



Invited Paper

The Gordian Knot of Mountain Lion Predation and Bighorn Sheep

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ABSTRACT The objective of this review is to generate a synthesis of research conducted on predation of bighorn sheep (*Ovis canadensis*) and to suggest directions for future research relative to current knowledge gaps and a novel hypothesis. This review is primarily based on literature from the last 60 years on desert bighorn sheep (*O. c. nelsoni*), Rocky Mountain bighorn sheep (*O. c. canadensis*), and mountain lion (*Puma concolor*) predation. Although, many predators kill bighorn sheep, only mountain lions are currently considered to be the primary proximate cause of mortality for many bighorn sheep populations. The ultimate cause of this phenomenon has vexed wildlife managers for >40 years. There are 3 primary reasons for increased predation on bighorn sheep by mountain lions. First, there is an increased presence of mountain lions in habitats where they were historically absent or rare because of the expansion of mule deer (*Odocoileus hemionus*) following the extensive conversion of fire-maintained grasslands to shrublands in the late-1800s. Second, is the extirpation of the 2 dominant apex carnivores (wolves [*Canis lupus*] and grizzly bears [*Ursus arctos*]) during this same time period and a hypothesized numerical response of mountain lions to those extirpations. Finally, the response of mountain lions to the cessation of >70 years of intensive predator control has often resulted in unsustainable mountain lion-bighorn sheep ratios, especially for desert bighorn sheep. Additionally, the effect of mountain lion predation is exacerbated by declines in bighorn sheep that do not result in declines in mountain lions because of their ability to prey switch to mule deer, elk (*Cervus canadensis*), or domestic cattle; kleptoparasitism of mountain lions kills, by ursids and canids, resulting in higher kill rates for mountain lions; and a possible ecological trap where adaptations derived over evolutionary time are no longer adaptive because of human-induced changes in the sympatric apex predator guild. Control of mountain lions, when mountain lion-ungulate ratios are high, might be required to protect small or endangered bighorn sheep populations, and to produce bighorn sheep for restoration efforts. © 2017 The Wildlife Society.

KEY WORDS apparent competition, bighorn sheep, ecological trap, kleptoparasitism, mountain lion, Native American fire, predation, predator control, predator-prey ratio.

Predation on bighorn sheep (*Ovis canadensis*), specifically mountain lion (*Puma concolor*) predation on isolated populations of bighorn sheep, has hindered restoration efforts for bighorn sheep in western North America. This review paper synthesizes our current knowledge and includes a novel hypothesis for the ultimate cause of high mountain lion predation that has confounded wildlife managers for >4 decades. This review is derived primarily from historical literature published in the last 60 years on desert bighorn sheep (*O. c. nelsoni*), Rocky Mountain bighorn sheep (*O. c. canadensis*), and mountain lion predation.

Predation has a profound influence on prey population dynamics in many ecosystems. Laboratory, mesocosm, or natural experiments have assessed the role of predation on non-ungulate prey including relationships between starfish

(*Pisaster* spp.) and tidal pool prey (Paine 1969), mites (*Typhlodromus occidentalis*) and mite prey (*Tarsonemus pallidus* and *Eotetranychus sexmaculatus*; Huffaker 1958), mesocarnivores and waterfowl (Garrettson and Rohwer 2001), weasels (*Mustela nivalis*) and voles (*Microtus agrestis*; Graham and Lambin 2002), mountain lions and porcupines (*Erethizon dorsatum*; Sweitzer et al. 1997), lynx (*Lynx canadensis*) and snowshoe hares (*Lepus americanus*; Krebs et al. 1995), and numerous other species. Hairston et al. (1960:424) noted “herbivores are seldom food-limited and appear most often to be predator-limited.” Excluding anthropogenic associated mortality, only disease has the potential for greater population-level consequences on prey populations (Pedersen et al. 2007).

The scientific literature on predation and ungulates is replete with evidence of the depressive effects that carnivores can have on ungulate populations (Gasaway et al. 1992, Harrington et al. 1999, Hayes et al. 2003, Wittmer et al. 2005, Bergerud et al. 2007). For example, some species of African ungulates increased ≥ 7 times following the removal

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of apex carnivores and all prey species <150 kg declined to near pre-removal densities after those predators were reestablished (Sinclair et al. 2003).

Asymptotic densities of ungulate populations, including bighorn sheep, on predator-free islands and in predator-free enclosures are examples of the profound influence the absence of predation can have on prey density. In North America, maximum ungulate densities in those settings are remarkably similar across an array of ecosystems and study area sizes ranging from 2.5–8,000 km² (McCullough 1979, Bowyer et al. 1999, Bergerud et al. 2007, Simard et al. 2010, Rominger 2015). In predator-free environments the median maximum density of deer-size ungulates is approximately 35 individuals/km² and compared to adjacent mainland areas with predators, ungulate densities are generally an order of magnitude, or more, greater (Rominger 2015).

High ungulate densities in the absence of predation have been documented in many cases for decades (Matthews 1973, New Mexico Department of Game and Fish [NMDGF], unpublished data) and for 80–130 years in the case of the Slate Islands, Ontario, Canada, Anticosti Island, Quebec, Canada, and Antelope Island, Utah, USA (Wolfe and Kimball 1989, Potvin et al. 2003, Bergerud et al. 2007) despite dramatic changes in vegetation composition. In other northern hemisphere predator-free islands, the non-irruptive mean ungulate density is like that reported on North American islands (Kaji et al. 2004). Density of tropical fauna is also 10 to 100 times greater on tropical predator-free islands compared with adjacent mainland densities, which mirrors the ratio of ungulate densities on temperate islands to adjacent mainlands (Terborgh et al. 2001).

The predator evasion strategy of bighorn sheep relies on the combination of keen eyesight to detect predators at distance and the ability to navigate steep terrain and outmaneuver predators following visual detection (Geist 1999). Sexual segregation of female and juvenile bighorn sheep, from male bighorn sheep, is hypothesized to be related to anti-predator behavior that includes proximity to steep escape terrain (Bleich et al. 1997). Both strategies are more effective, and therefore likely to have evolved, in response to coursing predators (e.g., wolves [*Canis lupus*]; Festa-Bianchet 1991). These strategies are less effective against a stalking predator (e.g., mountain lions).

Bighorn sheep-predator relationships are associated with potential proximate and ultimate causes. High mountain lion predation on bighorn sheep, particularly desert bighorn sheep and Sierra Nevada bighorn sheep (*O. c. sierrae*) has been the proximate factor hindering restoration in many historical ranges (Wehausen 1996, Hayes et al. 2000, Kamler et al. 2002, Rominger et al. 2004). High mountain lion predation on bighorn sheep, seen since the 1970s, appears to be related to the cessation of intensive predator control used during much of the twentieth century. This release of mountain lions from predator control has resulted in increased mountain lion-bighorn ratios that can be unsustainable based on native ungulate density, especially for desert bighorn sheep (Rominger 2013).

The ultimate cause of high mountain lion predation on bighorn sheep appears to be related to a restructuring of the apex predator guild following the extirpation of wolves and grizzly bears (*Ursus arctos*; Young and Goldman 1944, Brown 1985), major shifts in biotic communities (Berger and Wehausen 1991, McPherson 1995), and the associated restructuring of the ungulate guild across much of western North America. This restructuring has been primarily influenced by the cessation of widespread Native American burning and hunting (Turner 1991, Kay 1995, Stewart 2002), the introduction of livestock and feral equids (Berger and Wehausen 1991, Brown 1994), and the resulting expansion of mule deer (*Odocoileus hemionus*) and mule deer habitats.

Other ecological factors affecting predation and bighorn sheep include apparent competition (Rominger et al. 2004, Johnson et al. 2013), specialist predators (Ross et al. 1997, Logan and Sweaner 2001, Knopff and Boyce 2007, Knopff et al. 2010), kleptoparasitism (Elbroch et al. 2015), vulnerability of small populations (Berger 1990), subsidized predators (Rominger et al. 2004), indirect effects of predation (Bourbeau-Lemieux et al. 2011), and declining native prey (Unsworth et al. 1999). The extirpation of wolves and grizzly bears from the predator guild associated with bighorn sheep resulted in mountain lions becoming the primary bighorn sheep predator. This human-induced change might have resulted in an ecological trap (Dwernychuk and Boag 1972, Schlaepfer et al. 2002). Continued restoration of wolf and grizzly bear populations throughout Rocky Mountain and desert bighorn sheep habitat will add complexity associated with multi-predator, multi-prey systems (Knopff and Boyce 2007, Kortello et al. 2007, Knopff et al. 2010, Ruth et al. 2011) compared to many systems that only have had mountain lions as a resident apex carnivore for most of the last century.

Virtually all predators, sympatric with bighorn sheep, ranging in size from gray fox (*Urocyon cinereoargenteus*) to grizzly bear, have been documented to prey upon bighorn sheep (Sawyer and Lindzey 2002) and except for foxes, have been documented to prey on adults and juveniles. Although smaller predators (e.g., coyotes [*Canis latrans*], bobcats [*Lynx rufus*], and golden eagles [*Aquila chrysaetos*]), and less cursorial predators (e.g., black bear [*U. americanus*] and grizzly bear) are likely more effective predators of neonates, mountain lions have been documented as the primary predator of lambs (Parsons 2007, Smith et al. 2014, Karsch et al. 2016).

The consensus in the earliest review of the effects of predation on desert bighorn sheep was that no predators had population-level consequences (Desert Bighorn Council [DBC] 1957). At the inaugural DBC meeting, a special session on predation concluded that bobcats and golden eagles were the primary predators of desert bighorn sheep but that neither species limited population demographics (DBC 1957). Most biologists working on desert bighorn sheep thought that mountain lion numbers were so low, and the predator-control programs so strict (private and government year-round trapping and hunting, bounties, poisons), that

mountain lions simply could not induce population declines. The first monograph and 2 of the earliest books on Rocky Mountain and desert bighorn sheep ecology (Buechner 1960, Geist 1971, Monson and Sumner 1980) were written during a period when mountain lions were unprotected, or just recently protected by law, and wolves had been extirpated from all bighorn sheep habitats in the conterminous United States (Young and Goldman 1944). Mountain lion predation was not considered to be an important influence on bighorn sheep population dynamics.

In contrast, 5–6 decades later, a different predator-management paradigm, with mountain lions protected throughout the United States (except TX) and Canadian provinces, has shifted our interpretation of the consequences of predation. The demographic recovery of mountain lions in virtually all bighorn sheep ranges, and the advent and use of radio-telemetry to assess mortality causes, has resulted in multiple examples of population-level effects of mountain lion predation on bighorn sheep (Harrison and Hebert 1988, Wehausen 1996, Hayes et al. 2000, Rominger et al. 2004, Festa-Bianchet et al. 2006). In a recent review, Sawyer and Lindzey (2002) determined that mountain lions were capable of depressing bighorn sheep populations and numerous publications have corroborated that conclusion (Kamler et al. 2002, McKinney et al. 2006, Foster and Whittaker 2010, Brewer et al. 2013, Johnson et al. 2013).

CHANGES IN THE PREDATOR-PREY COMMUNITY

Predation on bighorn sheep hypothetically has been influenced by a change in the apex predator guild following the extirpation of wolves and grizzly bears and a change in the ungulate guild following the conversion of much of western North America from a grassland ecosystem maintained with fire by Native Americans to a shrub-dominated ecosystem. Changes in the ungulate guild are primarily related to the extensive range expansion of mule deer throughout large portions of bighorn sheep range (Berger and Wehausen 1991, Turner 1991, McPherson 1995, Kay 1995, Stewart 2002).

Changes in Predator Guild

Grizzly bear and wolf distribution overlapped nearly all Rocky Mountain bighorn sheep range and some desert bighorn ranges (Young and Goldman 1944, Lamb et al. 2017). These 2 predators were absent only from the most xeric parts of Mexico, western Arizona, California, and Nevada (Young and Goldman 1944, Lamb et al. 2017). The extirpation of wolves (Young and Goldman 1944) and near extirpation of grizzly bears (Brown 1985, Lamb et al. 2017) is well documented. Mountain lions are subordinate to wolves and bears (Boyd and Neale 1992, Kortello et al. 2007, Ruth et al. 2011, Elbroch et al. 2015) and much like the well documented response of subordinate coyotes to the absence of wolves (Berger and Gese 2007, Merkle et al. 2009), mountain lions almost certainly have responded numerically to competitive release from these 2 dominant carnivores. Evidence of this subordination is the observation

that when pursued by hounds, mountain lions in North America will climb trees. In South America, where mountain lions did not evolve with a large canid predator, they do not climb trees when pursued by hounds (B. M. Jansen, Arizona Game and Fish Department [AZGFD], personal communication.). Although the total cost to mountain lions of sympatry with wolves has not been assessed, it is hypothesized that interactions could affect reproduction, survival rates, habitat selection, and home range size (Kortello et al. 2007, Ruth et al. 2011). Mountain lion survival was negatively affected by increasing annual wolf use, wolves were responsible for 15% of adult mountain lion deaths, and wolf predation decreased annual kitten production 10–39% (Ruth et al. 2011).

Anecdotal evidence suggests that mountain lions and coyotes were rare or absent where grizzly bears and wolves occurred in New Mexico (Barker 1953, Stevens 2002). Stevens (2002) hunted grizzly bears, black bears, and mountain lions with dogs throughout the late 1800s, in the portion of New Mexico that is now the Gila Wilderness, but only mentioned 2 mountain lions in his book. In 1882, a Professor Dyche from the University of Kansas came to New Mexico to collect grizzly bears in what is now the Pecos Wilderness. Using a tree blind and a deer for bait, Dyche reported bobcats and foxes but not a single coyote in his diary, although they became common after the turn of the century following the extirpation of wolves (Barker 1953).

Extirpation of wolves and grizzly bears was facilitated by intensive predator control. Private predator control efforts began in the western United States soon after livestock was introduced following the end of warfare with Native Americans. In 1914, following a Congressional appropriation, federal agencies employed 300 predator control agents to protect livestock and remnant wild ungulate populations (Brown 1992). Control efforts included year-round trapping, poisoning, hunting with hounds, denning, and bounties paid from private and government sources (Buechner 1960, Brown 1992).

Xeric ecoregions with sufficient numbers of deer to maintain resident mountain lions, but without wolves or grizzly bears, presumably functioned much like systems where high mountain lion predation on bighorn occurs today. Historical accounts suggest that native ungulate densities may have been low in multi-prey ecosystems with sympatric mountain lions as the primary apex predator. As Charles Sheldon embarked on a bighorn sheep hunt into Mexico in 1915, his guide remarked that he had recently been to the Sierra Pintas in Arizona and “lions are numerous there but sheep are scarce” (Sheldon 1979:66). During the 1907 William Hornaday expedition from Tucson, Arizona to the Pinacate Mountains in Sonora, Mexico, a single adult deer was seen in a trip that lasted more than 30 days (Hornaday 1908).

Mountain lions may have been less common historically because of interspecific competitors (Stevens 2002, Riley et al. 2004, Wittmer et al. 2005) and a much more limited distribution of mule deer (Berger and Wehausen 1991, Potter 1995, Heffelfinger and Messmer 2003). Although

mountain lion abundance might have been briefly released following the extirpation of wolves, >70 years of intensive predator control kept numbers low. Quantifying abundance of mountain lions is difficult (Logan and Sweaner 2001) and there are no reliable estimates from periods of intensive predator control. Bounty records from 1902–1906 in Montana indicate that bounties paid for wolves outnumbered those paid for mountain lions by >30:1. By region, there was an inverse relationship between the number of wolves and mountain lions for which a bounty was paid suggesting that in areas where wolves were prevalent, mountain lions were rare (Riley et al. 2004).

Changes in Prey Guild

Grasslands were maintained across western North America with fire by Native Americans for millennia (Turner 1991, Kay 1995, McPherson 1995, Stewart 2002). Shrubs, which are the primary forage of mule deer, were an inconspicuous component of desert grasslands prior to 1880 (McPherson 1995). Reports of mule deer were rare in the diaries of early travelers and were reported to be a minor component of Native American diets (Berger and Wehausen 1991, Potter 1995, Heffelfinger and Messmer 2003, Kay 2007). The landscape conversion, of historical grasslands to shrub or chaparral, was influenced by grazing of excessive numbers of livestock and feral equids (Berger and Wehausen 1991). This conversion resulted in range expansion of mule deer and concomitantly the presence of mountain lions (Berger and Wehausen 1991). This conversion of grasslands to chaparral and shrublands occurred throughout bighorn sheep ranges in western North America. Range expansion of mountain lions following invasion by white-tailed deer (*Odocoileus virginianus*) into areas of clear-cut old-growth forests converted to shrub-dominated habitats also has been documented (Compton et al. 1995, Wittmer et al. 2005).

The 500,000-km² Great Basin ecoregion is hypothesized to have been void of deer and mountain lions because grass-dominated basin and range habitats, maintained by burning by Native Americans, did not support deer (Berger and Wehausen 1991). The Great Basin contains extensive bighorn sheep habitat and pronghorn (*Antilocapra americana*) and bighorn sheep were likely the primary ungulates present in this vast landscape. Therefore, bighorn sheep in the Great Basin may have encountered little predation by mountain lions just 125 years ago. Niche separation between pronghorn and bighorn sheep would have resulted in this ecosystem functioning much like a single-prey system. Analysis of Native American diets at 2 pueblo sites in New Mexico reported the ratio of pronghorn specimens to deer specimens was 25:1 and 79:1, respectively (Potter 1995).

Mountain lions are most effective at limiting bighorn sheep populations when they are able to prey switch onto deer, elk, or cattle and there is little evidence that mountain lions can limit bighorn sheep populations without alternative prey (Berger and Wehausen 1991, Wehausen 1996). Resident mountain lions were undocumented in bighorn sheep habitat of the Providence and New York Mountains, California, United States, until the introduction of mule deer (R. A. Weaver,

California Department of Fish and Wildlife, personal communication). Mountain lion predation is rare in the most xeric mountain ranges without sympatric deer or livestock (Berger and Wehausen 1991, Cronin and Bleich 1995).

THE PARADOX OF MOUNTAIN LION DENSITY

Regardless of the mechanisms that have resulted in the predator-prey guilds present today, it is the current ratio of mountain lions to native ungulate populations that appears to influence the primary proximate cause of mortality for bighorn sheep. Following decades of intensive predator control, mountain lions have increased numerically and in distribution (Fecske et al. 2011, Knopff et al. 2014). Predator control across North America was initially directed primarily toward wolves; however, the emphasis switched to mountain lions, black bears, and coyotes following the near-extirpation of wolves. Some states paid higher bounties for female mountain lions to incentivize population reduction (Buechner 1960). Until the cessation of large-scale predator control, mountain lion predation on bighorn sheep populations was insignificant (DBC 1957).

In a review of 12 studies assessing the effects of sport hunting on mountain lions, the range of densities was 1.1–7.1 mountain lions/100 km², although the low density does not include subadults or kittens (Cooley et al. 2011). A density of 1–3 mountain lions/100 km² when coupled with a standard ungulate kill rate (Wilckins et al. 2016) may have a profound influence on ungulate population dynamics (Table 1).

Global positioning system (GPS) collaring of mountain lions has allowed for a refinement of kill rates by visiting waypoint clusters associated with kills and most studies have confirmed that mountain lions kill about 1 ungulate/week (Anderson and Lindzey 2003, Knopff et al. 2009, Wilckins et al. 2016). This value is used as the mean for calculating the number of ungulate kills/100 km² with the 95% confidence interval for a high and low kill rate (Table 1; Wilckins et al. 2016). At a high density of 3 mountain lions/100 km² and a high kill rate of 1.1 ungulate/week, there would be a predicted 172 kills/100 km² annually (Table 1). Most small desert bighorn sheep populations in New Mexico were predicted to go extinct with 5% additive mountain lion mortality (Fisher et al. 1999). For 172 kills to be 5% of a wild ungulate population, the density required would be 3,440 ungulates/100 km². At a low density of 1 mountain lion/100 km² and a low kill rate of 0.9 ungulate/week there would be 47 kills annually (Table 1). For 47 kills to be 5% of a wild ungulate population, the density required would be 940 ungulates/100 km². Both numbers are essentially 1–2 orders of magnitude greater than currently estimated ungulate densities in desert bighorn sheep ranges in New Mexico (Bender et al. 2012, Rominger 2013). This is the paradox that influences high mountain lion predation in desert bighorn sheep ranges. Cunningham et al. (1999) estimated that 44% of mountain lion dietary biomass was comprised of livestock at an Arizona study area. The fact that mountain lions are a subsidized predator (Soule et al. 1988) is a partial explanation for their ability to persist despite low native

Table 1. Kills as a percentage of 3 hypothetical deer-size ungulate-prey population densities using 3 values of mountain lion density and 3 values of kill rates (e.g., low lion density [1.0] × low kill rate [0.9] × 52 weeks = 47 kills/annually). The final column is number of deer-size ungulates/100 km² required for the number of kills to be a 5% mortality rate (e.g., 47 kills/5 × 100) = 940.

Mountain lion density/100 km ^{2a}	Mountain lion weekly kill rates ^b (no. prey)	No. annual kills	Annual % mortality ^c at 50 prey/100 km ²	Annual % mortality ^c at 100 prey/100 km ²	Annual % mortality at 200 prey/100 km ²	No./100 km ² if % mortality = 5%
1	0.9	47	94	47	24	940
1	1.0	52	>100	52	25	1,040
1	1.1	57	>100	57	28	1,140
2	0.9	94	>100	94	47	1,880
2	1.0	104	>100	>100	52	2,080
2	1.1	114	>100	>100	57	2,280
3	0.9	140	>100	>100	70	2,800
3	1.0	156	>100	>100	78	3,120
3	1.1	172	>100	>100	86	3,440

^a These values lower than most values in Cooley et al. (2011).

^b Mean kill rate ±95% confidence intervals from Wilkins et al. (2016).

^c >100 indicates the estimated annual kill exceeds population size.

ungulate densities (Cunningham et al. 1999, Rominger et al. 2004).

In the Fra Cristobal Mountains, New Mexico, mountain lion control conducted from 1999 until 2013 resulted in the highest estimated ungulate density of any desert mountain range in the state (New Mexico Department of Game and Fish [NMDGF], unpublished data). The combined bighorn sheep and mule deer density is approximately 400/100 km² (NMDGF, unpublished data). From 2003 to 2013, an average of 3.3 mountain lions were killed annually on the 107-km² mountain range (NMDGF, unpublished data). However, even at this high ungulate density, 2 resident mountain lions could potentially kill nearly 25% of the resident ungulates annually.

A long-term mountain lion study on the San Andres Mountains, New Mexico documented 1.72–4.25 mountain lions/100 km² including adults, subadults, and cubs. This study was completed in 1995 just as high mountain lion predation adversely affected mule deer density and was also the predominant mortality cause associated with the biological extinction of desert bighorn sheep (Logan and

Swanor 2001, Rominger and Weisenberger 2000). Following this study, mule deer density declined to one of the lowest ungulate densities reported in North America with an estimated 10–12 deer/100 km² (Bender et al. 2012, Rominger 2013). Although mountain lion density in the San Andres Mountains is currently unknown, they persist in this habitat despite a very low deer density. There has been no discernable recovery of mule deer in >20 years.

DIRECT PREDATION

Although predation by mountain lions had been anecdotally noted by several authors (Leopold 1933, DBC 1957, Blaisdell 1961), it was not until the earliest stages of the restoration of desert bighorn sheep in Texas that high mountain lion predation was documented to cause population declines (Kilpatrick 1976). In rapid succession, other western states and provinces began documenting instances of high mountain lion predation (Table 2). Most early data are reported as a percentage of radio-collared bighorn sheep killed annually (Muñoz 1982, Harrison and Hebert 1988, Creeden and Graham 1997, Ross et al. 1997).

Table 2. Examples of high mountain lion predation on bighorn sheep (bhs) in western North America.

Location	Year	Citation	Specifics
TX	1975	Kilpatrick (1976, 1982)	21 bhs killed inside captive breeding facility by mountain lions at Black Gap State Wildlife Area; the wild population estimated to have declined from 20 to <10
NM	1979	Muñoz (1982)	9 of 25 (36%) bhs killed by mountain lions in 14 months
NM	1980–1989	Hoban (1990)	22 of 43 bhs mortalities attributed to mountain lion predation
NM	1996–1997	Rominger and Weisenberger (2000)	Bhs decline from ~25 to 1 resulting in biological extinction. Mountain lion predation the primary cause of death
BC	1986–1988	Harrison and Hebert (1988)	2 female mountain lions kill a minimum of 21 bhs in 14 months
CO	1995	Creeden and Graham (1997)	5 of 14 (36%) radio-collared bhs killed by mountain lions within 12 months
AB	1985–1994	Ross et al. (1997)	13% of winter bhs population killed; 1 female mountain lion killed 9% of total population and 26% of lambs in 1 winter
OR	1995–2002	Foster and Whittaker (2010)	Hart Mountain bhs herd declined from 600 to 125 with mountain lion predation the primary cause of mortality
CA	1997–1999	Schaefer et al. (2000)	Mountain lion predation cause of 75% of bhs mortality
CA	1976–1988	Wehausen (1996)	49 bhs documented killed by mountain lions without telemetry
AZ	1979–1997	Kamler et al. (2002)	In meta-analysis of 365 translocated bhs, 66% of mortality was mountain predation

Table 3. Cause-specific mortality rates (CSMR) on bighorn sheep (bhs) attributed to mountain lion predation in western North America.

Location	Year	Citation	Mortality rates
CA	1988–1995	Wehausen (1996)	CSMR due to mountain lions was 0.38
AZ	1979–1997	Kamler et al. (2002)	In meta-analysis of 365 translocated bhs, the highest CSMR due to mountain lions was 0.29
AZ	1993–1996	Bristow and Olding (1998)	CSMR due to mountain lions was 0.12 for females and 0.15 for males
NM	1992–2000	Rominger et al. (2004)	CSMR due to mountain lions was 0.13 for males and 0.09 for females in desert habitat
OR	2004	Foster and Whittaker (2010)	CSMR due to mountain lions for 44 radio-collared bhs was 0.17 for males and 0.10 for females
AB/MT	1983–2003	Festa-Bianchet et al. (2006)	During years of high mountain lion predation, the CSMR due to mountain lions was 0.26 for males and 0.32 for females
CA	1992–1998	Hayes et al. (2000)	CSMR due to mountain lions for 113 radio-collared bhs ranged between 0.08 and 0.26

The development of survival models (Heisey and Fuller 1985, White and Burnham 1999) that incorporate data from telemetrically monitored bighorn sheep, allow researchers to calculate cause-specific mortality rates (CSMR; Table 3). Mountain lion-specific mortality rates of adult bighorn sheep have been as high as 0.26 (Hayes et al. 2000), 0.29 (Kamler et al. 2002), and 0.31 (Goldstein and Rominger 2012) in some ranges. Statewide lion-specific mortality rates for desert bighorn sheep in New Mexico between 1992 and 2002 were 0.16 (Goldstein and Rominger 2012) and 88% of New Mexico desert bighorn sheep populations went extinct or declined to <10 females during this period.

The high mortality rates on state-endangered desert bighorn, attributed to mountain lion predation, in New Mexico during the 1990s were unsustainable and caused populations to decline rapidly (Goldstein and Rominger 2012). However, substantially lower mountain lion mortality rates are projected to be detrimental to the persistence of small populations of bighorn sheep. A Vortex model for state-endangered desert bighorn sheep in New Mexico predicted that all extant populations had a 100% probability of extinction with just 10% mountain lion predation added to baseline non-predation demographic parameters (Fisher et al. 1999). Initial population sizes of these small herds ranged from 10–120 and just a 5% mountain lion predation rate induced an extinction probability of 0.82–1.0 for 6 extant herds (Fisher et al. 1999).

Following the initiation of mountain lion control in desert bighorn sheep ranges in New Mexico, numbers increased from <170 in 2001 to >1,100 in 2016 (Fig. 1; Ruhl and Rominger 2015). After 31 years on the New Mexico threatened and endangered species list, desert bighorn sheep were delisted in 2012 and returned to a state-protected game species (Rominger et al. 2009, Goldstein and Rominger 2013).

Predation is the dominant cause of mortality for ungulate neonates (Smith et al. 1986, Scotton 1998, Gustine et al. 2006, Quintana et al. 2016). Predation caused 82% and 86% of mortality of desert bighorn sheep lambs in 2 studies in New Mexico (Parsons 2007, Karsch et al. 2016). In both studies, mountain lions were the apex predator.

Although wolves are currently considered to be a predator of minor consequence, as mountain lions were in 1957, wolves are still recolonizing many Rocky Mountain bighorn sheep ranges and have just begun to re-occupy historical

desert bighorn sheep ranges in Arizona and New Mexico. The ecological relationship between wolves and mountain lions is not well understood (Hussemann et al. 2003, Kortello et al. 2007, Ruth et al. 2011, Krawchuck 2014) and research has been primarily conducted in ecosystems recently recolonized by one or both predators, or where both carnivores have responded to less intensive predator control (Knopff and Boyce 2007, Kortello et al. 2007, Ruth et al. 2011). Most of these studies have reported mountain lions to be subordinate to wolves resulting in usurpation of kills, direct mortality of adult and juveniles, and constriction of home ranges (Boyd and Neale 1992, Kortello et al. 2007, Ruth et al. 2011).

In North American ecosystems occupied by Dall's sheep (*O. dalli dalli*), the primary predator is the wolf and there is little evidence of consistent population-level consequences of predation (Barichello and Carey 1988, Hayes et al. 2003), although Bergerud and Elliot (1998) reported improved recruitment of Stone's sheep (*O. d. stonei*) following the reduction of wolf numbers in British Columbia. Barichello and Carey (1988) reported no evidence that a substantial reduction in wolf density influenced demographics of Dall's sheep. However, Arthur and Prugh (2010) reported high

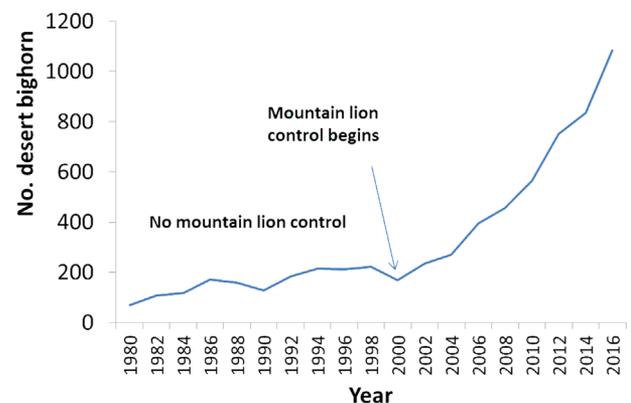


Figure 1. Desert bighorn sheep population estimates, New Mexico, 1980–2016. From 1979–1999, there were 253 desert bighorn sheep released into wild populations. From 2000–2016, there were 274 desert bighorn sheep released into wild populations. Mountain lion control began in 1999 in all endangered desert bighorn sheep herds when statewide population estimates declined to <170 in 6 herds.

levels of Dall's sheep lamb mortality by coyotes, which are hypothesized to have increased because of wolf control.

Coyotes are reported to kill adult and juvenile ungulates (Hass 1989, Kelley 1980) and were the second-most important predator of juvenile desert bighorn sheep after mountain lions in the Peloncillo Mountains, New Mexico (Karsch et al. 2016). Coyotes may be more effective predators than wolves on wild sheep neonates (Arthur and Prugh 2010) and the extirpation of wolves has resulted in a competitive release of coyotes (Berger and Gese 2007). Hebert and Harrison (1988) reported coyote predation as a major source of lamb mortality in British Columbia, Canada, and that predator control targeting coyotes was responsible for a 2–2.5-fold increase in lamb:female ratios. Bobcats are reported to kill adult and juvenile ungulates (Kelley 1980, DeForge 2002); however, there is little evidence that they have population-level effects on bighorn sheep populations. Bobcats were not confirmed to have killed desert bighorn sheep lambs in the 2 New Mexico studies (Parsons 2007, Karsch et al. 2016).

Most bighorn sheep herds are comprised of <100 individuals (Berger 1990) and therefore may be more vulnerable to extinction (Berger 1990, Fisher et al. 1999), although Wehausen (1999) found less support for a strong population size effect on extinction probability. High levels of predation can cause the extirpation of small isolated populations of bighorn sheep (Rominger and Weisenberger 2000), woodland caribou (*Rangifer tarandus*; Kinley and Apps 2001), and other species (Williams et al. 2004). However, bighorn sheep populations >100 also have been documented to decline substantially, with mountain lion predation the primary cause of mortality (Wehausen 1996, Hayes et al. 2000, Foster and Whittaker 2010).

Bighorn sheep populations with sympatric deer have been documented to decline to low density, with mountain lion predation the primary mortality factor (Wehausen 1996, Foster and Whittaker 2010, Rominger 2013). This apparent competition in multiple-prey systems was first described by Holt (1977) and has been documented in bighorn sheep populations (Rominger et al. 2004, Johnson et al. 2013) and other ungulates (Bergerud and Elliot 1986, Harrington et al. 1999, McLellan et al. 2010, Wittmer et al. 2014). For Sierra Nevada bighorn sheep, the more common prey species is mule deer (Johnson et al. 2013); however, in most desert bighorn sheep habitats in Arizona and New Mexico, domestic cattle, usually juveniles, are also alternative prey (Cunningham et al. 1999, Rominger et al. 2004).

The usurpation of mountain lion kills by interspecific competitors, primarily bears or wolves, can influence predation dynamics. In Colorado and California, mountain lion kill rates increased 48% in the presence of sympatric black bears because of kleptoparasitism, with bears detected at 48–77% of mountain lion kills (Elbroch et al. 2015). Although mountain lions may occasionally kill small black bears at cache sites, it appears that mountain lions generally depart permanently following the arrival of larger black bears (Elbroch et al. 2015). Wolves were documented to usurp 12% and scavenge 28% of mountain lion kills during a 4-year

period (Kortello et al. 2007). In southern British Columbia, where wolves and grizzly bears were extirpated, or greatly reduced, mountain lions are the dominant predator of woodland caribou (Compton et al. 1995, Kinley and Apps 2001, Wittmer et al. 2005). However, in north-central British Columbia, where wolves and grizzly bears persist, mountain lions are not the dominant predator (Wittmer et al. 2005).

After work by Ross et al. (1997) that documented high mortality on a wintering bighorn sheep herd by an individual mountain lion, it has been debated whether most predation on bighorn sheep is a function of specialist mountain lions. Although, specialist predators exist (Ross et al. 1997, Logan and Sweanor 2001, Knopff and Boyce 2007), other data suggest that most sympatric mountain lions will kill bighorn sheep. In the Peninsular Ranges of California, 18 of 23 individually identified mountain lions were associated with bighorn sheep kills (Ernest et al. 2002) and in the Fra Cristobal Mountains, New Mexico 16 of 18 radio-collared mountain lions either killed or attempted to kill desert bighorn sheep (NMDGF, unpublished data).

The predator-evasion strategy of bighorn sheep is far more effective against a coursing predator than a stalking predator (Festa-Bianchet 1991) and the abrupt removal of wolves and widespread replacement by mountain lions may have resulted in an evolutionary trap where past selection pressures shaped cue-response systems that were adaptive but no longer are in the face of human-induced changes. Additionally, the sexual segregation behavior of bighorn sheep might be associated with the potential for an ecological trap. Mortality rates for female bighorn sheep, attributed to mountain lion predation can be as high or higher than those for males, suggesting the benefit of this sexual segregation strategy is not particularly effective against mountain lion predation (Krausman et al. 1989, Hayes et al. 2000, Kamler et al. 2002, Festa-Bianchet et al. 2006).

DISCUSSION

Recent studies throughout western North America provide evidence that direct predation by mountain lions is a primary proximate mortality factor of bighorn sheep. The increase in mountain lion predation on bighorn sheep has followed the demographic recovery of mountain lion populations following the cessation of intensive predator control efforts. The recovery of mountain lions was preceded by expansion of their primary prey, mule deer, following the vast conversion of grasslands that had been maintained with fire by Native Americans. This shift in the mountain lion prey guild allowed for range expansion of mountain lions into habitats where wolves and grizzly bears have been extirpated. The combination of restructured predator-prey guilds and elimination of Native American fire and hunting has resulted in bighorn sheep with sympatric mountain lion densities unlikely to have occurred previously.

Additionally, livestock and feral equids responsible for conversion of grasslands contribute to the alternative prey-base for mountain lions. In ecosystems with low densities of native prey, cattle subsidize mountain lion populations and

may comprise >40% of the biomass in mountain lion diets, precluding a decline in mountain lion numbers despite declining native ungulate populations (Cunningham et al. 1999, Rominger et al. 2004). Feral equids are also reported to subsidize mountain lion populations, although they are much less numerous than cattle (Berger 1986, Turner et al. 1992, Knopff and Boyce 2007). Low densities of native ungulates are correlated with increased depredation of livestock by felids and canids (Brown 1992, Khorozyan et al. 2015).

The intensity of mountain lion predation has been reported to be nearly continuous in some ecosystems and more pulse-like in other ecosystems (Ross et al. 1997, Rominger et al. 2004). Because bighorn sheep density is rarely but a fraction of that observed on predator-free islands and predator-free enclosures, most predation is considered additive mortality, especially at low bighorn sheep densities. The stalking hunting style of mountain lions is hypothesized to result in more prime-age bighorn sheep kills compared to the effect of a coursing hunting style (e.g., wolves), which exposes compromised individuals. Additionally, the encroachment of woody vegetation due to the exclusion of fire for more than a century has enhanced stalking cover for mountain lions (Wakelyn 1987).

Increased mountain lion predation and related declines in New Mexico desert bighorn sheep populations have been correlated with declines in sympatric mule deer. These populations declined sharply in the mid-1990s and there has been no discernable recovery in the last 20 years (Rominger and Weisenberger 2000, Bender et al. 2012, NMDGF, unpublished data). Observations of deer during helicopter surveys in the San Andres Mountains were as high as 150 deer/hour and have declined to <5.5 deer/hour for all bighorn sheep surveys flown since 1996 (NMDGF, unpublished data). The estimated deer density in the San Andres has declined to 0.08–0.11 mule deer/km², making this one of the lowest densities of North American ungulates ever reported (Bender et al. 2012, Rominger 2013). Because of this low density, there has been no deer hunting on the entire 8,300-km² White Sands Missile Range, New Mexico since 1999. Similarly, low mule deer observation rates have been recorded in all other desert bighorn sheep surveys in New Mexico for the last 20 years (NMDGF, unpublished data). However, it was the ratio of mountain lions to these very low-density ungulates that precluded recovery and has required mountain lion control to increase desert bighorn sheep numbers.

Declines in bighorn sheep populations, due to mountain lion predation, have been reported for nearly every state and province where this species occurs. There is little evidence that these populations recover in the absence of predator control. One exception appears to be the federally endangered Peninsular bighorn sheep population. Although this herd is still listed as endangered, it has increased from approximately 275 (Rubin et al. 1998) to approximately 980 (Botta 2011) without mountain lion control. Peninsular bighorn sheep have an elevational niche separation from mule deer that use habitat at higher elevations in the Peninsular Ranges (Hayes et al. 2000), much like the niche

separation of pronghorn and bighorn sheep in the Great Basin (Berger and Wehausen 1991). Thus, mountain lions hunting in low-elevation desert bighorn habitat have virtually no opportunity to prey switch onto deer without vacating bighorn sheep habitat.

Management of predation deemed excessive relative to bighorn sheep population objectives generally involves lethal predator control. Controlling apex carnivores is much more controversial than culling mesocarnivores (Reiter et al. 1999, Rominger 2007) despite documented success in the protection and recovery of endangered species (Hecht and Nickerson 1999, Rominger et al. 2009, Johnson et al. 2013, Hervieux et al. 2014).

Predator control is used by most western state and provincial wildlife agencies to protect endangered ungulate species (Hervieux et al. 2014) and big game populations (Rominger 2007). Predator control to protect translocated desert bighorn was first advocated by Wilson et al. (1973) and has been used to aid the restoration of bighorn sheep in New Mexico, California, Texas, Arizona, Utah, and elsewhere (Rominger 2007). High levels of mountain lion predation associated with desert bighorn sheep translocations and some Rocky Mountain bighorn sheep translocations (Krausman et al. 1999, Rominger et al. 2004, McKinney et al. 2006) can be reduced by removing resident mountain lions prior to translocation. After multiple failed translocations due to mountain lion predation, NMDGF no longer translocates desert bighorn sheep without a pre-treatment mountain lion control program to reduce the density of resident mountain lions, usually beginning 3–4 months prior to translocation.

Following the extirpation of desert bighorn sheep in the Catalina Mountains, Arizona in the 1980s, desert bighorn sheep were released into historical habitat in 2013 (Krausman 2017). The initial translocation, done without a pre-treatment removal of resident mountain lions, had high mortality with mountain lions killing 15 of 30 radio-marked bighorn sheep within 4 months. Post-release control of offending mountain lions resulted in the lethal removal of 7 mountain lions. To date, mountain lions have killed a minimum of 27 of 86 radio-marked bighorn sheep from 3 releases. In the absence of mountain lion control, this attempted restoration of a native faunal component would have almost certainly failed.

Ernest et al. (2002) modeled predator control management options to mitigate mountain lion predation and determined that for populations or subpopulations with <15 females, range-wide control (habitat control) of mountain lions was the most effective paradigm. At higher female numbers, less strict take of mountain lions was recommended (e.g., only remove offending mountain lions [kill-site removal]). However, this model assumes that a documented offending mountain lion will be removed prior to making additional kills. A large data set from NMDGF suggests this is unlikely and offending mountain lions were taken at <20% of bighorn sheep kills (Rominger et al. 2011). During a period of range-wide mountain lion control, 68 mountain lion-killed bighorn sheep with very high frequency (VHF)

radio-collars were documented. However, only 13 (19%) offending mountain lions were culled.

The 2 primary reasons mountain lions were not culled were the bighorn sheep kill was not detected and located prior to the mountain lion departing (59% of all kills) and the mountain lion was present but missed at the kill site (54% of attempted removals were unsuccessful because the mountain lion did not step into snare, substrate was not conducive to snare placement, hounds were unable to tree or bay mountain lion). Although sample sizes were substantially reduced, the data set was partitioned between attempts to snare offending mountain lions and attempts to hound-hunt offending mountain lions. Use of hounds was successful in 5 of 14 attempts, whereas use of snares was successful in 8 of 14 attempts (Rominger et al. 2011). Culling offending mountain lions in the Catalina Mountains, Arizona restoration project has been successful in 6 of 15 attempts and this higher success rate is attributed to the use of GPS collars that alerted managers to mountain lion kills more quickly than VHF radio-collars (B. D. Brochu, AZGFD, personal communication).

Trapping and translocation is the primary management tool used to reestablish bighorn sheep populations into unoccupied habitats (Foster 2004). Currently, most bighorn sheep used for translocation come from mountain lion-free islands (e.g., Tiburon Island, Sonora, Carmen Island, Baja California Sur, MX; Wild Horse Island, MT, USA, Antelope Island) or predator-free enclosures (e.g., Red Rock, NM, USA and Pilares, Coahuila, MX). Very few desert bighorn sheep populations with uncontrolled sympatric mountain lions produce surplus bighorn sheep for translocations.

Restoration of natural grasslands, maintained by frequent fires, at scales that would substantially reduce deer numbers is unlikely to be a near-term management option. However, most state and provincial agencies have developed habitat management plans to reduce woody vegetation to increase bighorn habitat, and potentially reduce stalking habitat for mountain lions. Although, mountain lion predation seems to be lowest in single-prey systems in the most xeric habitats, most bighorn sheep currently occur in habitats with multiple sympatric ungulates. It is hypothesized that high levels of alternative buffer prey are preferable to low-density buffer prey when habitats have high mountain lion density.

Kill rates may increase substantially in ecosystems with high levels of kleptoparasitism and if deemed excessive, population reduction of kleptoparasites, specifically bears, would be a novel management action. The cumulative effects of predation on all sex and age classes of a bighorn sheep population must be recognized. Total predation in ecosystems with a diverse predator guild may have a much more profound influence on bighorn sheep demography; therefore, wildlife managers must decide on the appropriate response relative to management needs (Griffin et al. 2011). Small, isolated bighorn sheep herds, reduced to very low numbers by predation, will require human-mediated translocations to mitigate genetic loss and demographic declines.

Factors that influence rates of mountain lion predation should be examined experimentally to enable managers to better understand this complex system that appears to be substantially altered by anthropogenic causes. Experiments should be designed and conducted in bighorn sheep herds that are large enough to sustain high levels of predation without the need to manipulate mountain lion numbers during the experiment. Understanding the role of alternative prey, including livestock, will be a potential research direction. Understanding the influence of wolf restoration on bighorn sheep and mountain lions, particularly the effect on recruitment of adult female mountain lions, will be important. Because mountain lions are relatively long-lived, this research should be conducted over long periods following the reestablishment of wolves.

MANAGEMENT IMPLICATIONS

Productive bighorn sheep populations are required for restoration via translocation, sport hunting, and endangered species recovery. Management practices to decrease mountain lion densities that adversely affect bighorn sheep populations can be ideally addressed via sport harvest levels regulated by state wildlife agencies. In habitats or states (e.g., CA) where sport harvest does not meet management objectives, facilitated mountain lion control may be required to prevent population declines of bighorn sheep. Removal of resident mountain lions, prior to translocation of desert bighorn sheep, has increased the probability of successful restoration (Rominger et al. 2009).

There is still the potential that bighorn sheep can remain a viable faunal component in the North American west. If the public and wildlife managers are interested in keeping and restoring bighorn to their native ranges for viewing, hunting, and as source populations for recovery in landscapes that have been anthropogenically altered, difficult decisions will have to be made. Continued research on predation and other ecological factors will aid in the conservation of this species.

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