheep was open pinyon (*Pinus edulis*)–juniper (*Juniperus monosperma*) woodland community (Dick-Peddie 1993). Although no evidence exists of historical occupancy, Sierra Ladron was evaluated as desert bighorn sheep habitat prior to translocation (Sandoval 1979, Dunn 1994). An estimated 51 km^2 of bighorn sheep habitat was available in the Sierra Ladron (Dunn 1994). Bighorn sheep habitat was 93% public land managed by the Bureau of Land Management (BLM) and U.S. Fish and Wildlife Service (USFWS) and 7% private (Dunn 1994). Sympatric wild ungulates were mule deer (*Odocoileus hemionus*) and pronghorn (*Antilocapra americana*). Approximately 1,000 domestic cow–calf pairs were grazed year-round on BLM allotments that overlapped the areas of bighorn sheep use (D. Heft, BLM, personal communication).

Wheeler Peak Wilderness is in the Sangre de Cristo Mountains, north-central New Mexico (Fig. 1). Bighorn sheep occupied the Wheeler Peak area until the late 1800s (Bailey 1931). All bighorn sheep habitat was above timberline between 3,508 and 4,014 m. Johnson (1980) described New Mexico alpine vegetation. Bighorn sheep have occupied essentially all 52 km^2 of habitat estimated by Dunn (1993). Bighorn sheep habitat is 70% public land managed by the U.S. Forest Service (USFS), 27% Taos Pueblo reservation land, and 3% private (Dunn 1993). Sympatric wild ungulates are mule deer and elk (*Cervus elaphus*). Fewer than 100 domestic cow–calf pairs grazed a portion of the bighorn sheep range during summers (USFS, unpublished data).

METHODS

We captured desert bighorn sheep from RRWA using the helicopter net-gun technique (Barrett et al. 1982). Bighorn sheep were flown to a processing site, sampled for disease, trailered, and driven about 5 hr to a release site in the Sierra Ladron (Fig. 1). In October 1992, we released 23 bighorn sheep (16 F, 7 M). In October 1993, we augmented this population with 8 bighorn sheep (4 F, 4 M) from RRWA. Releases of males from RRWA occurred in 1997 ($n = 8$) and 1999 ($n = 3$). All bighorn sheep, except those released in 1993, were fitted with radiocollars with mortality sensors (Telonics, Mesa, Arizona, USA). We fitted bighorn sheep released in 1993 with colored neckbands. In November 1999 and May 2000, we captured and radiomarked 6 bighorn sheep (5 F, 1 M) to facilitate more intensive monitoring.

We captured Rocky Mountain bighorn sheep in the Pecos Wilderness in the Sangre de Cristo Mountains using the drop-net technique (Schmidt et al. 1978). In August 1993, 33 bighorn sheep (21 F, 9 M, and 3 M lambs) were ferried by helicopter to a processing site, sampled for disease, and driven about 5 hr to a release site on private land adjacent to Wheeler Peak Wilderness (Fig. 1). All adults were fitted with radiocollars with mortality sensors (Telonics, Mesa, Arizona, USA). One radiomarked female died a day after the release. In 1994, 3 nonradiomarked bighorn sheep were observed in the Wheeler Peak herd (NMDGF, unpublished data). These bighorn sheep, 1 female and 2 mature males, were assumed to be remnants from an unsuccessful translocation from Wyoming in 1970. Therefore, the founder population in the Wheeler Peak population was 21 adult females and 11 adult males.

After release, bighorn sheep in both populations were monitored daily for 2 field seasons (NMDGF, unpublished data). From September 1996 to December 2000, we monitored radiomarked bighorn sheep during monthly aerial fixed-wing flights. We located radiocollars in mortality mode from the air and subsequently relocated them on the ground. In the Wheeler Peak population, we conducted annual ground censuses in September from 1996 to 2000. In the Sierra Ladron population, a ground census was conducted from January to March 1993 to 1995. Since 1996, we surveyed the population annually in October by helicopter.

We investigated bighorn sheep mortalities in both populations to determine causes of death. We determined mountain lion predation by the following kill-site characteristics: a dragline from kill site to cache site, mountain lion tracks at kill or cache site, mountain lion scat at cache site, canine puncture wounds in neck or face, canine punctures or claw slices in radiocollar, rumen extracted and uneaten or buried, carcass partially or completely buried (i.e., rocks, sticks, grass, raked over carcass), broken neck (generally at cervical vertebrae 1, or more rarely 2), rostrum bones eaten back >10 cm, braincase cracked in female sheep (never males), humerus and/or femur cracked, mountain lion hair present at kill or cache site, mountain lion scrapes at or near cache site, hair plucked from carcass, and multiple cache sites.

If mountain lion sign was documented at a kill site, we assumed predation unless evidence of scavenging was detected. The potential for misidentifying a scavenging event as a mountain lion kill existed; 2 bighorn sheep scavenged by mountain lions have been documented in >100 bighorn sheep mortalities in New Mexico since 1995 (NMDGF, unpublished data). However, an approximate scavenging rate of <2% would make misclassification of a scavenging event as mountain lion predation unlikely.

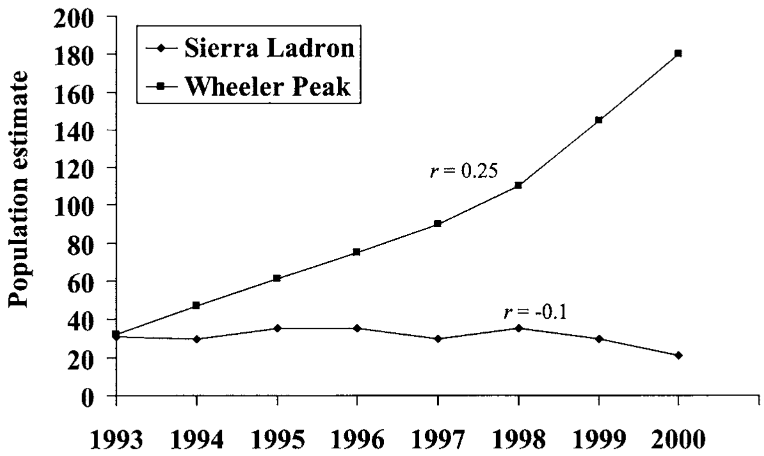

Fig. 2. Population estimates and mean exponential growth rate (r) of bighorn sheep herds in the Sierra Ladron and Wheeler Peak Wilderness, New Mexico, USA, 1993–2000.

We calculated survival and cause-specific mortality rates using MICROMORT (Heisey and Fuller 1985). We calculated radio-days to the midpoint between the last-known live signal and the initial mortality signal, unless refined by observation of the decomposed carcass. We calculated exponential rates of increase using annual population estimates. We compared annual lamb:ewe ratios between the 2 populations using a t-test for unequal sample sizes.

RESULTS

The Wheeler Peak population increased from 32 adults and 3 lambs in 1993 to 180 bighorn sheep including lambs in autumn 2000 (Fig. 2). Mean exponential growth rate was 0.25, indicating a rapidly expanding population. Based on estimated available habitat, bighorn sheep density was 3.5 sheep/km^2 in 2000. We did not document predation on bighorn sheep in the Wheeler Peak population (Table 1).

Table 1. Causes of mortality for radiomarked bighorn sheep in Sierra Ladron (n = 21) and Wheeler Peak Wilderness (n = 5), New Mexico, USA, 1992–2000.

Range/gender	Lion kill	Unknown	Poach	Accident	Legal harvest
Sierra Ladron					
Males	6	2	2	0	0
Females	6	3	0	2	0
Wheeler Park					
Males	0	0	0	0	1[a]
Females	0	3	0	0	1[b]

[a] Male legally harvested after radiocollar failure.
[b] Female harvested on Taos Pueblo, New Mexico.

The Sierra Ladron population declined from 31 to 21 individuals by autumn 2000, despite augmentation with 11 males (Fig. 2). Mean exponential growth rate was –0.1. Based on estimated available habitat, bighorn sheep density was 0.4 sheep/km^2 in 2000. Autumn lamb:ewe ratios in the Sierra Ladron population (29.7:100) were lower ($P < 0.001$) than those observed in Wheeler Peak (66.7:100). Adult survival in the Sierra Ladron population (0.784) was lower ($P < 0.005$) than in the Wheeler Peak population (0.955).

We calculated annual cause-specific mortality rates from 37,614 radio-days (n = 29 individuals) in the Wheeler Peak population and 31,428 radio-days (n = 40 individuals) in the Sierra Ladron population. From 1992 to 2000, predation by mountain lions was the major (75%) source of 16 known-cause mortalities of radiomarked bighorn sheep in the Sierra Ladron population (Table 1). The annual cause-specific mortality rate due to mountain lion predation in Sierra Ladron was 0.13 for males, 0.09 for females, and 0.11 for all adults. Mountain lion predation was documented for 12 radiomarked bighorn sheep and for 3 adults and 2 lambs that were not radiomarked. We observed 3 mountain lions during 5 autumn helicopter surveys of the Sierra Ladron bighorn population from 1996 to 2000.

DISCUSSION

The bighorn sheep translocation to the Sierra Ladron has been unsuccessful primarily because of high levels of adult mortality due to mountain lion predation. Although lambs were killed by mountain lions, no lambs were radiomarked, and we therefore could not calculate the effect of mountain lion predation on low lamb:female ratios. Since 1993, this population has incurred an annual mortality rate of 11%, and half the bighorn sheep translocated from RRWA were estimated to be alive in 2000. An increasing, inversely density-dependent, predation rate could occur with a declining bighorn sheep population and a stable mountain lion population.

Radiomarked desert bighorn sheep from RRWA (n = 98) were released into 4 other desert bighorn sheep herds in New Mexico from 1995 to 1999. Mountain lion predation was documented in 95% of 37 mortalities between 1995 and 2000 (NMDGF, unpublished data). Data collected since 1993 on 33 radiomarked desert bighorn sheep born in the wild also determined mountain lion predation to be the principle cause of mortality. Mountain lion predation was the cause of 86% of 21 mortalities on wild-born desert bighorn sheep (Rominger and Weisenberger 2000; NMDGF, unpublished data).

The bighorn sheep translocation to Wheeler Peak has been successful. The population is near the estimated carrying capacity (Dunn 1993), provides viewing and hunting opportunities, and has been used as a source of bighorn sheep for translocation (NMDGF, unpublished data). No mortality due to predation was documented in the Wheeler Peak population despite the presence of mountain lions based on harvest records (NMDGF, unpublished data).

Domestic cattle occur year-round on, or adjacent to, all desert bighorn sheep ranges in New Mexico, including the Sierra Ladron. Presence of cattle has been negatively correlated with success of bighorn sheep translocations (Singer et al. 1999). This generally is assumed to result from direct competition or possibly disease (Albrechtsen and Reese 1970, Gallizioli 1977, Onderka et al. 1988, Bissonette and Steinkamp 1996). We propose an alternate hypothesis for the role of domestic livestock in desert bighorn sheep range. The ability of mountain lions to prey-switch to domestic calves may enable resident mountain lion populations to persist in areas surrounding bighorn sheep habitat despite low densities of native ungulates. Resident mountain lions are able to prey-switch to desert bighorn sheep during incidental encounters or periods when domestic calves are removed from the range. Drought also may exacerbate this problem because fewer cattle are present and calves are frequently removed. Drought also may induce a decline in native prey species, particularly deer.

Predation on cattle by mountain lions in the western United States is well documented (Sitton and Weaver 1977, Shaw 1982, Torres et al. 1996, Cunningham et al. 1999) and may increase when native prey density decreases (Sweitzer et al. 1997). Cattle are reported as important prey of mountain lions in other ecosystems (Iriarte et al. 1990, Polisar et al. 2003). Cattle were estimated to comprise 44% of the diet of mountain lions in southeast Arizona, and 90% of the cattle killed were calves (Cunningham et al. 1999). In the Peloncillo Mountains desert bighorn sheep range in New Mexico, 6 of 14 mountain lions harvested between 2001 and 2004 were pursued directly from beef calf kills (NMDGF, unpublished data). Predation on an exotic ungulate (e.g., cattle) results in mountain lions being a subsidized predator *sensu* Soulé et al. (1988) in these ecosystems. Subsidized predators, such as mountain lions in the Sierra Ladron, are able to remain at densities much higher than would be supported by low numbers of native ungulates.

MANAGEMENT IMPLICATIONS

Recently published models on effects of mountain lion predation on small bighorn sheep populations suggest that intensive management may be required to minimize the risk of extinction (Fisher et al. 1999, Ernest et al. 2002). Management costs of implementing effective control of mountain lions may be high; however, we contend that the costs of translocation failures due to mountain lion predation also are high.

Predator control of mesocarnivores including raccoons (*Procyon lotor*), red foxes (*Vulpes vulpes*), and striped skunks (*Mephitis mephitis*) has been recommended to protect rare or endangered species (Hecht and Nickerson 1999). The same biological principle would apply to predator management of larger carnivores including mountain lions, bears (*Ursus* spp.), and wolves (*Canis lupus*) that prey on endangered ungulates including Selkirk woodland caribou (*Rangifer tarandus caribou*) or Peninsular desert bighorn sheep (*O. c. nelsoni*). Although the 2 situations are biologically equivalent, the sociopolitical ramifications of management affecting large carnivores are substantially greater (Reiter et al. 1999).

Management of mountain lion numbers may be required to mitigate the proximate cause of desert bighorn sheep mortality in the short term. Potential long-term management alternatives to mitigate ultimate causes of mortality include habitat manipulation to reduce woody vegetation and perhaps reduce ambush opportunities and conversion of overlapping domestic cow–calf operations to steer operations or the removal of livestock. Additionally, management agencies must recognize that a sudden decline in alternate prey species, either native or exotic, may increase the prey-switching behavior of resident mountain lions, resulting in substantial predation and an increased risk of extinction for small populations of bighorn sheep.

No short-term alternatives to high mountain lion predation—other than control—may be available, particularly if mountain lion populations are subsidized and at unnaturally high densities. The short-term removal of mountain lions to allow small populations of desert bighorn sheep to increase may be the best option for populations at risk of extinction due to mountain lion predation (Ernest et al. 2002). The alternative to predator management may be the loss of integral faunal components within ecosystems, such as porcupines (*Erethizon dorsatum*) or desert bighorn sheep (Sweitzer et al. 1997, Rominger and Weisenberger 2000).

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