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Factors Limiting a Bighorn Sheep Population in Montana Following a Dieoff

Abstract

Conservation and management of bighorn sheep populations is complicated by the species' susceptibility to a multitude of pathogens and the long-term influence of disease upon population dynamics. Small, post-dieoff sheep herds are often unable to fully recover to pre-dieoff densities, and researchers have identified several factors limiting such populations including disease, predation, competition, climate, nutritional deficiencies, and loss of genetic variability. We studied a small bighorn sheep herd in west central Montana from 1995 to 1997 to identify the mechanisms responsible for poor population performance subsequent to a dieoff in 1984. In contrast to the migratory pre-dieoff population, the current sedentary population was restricted to a small area of low elevation range throughout the year. Whereas we observed limited annual adult mortality due to disease and predation, ewe productivity and lamb recruitment rates were low in all years. Lamb production and survival were highly correlated with summer climatic conditions, with the highest rate of disease-mediated lamb mortality occurring during a summer drought and the lowest rate of ewe productivity occurring subsequent to this drought. Our data suggest that disease continues to play a significant role this bighorn sheep population, and nutritional quality of summer forage influenced not only sheep immunocompetence and susceptibility to disease but also herd productivity. Winter is generally considered the critical season for ungulate populations in the northern Rocky Mountains, yet summer climatic conditions can have important implications for performance of sedentary, low elevation sheep populations. We suggest that an understanding of population-specific limiting factors is essential to successful management of post-dieoff bighorn sheep herds. Data obtained through rigorous field studies facilitate the development and implementation of efficient, biologically sound strategies to improve performance of these populations.

Introduction

Susceptibility to disease is a distinguishing feature of bighorn sheep ecology throughout the western United States, and epizootics/dieoffs have contributed greatly to the decline of both montane and desert subspecies over the past century (Buechner 1960). Disease processes can result in significant adverse demographic impacts, including high rates of mortality (>70% of the population) and reduced population vigor (Onderka and Wishart 1984, Ryder et al. 1992), which compromise the viability of small post-dieoff sheep herds (Gilpin and Soule 1986, Berger 1990, Seebeck et al. 1990). Subsequent to a disease event, sheep populations often stabilize at relatively low equilibrial densities and exhibit poor population performance due to low recruitment rates (Cook 1990, Coggins and Matthews 1992, Ryder et al. 1992). Factors ultimately limiting such populations are population-specific and include loss of genetic variability, nutritional deficiencies, disease, predation, competition, and climate (Beuchner 1960, Berwick 1968, Geist 1971, Woodard et al. 1974, Horejsi 1976, DeForge and Scott 1982, Skiba and Schmidt 1982, Douglas and Leslie 1986, Hass 1989, Jones and Worley 1992, Wehausen 1996).

Detailed knowledge of local population dynamics is essential in the conservation and recovery of small wildlife populations (Clark et al. 1990, Minta et al. 1990). Management programs to improve the viability of small post-dieoff bighorn sheep herds have had limited success, largely due to an inadequate understanding of population–specific limiting factors (Wishart 1975, Risenhoover et al. 1988, Armstrong and McLean 1995). We studied bighorn sheep population dynamics on the Beartooth Wildlife Management Area (BWMA) from 1995 to 1997 in an effort to identify the factor(s) responsible for poor population performance subsequent to a dieoff event in 1984. Primary study objectives included identifying sheep range use, determining annual rates

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of reproduction and cause-specific mortality, evaluating individual lungworm burdens and nutritional status throughout the year, and modeling sheep population trends. The study was conducted coincident with a Montana Department of Fish, Wildlife and Parks (MFWP) sheep augmentation program, and we refer to the relocated sheep as "transplants" and the sheep that inhabited the BWMA prior to augmentation as "residents".

Study Area

The study area encompassed 18,390 ha in west central Montana approximately 36 km north of Helena (Figure 1). Eighty percent of the study area was within the BWMA, 13% in the Gates of the Mountains Wilderness Area, and 7% on private lands, and the Missouri River represented the western boundary. Elevations ranged from 1,091 msl along the Missouri River to >2,400 msl at the southeast boundary, and slopes varied from nearly level meadows to steep limestone cliffs. The study area was characterized by parallel southeast-northwest rocky ridges interspersed by bunchgrass meadow on southerly aspects and coniferous forest on northerly aspects.

The local climate is semi-arid, with mean annual precipitation of 31 cm. Fifty-nine percent of total annual precipitation falls during summer months (May-August), and summer precipitation determines growing season duration and the availability of nutritious forage for herbivores on the BWMA (Pyrah 1985). Winter climatic conditions are relatively mild due to warm Chinook winds. Mean temperatures are +18° C and -1° C in summer and winter, respectively. Whereas winter temperatures and snowfalls were relatively normal during this study, summer climatic conditions varied considerably. The summers of 1995 and 1997 were relatively wet with precipitation 42% and 54% above the 30-year average. Precipitation during the summer of 1996 was 38% below average, and drought conditions continued into early fall as cumulative September and October precipitation was 43% below normal.

The study area includes extensive grasslands interspersed by small forest communities. Grasslands primarily contained bluebunch wheatgrass (*Agropyron spicatum*) at lower elevations and fescue (*Festuca scabrella* and *F. idahoensis*) at higher elevations. Forest communities included ponderosa pine (*Pinus ponderosa*) savanna on southerly aspects and Douglas-fir (*Pseudotsuga mensezeii*) on northerly aspects. Higher elevations of the BWMA represented critical winter range

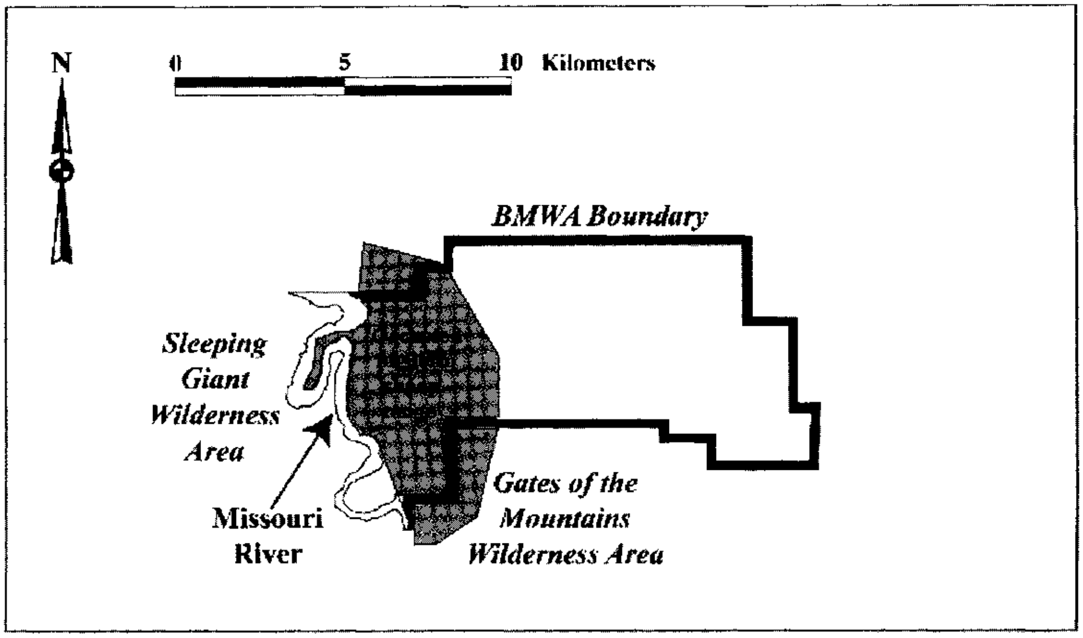

Figure 1. Study area location map.

for 1,700 elk (*Cervus elaphus*) and 500 mule deer (*Odocoileus hemionus*). Approximately six mountain lions (*Felis concolor*) held territories within bighorn sheep range during winter months (Enk 1999). A small bighorn sheep population (<40 individuals) occupied the adjacent Sleeping Giant Wilderness Area. Domestic sheep are raised at two ranches located 5 km north and 8 km east of the study area.

Herd History

Lewis and Clark observed bighorn sheep along the Missouri River near the Gates of the Mountains area in 1805 (Coues 1893). There are no historic estimates of the size of this population, which was extirpated by disease and market hunting in the early 1930s. The population was subsequently re-established following the translocation of 113 individuals to the Gates of the Mountains area in the 1970s (Rognrud 1983, Hilger 1996). Results from MFWP bighorn sheep surveys indicated that the population grew rapidly between 1978 and 1983 (r = + 0.202) and approached 300 individuals. During this period, the population also expanded onto the adjacent BWMA and established seasonal elevational migrations (Enk 1999). Population growth was spurred by high recruitment rates, as the mean spring lamb-ewe ratio during this period was 58 lambs:100 ewes.

A dieoff in 1984 resulted in 80% herd mortality, and only 51 survivors were counted in the fall of 1984. Clinical symptoms of respiratory disease were observed in the field during the dieoff. Necropsies conducted on two rams recovered in September 1984 determined that both individuals were in poor nutritional condition and *Pasteurella* spp. were isolated from each. Causes of death included verminous pneumonia and Pasteurellosis.

During the post-dieoff period (1985-1993), the population was relatively stable (r = + 0.002) and appeared to fluctuate around an equilibrial density of approximately 50 individuals.

Spring lamb-ewe ratios averaged 21:100 during this period, suggesting that recruitment rates were inadequate to stimulate population growth. The herd also ceased seasonal migrations subsequent to the dieoff. Necropsy of a dead lamb found in July 1991 diagnosed the cause of death as streptococcal pneumonia, and these results suggested that disease continued to influence bighorn sheep ecology on the BWMA long after the primary dieoff event.

Methods

In March 1995 and March 1996, 15 ewes and 4 rams were captured from the Perma-Paradise herd near Plains, Montana and 14 ewes and 6 rams were captured from the Rock Creek herd near Phillipsburg, Montana, respectively. Both herds were growing and relatively healthy at the time, and histological/serological analyses indicated no significant disease among captured individuals. Sheep were captured via helicopter netgun by Helicopter Wildlife Management, Inc. (Salt Lake City, Utah) and fitted with either a radio transmitter (n = 17) or an individually identifiable neckband (n = 22). Transplants and residents were relocated during bi-weekly relocation flights (n = 28) between January and December 1996 and May and September 1997, and from the ground throughout the study. We obtained 1,518 visually confirmed, individual relocations that were plotted on United States Geological Survey topographic maps (1:24,000) with Universal Transverse Mercator (UTM) grid overlays. UTM coordinates, date, group size and composition, and physical environmental characteristics were recorded for all locations. Statistical dependence was minimized by maintaining a minimum of 24 hours between successive relocations of a given individual (Thomas and Taylor 1990).

Relocation data were used to determine sheep movements and distribution. Individual movements were classified as either exploratory movements or dispersal events depending on whether emigration from the study area was temporary or permanent, respectively. Dispersal events (n = 11) involved sheep swimming across the Missouri River to the Sleeping Giant Wilderness Area, and most dispersers (n = 8) joined the Sleeping Giant bighorn sheep herd. The program CALHOME (Kie et al. 1994) was used to analyze overall sheep distribution via minimum convex polygon (MCP; Mohr 1947) and to identify core ranges via 90% harmonic mean (HM; Dixon and Chapman 1980).

Lamb production in 1996 and 1997 was quantified by actively monitoring lambing grounds until all ewes and lambs departed. Lamb production for 1995 was estimated based upon MFWP classification data, and summer (peak) and subsequent spring lamb-ewe ratios were calculated in all three years. Productivity of individual ewes was analyzed to determine whether this population exhibited alternate year reproduction (Heimer 1978). We conducted linear regression analyses to examine relations among climate and lamb production and lamb survival (*P*= 0.05) using the software package STATISTICA® (StatSoft, Inc., Tulsa, Oklahoma). Kaplan Meier survivorship curves (Pollock et al. 1989) were generated to quantify annual adult and lamb survival and to identify critical periods of lamb mortality. Causes of mortality were classified as disease, predation, or unknown based on field investigations, and necropsies were performed at the MFWP Research Laboratory in Bozeman when feasible. Mortality data were analyzed to identify seasonal trends and the relative roles of disease and predation in local population dynamics.

Sheep pellet groups (n = 152) were randomly collected from known individuals between March 1996 and August 1997. Pellets were air-dried for >90 days, and the Baermann technique (Beane and Hobbs 1983) was used were to determine the presence and abundance of first-stage Protostrongylid larvae on 5-gram sub-samples. Baermann results, expressed as larvae per gram (LPG), were transformed prior to statistical analyses (Uhazy et al. 1973). Sixty adult pellet groups were submitted to the Montana State University-Plant and Soils Analytical Laboratory for fecal nitrogen analysis via the Kjeldahl method (Horowitz 1975), with results expressed as %TKN. We used a stratified sampling approach across seasons to select pellet groups for Kjeldahl analyses. Baermann and Kjeldahl results were statistically analyzed using Student's t-tests and ANOVA (*P* = 0.05) to detect differences in individual Protostrongylid burdens and fecal nitrogen levels between seasons and to compare these factors among different sex and age cohorts.

Lincoln-Peterson estimates (Lancia et al. 1994), surveys of the minimum number known alive, and annual MFWP spring censuses were used to determine population trends. Lincoln-Peterson estimates were developed from aerial and ground surveys in which >60% of marked sheep were relocated. We used the program BOPEEP (McCarty and Miller 1998) to generate deterministic, discrete population models based upon annual reproduction and mortality rates. We developed alternative population scenarios including: an "expected" trajectory using population parameters from McCarty and Miller (1998); an "observed" trajectory using parameters obtained during this study; and a "no predation" trajectory in which we simulated the elimination of mountain lion predation (n = 4 annual events). While we acknowledge that the study duration limits model robustness, we do suggest that the model scenarios are valuable in identifying general trends and determining the relative importance of predation in this population.

Results

Sheep Distribution

Analyses of telemetry and observational data indicated that sheep distribution was limited to 6,000 ha in the western portion of the BWMA and adjacent lands (Figure 2). The population included two sub-groups that exclusively utilized distinct portions of the study area, and there was little interaction between these subgroups. Transplanted sheep did integrate with the resident sub-groups, and transplants and residents exhibited similar distribution and range use patterns (Enk 1999). Summer and winter distributions were similar, with sheep activities concentrated in 3,374 ha of low elevation "winter range" habitat (< 1,650 m) throughout the year. The data indicate that the population has not re-established seasonal elevational migrations.

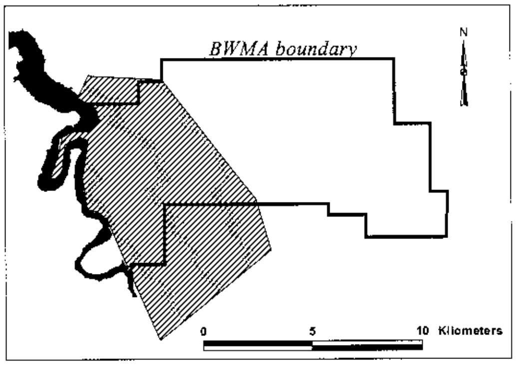

Figure 2. Bighorn sheep distribution on the BWMA.

Lamb production

Total annual reproduction varied between 11 and 19 lambs, with corresponding peak lamb:ewe ratios of 35-40 lambs:100 ewes (Table 1). Annual

TABLE 1. Annual production and mortality of bighorn sheep lambs between 1995 and 1997.

	1995	1996	1997
Number of mature ewes	37	47	31
Number of lambs produced	14	19	11
Number of lambs recruited	8	6	7
Lamb:ewe ratio[1]	38:22	40:13	35:23
Unmarked survival[2]	NA	3/9	3/4
Marked survival[2]	NA	3/10	4/7

[1] Number of lambs per 100 ewes at peak of lambing/subsequent spring.

[2] Number survived/number produced.

variability in total lamb production reflected changing densities of mature ewes in the BWMA population, with an increase subsequent to augmentation in 1996 and a decrease in 1997 due to ewe dispersal and mortality (Table 1). Lamb production was similar between transplant and resident ewes (Table 1). Intensive monitoring of lambing grounds indicated that low lamb production reflected poor reproductive success rather than post-partum mortality, although it is unknown whether this was associated with failure to conceive or fetal resorption. Over the 3-year study period, lamb production was positively correlated with total precipitation during the previous July ($r = 0.999$, $P = 0.018$) and was negatively correlated with maximum temperatures during the previous August, although this result was not significant ($r = 0.981$, $P = 0.112$).

The proportion of mature ewes producing lambs was low in all years ($\bar{x}$ = 38%, SD = 2.0), and remained relatively unchanged subsequent to augmentation (Table 1). Annual proportions of transplant and resident ewes producing lambs were similar, suggesting that factors responsible for low productivity were not inherent to BWMA sheep. Individual ewes exhibited considerable variability, producing 0, 1, or 2 lambs during the study, and there was no correlation between previous year reproductive status and subsequent year success. As a group, none of the 1995 transplant ewes produced lambs in 1996 whereas 73% produced lambs in 1997. Seventy-eight percent of the 1996 transplant ewes produced lambs in 1996 and only 25% produced lambs in 1997. While these data are suggestive of alternate year reproduction (Heimer 1978), the duration of this study precluded analyses of ewe reproductive patterns.

Lamb survival

Annual survival of lambs to age one varied between 0.32 and 0.64 during this study (Table 1). Survivorship curves (Figure 3) identified a critical period of lamb mortality between July 15 and September 15 in 1995 and 1996. Cumulatively, 91% of the lambs surviving to September 15 lived to age one during the three-year study period. Lambs born to resident and transplant ewes had similar survival rates in all years (Table 1). Results from regression analyses indicated that lamb survival rates were significantly correlated with same-year April/May precipitation and maximum August temperatures for the 13 years following the dieoff ($r = 0.844$, $P = 0.007$, $n = 13$). There was no correlation between lamb survival and these climatic variables for the 7 years prior to the dieoff ($r = 0.354$, $P = 0.818$, $n = 7$).

Four lamb mortalities were investigated in 1996 ($n = 2$) and 1997 ($n = 2$). The 1996 mortalities occurred in late July/early August when the lambs were approximately 8-9 weeks old, and were both associated with disease processes. Necropsy of a male lamb that died on 6/29/96 indicated that the individual had a low lungworm burden and was in fair nutritional condition at the time of death. Pleuritis was suggestive of pneumonia processes, but tissue autolysis prevented histologic and bacteriologic analyses (Enk 1999). July and August of 1996 represented a period of significant lamb mortality, and 68% of all lambs born in 1996 were dead by October 1 (Figure 3). This mortality period coincided with the observation of clinical symptoms of respiratory disease, including coughing, sluggish behavior, and ragged appearance (Woodard et al. 1974) among both lambs and ewes. Cumulatively, necropsy results and observational data indicated that 1996 lamb mortalities were due to pneumonia processes.

Although analyses of coyote and mountain lion scats indicated minimal lamb predation during all years of this study (Enk 1999), the 1997 lamb mortalities were due to predation (species unknown) while lambs were on/adjacent to lambing grounds in late June. Lamb survivorship was relatively high in 1997 (Figure 3), and there was no evidence that disease caused lamb mortality during this year.

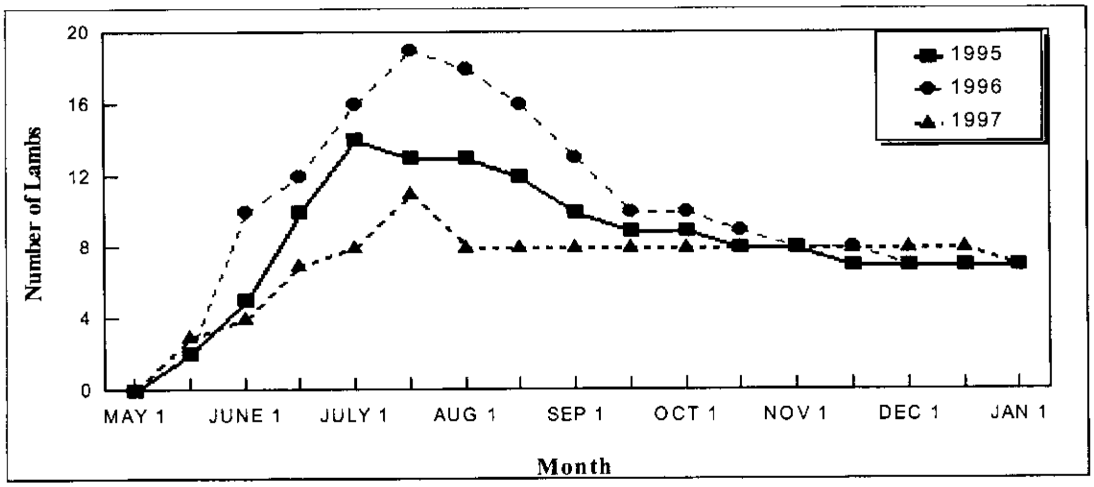

Figure 3. Lamb survivorship curves.

Adult survival

Mean annual adult survivorship for marked individuals during this study was 0.84, but dispersal of 28% of all transplanted sheep reduced the ewe densities within the study area. Thirteen adult mortalities were investigated, including 4 dispersers outside the study area (Table 2). Mortalities within the study area occurred either in spring (March-May) and fall (October-November), and were associated with mountain lion predation (n = 5), disease (n = 3), and unknown causes (n = 1). Throughout the study, all spring mortalities were due to mountain lion predation and all fall mortalities were caused by disease (Table 2). The sole exception to this temporal pattern was a dispersing ewe that died subsequent to her association with domestic sheep in June 1996. Sheep mortalities were located within a variety of habitat types (Table 2). Predation sites were characterized by vegetative or topographic features that limited sheep vision of the surrounding environment.

TABLE 2. Dates and causes of adult sheep mortalities during the study. Cover type refers to general characteristics of mortality locations.

Sex	Date	Cause	Cover type
Ewe	11/15/95	Unknown	Grassland/Shrub
Ram	3/1/96	Predation	Forest
Ram	3/9/96	Predation	Rock/Talus
Ewe	3/29/96	Predation	Riparian
Ewe	4/16/96	Predation	Riparian
Ewe[1]	5/14/96	Predation	Rock/Talus
Ewe[1]	7/3/96	Disease	Grassland
Ewe	10/21/96	Disease	Burn
Ewe[2]	11/20/96	Disease	NA
Ewe[2]	11/20/96	Disease	NA
Ewe[1]	11/23/96	Predation	Forest
Ram[1]	3/15/97	Predation	Rock/Talus
Ewe	5/29/97	Predation	Rock/Talus

[1] Located outside study area.

[2] Location unknown and date of death approximate.

All disease-related mortalities of adult sheep occurred coincident with the 1996 drought, and affected only transplant ewes. Necropsy of a transplant ewe that died in October 1996 indicated the individual supported a "low" lungworm burden and was in poor nutritional condition. Severe lung adhesions, suggestive of a chronic illness, were observed and *Streptococcus* spp. were isolated via histological analyses. The cause of death was attributed to bacterially induced bronchopneumonia, although the specific bacteria involved were unknown (Enk 1999). Relative to lungworm burden, nutritional status, and general cause and season of death, these findings are similar to results of necropsies conducted on BWMA sheep in 1984 and 1991 (Enk 1999), and suggest that disease has continued to affect this population since the 1984 dieoff.

Fecal Analyses

Protostrongylid larvae were present in 98% of adult sheep pellet samples (n = 83). Results from Baermann analyses indicated moderate levels of lungworm infection ($\overline{x}$ = 86 LPG; range = 0-535 LPG) and only 14% of adult samples exceeded

100 LPG. Individual shedding rates were highly variable and exhibited no discernible seasonal patterns (Enk 1999). Lamb samples (n = 45) were negative for Protostrongylid larvae until August, and shedding rates remained low throughout their first 8 months ($\bar{x}$ = 7 LPG; range = 0-44 LPG).

Mean adult fecal nitrogen levels were generally low (Table 3), and mean fecal nitrogen differed between seasons ($P = 0.001$). Fecal nitrogen levels peaked in May ($\bar{x}$ = 2.34) and declined through October 1996 ($\bar{x}$ = 1.29). Levels remained below 1.3% through the winter months and then rose slightly in March and April ($\bar{x}$ = 1.36). Ram and ewe levels were similar in throughout the year ($P = 0.426$). Mean fecal nitrogen levels for the June-September period were higher in 1997 ($\bar{x}$ = 2.14; SD = 0.36; n = 11) than in 1996 ($\bar{x}$ = 1.92; SD = 0.34; n = 13). Late summer-early fall individual fecal nitrogen levels declined more rapidly in 1996 compared to 1997 (Enk 1999). These data likely reflect the influence of drought conditions on forage quality and associated individual nutritional status in 1996. Data limitations precluded correlation analyses of precipitation and fecal nitrogen levels.

TABLE 3. Results (%TKN) of Kjeldahl analyses on fecal samples from adult bighorn sheep.

	Mean (SE)	Range
All (n=49)	1.60 (0.06)	0.73-3.19
Ewes (n=36)	1.73 (0.08)	0.90-3.19
Rams (n=13)	1.53 (0.49)	0.73-2.54
Season		
Winter (n=15)	1.24 (0.03)	1.00-1.37
Spring (n=9)	1.66 (0.18)	1.18-2.03
Summer (n=12)	2.08 (0.11)	1.77-3.19
Fall (n=13)	1.41 (0.09)	0.73-1.88

Population Estimates and Models

All estimators indicated that the sheep population declined over the study period (Table 4). Although confidence intervals on Lincoln-Peterson estimates were relatively large, the minimum number known alive and MFWP census data revealed similar declining trends. Population trajectories differed significantly depending upon the parameters utilized to construct the model (Figure 4). The expected trajectory indicated steady population growth (r = +0.116) throughout the modeling period and ends with a final population of 211. The observed trajectory indicates a declining population (r = – 0.068) and concluded with a final population of 17. The no predation trajectory indicates that eliminating mountain lion predation, while slightly improving sheep population trends, did not induce growth (r = – 0.004). This model ended with a final population of 63 sheep.

TABLE 4. Population estimates of the BWMA bighorn sheep herd for 1995, 1996, and 1997.

	1995	1996	1997
Lincoln-Peterson (95% CI)	68 (35-100)	64 (38-89)	38 (27-48)
Minimum number alive	52	42	35
MFWP census	45	30	20

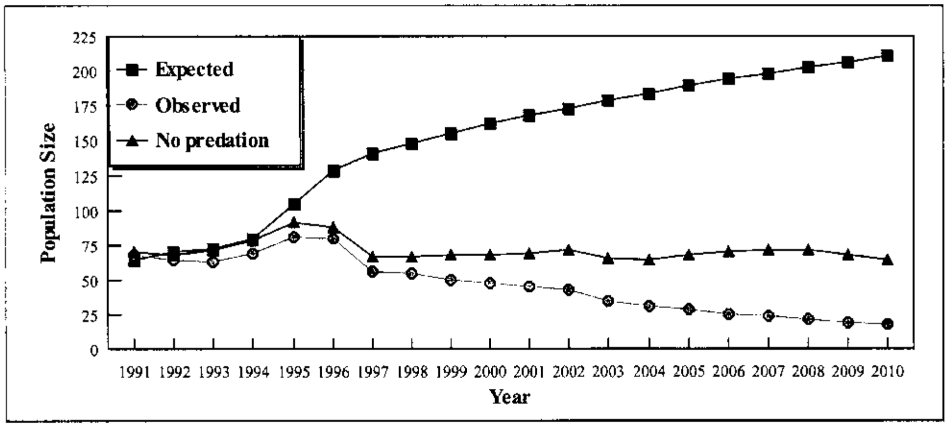

Figure 4. BWMA bighorn sheep population trajectories.

Discussion

The BWMA bighorn sheep herd has performed poorly subsequent to the 1984 dieoff, and evidence suggests that this population has been exposed to disease-inducing pathogens since the dieoff. Our data indicate that the primary limiting factors during the study period included low lamb production, disease mortalities during periods of nutritional stress, and predation upon adult sheep.

Quality of herbivore populations is largely determined by female nutritional status (Verme 1969, Geist 1971, Gunn 1983, Cook 1990, Sodor et al. 1995), and rates of lamb production observed during this study were characteristic of a low quality population (Geist 1971). In semi-arid habitats, climate mediates nutritional quality of native forages and is a primary determinant of ungulate reproductive success (Talbot and Talbot 1963, Verme 1967, Sadlier 1969, Thorne et al. 1979, Clutton-Brock et al. 1982, Hamlin and Mackie 1989, Hengel et al. 1992).

Our results support the assertion that nutritional constraints during late summer and early fall can reduce herd productivity and lamb survival in sedentary, low elevation bighorn sheep populations following a dieoff (Douglas and Leslie 1986, Festa-Bianchet 1986, Cook 1990, Goodson et al. 1991, Hengel et al. 1992, Kissel 1996). Lamb production was correlated with July precipitation in all three years. While we agree that correlation does not imply causality, particularly during a study of limited duration, we do provide additional evidence of a strong relationship between summer climatic conditions and ewe productivity. Fecal nitrogen was slightly above maintenance levels during this period (Irwin et al. 1993), suggesting that forage quality was likely inadequate for ewes to attain the physiological condition necessary to produce a lamb the following year. Domestic lamb production on an adjacent ranch declined by 30% due to drought and associated nutritional deficiencies during the summer of 1996 (Scott Blackman, Sterling Ranch Company, Craig, Montana, personal communication). Additionally, MFWP observed improved productivity in a year with "good" summer climatic conditions after this study had concluded (Jim Williams, MFWP, personal communication).

Rocky Mountain bighorn sheep are typically migratory (Festa-Bianchet 1986), and the cessation of seasonal elevational migrations by the BWMA population has important nutritional implications. Elevational migrations allow individuals to follow plant phenological development, prolonging availability of nutritional forages through summer months (Hebert 1973, Shackleton 1973, Stelfox 1976) and facilitating access to high quality alpine forages (Klein 1965). The loss of seasonal migratory behaviors has been observed in other bighorn populations (Wakelyn 1984). On the BWMA, the cessation of seasonal migrations has restricted the current population to a small area of low elevation habitat throughout the year, precluding access to nutritional forages at higher elevations and forcing sheep to rely on low quality forages for much of the year. The loss of migratory behavior has likely negatively influenced the overall nutritional balance and, accordingly, performance of this sheep population (Hebert 1973, Shackleton 1973, Schwartz and Hobbs 1985).

Disease-mediated lamb mortality is a common residual effect of dieoff events (Couey 1950, Forrester and Senger 1964, Woodward et al. 1972, Woodard et al. 1974, Spraker and Hibler 1977, DeForge and Scott 1982, Onderka and Wishart 1988, Foreyt 1988, Akenson and Akenson 1992, Coggins and Matthews 1992). Survivorship curves indicated a critical lamb mortality period on the BWMA between late July and early September, and in conjunction with necropsy results and observations of respiratory disease symptoms, suggest that disease processes continued to adversely affect local population dynamics.

Mortality of lambs and adults due to disease, primarily during a drought period, suggested increased susceptibility during periods of poor forage quality. Between 1985 and 1997, lamb survival rates were highly correlated with summer climate (April/May precipitation and August temperatures). In the study area, April/May precipitation determines forage quality and ewe nutritional status during the last two months of gestation, and influences lamb survival by determining birth weights and colostrum production (Robinson 1983, Subandriyo 1984, Foreyt 1988, Burfening and Kott 1993, Sodor et al. 1995). August temperatures affect plant senescence and the availability of quality forage during a period when lambs are physiologically-stressed due to increased reliance on native forage and waning colostral immunities (Foreyt 1988). These factors are particularly crucial in sedentary populations with exposure to pathogens. Necropsy results and fecal nitrogen analyses support the assertion that nutritional stress increased lamb susceptibility to disease (Chandra and Newburne 1977, Foreyt 1988).

Necropsies conducted on BWMA sheep between 1984 and 1996 indicate that disease has been present in this population since the primary dieoff. During this study, disease-related mortality of adults was limited to transplants and only occurred coincident with summer drought. Resident sheep were not evaluated for presence of disease prior to the augmentation program, and all transplants tested negative for pathogens prior to translocation. Although residents appeared to be healthy, survivors of dieoff events can shed pathogenic bacteria for extended periods despite appearing clinically normal (Foreyt 1988). Presumably, resident sheep have acquired relative immunity to pathogens that were lethal to transplanted sheep. The timing of disease mortalities indicated that disease affected adult sheep during periods when nutritional stress compromised individual immunocompetence.

While pathogen source(s) are unknown, dispersal and exploratory movements resulted in at least two individuals coming into contact with domestic sheep. Although one of these individuals died in a domestic sheep pasture, the other did return to the BWMA after approximately two weeks. Given that domestic sheep carry diseases that are lethal to bighorns (Foreyt 1989), contact with domestic sheep may result in chronic persistence of pathogens in this bighorn population.

We estimate that mountain lions killed 3-5 adult sheep annually on the BWMA. Predation was limited to winter and spring seasons, and our data support the conclusions of Williams (1992) and Ross et al. (1997) that sheep can be a seasonal prey item for some mountain lion populations. While this predation rate was low relative to mountain lion densities on bighorn range (~ 6 individuals), annual predation losses accounted for approximately 10% of the adult sheep population. During the study period, predation losses offset annual lamb recruitment.

Population models were based upon three years of data and, while projections should be interpreted with caution, they provide some interesting trend information. All estimators reflected a population decline between 1995 and 1998, despite the addition of 39 individuals through the augmentation program. Models indicated that local bighorn sheep demographic parameters differed considerably from those reported in the literature (McCarty and Miller 1998). Simulations in which predation was eliminated slowed the population decline but did not induce growth, confirming our conclusion that losses to mountain lion predation generally offset annual recruitment. The observed model, using parameters obtained during this study, ended with an extremely small population. As local population dynamics appear correlated with summer climate and susceptibility to disease, the actual population trajectory will likely track annual climatic variability and be somewhat better than model forecasts.

During this study period, the BWMA bighorn sheep population was proximately regulated by low reproductive success, poor recruitment rates, and adult mortality. This sedentary, post-dieoff herd appears to be ultimately limited by disease and mountain lion predation. Our data support the conclusions of Cook (1990) and Kissel (1996) that nutritional quality of forage in late summer and early fall summer can limit low elevation bighorn sheep populations. We suggest that differences between pre- and post-dieoff population performance largely reflects continued exposure to pathogens. Lamb survival was correlated with summer climate following, but not prior to, the dieoff, which likely reflects the presence of lethal pathogens during the post-dieoff period that cause mortality during periods of nutritional stress. The pre-dieoff population was not subjected lethal pathogens, and seasonal elevational migrations likely mediated late summer nutritional stress by providing access to nutritious forage at higher elevations.

Although this study was not designed to address the roles of inter-specific competition and loss of genetic variability in local population dynamics, anecdotal data suggest these factors are of limited significance. Limited spatial and temporal overlap of elk and deer with bighorn sheep on the study area (Feist et al. 1994, Enk 1999) resulted in a low potential for competition. Poor reproductive performance was not likely due to inherent genetic problems in this population as: 1) the herd was founded from the genetically diverse Sun River sheep population (Luikart and Allendorf 1996) and the population has been augmented from 2 other Montana herds; and 2) overall reproductive success did not improve subsequent to augmentation, and transplant and resident ewes reproductive rates were similar (Enk 1999).

Winter is traditionally considered to be the critical season relative to ungulate survival and population dynamics in the northern Rocky Mountains (Chappel and Hudson 1978), and studies have demonstrated the adverse effects of severe winter climatic conditions on bighorn lamb survival (Picton 1984). Our results suggest that in certain ecological settings, summer can be a critical period for bighorn sheep populations in this region. Sedentary, low elevation populations are particularly vulnerable to nutritional stress, which increases susceptibility to disease and reduces reproductive performance.

Management programs aimed at improving the viability of small, post-dieoff bighorn sheep populations have had limited effectiveness largely due to inadequate understanding of local population ecology (Armstrong and McLean 1995). A crucial step towards developing effective bighorn sheep management strategies is *a priori* identification of population-specific limiting factors. Augmentation on the BWMA had limited potential for improving local sheep population dynamics given the current limiting factors. We suggest that data obtained through traditional semi-annual population surveys are inadequate for the rigorous evaluation of bighorn sheep management strategies, and encourage more intensive field efforts to gather the data necessary for biologically-sound management actions. In the absence of requisite population-specific data, contemporary efforts to improve the viability of small, post-dieoff bighorn sheep populations will continue to be inefficient.

Acknowledgements

We thank B. Michaelson and T. Antonich for field assistance. B. Wilmer and D. Gustafson provided technical support and the Craighead Environmental Research Institute donated telemetry equipment. K. Aune conducted necropsies and D. Worley assisted with lungworm analyses. The Montana Department of Fish, Wildlife & Parks, MFWP bighorn sheep permit fund, and Montana State University funded research. L. Irby reviewed the manuscript and provided valuable insights.

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Received 22 March 2000
Accepted for publication 27 March 2001

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