Journal of Wildlife Diseases, 44(2), 2008, pp. 388–403

EPIDEMIC PASTEURELLOSIS IN A BIGHORN SHEEP POPULATION COINCIDING WITH THE APPEARANCE OF A DOMESTIC SHEEP

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ABSTRACT: A pneumonia epidemic reduced bighorn sheep (*Ovis canadensis*) survival and recruitment during 1997–2000 in a population comprised of three interconnected wintering herds (Kenosha Mountains, Sugarloaf Mountain, Twin Eagles) that inhabited the Kenosha and Tarryall Mountain ranges in central Colorado, USA. The onset of this epidemic coincided temporally and spatially with the appearance of a single domestic sheep (*Ovis aires*) on the Sugarloaf Mountain herd's winter range in December 1997. Although only bighorns in the Sugarloaf Mountain herd were affected in 1997–98, cases also occurred during 1998–99 in the other two wintering herds, likely after the epidemic spread via established seasonal movements of male bighorns. In all, we located 86 bighorn carcasses during 1997–2000. Three species of *Pasteurella* were isolated in various combinations from affected lung tissues from 20 bighorn carcasses where tissues were available and suitable for diagnostic evaluation; with one exception, β-hemolytic *mannheimia* (*Pasteurella*) *haemolytica* (primarily reported as biogroup 1^{G} or $1^{\alpha G}$) was isolated from lung tissues of cases evaluated during winter 1997–98. The epidemic dramatically lowered adult bighorn monthly survival in all three herds; a model that included an acute epidemic effect, differing between sexes and with vaccination status, that diminished linearly over the next 12 mo best represented field data. In addition to the direct mortality associated with epidemics in these three herds, lamb recruitment in years following the pneumonia epidemic also was depressed as compared to years prior to the epidemic. Based on observations presented here, pasteurellosis epidemics in free-ranging bighorn sheep can arise through incursion of domestic sheep onto native ranges, and thus minimizing contact between domestic and bighorn sheep appears to be a logical principle for bighorn sheep conservation.

Key words: Bighorn sheep, domestic sheep, epidemic, *Mannheimia* spp., *Ovis canadensis*, *Pasteurella* spp., pasteurellosis, survival, vaccine.

INTRODUCTION

Epidemics caused by *Pasteurella* spp. and other pathogens have plagued bighorn sheep (*Ovis canadensis*) populations for at least a century, and have played a significant role in declines of bighorn populations throughout western North America (Warren, 1910; Grinnell, 1928; Shillinger, 1937; Buechner, 1960; Post, 1962; Miller, 2001). Disease epidemics in bighorn sheep were reported to follow European settlement and establishment of domestic livestock grazing (Warren, 1910; Grinnell, 1928; Shillinger, 1937). This trend may reflect historic introduction of novel pathogens (including some *Pasteurella* spp. strains) into naive bighorn populations beginning in the late 1800s (Warren, 1910; Grinnell, 1928; Shillinger, 1937; Marsh, 1938; Honess and Frost, 1942; Buechner, 1960; Goodson, 1982; Miller, 2001). Although pasteurellosis was first diagnosed in free-ranging bighorns in 1935 (Potts, 1937), earlier unconfirmed epidemics (e.g., Warren, 1910; Rush, 1927; Grinnell, 1928; Honess and Frost, 1942; Spencer, 1943; Buechner, 1960) seem likely (Post, 1962).

Native North American wild sheep species appear exquisitely susceptible to pasteurellosis (Onderka and Wishart, 1988; Onderka et al., 1988; Foreyt, 1989; Foreyt et al., 1994, 1996). Based on contemporary taxonomic classifications, three species of *Pasteurella*, *Pasteurella haemolytica* (recently reclassified and renamed *Mannheimia haemolytica*; Angen et al., 1999), *Pasteurella trehalosi* (formerly *P. haemolytica*, biotype T; Sneath and Stevens, 1990), and *Pasteurella multocida*, have been isolated from both healthy and ill bighorns (Jaworski et al., 1998; Miller, 2001; Kelley et al., 2007). All three species can cause pneumonic and septicemic pasteurellosis in bighorn sheep, but the commensal nature, ubiquitous distribution, and heterogeneity of *Pasteurella* spp. among bighorn sheep and other mammalian hosts obscure several features of their transmission and epidemiology. Whether highly pathogenic *Pasteurella* spp. strains are "normal" flora in North American wild sheep populations on an evolutionary timescale seems questionable (Miller, 2001; Jenkins et al., 2007).

Because *Pasteurella* spp. can function as endemic, opportunistic pathogens, predisposing factors like trauma, stress, or intercurrent disease may contribute to isolated or epidemic pasteurellosis in bighorn sheep (Feuerstein et al., 1980; Spraker et al., 1984; Festa-Bianchet, 1988; Ryder et al., 1992). In some cases, however, pasteurellosis can arise in bighorn sheep in the apparent absence of significant predisposing factors. In these situations, it appears that individual carriers (most likely either a domestic ruminant or a bighorn sheep) introduce a pathogenic and perhaps novel *Pasteurella* spp. strain into a susceptible host population (Foreyt and Jessup, 1982; Miller et al., 1991; Miller, 2001). Although stressors could still play a role in precipitating the shedding of *Pasteurella* spp. or clinical disease in carriers under such circumstances, they are not necessary to sustain such epidemics. Some *M. haemolytica* and *P. trehalosi* strains carried as normal commensal flora by healthy domestic sheep are highly pathogenic in bighorn sheep and Dall sheep (*Ovis dalli*; Onderka and Wishart, 1988; Onderka et al., 1988; Foreyt, 1989; Foreyt et al., 1996). It follows that introduction of such strains could lead to catastrophic epidemics in susceptible bighorn populations, and that some of these strains may become endemic and continue cycling in affected populations (Miller et al., 1991; Hobbs and Miller, 1992; Miller et al., 1995; Miller, 2001). Here, we describe a pasteurellosis epidemic and its effects on population performance in a Colorado bighorn sheep population; the onset of this epidemic coincided in both time and space with the appearance of a single domestic sheep (*Ovis aires*) on occupied bighorn winter range.

METHODS

Population structure and demography

Radiotelemetry studies of free-ranging bighorn sheep residing in the Tarryall and Kenosha Mountains located in Park County, Colorado, USA (39°N, 105°W) (Fig. 1) were conducted from 1991–2000 in conjunction with a series of field studies (George et al., 1996; George, 1997; Miller et al., 2000). From 1991 to 1998, we captured bighorns and marked them with radiocollars, radio ear tags, and/or unique plastic ear tags annually to maintain adequate sample sizes for these studies; capture and associated field methods were described in detail elsewhere (George et al., 1996; George, 1997; Miller et al., 2000). All radiomarks were equipped with mortality signals. Radiocollared adult females ($\geq$3 yr old) were present in the study area during the entire time period; radiocollared adult males ($\geq$3 yr old) were present from 1995 to 2000, and radiocollared subadults ($<$3 yr old) of both sexes were present from 1996 to 2000.

Radiocollared bighorn sheep were both observed and monitored remotely for mortality signals year-round. For each visual observation, technicians recorded date, time, group size, age and sex of animals in the group, identification of marked animals, habitat type, and location. Visual observations were made from a distance with the use of binoculars and spotting scopes to minimize disturbance. The frequency of visual observations varied and was dependent on design of specific studies. From May to October 1991–97, females and males were observed approximately once every 2 wk,

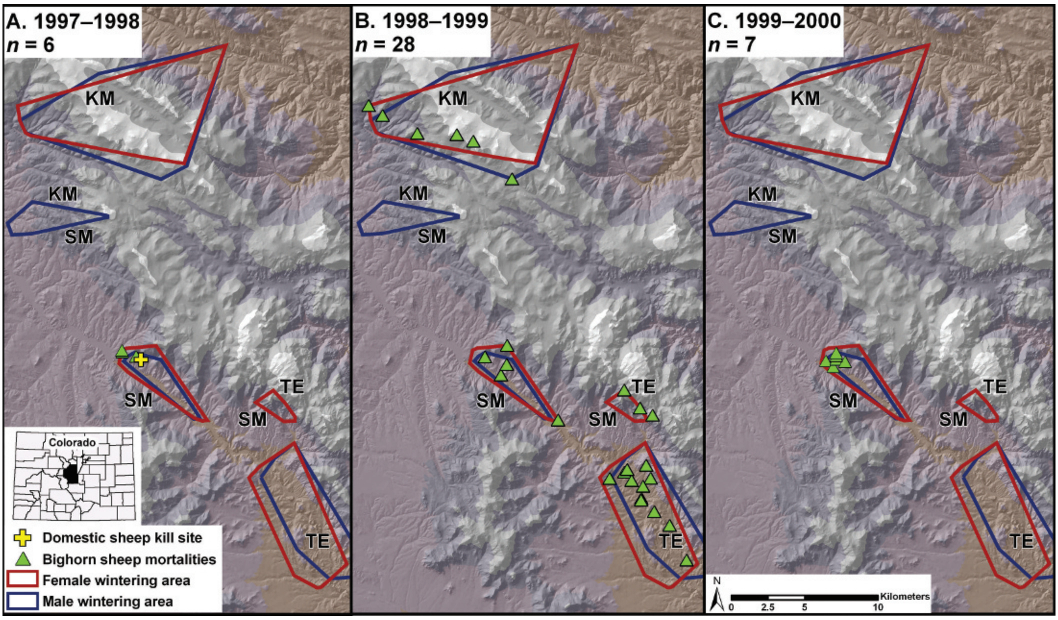

FIGURE 1. Spatial and temporal distribution of 41 carcasses attributed to pneumonia among radiocollared bighorn sheep in the Tarryall and Kenosha Mountains, Colorado, during the winters of (A) 1997–1998, (B) 1998–1999, and (C) 1999–2000, and their relationship to the location where a single domestic sheep was associated with bighorns on range in December 1997. Primary winter ranges (KM = Kenosha Mountains, SM = Sugarloaf Mountain, TE = Twin Eagles) and two areas of intermediate winter use were delineated with minimum convex polygons by using all radiocollared bighorn sheep locations between December and March, 1992–2000 (females) and 1994–2000 (males). Locations of four radiocollared carcasses were not reported.

although this was not possible in winter. From 1998 to 2000, visual observations were made less frequently, varying from once every 2 wk to once every several months. Mortality signals were monitored more frequently in all seasons and years. All mortality signals were investigated promptly and, when possible, carcasses were necropsied either in the field or at the Colorado State University Diagnostic Laboratory (CSUDL; Fort Collins, Colorado, USA).

Based on data gathered during these studies and on prior knowledge about bighorn sheep in our study area (Bear and Jones, 1973; Bailey, 1990), the Tarryall-Kenosha Mountains bighorn population was comprised of three distinct female groups (referred to here as the Kenosha Mountains, Sugarloaf Mountain, and Twin Eagles herds; Fig. 1). The Sugarloaf and Twin Eagles herds occupied largely separate ranges in the Tarryall Mountains with elevations ranging from 2,400 to 3,800 m. The Sugarloaf Mountain herd ranged over about 165 km^2, but bighorns congregated at lower elevations along Tarryall Creek near Sugarloaf Mountain during winter. The Twin Eagles herd ranged over about 139 km^2 south and east of the Sugarloaf Mountain herd, also congregating at lower elevations along Tarryall Creek during winter about 15 km downstream from the Sugarloaf Mountain herd. Although the Sugarloaf Mountain and Twin Eagles herds' ranges overlapped slightly during seasonal movements, interchange between herds appeared minimal, particularly among females. The Kenosha Mountains herd ranged over about 65 km^2 in the Kenosha and Platte River Mountains between 2,800 and 3,400 m in elevation. This herd primarily used alpine habitat throughout the year, but occasionally congregated in subalpine habitats in late winter or spring in Black Canyon and

Long Gulch. The Kenosha Mountains herd's range was separated from the other two herds by at least 10 km during all seasons. Although male movements largely overlapped with those of their corresponding female herds during winter (Fig. 1), there also were some seasonal male movements among herds, primarily between the Kenosha Mountains and the Sugarloaf Mountain herds. A portion of the males associated with the Sugarloaf Mountain females in winter migrated and associated with resident Kenosha Mountains males during summer. Other males that associated with the Kenosha Mountains females during the fall breeding season moved to the north end of the Tarryall Mountains and associated with males from Sugarloaf Mountain on a distinct late winter/spring range (Fig. 1).

Bighorn sheep numbered about 150 (90% confidence interval [CI]=136–164) in the Tarryall Mountains and about 100 (90% CI=97–115) in the Kenosha Mountains in March 1995 based on mark-resight inventory methods (George et al., 1996). Annual adult female survival rates from 1991–95 in the Tarryall Mountain herds were 0.82–0.98 (standard error [SE]=0.02–0.09) based on an annual sample size of 30 radiocollared females (15/herd; Miller et al., 2000). Of the 10 mortalities among radiocollared Tarryall bighorns from 1991–1995, six resulted from probable mountain lion predation and the other four were from unknown causes (Miller et al., 2000). Of the 17 radiocollared bighorns (10 females, seven males) in the Kenosha Mountains, there were three mortalities during 1995–1997. One of these was killed by lighting, another by a hunter, and one from an unknown cause that may have been related to recapture. No consistent health problems were detected among marked animals and no cases of pneumonia were diagnosed from 1991 to 1996 within the study area (George, 1997; Miller et al., 2000; Colorado Division of Wildlife [CDOW], unpubl. data).

Management intervention

Soon after the epidemic began in December 1997 as described below, we considered possible management actions that might be undertaken to minimize its spread and adverse effects. Based on knowledge of bighorn movement patterns in our study area gained from radiotelemetry data and ongoing field studies, we anticipated that late winter and summer movements of male bighorns would spread the responsible pathogen(s) from the Sugarloaf Mountain herd to the neighboring Kenosha Mountains and Twin Eagles herds by the winter of 1998–99. In an effort to lessen the effects of this epidemic by boosting herd immunity to pasteurellosis, 20 bighorns at Twin Eagles, 19 in the Kenosha Mountains, and seven at Sugarloaf Mountain were vaccinated with a multivalent *P. haemolytica* subcomponent vaccine (Miller et al., 1997; Kraabel et al., 1998; McNeil et al., 2000) in February and March 1998 in anticipation of the epidemic spreading in the months to follow. Vaccine doses equivalent to 2 ml were delivered by hand injection, projectile syringe, or biobullet to bighorns uniquely identified by ear tags or radiocollars.

Laboratory assessment

Carcasses that were not too heavily scavenged or decomposed to yield tissues for diagnostic evaluation were either necropsied in the field or submitted to the CSUDL for postmortem examination. In 20 cases where adequate tissues were available and suitable for diagnostic evaluation, lung and other representative tissues were collected and subsamples preserved either refrigerated for bacteriology and virus isolation or in 10% neutral buffered formalin for histopathology. For some cases, samples for bacteriology also were submitted to the University of Idaho Caine Veterinary Teaching Center (CVTC; Caldwell, Idaho); there, *Pasteurella* spp. were isolated and characterized

TABLE 1. Models and hypotheses considered for the bighorn sheep radiotelemetry survival analysis; models 20 and 21 were developed post hoc to consider additional hypotheses about bighorn sheep survival.

Model	Hypothesis	Model structure
1	Four-month acute epidemic effect	epi(acute)
2	Four-month acute epidemic effect with differences by vaccination status	epi(acute)+vaccine
3	Four-month acute epidemic effect with differences by sex	epi(acute)+sex
4	Four-month acute epidemic effect with differences by age	epi(acute)+age
5	Four-month acute epidemic effect with differences by sex and age	epi(acute)+sex+age
6	Acute effect with 12-mo linearly decreasing epidemic effect	epi(trend)
7	Acute effect with 12-mo linearly decreasing epidemic effect with differences by vaccination status	epi(trend)+vaccine
8	Acute effect with 12-mo linearly decreasing epidemic effect with differences by sex	epi(trend)+sex
9	Acute effect with 12-mo linearly decreasing epidemic effect with differences by age	epi(trend)+age
10	Acute effect with 12-mo linearly decreasing epidemic effect with differences by sex and age	epi(trend)+sex+age
11	Chronic epidemic effect	epi(chronic)
12	Chronic epidemic effect with differences by vaccination status	epi(chronic)+vaccine
13	Chronic epidemic effect with differences by sex	epi(chronic)+sex
14	Chronic epidemic effect with differences by age	epi(chronic)+age
15	Chronic epidemic effect with differences by sex and age	epi(chronic)+sex+age
16	Constant survival (null)	Constant
17	Survival differences by sex	Sex
18	Survival differences by age	Age
19	Survival differences by sex and age	sex+age
20	Four-mo acute epidemic effect with differences by sex and by winter season	epi(acute)+sex+winter
21	Acute effect with 12-mo linearly decreasing epidemic effect with differences by sex and by vaccination status	epi(trend)+sex+vaccine

via a modified biogrouping classification system with the use of established methods (Kilian and Frederiksen, 1981; Bisgaard and Mutters, 1986; Ward et al., 1986, 1997; Jaworski et al., 1998). We report all isolates as *Pasteurella* spp. as per the original laboratory reports, although some of these strains are now classified as *Mannheimia* spp. Virus and *Mycoplasma* spp. isolations were attempted at CSUDL and CVTC with the use of established methods (Spraker et al., 1984). For histopathology, fixed tissues were embedded in paraffin, cut into 5–6-µm sections, mounted on glass slides, and stained with hematoxylin and eosin.

Survival data analysis

To assess the effects of this pasteurellosis epidemic on the Tarryall-Kenosha bighorn population, we analyzed radiotelemetry data with the use of a ragged telemetry approach in Program MARK (White and Burnham, 1999). The ragged telemetry analysis allowed for the fact that some bighorns may not have been found dead during the month that they died because field conditions interfered with carcass recovery; this was accommodated by allowing for all possible combinations of potential months of death in the statistical likelihood, an approach mathematically analogous to the nest survival model of Dinsmore et al. (2002). We constructed explanatory models of observed mortality patterns that included an effect of the epidemic event in the years that it occurred, variation among sexes and ages (categorical 1, 2, 3, ≥4 years old), with an effect of vaccination on survival (Table 1). Variation among the three herds was included in all models. The epidemic effect was modeled to reflect three hypotheses about the form of the effect: 1) as an acute effect lasting for 4 mo (December–March) during the winter of first occurrence, with survival then returning to a "normal" level; 2) as an acute effect with a linearly increasing trend in survival that returned to normal survival after 12 mo; and 3) as a chronic effect on survival that continued until the end of the study period in 2000. We also included a null hypothesis of no effect of the epidemic on survival. The Sugarloaf Mountain herd suffered three epidemic events that were modeled separately to account for the potential differences in the repeated effect of the outbreak on the population. After arriving at the "best" model, we added an effect of winter on survival to test whether all winters or only epidemic winters were affecting survival, and we also added a vaccination effect to the top-ranked model. We used a logit link function to model survival as a function of the effects listed above, basing model selection on the minimum Akaike's information criterion (AIC) corrected for small sample size (AIC_c; Burnham and Anderson, 2002). Thirty six, 52, and 55 bighorn sheep were radiocollared in the Kenosha, Sugarloaf and Twin Eagles herds, respectively.

RESULTS

Bighorn sheep population structure and demography

An unusual pattern of mortality for bighorn sheep residing in the study area began on 2 December 1997, when a radiocollared yearling female was found dead on Sugarloaf Mountain. The carcass was necropsied at CSUDL the following day and diagnosed with "severe hemorrhagic necrotizing suppurative bronchopneumonia"; the microscopic lesions were "suggestive of bronchopneumonia due to *Pasteurella hemolytica* [sic]" (CSUDL No. 978-17470). From 8–19 December, eight more bighorn sheep carcasses (four radiocollared, one ear tagged, and three unmarked) were found dead within about 1 km of the first carcass. Two of these eight mortalities, a 3-yr-old male and a male lamb found on 18 December, were necropsied and also diagnosed with "acute fibrinous bronchopneumonia"; the other six carcasses were heavily scavenged and unsuitable for necropsy.

On 18 December, while radiotracking bighorn sheep, a field technician observed a male domestic sheep on Sugarloaf Mountain. The domestic sheep was more difficult to see on the snow-covered terrain than the darker bighorn sheep. When first observed, the domestic sheep appeared to be following the technician. However, when the technician tried to approach the domestic sheep it fled and joined a nearby group of bighorn sheep. According to his notes, "Several attempts were made by the bighorns to keep the domestic male away but it was persistent and eventually allowed to graze with them." (T. Verry, unpubl. field notes, CDOW and United States Forest Service). We made unsuccessful attempts to capture the domestic sheep and to locate its owner later that day and again on the morning of 19 December. We subsequently shot the domestic sheep on 19 December while it was still associated with a group of bighorn sheep (Fig. 1A). The carcass of the domestic sheep was transported to CSUDL for necropsy. This was the first (and only) time during our 10-yr study that a domestic sheep was found with bighorn sheep on range in the study area.

After removal of the domestic sheep, pneumonia-related bighorn mortalities continued at Sugarloaf Mountain for 3 wk, with seven additional bighorn carcasses (one radiocollared, two ear tagged, and four unmarked) found between 23 December 1997 and 13 January 1998 (Fig. 1A). Of these seven, the relatively intact carcass of a 3-yr-old female found on 23 December was transported to

CSUDL for necropsy and also was diagnosed with acute fibrinous bronchopneumonia. No additional pneumonia-related mortalities were documented between 13 January 1998 and 24 November 1998 at Sugarloaf Mountain or elsewhere in the study area.

Unusually high numbers of bighorn mortalities resumed in the Sugarloaf Mountain herd during the winter of 1998–99, and also began as predicted in the Twin Eagles and Kenosha herds (Fig. 1B). We found 13 bighorn carcasses (five radiocollared, two ear tagged, and six unmarked) on the Sugarloaf Mountain winter range between 16 December 1998 and May 1999. At Twin Eagles, we found 27 bighorn carcasses (17 radiocollared, four ear tagged, and six unmarked) and one sick unmarked female was shot, between 24 November 1998 and May 1999; seven of these were necropsied and diagnosed with multifocal to confluent necrosuppurative pneumonia. In the Kenosha Mountains, ten of 23 radiocollared bighorns (43%) died between January and May 1999, and the carcasses of two ear tagged and four unmarked bighorns also were located the same winter. Because of difficult access and greater snow accumulations in the Kenosha Mountains, no carcasses were necropsied, and four of the carcasses were not recovered until spring or summer 1999. The unusually high mortality rate continued on the Sugarloaf Mountain winter range during the winter of 1999–2000, with 13 carcasses (seven radiocollared, one ear tagged, and five unmarked) located from 22 to 30 December 1999, but subsided on the Twin Eagles and Kenosha winter ranges (Fig. 1C).

In all, we found 86 bighorn carcasses (including 45 radiocollared individuals) during the course of the epidemic. Undoubtedly there were additional mortalities of nonradioed animals that were not detected, especially in the less accessible Kenosha Mountains. The source of the domestic sheep was never determined—although we did subsequently identify a small private collection of domestic sheep about 14 km from Sugarloaf Mountain that could have been the source, we could neither confirm nor eliminate the possibility that the animal came from elsewhere.

In addition to the direct mortality associated with epidemics in these three herds, lamb recruitment in years following the pneumonia epidemic decreased. In the Kenosha Mountains, winter lamb:ewe ratios dropped from an average of 46 lambs:100 females (range 39–56 lambs:100 females) during 1992–1996 to zero lambs:100 females from 1999–2001, then improved to a 5-yr average (2002–2006) of 32 lambs:100 females (range 20–50). Similar poor lamb recruitment was qualitatively noted in the Tarryall Mountains following epidemics in the Twin Eagles and Sugarloaf Mountain herds: recruitment had been consistently high ($\geq$0.53; Miller et al., 2000) prior to the epidemic, but by 2006–2007 winter ratios were only about 23 lambs:100 females.

Although mark-resight survey methods were not applied after the epidemic to estimate bighorn population size, a standardized annual winter composition survey showed a 50% decline in the Kenosha Mountain herd after the epidemic: during the 5 yr of surveys in 1992–1996, prior to the epidemic, an average of 90 bighorn (range 79–96) were observed each year; in contrast, during the 5 yr following the epidemic (1999–2003) an average of 42 (range 39–49) bighorns were observed annually. A survey conducted in winter 2006–2007 using the same methods as previous surveys located 45 bighorns, indicating that 7 yr postepidemic this herd had not recovered to numbers observed in years prior to the epidemic. Population recovery in the Tarryall Mountains herds was comparable to recovery in the Kenosha Mountains: The numbers of bighorn classified on standardized surveys were 66 in 2003, 76 in 2004, 84 in 2005, and 64 in 2006, indicating that after 9 yr bighorn abundance was only about half of that estimated in the Tarryall Mountains before the epidemic.

Laboratory findings

Among bighorn carcasses examined either in the field or at CSUDL, gross lesions consistently included varying degrees of consolidation and adhesion of dependent lung lobes, as well as various defects consistent with scavenging in many of the cases examined. Histologic lesions of severe, hemorrhagic, necrotizing, suppurative bronchopneumonia or acute fibrinous bronchopneumonia were described in all cases from the Sugarloaf Mountain herd examined in the winter of 1997–98; in some cases, accumulations of oat-shaped macrophages were observed. Similarly, cases from the Twin Eagles herd also showed acute to subacute necrotizing, suppurative bronchopneumonia. Either gross or histologic evidence of lungworms (*Protostrongylus* spp.) were noted in some cases. The domestic sheep appeared grossly normal, and histopathology of lung tissue revealed only congestion and atelectasis, with some small areas of neutrophils or lymphoid cell infiltration.

Three species of *Pasteurella* were isolated in various combinations from affected lung tissues from pneumonic bighorns. With one exception, β-hemolytic *P.* (m.) *haemolytica* (primarily reported as biogroup 1^{G} or $1^{\alpha G}$) was isolated from lung tissues of cases evaluated during winter 1997–1998; in the exceptional case, only "very hemolytic" *Escherichia coli* was isolated from lung (and tonsil) tissue. β-hemolytic *P.* (m.) *haemolytica*, hemolytic and nonhemolytic *P. trehalosi*, *P. multocida multocida* b, nonhemolytic or β-hemolytic *E. coli*, and *Pseudomonas fluorescens* were isolated in various combinations from pneumonic bighorns sampled opportunistically throughout the epidemic; in some cases, culture results appeared to be influenced by postmortem carcass condition or delays in shipping and laboratory processing. The domestic sheep yielded various combinations of β-hemolytic *P.* (m.) *haemolytica* (reported as biogroup 3^{A}), nonhemolytic *P. trehalosi*, *Streptococcus bovis*, and *P. fluorescens* from nasal, sinus, and pharyngeal swabs and tonsil tissue, but no bacteria were isolated from lung tissue. No viruses were isolated from any of the bighorn or domestic sheep samples, but an uncharacterized *Mycoplasma* spp. was isolated from two of the seven carcasses from the Twin Eagles herd.

Epidemic effects on survival

The model that included an acute effect with a 12-mo linearly decreasing effect of the outbreak on survival and differing survival by sex was selected as the best model by AIC_c (Table 2). The AIC_c weights suggested the acute effect with a 12-mo linearly decreasing effect was 2.2× more likely than an acute effect alone (Table 2). Parameter estimates suggested a strong negative effect of the epidemic on survival ($slope=-0.18$, $SE=0.02$, Fig. 2). Survival patterns after epidemics were similar across herds, and the subsequent outbreaks on the Sugarloaf Mountain winter range were similar to the first. Males showed lower survival than females (-0.50, $SE=0.23$, Fig. 2). Models that included a long-term chronic effect on survival or no epidemic effect on survival received no support (Table 2). There was no support for winter survival differing from nonwinter months in nonepidemic years (0.464, $SE=0.37$, Table 3). There was support for a small, positive influence of vaccination on bighorn survival (0.007, $SE=0.003$, 4.39 AIC_c units smaller than the model without a vaccine effect; Table 3).

DISCUSSION

Epidemic pasteurellosis and the resulting depression in the Tarryall-Kenosha Mountains bighorn population's survival, recruitment, and size followed the appearance of a single domestic sheep on native bighorn winter range and occurred in the absence of other known or suspected

TABLE 2. A priori models, model selection results (AIC_c), model weights (w), numbers of estimated parameters (K), and deviance for the bighorn sheep radiotelemetry analysis.

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
epi(trend)+sex	785.22	0.00	0.29	6	773.20
epi(acute)+sex	786.80	1.58	0.13	6	774.79
epi(acute)+sex+age	786.99	1.77	0.12	9	768.96
epi(trend)+vaccine	787.06	1.84	0.12	6	775.05
epi(trend)	787.67	2.45	0.09	5	777.66
epi(trend)+sex+age	788.33	3.11	0.06	11	766.28
epi(trend)+age	789.44	4.23	0.04	10	769.40
epi(acute)	790.07	4.85	0.03	5	780.06
epi(acute)+vaccine	791.37	6.15	0.01	6	779.35
epi(acute)+age	792.18	6.96	0.01	10	772.13
epi(chronic)+sex	815.28	30.06	0.00	5	805.27
epi(chronic)+sex+age	819.39	34.17	0.00	10	799.34
epi(chronic)+vaccine	819.39	34.17	0.00	5	809.38
epi(chronic)	820.28	35.06	0.00	4	812.28
epi(chronic)+age	821.86	36.64	0.00	9	803.82
Sex	829.99	44.77	0.00	4	821.98
sex+age	837.00	51.78	0.00	9	818.96
Constant	838.03	52.81	0.00	3	832.02
Age	840.15	54.93	0.00	8	824.12

inciting factors, illustrating the potential consequences of contact between these species under natural conditions. Our observations provide one more replicate of epidemiologic and mortality patterns reported following association of these two species in Colorado and elsewhere for over a century (Warren, 1910; Grinnell, 1928; Shillinger, 1937; Buechner, 1960; Bear and Jones, 1973; Foreyt and Jessup,

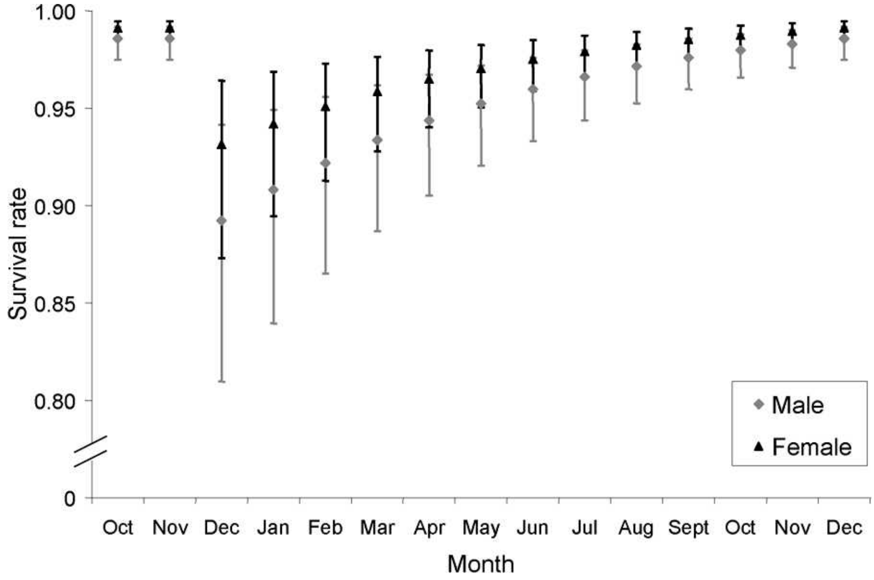

FIGURE 2. Monthly survival estimates for male (gray diamonds) and female (black triangles) bighorn sheep in the Kenosha Mountains herd from October 1998 to December 1999, showing an example of the change in survival prior to, during, and following the disease outbreak. Bars are 95% confidence intervals on point estimates of survival.

TABLE 3. Post hoc models considering additional hypotheses about bighorn sheep survival, model selection results (AIC_c), model weights (w), numbers of estimated parameters (K), and deviance for the bighorn sheep radiotelemetry analysis. The epi(trend)+sex model was the top-ranked model from the a priori analysis (Table 2).

Model	AIC_c	ΔAIC_c	w_i	K	Deviance
epi(trend)+sex+vaccine	780.82	0.00	0.87	7	766.802
epi(trend)+sex	785.22	4.39	0.10	6	773.203
epi(acute)+sex+winter	787.06	6.24	0.04	5	773.042

1982; Goodson 1982; Coggins, 1988; Brown, 1989, deVos, 1989; Beecham et al., 2007). Previous studies have consistently linked contact with domestic sheep to occurrences of pneumonia in captive bighorns (Foreyt and Jessup, 1982; Onderka and Wishart, 1988; Foreyt, 1989; Callan et al., 1991; Foreyt et al. 1994), but this phenomenon has not been produced experimentally in natural bighorn populations because intentional manipulations that likely would result in the loss of a large number of free-ranging bighorn sheep are neither politically, ethically, nor logistically feasible. Although the situation we described here was not a true experiment, the spatial and temporal relationship between epidemic onset and discovery of a domestic sheep on the affected winter range was clear (Fig. 1). Ecologic patterns that occur repeatedly—like pneumonia in bighorn sheep following association with domestic sheep—are meaningful even though they may not arise from experimentation, and such patterns should not be ignored in conservation and resource management decision making.

The mortality and subsequent depressed recruitment patterns observed during and after the 1997–2000 Tarryall-Kenosha Mountains pneumonia epidemics are similar to patterns reported by others (Coggins, 1988; Festa-Bianchet, 1988; Coggins and Matthews, 1992; Ryder et al., 1994; Cassirer et al., 1996; Enk et al., 2001). Mortality during the Tarryall-Kenosha Mountains epidemic resulted in the direct loss of at least 72 individuals, representing about 28% of the estimated population. Bighorn losses incurred during recent pneumonia epidemics reported elsewhere ranged from about 25% at Whiskey Mountain, Wyoming (Ryder et al., 1994), 35–40% at Sheep River, Alberta (Festa-Bianchet, 1988), 50–75% in Hell's Canyon, Idaho (Cassirer et al., 1996), about 67% of an Oregon herd (Coggins, 1988), to about 80% of a Montana population (Enk et al., 2001). In the Tarryall-Kenosha Mountains bighorn population and elsewhere, pneumonia epidemics tended to occur in fall and winter with index cases detected in November or early December (Coggins, 1988; Festa-Bianchet, 1988; Ryder et al., 1992; Cassirer et al., 1996; Enk et al. 2001; this study). Although epidemics depressed adult survival for <1 yr, lamb recruitment was very low for 2–3 yr following epidemics in our herds and in others (Onderka and Wishart, 1984; Festa-Bianchet, 1988; Coggins and Matthews, 1992; Ryder et al., 1994). Consequently, as of winter 2006–2007 the Tarryall-Kenosha Mountains bighorn population's estimated size remained about half of that estimated before the epidemic, similar to trends observed in other bighorn populations (Coggins and Matthews, 1992; Enk et al., 2001).

The seasonal pattern of pneumonia-associated mortalities in the Twin Eagles and Kenosha Mountains herds, as well as the recurrence of pneumonia-associated mortality in the Sugarloaf Mountain herd in the two winters following the initial epidemic, suggest that environmental and/or social conditions coinciding with or subsequent to the introduction of novel pathogens can contribute to the development of clinical pneumonia in bighorn sheep. In the Kenosha Mountains herd, exposure most likely first occurred during the summer following the initial 1997–98 epidemic in the Sugarloaf Mountain herd as males made seasonal movements and joined with males from other herds on summer range (Fig. 1); however, pneumonia-associated mortalities were not detected until December–January. Coggins (1988) reported a similar delay between suspected exposure and subsequent mortalities in the Lostine bighorn herd: There, exposure likely occurred in early October when a female domestic sheep was seen associated with three bighorn sheep (two males and one female) on summer range, but the epidemic was not detected until late November after bighorns returned to winter range and the breeding season was in progress. After observing that chronic, sporadic pneumonia-associated mortality in adult bighorns occurred in fall and early winter (October–January) in the Hells Canyon population, Cassirer and Sinclair (2007) hypothesized that "seasonal increase in disease could be due to variation in immunocompetence caused by energy availability or stressors or to seasonal behavior patterns that might facilitate pathogen transmission." Seasonal declines in immunity within individuals in late fall and winter and increased contact between individuals because of breeding behavior may explain the relatively common timing of most pneumonia epidemics in free-ranging bighorn populations, regardless of whether these epidemics arise from endemic or introduced pathogens.

Our experiences suggest that contact between bighorn sheep and domestic sheep may go undetected on native ranges. The Tarryall and Kenosha Mountains, like most bighorn ranges, include remote areas of broken terrain that have little human presence in winter. At the time of the initial epidemic at Sugarloaf Mountain, a full-time technician was living within 4 km of where bighorn mortalities occurred, and radiocollars were monitored on a regular basis. With the exception of one small band, this entire herd had remained within ~1.6 km of Sugarloaf Mountain since early November 1997, and of the seven marked bighorns that died in December, all were seen associated with one another in a group on either 5 or 13 November. Even with such intensive monitoring, given the domestic sheep's recalcitrance and the difficulty of observing it against the snow pack, we believe this animal may have been present somewhere on the Sugarloaf Mountain winter range for several weeks prior to being detected. If the same contact and mortality event had occurred outside of our study, we doubt that the epidemic would have been detected until some time after the domestic sheep had disappeared because of predation or another cause. It follows that when pneumonia epidemics occur in free-ranging native North American wild sheep it may not be possible to conclude that contact with domestic sheep did not occur, but only that contact was not detected.

Our attempted management interventions in the Tarryall-Kenosha Mountains bighorn population, including removing the domestic sheep and vaccinating a proportion of the bighorns in two herds prior to exposure and onset of epidemics, did not prevent significant mortality or poor recruitment in following years. Although the subcomponent vaccine we used had previously been shown effective under experimental conditions (Kraabel et al., 1998), a single dose of vaccine provided perhaps 8 mo or more prior to exposure appeared to confer only limited protection under field conditions. Research should continue toward developing effective vaccines or therapeutic tools, but until effective intervention or treatment protocols are available management efforts are best focused on disease prevention. Research and management efforts also should focus on long-term studies in selected free-ranging bighorn populations (e.g., Jorgenson et al., 1997; Cassirer and Sinclair, 2007). Long-term studies could provide valuable information on population dynamics in both the absence and presence of epidemics. In retrospect, either annual or biennial population estimates based on mark-resight techniques, as well as more careful estimation of recruitment in all three affected herds, would have afforded us more certainty in measuring the overall effects of this epidemic on the Tarryall-Kenosha Mountains bighorn population.

The dominant strain of *P.* (m.) *haemolytica* isolated from bighorn carcasses in December 1997 had not been isolated previously from either the Tarryall-Kenosha Mountains bighorn population or from other Colorado bighorn populations (Miller et al., 1995; Green et al., 1999), suggesting it may have been a novel pathogen introduced at the time the epidemic began. (Alternatively, some other unidentified pathogen may have been introduced.) Mannheimia *haemolytica* biogroup 1 is the most common biovariant isolated from domestic sheep, and is comparatively rare in wild sheep (Jaworski et al., 1998). Although these findings were consistent with other field evidence implicating the domestic sheep that appeared on the Sugarloaf Mountain herd winter range as the inciting cause of this epidemic, only *P.* (m.) *haemolytica* biogroup 3, a remarkably rare biovariant among domestic sheep (Jaworski et al., 1998), was isolated from the carcass of that animal. Thus, despite gathering overwhelming circumstantial epidemiologic evidence regarding the most plausible and parsimonious explanation for the origins of this epidemic, laboratory findings failed to “prove” this apparent explanation.

Our laboratory findings raise questions about interpreting data from fine-scale phenotypic strain classifications like biogrouping in field investigations of pasteurellosis epidemics in bighorn sheep. Although such approaches have been shown as useful adjuncts to studies of pasteurellosis in captive bighorn sheep (e.g., Kraabel et al., 1998), their ability to track an introduced *Pasteurella* spp. strain through the course of an epidemic under natural conditions has not been demonstrated experimentally. We identified several potential sources of bias in laboratory results arising from our field samples. With respect to recovery of isolates for characterization, we noticed that *Pasteurella* spp. strains originally isolated at CVTC and CSUDL were quite different despite temporal and spatial proximity of cases, suggesting that differences in techniques between laboratories may influence primary culture results. In addition, delays in shipping of some specimens also appeared to hamper recovery of some *Pasteurella* spp. strains. Differences in disease progression and carcass preservation may have further influenced recovery of *Pasteurella* spp. Beyond the limitations of recovery methods, the use of phenotypic strain classification data in field investigations is based on assumptions that relative strain abundance is static within hosts and that trait expressions within strains are not altered with interspecies or serial intraspecies passage; the former does not appear to be true, at least in captive bighorn sheep (Miller et al., 1997), and the latter has not been studied under natural conditions. Interpretations of phenotypic strain classification data are further confounded by observations (Kelley et al., 2007) that apparently identical biovariants can have divergent phylogenetic relationships and yet different biovariants can be quite closely related: For example, in comparing three biovariant 1 isolates (I26, I45, and I49), Kelley et al. (2007, Fig. 1) genetically identified one as a different species (*P. trehalosi*) and showed that two isolates (I30, I26) classified as biovariants 3 and 1, respectively, appeared more closely related than the three aforementioned biovariant 1 isolates. Moreover, evidence of horizontal transfer of the *lkt*A gene—the gene that encodes leukotoxin production in Pasteurellaceae—among *Pasteurella* spp. and *Mannheimia* spp. isolates from bighorn and domestic sheep (Kelley et al., 2007) suggests that endemic and introduced strains can exchange genetic material (including coding for virulence factors), thereby altering both phenotypic traits and pathogenicity and further confounding epidemiology. Based on the findings presented here and elsewhere, it follows that the failure to match *Pasteurella* spp. and *Mannheimia* spp. strains between domestic sheep and affected bighorns precisely does not necessarily preclude the involvement of domestic sheep in precipitating pasteurellosis epidemics in bighorns.

Epidemic pasteurellosis can cause widespread mortality that may hamper effective population or species management, as we observed in the Tarryall-Kenosha Mountains bighorn population and as has been observed elsewhere (Jorgenson et al., 1997; McCarty and Miller, 1998; Singer et al., 2000). In some cases the effects of epidemics are limited and/or ephemeral, and present only temporary obstacles to resource management. Overall, however, bighorn sheep abundance appears to be limited by recurrent pasteurellosis epidemics (Hobbs and Miller, 1992; Jorgenson et al., 1997; McCarty and Miller, 1998; Singer et al., 2000). The immediate impact of significant mortality exacted across all age classes during these epidemics is compounded by pneumonia and septicemia in neonatal lambs that may suppress recruitment for years afterward, thereby impairing population recovery and stability. In addition to intensive population management designed to keep some bighorn herds below perceived density-dependent epidemic thresholds, livestock grazing policies on some public lands in the western United States (Bureau of Land Management, 1992; Schommer and Woolever, 2001; Beecham et al., 2007; Western Association of Fish and Wildlife Agencies, 2007) have been modified to prevent contact between bighorn and domestic sheep in an attempt to reduce the frequency and severity of these epidemics via introduction of novel pathogenic *Pasteurella* spp. and *Mannheimia* spp. strains and other respiratory pathogens. Such segregation is not likely to prevent all pasteurellosis epidemics in bighorns, but should help reduce both the frequency and, in many cases, the severity of epidemics in free-ranging populations.

ACKNOWLEDGMENTS

Our study was supported by Federal Aid in Wildlife Restoration Project W-153-R, Colorado bighorn sheep auction and raffle funds, the Rocky Mountain Bighorn Society, the Foundation for North American Wild Sheep, the United States Forest Service and the Colorado Division of Wildlife. We thank T. Verry, J. Vayhinger, S. Roush, V. Jurgens, A. Torres, N. Howard, S. Tracey, P. Krumm, S. Berry, T. Sandmeier, J. Duran, B. Davies, M. Elkins, R. Green, M. Lamb, R. Myers, R. Zaccagnini, S. Ogilvie, G. Schoonveld, K. Green, R. Mason, S. Werner, W. Adrian, K. Larsen, L. Carpenter, and others for field assistance. We also thank T. Spraker, D. Gould, A. Ward, G. Weiser, E. Williams, and others for diagnostic assistance, D. Browne for geographic information system (GIS) assistance, and M. Schuette for revising and improving Figure 1. B. Davies, D. Walsh, F. Cassirer, and two anonymous reviewers provided valuable comments on earlier drafts of this manuscript.

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Received for publication 13 April 2007.