A Review of Predation on Bighorn Sheep (*Ovis canadensis*)

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Wyoming Animal Damage Management Board
Wyoming Domestic Sheep and Bighorn Sheep Interaction Working Group
Wyoming Game and Fish Department

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INTRODUCTION

Mountain sheep *(Ovis* spp*.)* are medium-sized ungulates that range from northern Alaska to Mexico, where they rely on steep, precipitous and usually non-forested terrain to detect and escape predators (Geist 1971). North American mountain sheep are divided into two basic groups: the thinhorn sheep of Alaska and northwest Canada, and the bighorn sheep of the western mountains and deserts (Krausman and Shackleton 2000). Thinhorn sheep include Dall's *(O. dalli)* and Stone's sheep *(O. d. stonei)*. Among bighorn sheep there are several different subspecies; the Rocky Mountain bighorn *(O. c. canadensis)*, the California bighorn *(O. c. californiana)*, and four sub-species collectively called desert bighorns *(O. c. nelsoni, O. c. mexicana, O. c. cremnoboates, and O. c. weemsi)*. For specific taxonomic information on bighorn sheep in northern and southern ranges refer to Wehausen and Ramey (2000) and Ramey (1995), respectively.

Although bighorn sheep occupy only a portion of their historical range (Fig. 1), the contiguous United States supports an estimated 48,000 bighorn sheep, of which approximately 53% are Rocky Mountain bighorns, 10% California, and 37% desert (Valdez and Krausman 1999). Most bighorn sheep in desert environments occur in small (<100) populations in isolated habitats (Krausman and Leopold 1986, Etchberger et al. 1989, Bleich et al. 1990). Small populations are generally predisposed to greater risks of extinction (Berger 1990, Berger 1999), however population size alone may not always be an accurate indicator of bighorn sheep persistence (Krausman et al. 1996, Wehausen 1999). Habitat loss is likely the most serious threat to bighorn sheep populations (Risenhoover and Bailey 1985, Wakelyn 1987, Risenhoover et al. 1988, Etchberger et al. 1989).

Mountain sheep have evolved with a variety of potential predators, including the wolf *(Canis lupus)*, coyote *(Canis latrans)*, gray fox *(Urocyon cinereoargenteus)*, bobcat *(Lynx rufus)*, lynx *(Lynx canadensis)*, cougar *(Puma concolor)*, black bear *(Ursus americanus)*, grizzly bear *(Ursus arctos horribilis)*, jaguar *(Panthera onca)*, ocelot *(Leopardus pardalis)*, wolverine *(Gulo gulo)*, and golden eagle *(Aquila chrysaetos)* (Kelly 1980, Nichols and Bunnell 1999). The fact that bighorn sheep are preyed upon is well documented, however studies addressing the impacts of predation on bighorn sheep populations are limited. Recent studies have demonstrated that predation can be an important source of mortality in bighorn sheep herds and, in some cases, may have population-level impacts (Hoban 1990, Wehausen 1996, Ross et al. 1997, Hayes et al. 2000, Rominger and Weisenberger 2000, Logan and Sweanor 2001). The effects of predation on wild ungulates, whether perceived or realized, influence how wildlife populations are managed. ***The purpose of this report is to provide an objective review of available literature concerning bighorn sheep predation, including an evaluation of findings and management recommendations pertinent to bighorn sheep populations.***

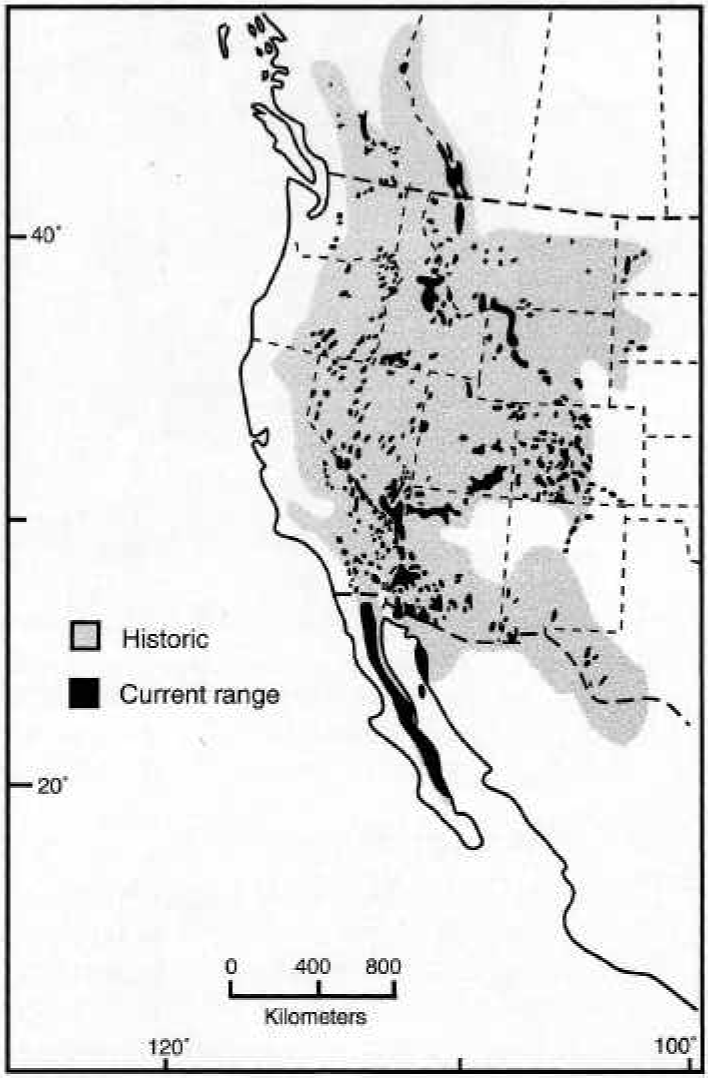

Figure 1. Historic and current ranges of bighorn sheep in North America (from Krausman and Shackleton 2000: fig 25-2).

We searched literature databases to compile citations relevant to bighorn sheep predation. More than 60 citations were found pertaining to mountain sheep predation (Table 1). Most, however, were incidental or observational accounts that simply documented the fact that predation occurs. Not all observational accounts of bighorn sheep predation were included in this review. Our intention was to focus search effort on peer-reviewed studies that specifically examined bighorn sheep predation (Table 2). Although the utility of observational or anecdotal data are limited when attempting to understand the effects of predation, they are useful for determining what predators kill wild sheep and under what circumstances. We used all available information, including observational data, to determine what predator(s) may have population-level effects on bighorn sheep populations. Once predator(s) capable of causing significant mortality to bighorn sheep populations were identified, we attempted to synthesize available knowledge of the effects of predation on bighorn sheep. For this, we used only studies that met the following criteria: 1) study objectives included an examination of bighorn sheep predation, 2) studies were conducted on free-ranging bighorn sheep (*O. canadensis*) rather than other mountain sheep species or sub-species, and 3) study results were peer-reviewed.

BIGHORN SHEEP PREDATION

An Overview:

Much of the literature suggests that efficient anti-predator strategies of bighorn sheep greatly reduce their vulnerability to predation (Buechner 1960, Hornocker 1970, Geist 1971, Jorgenson et al. 1997). Disease transmission, human disturbance, overgrazing, and habitat loss are often cited as factors responsible for declines in bighorn sheep abundance and distribution, while predation is rarely considered a significant mortality factor (Wishart 1975, 1978). The fact that bighorn sheep are preyed upon is well documented, but there is little information available concerning the effect(s) of predation on bighorn sheep populations. Numerous citations document a variety of predators stalking and/or killing bighorn sheep (Table 1). Most accounts of bighorn sheep predation involve coyotes or cougars, with occasional reports of golden eagle, lynx, bobcat, gray fox, wolf, or bear predation. Although coyote and cougar are the most common predators of bighorn sheep, cougars appear to be the only predators capable of causing significant mortality in bighorn sheep populations that occupy suitable habitats. Coyote predation appears to be incidental, primarily restricted to lambs, and most often reported in areas that lack suitable escape terrain. Wolves occasionally prey upon thinhorn sheep (Holleman and Stephenson 1981, Heimer and Stephenson 1982, Gasaway et al. 1983, Huggard 1993, Nichols and Bunnell 1999), but have not been reported as a significant source of mortality in bighorn sheep populations. Gregariousness and the use of steep rugged terrain appear to be effective adaptations to avoid predation by coursing predators such as wolves and coyotes (Wishart 2000). Stalking predators like cougars however, may be able to circumvent these strategies, and predation losses in some herds may be high if individual cougars specialize in preying upon bighorns (Ross et al. 1997).

Cougar predation on bighorn sheep is highly sporadic and varies annually (Ross et al. 1997, Logan and Sweanor 2001). The small size of most bighorn sheep populations and changes in availability of alternative prey likely result in variable predation rates among bighorn populations and among years for the same population (Jorgenson et al. 1997). The impacts of cougar predation on bighorn sheep may be direct (mortality) or indirect (changes in distribution). Recent studies have demonstrated that cougar predation can be an important source of mortality in bighorn sheep populations (Wehausen 1996, Ross et al. 1997, Hayes et al. 2000, Logan and Sweanor 2001). Available evidence in California suggests that impacts of cougar predation on bighorn sheep populations are restricted to areas where bighorn sheep and mule deer are sympatric (Schaefer et al. 2000).

Table 1. References of mountain sheep-predator interactions.

Author(s)	Location	Predator(s)	Study Objective
Akenson and Akeson (1992)	Idaho	Golden Eagle, Coyote	Bighorn sheep movements and lamb mortality
Ashcroft (1986)	British Columbia	Coyote	Observational note
Barichello and Carey (1988)	Yukon	Wolf	Effect of wolf reduction on thinhorn sheep
Bear and Jones (1973)	Colorado	Coyote, Cougar	History and distribution of bighorn sheep in Colorado
Berger (1978)	Coyote		Observational note
Berger (1991)	various	Coyote, Wolf, Bear, Cougar	Pregnancy incentives for bighorn sheep
Bleich (1996)	California	Coyote	Observational note
Bleich et al. (1997)	California	Cougar	Sexual segregation in mountain sheep
Bleich (1999)	various	Coyote	Predator evasion strategies of bighorn sheep
Burles and Hoefs (1984)	Yukon	Coyote, Wolf	Winter mortality of thinhorn sheep
Cashman et al. (1992)	Arizona	Cougar	Cougar food habits
Child et al. (1978)		Wolf	Observational note
Coggins et al. (2000)	Oregon/Idaho	Cougar	Status of transplanted bighorn sheep population
Creeden and Schmidt (1983)	Colorado	Cougar, Coyote	Status of transplanted bighorn sheep population
Cunningham (1970)	Alberta	Golden Eagle	Observational note
Cunningham et al. (1989)	Arizona	Cougar	Arizona bighorn sheep reintroductions
Cunningham et al. (1999)	Arizona	Cougar	Diet selection of cougars
Dekker (1986)	Alberta	Coyote	Observational note
Demarchi and Mitchell (1973)	British Columbia	Coyote, Cougar, Black Bear	Population dynamics of bighorn sheep
Fairaizl (1980)	North Dakota	Coyote	Population characteristics of a transplanted bighorns
Festa-Bianchet (1988)	Alberta	Coyote	Seasonal range selection of bighorn sheep
Frid (1997)	Yukon	Coyote, Wolf Grizzly Bear	Vigilance behavior of female thinhorn sheep
Gasaway et al. (1983)	Alaska	Wolf	Wolf-prey relationships in Alaska
Harrison and Hebert (1988)	British Columbia	Cougar	Cougar predation on bighorn sheep
Hass et al. (1989)	Montana	Coyote	Coyote predation on bighorn sheep
Hayes et al. (2000)	California	Cougar	Cougar predation on bighorn sheep

Table 1 (cont). References of mountain sheep-predator interactions.

Author(s)	**Location**	**Predator(s)**	**Study Objective**
Hebert and Harrison (1988)	British Columbia	Coyote	Coyote predation on bighorn sheep
Heimer and Stephenson (1982)	Alaska	Wolf	Wolf predation on thinhorn sheep
Hoban (1990)	New Mexico	Cougar	Review of desert bighorn sheep in New Mexico
Hoefs and Cowan (1979)	Yukon	Wolf	Ecology of thinhorn sheep
Hoefs et al. (1986)	Yukon	Wolf	Observational note
Holleman and Stephenson (1981)	Alaska	Wolf	Prey selection of wolves
Holt (1994)	Montana	Cougar	Observational note
Hornocker (1969)	Idaho	Bobcat	Observational note
Hornocker (1970)	Idaho	Cougar	Analysis of cougar predation on mule deer and elk
Huggard (1993)	Alberta	Wolf	Prey selectivity of wolves
Jones and Worley (1994)	Montana	Cougar	Limiting factors of a bighorn sheep population
Kelly (1980)	various	Coyote, Gray Fox, Bobcat, Cougar, Golden Eagle	Observational notes
Kennedy (1948)	New Mexico	Golden Eagle	Observational note
Kilpatric (1982)	Texas	Cougar	Status of transplanted desert bighorn sheep population
Krausman et al. (1989)	Arizona	Cougar	Desert bighorn sheep habitat relationships
Legg et al. (1996)	Wyoming	Cougar	Factors for decline in a bighorn sheep population
Leopold and Krausman (1983)	Texas	Cougar	Status of a transplanted sheep population
Logan and Sweanor (2001)	New Mexico	Cougar	Cougar ecology, including desert bighorn sheep predation
McCann (1956)	Wyoming	Coyote	Ecology of bighorn sheep
Murie (1944)	Alaska	Wolf	Observational note
Murphy (1998)	Wyoming	Cougar	Cougar ecology/food habits/predation rates
Nette et al. (1984)	Alaska	Golden Eagle	Observational note
Nichols and Bunnell (1999)	Alaska	Wolf	Natural history of thinhorn sheep
Oldemeyer (1966)	Wyoming	Coyote, Black Bear	Winter ecology of bighorn sheep in Yellowstone
Ostovar and Irby (1998)	Wyoming	Cougar, Coyote, Golden Eagle	Effects of predation on bighorn sheep

Table 1 (cont). References of mountain sheep-predator interactions.

Author(s)	Location	Predator(s)	Study Objective
Remington (1983)	Arizona	Cougar	Status of transplanted bighorn sheep population
Rominger and Weisenberger (2000)	New Mexico	Cougar	Review of cougar predation on bighorn sheep
Ross et al. (1995)	Alberta	Cougar	Observational note
Ross et al. (1997)	Alberta	Cougar	Cougar predation on bighorn sheep
Ryder and Lanka (1997)	Wyoming	Cougar	Status of a bighorn sheep population
Schaefer et al. (2000)	California	Cougar	Survival/predation of mule deer and bighorn sheep
Shank (1977)	Alberta	Coyote	Observational note
Stephenson et al. (1991)	Alaska	Lynx	Observational note
Thorne et al. (1979)	Wyoming	Coyote	Status and population biology of a bighorn sheep herd
Tsukamoto (1975)	Nevada	Cougar	History and status of bighorn sheep in Nevada
Weaver and Mensch (1970)	California	Golden Eagle, Coyote, Bobcat	Observational note
Wehausen (1996)	California	Cougar	Effects of cougar predation on bighorn sheep
Whitfield (1983)	Wyoming	Coyote, Bobcat Golden Eagle	Ecology of bighorn sheep in the Teton Range
Williams et al. (1995)	Montana	Cougar	Cougar food habits and habitat use
Woolf and O'Shea (1968)	Wyoming	Coyote	Observational note

Table 2. Citation and geographic location of studies that have examined the effects of predation on mountain sheep.

Author(s)	Study Area	Predator Involved	Sheep Subspecies	Peer-Reviewed
Hayes et al. (2000)	Peninsular Ranges, California	cougar	bighorn	Yes
Logan and Sweanor (2001)	San Andres Mountains, New Mexico	cougar	bighorn	Yes
Ross et al. (1997)	Sheep River, southwest Alberta	cougar	bighorn	Yes
Schaefer et al. (2000)	San Bernardino Mountains, California	cougar	bighorn	Yes
Wehausen (1996)	Mojave Desert, California	cougar	bighorn	Yes
Hass et al. (1988)	Bison Range NWR, Montana	coyote	bighorn	Yes
Gasaway et al. (1983)	Interior Alaska	wolf	thinhorn	Yes
Barichello and Carey (1988)	Southwest Yukon	wolf	thinhorn	No
Heimer and Stephenson (1982)	Tanana Flats, Alaska	wolf	thinhorn	No
Hebert and Harrison (1988)	Junction Wildlife Area, British Columbia	coyote	bighorn	No
Harrison and Hebert (1988)	Junction Wildlife Area, British Columbia	cougar	bighorn	No
Hoban (1990)	San Andres Mountains, New Mexico	cougar	bighorn	No
Ostovar and Irby (1998)	Yellowstone National Park	cougar	bighorn	No
Rominger and Weisenberger (2000)	San Andres Mountains, New Mexico	cougar	bighorn	No

Wolf and Coyote Predation:

Murie (1944) believed wolves were the limiting factor for Dall's sheep populations in Denali National Park, and Heimer and Stephenson (1982) thought wolf predation limited Dall's sheep numbers in the Alaska Range. However, the more extensive work of Gasaway et al. (1983) found wolf predation had little impact on the Dall's sheep populations of interior Alaska. Additionally, when thinhorn sheep populations in areas where wolf numbers were controlled were compared with populations where wolves were abundant and uncontrolled, wolf control appeared to have negligible effects on Dall's sheep numbers (Gasaway et al. 1983). Gregariousness and the use of steep rugged terrain appear to be effective adaptations to avoid predation by coursing predators such as wolves. For other northern ungulates, such as moose *(Alces alces)* and caribou *(Rangifer sp.)*, that cannot seek protection from wolves in steep, rugged terrain, the effects of wolf predation are much more pronounced (Gasaway et al. 1992, Dale et al. 1994, Van Ballenberghe and Ballard 1994). Only when wild sheep seek forage away from escape terrain or in timbered areas where predators can approach undetected can wolves inflict considerable mortality (Nichols and Bunnell 1999). However, under most circumstances, wolf predation is not considered a major source of mortality or factor in the population regulation of thinhorn sheep populations (Nichols 1978, Bowyer et al. 2000). While wolves occasionally prey upon thinhorn sheep (Heimer and Stephenson 1982, Gasaway et al. 1983, Huggard 1993, Nichols and Bunnell 1999), they have not been found to be a significant source of mortality in bighorn sheep populations.

Second to wolves, coyotes are probably the most successful predator of thinhorn sheep (Nichols and Bunnell 1999), and next to cougars, they are probably the most successful predator of bighorn sheep. Predation by wolves and coyotes may increase during periods of deep snow (Burles and Hoefs 1984) if sheep are forced to feed away from escape terrain (Nichols and Bunnell 1999). Hass (1989) reported coyote predation to be a major cause of mortality of bighorn sheep lambs in northwest Montana. However, this study was conducted on the Bison Range National Wildlife Refuge; a 75 km^2-area enclosed by a 2.4-m game fence. Further, this area was likely not historic sheep range and lacked rugged, cliff terrain used by wild sheep for lambing and predator avoidance (Hass 1989). Because this sheep herd was not capable of immigration or emigration, inbreeding depression may have contributed to lamb mortality by increasing the number of still births and producing weak lambs more susceptible to predation or disease (Hass 1989). Although frequently cited, results from this study are likely not indicative of how coyote predation impacts free-ranging bighorn sheep populations that occupy habitats with suitable escape terrain. Rather, coyote predation appears to be incidental, primarily restricted to lambs, and not considered a limiting factor in bighorn sheep populations.

Thorne et al. (1979) found coyote predation to be the greatest identified cause of natural mortality during a 3-year study of the Whiskey Mountain bighorn sheep herd in Wyoming. This study was based on the observations and movements of 172 marked (151 neck bands, 21 radio-collars) bighorns. Bighorn sheep remains were found most frequently in coyote scats (40%) collected during spring and early summer. Scat analyses corresponded with observations that suggested most successful coyote kills on bighorn sheep occurred in late-May, when lambs were most vulnerable to predation. Although coyote predation was the leading cause of natural mortality, only 3 kills of sheep (2 lambs, 1 yearling) by coyotes were documented and multiple observations of coyote-bighorn sheep interactions indicated coyotes were inefficient predators of bighorn sheep and unlikely a limiting factor (Thorne et al. 1979).

Fairaizl (1980) reported coyote predation was the major cause of lamb mortality in 5 transplanted bighorn sheep herds in North Dakota. During this study of 4 lambs equipped with radio-collars, 2 were killed by coyotes, with 1 of these thought to be abandoned. Although coyote predation may have been the most prevalent, identified cause of lamb mortality, these limited data do not suggest coyote predation limits bighorn sheep populations or even that coyotes are effective predators of bighorn sheep.

Numerous other authors have documented coyote-bighorn sheep interactions (McCann 1956, Buechner 1960, Woolf and O'Shea 1969, Geist 1971, Demarchi and Mitchell 1973, Shank 1977, Berger 1978, Thorne et al. 1979, Kelly 1980, Creeden and Schmidt 1983, Whitfield 1983, Ashcroft 1986, Dekker 1986, Festa-Bianchet 1988, Berger 1991, Bleich 1996, Bleich 1999), but none suggested coyote predation limited bighorn sheep populations. Hebert and Harrison (1988) however, believed coyote predation was a major source of lamb mortality in British Columbia and that predator control was responsible for dramatic increases in lamb:ewe ratios recorded during 1987-1988. The authors believed that, *"A few instances of predator activity (coyotes chasing sheep or cougar predation on sheep) usually indicate an underlying predator problem"* and that, *"(coyote) removal programs can confirm the impacts of predators and can produce dramatic improvements in survival and growth (of bighorn sheep)….".* This study was not peer-reviewed and to the best of our knowledge, there are no peer-reviewed studies that suggest coyote predation limits the growth of free-ranging bighorn sheep populations.

While wolves, coyotes, and cougars are the most common predators of wild sheep, cougars appear to be the only predators capable of causing significant mortality in bighorn sheep populations that occupy habitats with suitable escape terrain. Therefore, the remainder of this report will focus on cougar predation on bighorn sheep.

Cougar Predation:

Because of the complexity of predator-prey relationships, the following is not intended to summarize the role of predation in ungulate population dynamics, but to synthesize available information specific to cougar predation on bighorn sheep. Recognize however, that bighorn sheep predation studies are typically done only where some concern about the sheep population already exists. There are many large, viable bighorn sheep populations where no predation studies have occurred.

Cougar Predation: Prey-class or sex and age vulnerability

Cougars are capable of preying upon all sex and age classes of bighorn sheep. Studies involving radio-collared bighorns and/or cougars indicate the vulnerability of prey-classes is variable and cougar prey selectivity is likely a function of individual cougar behavior (Hoban 1990, Ross et al. 1997, Logan and Sweanor 2001). Prey selection is generally influenced by size of available prey; smaller, less experienced cougars select smaller prey, and larger, more experienced adults kill larger prey (Iriarte et al. 1990, Murphy 1998).

Cougars in the San Andres Mountains of New Mexico killed 4 bighorn rams ranging in age from 0.8-4.0 years and 6 ewes ranging from 3-16 years (Logan and Sweanor 2001). Cougar predation was the single most identifiable cause of mortality in radio-collared sheep and accounted for 23% of total identified mortality. An adult male cougar (M23) killed 3 radio-collared bighorns in a 3-month time period and was subsequently removed. Following his removal, cougar(s) killed only 1 other radio-collared bighorn sheep. Between 1980-1989, Hoban (1990) worked in the same area and found cougar predation accounted for 51% (n=22) of mortality in radio-collared sheep. Cougars killed rams and ewes in proportion to their availability. Ages of bighorn sheep killed by cougars ranged from 1-17 years. Rominger and Weisenberger (2000) also reported cougar predation on both male and female bighorn sheep in the San Andres Mountains of New Mexico. Rominger and Weisenberger (2000) reviewed cougar predation on desert bighorn sheep herds in New Mexico. Between 1992-1997, 106 radio-collared bighorn sheep were transplanted into 4 populations. By 1999, 49 of 101 had died, of which 36 (74%) were killed by cougars.

Ross et al. (1997) reported 29 bighorns killed by cougars in southwest Alberta, 13 of which were lambs. The remaining sheep ranged in age from 1-17 years and included 9 ewes and 7 rams. During their study lambs represented 45% of cougar kills and 23% of the early winter sheep population. Adult ewes and rams comprised 44% and 24% of the population, and 31% and 21% of the kills, respectively. Yearling sheep of both sexes constituted 10% of the population and 3% of the kills. Cougars apparently selected lambs rather than killing all sex/age classes in proportion to their availability. However, of the 5 cougars intensively monitored, 2 never killed sheep, 1 killed only one, and another (F25) killed 17. The home range of the radio-collared cougar (F25) responsible for most bighorn sheep predation did not overlap areas used by rams. So, although cougars appeared to select lambs, prey-class vulnerability to cougar predation was largely due to the behavior of individual cougars, namely the single cougar (F25).

Hayes et al. (2000) monitored 113 radio-collared adult bighorns (16 males, 97 females) in the Peninsular Ranges of California and found no difference in cougar predation rates on the sexes. However, bighorns 1-4 or >9 years of age were more likely to be killed by cougars than other age classes. Of 61 sheep deaths, 42 (69%) were killed by cougars.

Bleich et al. (1997) found cougar predation in the eastern Mojave Desert of California was restricted to rams, however rams occupied habitats that likely predisposed them to higher predation rates than ewes. Nearby, in the San

Bernardino Mountains, Schaefer et al. (2000) also found rams were exposed to higher rates of predation than ewes. Higher rates of predation on rams is consistent with the reproductive-strategy hypothesis (Main and Coblentz 1996) that suggests sexual segregation is due to predator avoidance strategies of females with young and forage optimization by adult males (Geist 1982, Bowyer 1984, Jakimchuk et al. 1987, Skogland 1989, Bleich et al. 1997, Sawyer and Lindzey 2001). The theory predicts females should select habitats conducive to the survival of their offspring, while males seek out areas that maximize forage intake.

Harrison and Hebert (1988) reported cougar predation to be a major mortality factor in a bighorn sheep population in British Columbia and believed rams weak from rutting were the preferred prey of cougars. However, this 22-month study was based on the ground tracking (~4 locations per week) of 2 radio-collared adult female (both with 2 kittens) cougars and 40 identified cougar kills. Assuming an adult cougar with kittens will kill 1 deer or comparable-sized ungulate every 7-8 days (Hornocker 1970, Beier et al.1995, Murphy 1998, Nowak 1999), these 2 radio-collared cougars made a minimum of 176 kills during the study. Inference of prey selectivity based on 40 kills from a sample of 2 cougars should be interpreted with caution. Nonetheless, these 2 cougars killed 22 bighorn sheep (16 adult males, 5 adult females, 1 lamb) during the study.

Krausman et al. (1989) reported higher rates of cougar predation on female sheep in the Harquahala Mountains compared to the Little Harquahala Mountains in Arizona. Williams et al. (1995) documented cougar predation on both adult rams and ewes in northern Montana, but found ewes were the more frequent prey, likely due to the relative abundance of ewes compared to rams.

Because individual cougars are usually responsible for the majority of bighorn sheep predation within a given sheep population (Hoban 1990, Ross et al. 1997, Hayes et al. 2000, Rominger and Weisenberger 2000, Logan and Sweanor 2001), prey-class vulnerability to cougar predation, at least with bighorn sheep, is largely a function of the behavior of individual cougars and the sex and age class of bighorn sheep that occur within the cougars' home range. Cougars can kill any sex and age class of bighorn sheep. What they kill reflects bighorn sheep behaviors that make individual sex and age classes more or less vulnerable in a particular population.

Cougar Predation: Seasonal vulnerability

Lion predation on bighorn sheep is highly sporadic and varies annually (Ross et al. 1997, Logan and Sweanor 2001). Additionally, the small size of most bighorn sheep populations and changes in availability of alternative prey likely result in variable predation rates among bighorn populations and among years (Jorgenson et al. 1997). Although variable, cougar predation on bighorn sheep appears to be more prevalent during winter. Most (62%) cougar predation on bighorn sheep in the Peninsular Ranges of California (Hayes et al. 2000) occurred during winter (December–March). A greater proportion of bighorn sheep were preyed upon during winter and spring (75%) compared to summer and fall (25%) in the San Bernardino Mountains of California (Schaefer et al. 2000). Higher rates (0-57%) of cougar predation on bighorn sheep were also reported during the winter in Alberta (Ross et al. 1997). Jones and Worley (1994) reported 2 cases of cougar predation on bighorn sheep during the winter, however this study was restricted to winter range. Williams et al. (1995) reported more bighorn sheep killed by cougars during winter and spring (89%) compared to summer and fall (11%) in Montana, and suggested bighorn sheep may serve as a seasonally important prey resource during these months. Bighorn sheep represented 18% (n=10) of 53 documented kills and occurred in 20% of collected scats (n=27). The conclusions were based on a relatively small sample of kills (n=53) from 23 radio-collared cougars over a 2-year period. Fifty-three kills represents approximately 2% of the total kills (~2,400) likely made by 23 independent cougars over a 2-year time period, assuming a kill rate of 1 deer or comparable-sized ungulate every 7-8 days (Hornocker 1970, Beier et al.1995, Murphy 1998, Nowak 1999).

Cougar Predation: A function of prey density?

Cougars are the most widely distributed terrestrial mammal in the western hemisphere, covering 100^o of latitude; ranging from the tip of South America to British Columbia (Iriarte et al. 1990). Prey species may vary depending on local abundance and vulnerability, but deer are the primary food source for most cougars (Logan and Sweanor 2000), while bighorn sheep are generally considered alternate prey (Anderson 1983). Studies that have examined cougar predation on bighorn sheep have been conducted in areas where mule deer and bighorn sheep coexist (Table 2) (Wehausen 1996, Ross et al. 1997, Hayes et al. 2000, Schaefer et al. 2000, Logan and Sweanor 2001,). Additionally, with the exception of Ross et al.'s (1997) work in southwest Alberta, all of these studies were conducted in desert environments where bighorn sheep typically occur at low densities (Krausman and Leopold 1986, Etchberger et al. 1989, Bleich et al. 1990). Cougar predation on bighorn sheep can be a significant mortality factor, even at very low prey densities (Wehausen 1996, Hayes et al. 2000, Logan and Sweanor 2001). Ross et al. (1997) found no evidence that cougar predation could be explained by changes in bighorn sheep density or the availability of alternate prey, suggesting little relationship between sheep numbers and cougar predation. Additionally, there were no indications that other ungulate species in the study area had declined as sheep predation increased (Ross et al. 1997).

Most evidence however, suggests cougars permanently inhabit areas occupied by bighorns only where deer occur sympatrically and at densities adequate to provide a primary food source for cougars (Schaefer et al. 2000). Cougar predation on alternate prey species may increase when mule deer populations are depressed (Leopold and Krausman 1986). Thus, predation of bighorn sheep may be exacerbated when mule deer populations are low. Logan and Sweanor (2001) believed cougar predation on bighorn sheep was reduced when mule deer were abundant, and Rominger and Weisenberger (2000) found increased cougar predation on bighorn sheep associated with a rapid decrease in a mule deer population. The density of alternate prey (bighorn sheep) may not be nearly as important as the density of the primary food source (deer) in determining the level of cougar predation on bighorn sheep. Regardless of prey density, ecological or behavioral mechanisms may operate and make certain species or age and sex classes more vulnerable to cougar predation (Hornocker 1970).

Cougar Predation: A function of predator density?

Predator abundance has been cited as a primary factor influencing predation on, or limiting the recovery of wild sheep populations (Kilpatric 1982, Ostovar and Irby 1998, Bailey 2000). However, in studies where cougars have been radio-collared, researchers have found that predation on bighorn sheep is largely a function of the behavior of individual cougars (Hornocker 1970, Hoban 1990, Ross et al. 1997, Logan and Sweanor 2001) rather than the total number of cougars.

Cougar predation rates on bighorn sheep in New Mexico were not related to cougar density (Logan and Sweanor 2001). Rather, individual cougars demonstrated a propensity for killing bighorn sheep (Hoban 1990, Logan and Sweanor 2001). Five radio-collared bighorn sheep were killed by 1 adult female cougar within 4 months in 1981 (Hoban 1990). An adult male cougar (M23) killed 3 radio-collared bighorns in a 3-month time period and accounted for 100% of known radio-collared sheep deaths in 1989 (Logan and Sweanor 2001). Following his (M23) removal, only 1 other radio-collared bighorn sheep was killed by a cougar in August 1990 (Logan and Sweanor 2001). During a 4-year cougar food habit study in Idaho, only 2 kills of bighorn sheep were recorded and both sheep were killed by one female cougar (Hornocker 1970).

Although Wehausen (1996) and Hayes et al. (2000) examined mortality patterns of bighorn sheep without radio-collared cougars, their results indicated that even a small number of cougars may affect bighorn sheep survival, and population-level impacts may be exacerbated if adult female sheep are heavily preyed upon. Rominger and Weisenberger (2000) corroborate these findings and suggested individual behavior of predators may influence population dynamics of prey independent of predator density. Anderson et al. (2002) found similar predator-prey interactions with grizzly bears and cattle in northwest Wyoming, where 3 of 17 bears (all adult males) monitored were responsible for 90% of cattle deaths.

Indiscriminate removal or population-level reductions of cougars may not be successful in reducing the number of cougar-related bighorn sheep deaths

(Hoban 1990). However, identification and removal of individual cougars appears an effective method for minimizing cougar predation on bighorn sheep. Management based on the selective removal of problem individuals is dependent on the ability to define and identify them (Linnell et al. 1999). This type of management may be challenging with coyotes or wolves because they hunt in packs, or with bears because they are often difficult to trap and males may not be territorial. However, because cougars hunt individually, maintain consistent home ranges, and can be easily tracked with trained dogs, their identification and removal seems a viable management option.

Cougar Predation: Compensatory or Additive?

Compensatory mortality is the combined effect of 2 or more types of mortality (i.e., hunting, predation, starvation), in which each type may vary in magnitude, while total mortality remains constant (Bailey 1984). The theory of compensatory mortality is based on the concept that habitat resources determine the number of animals that can survive in a given area and when excess animals are produced, they must be removed from the population by some form of mortality, whether by starvation, hunting, disease, and/or predation. Additive mortality increases the total mortality, where compensatory mortality does not. Because predator-prey interactions are complex, dynamic systems influenced by both extrinsic and intrinsic factors (Odum 1959), determining whether predation is compensatory or additive is difficult. However, compensatory mortality is most likely to occur when populations approach ecological carrying capacity (Caughley 1979), when densities and mortality rates are high (Bartmann et al. 1992).

Logan and Sweanor (2001) estimated approximately 30% of desert bighorn mortality caused by cougars was compensatory. This estimate was based on the poor condition and/or old age (>12 years) of bighorns killed by cougars. Ross et al. (1997) reported >1/3 of cougar-killed bighorn sheep in Alberta had apparent disabilities; 4 lambs (29%), 4 ewes (44%), and 3 rams (50%) had anatomical or behavioral disabilities prior to being killed by cougars.

Between 1976-1988 Wehausen (1996) documented 49 bighorn sheep killed by cougars on the Mount Baxter winter range in California. No information was provided on the sex, age, or body condition of these sheep however. Because none of these sheep were radio-collared, and locating cougar kills for necropsy is difficult to accomplish in a timely manner without the aid of telemetry equipment, it is unlikely that any reliable estimate of compensatory mortality could be made from these data.

Generally, predation on the non-reproductive segment (i.e., lambs, rams) of the population has less impact on prey numbers because mortality to offspring should be more compensatory than mortality to adults (Murphy 1998). However, when ewes are heavily preyed upon, predation may become an additive source of mortality and population-level effects may be exacerbated (Hayes et al. 2000).

Cougar Predation: Studies of cougar predation

Understanding the effect(s) of predation on bighorn sheep population dynamics is a difficult task and hindered by:

- The tendency to accept the fact of predation as evidence of an effect of predation.
- Habitats of bighorn sheep and predators are continually changing.
- The suite of predators once sympatric with bighorn sheep has changed.
- Historic records are relatively recent in nature, and insufficient to capture the interplay of weather, predators, and habitat changes in the absence of European man.
- Wildlife researchers tend to study the relationship between bighorn sheep and predators only in sheep populations that are perceived as being in trouble.
- The effect of predation is difficult and costly to demonstrate, resulting in easily impeachable studies. However, the lack of sound studies that unequivocally demonstrate population-level effects does not necessarily mean the effects of predation are not more widespread than the few studies would suggest.

We attempted to summarize what is known about the effect(s) of cougar predation on bighorn sheep populations by evaluating studies that were peer reviewed and designed to examine predation on bighorn sheep (*O. canadensis*) (Table 2: Wehausen 1996, Ross et al. 1997, Hayes et al. 2000, Schaefer et al. 2000, Logan and Sweanor 2001). First, a brief synthesis of each study:

Wehausen (1996): This study was conducted on 2 small (4-150) bighorn sheep populations located in the Sierra Nevada and Granite Mountains of California. Between 1988-1995, 9 ewes were captured and radio-collared in the Granite Mountains. Additionally, fieldwork was done to determine the minimum number of ewes in the population and mark-resight population estimates were developed. Demographic variables for the Sierra Nevada area were collected during most years between 1976-1995, using direct counts of sheep while they were concentrated on winter ranges. Cougar tracks and kills were recorded during counts that occurred from 1976-1988. Dead sheep were considered cougar kills only if physical evidence was consistent with cougar predation. Fecal nitrogen indices to diet quality were developed from summer and winter samples.

Of 9 radio-collared ewes in the Granite Mountains, 5 were killed by cougars between 1989 and 1992. Annual survivorship of ewes for the first 3 years was 62.5%, with all deaths due to cougar predation. However, cougar predation ceased in 1992 and survival of radio-collared sheep increased to 100% over the next 3 years. The decline in cougar predation corresponded with a change in the rate that cougar tracks were detected. Cougar tracks were encountered 17% of the days prior to 1992, and 0% of the days after March 1992. A 1989 helicopter survey and 43 person-days of searching for bighorn sheep yielded 13 ewes, 7 of which were radio-collared.

The study population in the Sierra Nevada averaged 127 animals from 1977-1986, before a steep decline during 1987-1991. During the decline, bighorn sheep apparently abandoned use of their traditional winter range, after which population counts averaged <5 from 1991-1995. Concurrent with the bighorn sheep declines, the rate at which cougar tracks and kills were detected increased. Between 1976-1988, 49 cougar kills were documented on the winter ranges, representing 80% of all mortalities found. Additionally, 103 bighorn sheep were removed from this winter range for reintroductions from 1979-1888.

Results from the Granite Mountain area demonstrated that cougar predation could be a significant mortality factor even at very low bighorn sheep densities. Wehausen (1996) believed cougar predation in the Sierra Nevada area was responsible for the winter range abandonment and subsequent population crash of bighorn sheep. The population decline appeared to be a result of indirect effects of cougar predation, mediated through habitat selection by bighorn sheep. Fecal nitrogen levels of bighorn sheep were higher prior to winter range abandonment, suggesting bighorn sheep maintained higher nutritional planes and reproductive success when they seasonally migrated.

Ross et al. (1997): This study was conducted in southwest Alberta to examine cougar predation on a resident herd (>120) of bighorn sheep. Other ungulates in the area included mule deer (*O. hemionus*), white-tailed deer (*O. virginianus*), elk (*Cervus elaphus*), and moose (*Alces alces*). Winter food habits of cougars were studied from winters 1985-86 to 1993-94 by capturing 87 cougars, radio-collaring 60, and examining 320 kills. Only 11 cougars (8 female, 3 male) occupied home ranges that overlapped with bighorn sheep. The bighorn sheep population was censused by ground survey several times per year since 1981. Precise counts and classifications were possible because almost all sheep were marked (>94% of lambs, >97% of ewes, and >66% of rams).

Of the 320 cougar kills examined, 29 were bighorn sheep, 183 mule deer, 36 moose, 22 elk, and 19 white-tailed deer. There was no relationship between the number of bighorn sheep present and the number of known cougar kills. Of the 29 bighorn sheep killed, 13 (45%) were lambs and 16 (9 ewes, 7 rams) were ≥ 1 year old. Adult ewes represented 44% of the early-winter (December) population and 31% of cougar kills, while adult rams represented 24% of the population and 21% of kills, and yearlings of both sexes represented 10% of the population and 3% of kills. Lambs, however represented 22% of the population and 45% of all cougar kills. Cougars selected bighorn lambs over other sex and age classes. More than one-third of cougar-killed bighorn sheep had apparent disabilities.

Of 5 female cougars that were intensively monitored and had home ranges that overlapped areas occupied by bighorn sheep, 2 never killed a sheep and a third killed only 1. One female however, marked as F25, preyed heavily upon bighorn sheep and she alone killed 9% (n=11) of the early-winter sheep population in 1993-94, and 26% (n=6) of the lambs. The home range used by cougar F25 did not overlap with areas used by adult rams during winter, therefore she did not have the opportunity to prey upon rams. These data suggest prey-class vulnerability of bighorn sheep to cougar predation is largely a function of the individual cougars. Additionally, successful cougar predation on bighorn sheep appeared to be an individual acquired skill.

Annual cougar predation on bighorn sheep was highly variable and ranged from 0-13% of the population. Ross et al. (1997) believed the variability in cougar predation could not be explained by changes in sheep densities or the availability of alternative prey. They found no relationship between cougar predation and sheep numbers (prey density).

Hayes et al. (2000): The objective of this study was to examine survival and cause-specific mortality in an endangered bighorn sheep population in the Peninsular Ranges of California. Bighorn sheep occurred in arid, low-elevation habitats immediately below a dense, shrub-dominated coastal chaparral community inhabited by mule deer. Six subpopulations of sheep were identified and 113 bighorn sheep (16 rams, 97 ewes) were subsequently captured and radio-collared. Bighorn sheep were then monitored at least once per month from November 1992 through May 1998. Sixty-one radio-collared sheep died and cause of death was determined using field necropsy techniques.

Of the 61 deaths, 69% (n=42) resulted from cougar predation. The mean annual mortality rate from cougar predation was 14%, which was larger than any other single cause of death. Cougar predation was highest for bighorn sheep in the 1-4 and ≥ 9-year age class. Predation rates did not differ between rams and ewes. Most cougar predation occurred from December through March.

During this study adult survival was relatively low (79%) compared with other desert bighorn sheep populations, and cougar predation was the major cause of adult mortality. Hayes et al. (2000) suggested population-level effects were exacerbated when cougars killed reproductive-age females and their offspring, which was observed on several occasions (n=7). Sustained high levels of cougar predation apparently impeded the recovery of this sheep population.

Schaefer et al. (2000): The objective of this study was to examine the survival and cause-specific mortality of sympatric bighorn sheep and mule deer populations in the San Bernardino Mountains of California. Data were collected weekly from 26 radio-collared bighorn sheep (10 males, 16 females) and 34 mule deer (9 males, 25 females) from January 1992 through May 1996. Cause of death was determined using field necropsy techniques.

A total of 12 sheep (7 males, 5 females) and 17 deer (7 males, 10 females) died during the study. Cougar predation accounted for 55% of mule deer mortality. Of the 12 sheep deaths, 75% (n=9) were caused by cougar predation. Bighorn sheep had annual survival rates of 76% and 86% for males and females, respectively. However, the median survival for males (19 months) was significantly lower than females (>40 months), indicating a greater rate of mortality for males. Cougars killed a greater proportion of sheep during the winter-spring (75%) compared to summer-fall (25%).

Evidence from California suggests that effects of cougar predation on bighorn sheep are restricted to areas where mule deer occur sympatrically and at densities adequate to provide a primary source of prey for cougars. Schaefer et al. (2000) provided examples of other sympatric bighorn sheep and mule deer populations in California where low mule deer densities corresponded with low cougar predation on sheep.

Logan and Sweanor (2001): This long-term (1985-1995) study conducted in the San Andres Mountains of New Mexico examined, among other things, cougar predation on mule deer and desert bighorn sheep. Both mule deer and bighorn sheep populations were annually monitored using ground and helicopter counts. Additionally, 175 mule deer (91 males, 84 females), 43 sheep (16 males, 27 females), and 107 cougars (48 male, 59 female) were equipped with radio-collars. Research hypotheses included: 1) cougar predation was the most important proximate cause of mortality affecting bighorn sheep population growth, and 2) experimental removal of cougars in the treatment area should cause an increase in sheep survival rates that was linked to a reduction in cougar predation rates. These predictions were tested by quantifying cougar predation rates on radio-collared sheep relative to other causes of mortality, and measuring the relationship of cougar density to cougar predation rates.

The number of radio-collared sheep monitored each year comprised 36-83% of the number of adults and yearlings observed in annual surveys. The number of observed bighorn sheep in annual surveys ranged from 22 to 37. Cougars were responsible for the deaths of 10 (4 males, 6 females) of 26 radio-collared sheep that died. One male cougar (marked as M23) was responsible for at least a third of the kills. Cougar predation on radio-collared sheep appeared to decline following the removal of M23. Based on body condition and age, an estimated 30% of sheep killed by cougars was considered compensatory mortality. Removal of cougars from the treatment area and subsequent monitoring of radio-collared sheep demonstrated that cougar predation rates on sheep were not related to cougar densities. Because it was the single most identifiable cause of death, Logan and Sweanor (2001) concluded that cougar predation was one of several limiting factors (i.e., disease, drought) in this remnant desert bighorn population.

Following the years of intensive study (1985-1995), dynamics between cougars and sheep markedly changed. Beginning in 1996, 9 radio-collared sheep died in a 19-month period. Six (1 male, 5 female) of the 9 were killed by cougars. This decline in the bighorn sheep population coincided with a crash in the mule deer population. Logan and Sweanor (2001) believed the increased cougar predation resulted from concurrent mule deer declines that forced cougars to hunt more intensively, thereby increasing encounter rates with bighorn sheep. After 15 hours of helicopter surveys in December 1997, only 1 bighorn sheep was found; a radio-collared female. With only one remaining female, the desert bighorn sheep population in the San Andres Mountains was biologically extinct. The proximate cause responsible for the extinction, as indicated by radio-collared sheep, was cougar predation.

Cougar Predation: Effect(s) of cougar predation

Cougar predation on bighorn sheep is highly sporadic and varies annually (Ross et al. 1997, Logan and Sweanor 2001). Recent studies have demonstrated that cougar predation can be an important source of mortality in bighorn sheep populations (Wehausen 1996, Ross et al. 1997, Hayes et al. 2000, Logan and Sweanor 2001). Sustained high levels of cougar predation may impede the recovery of bighorn sheep populations (Hayes et al. 2000), induce population declines (Wehausen 1996), or in extreme cases, lead to the biological extinction of small (<40) sheep populations (Logan and Sweanor 2001). The potential for cougar predation to have a population-level effect appears greatest in small (<100) sheep populations that inhabit desert environments. The relationship between bighorn sheep population size and the degree of population-level effect(s) of cougar predation are illustrated in the above accounts. For example, Hayes et al. (2000) reported cougar predation slowed the recovery of an endangered sheep population in the Peninsular Ranges of California. This sheep population was estimated at 330 individuals (yearling and adult), and while cougar predation lowered adult survival rates to 0.79, it did not cause a population decline. However during the Wehausen (1996) study in California, cougar predation had a much more pronounced effect on bighorn sheep and elicited a population decline. One population in his study began with an estimated 11 sheep (ewes only), while the other area supported <50 (all sex/age classes), following removal of sheep for reintroduction efforts elsewhere. Cougar predation ultimately resulted in the biological extinction of a bighorn sheep population in New Mexico, where population estimates, during the early phases of the study, ranged from 22 to 37 (Logan and Sweanor 2001). An indirect effect of small population size may be the number of deaths attributed to cougar predation, based on predator avoidance strategies relative to group size (Hoban 1990). Not surprisingly, small isolated bighorn sheep populations appear more vulnerable to population-level effects caused by cougar predation.

Cougar predation has not been considered a significant source of mortality in the larger, migratory sheep populations that occupy high-elevation habitats of the interior Rocky Mountains. Studies of cougar prey selection and food habits in central Idaho (Hornocker 1970) and northwest Wyoming (Murphy 1998) found bighorn sheep were not an important food source for cougars. Small, isolated, or non-migratory populations appear more vulnerable to predators than larger populations in high quality habitat. Ross et al. (1997) recommended that managers should expect highly variable predation rates on sheep populations of less than 200 individuals.

Schaefer et al. (2000) suggested that effects of cougar predation on bighorn sheep populations in California were restricted to areas where bighorn sheep and mule deer were sympatric (Schaefer et al. 2000). Because bighorn sheep are not widely distributed and occur at relatively low densities, it is reasonable to assume that sheep serve as alternative prey to cougars, while other more abundant prey, whether it be deer or elk, function as the primary food source and allow cougars to persist in a given area. Nonetheless, because most bighorn sheep populations occur in areas sympatric with or adjacent to deer populations, most bighorn sheep herds are likely exposed to some level of cougar predation.

An indirect effect of predation is the restriction of range utilized by bighorn sheep to areas adjacent to escape terrain, and thus how bighorn sheep are distributed over their ranges. Wehausen (1996) believed increased cougar activity resulted in behavioral changes of bighorn sheep in California, where a small (<60) population of sheep abandoned historic winter ranges. The behavioral response to predation may have resulted in reduced nutrient intake and lower lamb survival, which led to an overall population decline. Bighorn distribution and the numbers that their ranges support are dependent on the assortment of predators that confine them to those ranges (Wishart 2000). However, this is not a unique situation to bighorn sheep, as predators influence the distribution and range of all prey species.

BIGHORN SHEEP STATUS IN WYOMING

Wyoming supports an estimated 6,300 bighorn sheep among 8 core native herds and 7 transplanted herds. Core, native herds are those populations that have never been extirpated and repopulated. The 8 core native herds account for 90% (~5,700) of the bighorn sheep in the state, while the remaining 10% (~600) occur in small, isolated transplanted populations (Table 3). Between 1949-1995, 1,489 bighorn sheep were captured from the Whiskey Basin winter range and relocated among 61 separate transplant efforts in Wyoming (Hurley 1996). During that time period, the only importation of bighorn sheep into Wyoming were 22 Rocky Mountain bighorns from Idaho released in Shell Canyon, along the west-slope of the Bighorn Mountains in 1992.

Table 3. Wyoming bighorn sheep population objectives and estimates for 15 herd units, post-season 2001.

Hunt Area(s)	Origin	Herd Unit	Objective	Estimate
1	Native	Clarks Fork	500	400
2	Native	Trout Peak	750	590
3	Native	Wapiti Ridge	1,000	980
4	Native	Younts Peak	900	909
5, 22	Native	Francs Peak	1,360	1,466
6	Native	Targhee	125	120
7	Native	Jackson	500	424
8, 9, 10, 23	Native	Whiskey Mountain	1,350	810
N/A	Transplant	Bighorn Mountains	100	50
11	Transplant	Temple Peak	250	30
17	Transplant	Ferris-Seminoe	300	20
18	Transplant	Douglas Creek	350	95
19	Transplant	Laramie Peak	500	300
21	Transplant	Encampment River	200	50
24	Transplant	Darby Mountain	150	45
		Totals:	**8,735**	**6,306**

Habitat loss and loss of traditional movement patterns appear to be the primary factors responsible for declines in bighorn sheep populations (Risenhoover et al. 1988). These problems tend to be exacerbated in transplanted herds that are often small (<100), isolated, and non-migratory. Transplanted bighorn sheep may fail to expand into adjacent habitats because of inadequate forage and/or unsuitable escape terrain (Risenhoover et al. 1988). Additionally, bighorn sheep have poor dispersal tendencies (Singer and Gudorf 1999) because of social bonding that favors traditional use of home ranges (Geist 1971). Sedentariness may increase predation rates on bighorn sheep because predator densities and/or distribution may be set by more numerous ungulates such as deer or elk, and because predators may repeatedly search small areas where they are likely to encounter bighorn sheep (Singer and Gudorf 1999). Further, when bighorn sheep are transplanted they may be predisposed to cougar predation because normal escape routes are unknown or unavailable (Krausman et al. 1999).

Transplanted bighorn sheep populations in Wyoming are no different and suffer from problems associated with small, sedentary herds (i.e., poor survival, low recruitment). Wyoming transplant efforts have taken place in low to mid-elevation areas where successional changes from relatively open habitats to dense shrub and conifer stands have reduced the amounts of high quality sheep habitat and blocked migration routes. Further, the mid-elevation mountain shrub communities are more likely to support high densities of mule deer and cougars, compared with the high-elevation alpine habitats that dominate the core native herd ranges. Because transplanted bighorn sheep herds in Wyoming occur at low densities (<100) and typically inhabit areas that support healthy deer and elk populations, in habitats with reduced visibility, they appear more susceptible to predation than bighorn sheep that occupy the native core ranges.

SUMMARY

- Recent studies have demonstrated that cougar predation can be an important source of mortality in bighorn sheep herds and, in some cases, may have population-level effects.

- Wolves occasionally prey upon thinhorn sheep, but have not been a significant source of mortality in bighorn sheep populations.

- Coyote predation appears to be incidental, primarily restricted to lambs, and not considered a limiting factor in bighorn sheep populations.

- Gregariousness and the use of steep, rugged terrain appear to be effective adaptations to avoid predation by coursing predators such as wolves and coyotes. Stalking predators like cougars, however, may be able to circumvent these strategies, and predation losses in some herds may be high if individual cougars specialize in preying upon bighorns.

- Available evidence suggests that impacts by cougars to bighorn sheep populations are restricted to areas where bighorn sheep and mule deer are sympatric.

- Most studies of bighorn sheep predation are conducted in sheep populations perceived to be in trouble.

- Cougars are capable of preying upon all sex and age classes of bighorn sheep. Studies involving radio-collared bighorns and/or cougars indicate that the vulnerability of prey-classes is variable and cougar prey selectivity is a function of individual cougar behavior.

- Although variable, cougar predation on bighorn sheep appears to be more prevalent during the winter.

- Identification and removal of individual cougars may be an effective method for minimizing cougar predation on bighorn sheep.

- Predation may become an additive source of mortality and population-level effects may be exacerbated if ewes are heavily preyed upon.

- Predation is more likely to be a limiting factor of bighorn populations inhabiting ranges without adequate escape terrain and is expected to be much less important in habitats where sheep can escape into cliffs and other rugged terrain.

- Compared to bighorns in the core native herds, transplanted bighorn sheep in Wyoming appear more susceptible to predation because they often inhabit areas with poor visibility that support healthy deer and elk populations, which serve as a primary food source for cougars.

MANAGEMENT CONSIDERATIONS

Bighorn sheep evade predation through their exceptional eyesight, climbing ability, and use of open areas adjacent to and within rugged terrain (Wishart 1978). Preference for habitats providing a high degree of visibility results from the predator-evasion strategy of bighorn sheep, in which predators are detected visually and the presence of danger is communicated among sheep by visual cues (Geist 1971). Apparent increases in bighorn sheep predation may be related to changes in plant communities. Decades of fire suppression have allowed many historic bighorn sheep ranges to become overgrown with tree and shrub communities that obstruct visibility and reduce the amount of high-visibility habitat needed by bighorn sheep (Risenhoover and Bailey 1985, Etchberger et al. 1989). The invasion by pinyon-juniper stands is believed to make bighorn sheep more vulnerable to ambush predators because of decreased visibility (Risenhoover and Bailey 1985, Wakelyn 1987). Encroachment of tall, dense shrubland and forest has caused loss of high-visibility habitat, open escape terrain, and migration routes on bighorn sheep ranges in Colorado (Wakelyn 1987).

Bighorn sheep populations that occupy areas with limited escape terrain may be vulnerable to high rates of predation. Lamb mortality in particular, may depend upon the availability and steepness of cliff terrain used for security cover (Shackelton et al. 1999). Predation is more likely to be a limiting factor of bighorn populations inhabiting ranges without adequate escape terrain (Hass 1989) and is expected to be much less important in habitats where sheep can escape into cliffs and other rugged terrain. Bighorn sheep are habitat specialists that depend on steep, rocky terrain with open visibility and generally shallow snow cover. Many bighorn sheep ranges require active management, particularly removal of tall, dense vegetation, to improve visibility and reduce bighorn sheep vulnerability to predation. A proactive approach should be taken to maintain suitable bighorn sheep habitats and improve those seasonal ranges with inadequate visibility and/or escape terrain.

Predator control is a valid management option only when problem individuals can be identified and removed. Because there is no evidence that wolves and/or coyotes are efficient predators of bighorn sheep or cause significant mortality in free-ranging bighorn populations, predator control or removal efforts should be limited to cougars; and then only in those situations where cougar(s) demonstrate a propensity for killing bighorns. Management based on the selective removal of problem individuals is dependent on the ability to define and identify problem individuals (Linnell et al. 1999). Predator control may be more readily needed and implemented in small or newly transplanted sheep herds, rather than well-established sheep populations. Ross et al. (1997) recommended that managers should expect highly variable predation rates on sheep populations less than 200 individuals. Predator management strategies should be implemented in ways that allow reliable evaluations of their effects upon bighorn sheep populations.

When predators exert a population-level effect on a bighorn sheep population, it is more likely a symptom of a greater illness rather than a disease in itself. Treating the symptom through predator control will likely only provide short-term relief for the population. Predator control is too often used because it generally meets the public's perception of what the problem is and it is a relatively easy way to show constituents that something is being done. Predator control is a tempting window dressing for agencies under political pressure and does not address any of the more prevalent problems (i.e., nutrition, habitat quality, habitat loss, migration routes, human disturbance, disease) associated with declines in bighorn sheep populations.

The major shortcoming of efforts to evaluate potential effects of predation on bighorn sheep is that they seldom are addressed in an experimental framework but, rather tend to be short-term and observational in nature. Future research should consider integrated telemetry and global positioning system (GPS) technology to determine predator effects on bighorn sheep populations. Recent advances in GPS-equipped telemetry equipment may allow researchers to obtain accurate data on predator kill sites, prey selection, food habits, predation rates, movement patterns, and other pertinent information related to predator-bighorn sheep interactions. Implementing GPS radio-collar studies may eliminate the inherent bias and guesswork associated with traditional methods (snow tracking, winter range transects, etc.) used to determine cougar food habits and establishing cause of death of prey species. Additionally, studies conducted in areas where predation is not perceived to be a problem may provide valuable insight as to the types of habitat conditions and ungulate dynamics that exist in areas where predation does not have population-level impacts on bighorn sheep.

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