Ecological correlates of pneumonia epizootics in bighorn sheep herds

Ryan J. Monello, Dennis L. Murray, and E. Frances Cassirer

Abstract: Bighorn sheep (*Ovis canadensis*) populations commonly experience pneumonia outbreaks caused by *Pasteurella* spp. that result in a partial or complete dieoff. Although several factors can contribute to *Pasteurella* spp. transmission or infectivity in bighorn sheep, to date the importance of such factors in population declines has not been rigorously examined. We evaluated the relationship between pneumonia-induced dieoffs in bighorn sheep and environmental and biological factors by analyzing demographic information for 99 herds across the species' geographic range. Our analysis revealed that 88% of pneumonia-induced dieoffs occurred at or within 3 years of peak population numbers, which implies that density-dependent forces such as food shortage or stress contribute to bighorns' susceptibility to pneumonia. There were few differences in the growth rates of dieoff and non-dieoff populations, suggesting that pneumonia did not manifest itself demographically prior to an outbreak. On average, abundance of lambs was most dramatically reduced post outbreak (–66%) relative to that of either rams (–35%) or ewes (–42%). Deviations in normal precipitation and temperature regimes were not associated with the onset of pneumonia outbreaks, but herds found in proximity to domestic sheep tended to be more susceptible to dieoff. Our results suggest that bighorn sheep herds are rendered vulnerable to pneumonia principally through density-dependent factors, as well as through horizontal transmission of *Pasteurella* spp. from domestic sheep serving as reservoir hosts.

Résumé : Les populations du Mouflon d'Amérique, *Ovis canadensis*, subissent souvent des épidémies de pneumonie causées par la présence de *Pasteurella* spp. qui déciment ou éliminent complètement la population. Bien que plusieurs facteurs puissent contribuer à la transmission de *Pasteurella* spp. ou à la sensibilité des mouflons à l'infection, l'importance de ces facteurs de déclin des populations n'a jamais été examinée rigoureusement à ce jour. Nous avons évalué la relation entre la mortalité attribuable à la pneumonie chez des Mouflons d'Amérique et les facteurs environnementaux et biologiques par l'analyse des informations démographiques obtenues chez 99 troupeaux provenant de l'ensemble de l'aire de répartition géographique de l'espèce. Notre analyse a révélé que 88 % des épisodes de forte mortalité due à la pneumonie se produisent 3 ans ou moins de 3 ans après une période de densité maximale, ce qui suppose que des facteurs reliés à la densité, tels une carence alimentaire ou un stress, contribuent à la sensibilité des mouflons à l'infection. Nous avons enregistré peu de différences des taux de croissance entre les populations affectées par la mortalité et les populations non affectées, ce qui indique que la pneumonie ne se manifeste pas par des différences démographiques avant l'épidémie. En moyenne, ce sont les agneaux qui se trouvent le plus décimés après une épidémie (–66 %) comparativement aux boucs (–35 %) ou aux brebis (–42 %). Les écarts des conditions normales de précipitations et de température ne sont pas associés au déclenchement des épidémies de pneumonie, mais les troupeaux de mouflons vivant à proximité des troupeaux de moutons domestiques sont plus sensibles aux épidémies létales. Nos résultats semblent indiquer que les troupeaux de mouflons sont rendus sensibles à la pneumonie surtout par l'action de facteurs dépendants de la densité, aussi bien que par transmission horizontale de *Pasteurella* spp. à partir des troupeaux de moutons domestiques qui servent de réservoirs.

[Traduit par la Rédaction]

Introduction

Bighorn sheep (*Ovis canadensis*) populations often experience irregular fluctuations in abundance involving periods of rapid growth followed by drastic declines (Buechner 1960; Stelfox 1971; Onderka and Wishart 1984; Festa-Bianchet 1988). Recently, numbers of bighorns have remained substantially depressed throughout much of their native range, with many populations having experienced extinctions or near-extinctions followed by a failure to recover to historical levels. Efforts at restoring bighorns to their former habitat through translocation have met with equivocal success, with

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R.J. Monello[1,2] and D.L. Murray. Department of Fish and Wildlife Resources, University of Idaho, Moscow, ID 83844–1136, U.S.A.
E.F. Cassirer. Idaho Department of Fish and Game, Lewiston, ID 83501, U.S.A.

[1]Corresponding author (e-mail: Ryan_Monello@nps.gov).
[2]Present address: National Park Service, Rocky Mountain National Park, 1000 West Highway 36, Estes Park, CO 80517–8397, U.S.A.

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many translocated herds experiencing repeated episodes of decline and extinction (e.g., Berger 1990). Consequently, the sustenance of viable bighorn populations remains a perplexing and important conservation issue across much of western North America.

The recognized proximate cause of bighorn mortality during most population dieoffs is pneumonia, a disease caused by the pathogen *Pasteurella* spp., which elicits respiratory distress, lethargy, and anorexia and ultimately results in death (Rosen 1981). Partial and complete dieoffs of bighorn herds due to pneumonia-induced mortality have been documented across most of the species' range (e.g., Bailey 1986; Coggins 1988; Ryder et al. 1992; Cassirer et al. 1996; Jorgenson et al. 1997; Ward et al. 1997), with the frequency and intensity of dieoffs in the northwestern United States being particularly severe. However, it is understood that *Pasteurella* spp. infections are not always manifested in disease, and indeed bighorns may possess infections of this microorganism without showing any clinical signs (Rosen 1981; Onderka and Wishart 1988; Dunbar et al. 1990; Wild and Miller 1991). Some strains of *Pasteurella* spp. may be more likely to cause pneumonia and thus be responsible for the majority of dieoffs; infection with such strains may be initiated through direct transmission from domestic sheep (Foreyt and Jessup 1982; Goodson 1982; Callan et al. 1991). The fact that bighorns infected with apparently pathogenic strains may show no clinical signs implies that disease outbreaks may only occur under certain ecological or environmental conditions (Festa-Bianchet 1988; Ryder et al. 1992). Although bighorn conservation is clearly reliant on understanding what factors cause *Pasteurella* spp. infections to translate into pneumonia outbreaks, limited research to date has shed light on this important and complex topic (Bailey 1990; Aune et al. 1998).

For bighorns, factors predisposing individuals to pneumonia may include lungworm (*Protostrongylus* spp.) or mite (*Psoroptes ovis*) infections, malnutrition, inbreeding, harsh weather conditions, or stress associated with overcrowding (Risenhoover et al. 1988; Bailey 1990; Belden et al. 1992; Jones and Worley 1994). Each of these factors may serve to compromise bighorn immunity, and thus either facilitate the shift from benign to lethal *Pasteurella* spp. infection or else enable the establishment of virulent forms that would otherwise be controlled by the immune system. In the present study, we analyze records of bighorn population attributes obtained from herds found across the species' range, to compare the biological and environmental factors associated with populations that had experienced a dieoff induced by pneumonia versus those that had not experienced a dieoff. Because many of these factors may show considerable spatial or temporal variation in their prevalence and severity, range-wide analyses should be important in revealing their large-scale role in bighorn population dynamics. Specifically, we aimed to test the following predictions: (*i*) contact with domestic sheep is a principal mode of infection with pneumonia-causing strains of *Pasteurella* spp. and thus outbreaks occur in proximity to domestic sheep grazing areas; (*ii*) density-dependent forces (i.e., food limitation, stress, competition) predispose bighorns to pneumonia outbreaks and thus herds experience dieoffs at or near population peaks; (*iii*) inclement weather predisposes bighorns to pneumonia outbreaks and thus herds experience dieoffs during periods of abnormal temperature or precipitation.

Methods

We collected data from aerial and ground surveys of bighorn populations that had been previously monitored by wildlife-management agencies. Data were obtained from the literature or by interviewing agency personnel and gaining access to their unpublished data.[3] All records were from recent (after 1980) herd observations, with surveys consisting of annual herd size estimates and simultaneous age- and sex-ratio counts. The timing of herd surveys did differ between agencies (spring vs. fall); however, seasonal differences primarily affect lamb numbers and surveys were consistent within agencies. Because our analyses were dependent on the numerical change between years, and not the actual value, differences between independent surveys did not affect our results. We used necropsy results and conducted interviews with state and provincial biologists to confirm the specific timing and proximate cause of alleged herd dieoffs. Dieoffs attributed to pneumonia outbreaks were characterized by observations of bighorn coughing and nasal discharge (Ryder et al. 1992) and sudden population declines that could only be explained by a disease outbreak (e.g., Coggins 1988). All herds were classified into one of the following categories: (*i*) "pneumonia-induced dieoff", (*ii*) "other dieoff" (i.e., due to unknown cause, predation, drought, scabies, etc.), or (*iii*) "non-dieoff" (i.e., the herd failed to undergo any notable decline). We did not set a lower limit on the size of a dieoff because pneumonia outbreaks can cause a dieoff ranging from less than 10% to 100% of the population (e.g., Bailey 1990; Cassirer et al. 1996; Aune et al. 1998). We considered herds from the non-dieoff category as controls and used these as a basis for comparison with dieoff herds. We also used interviews with agency personnel to approximate the distance from each bighorn herd's range to the nearest domestic sheep grazing allotment, and noted the likely presence of free-ranging cattle, goats, or llamas within the area occupied by the herd.

Demographic attributes

We only included in demographic analyses herds for which at least 2 years of pre- and post-peak/dieoff data were available. Thus, 5 years was the minimum survey data requirement, though the majority of herd records included in this study had more than 10 years of data (non-dieoff = 15.82 ± 1.79 (mean ± 95% CI), pneumonia-induced dieoff = 19.33 ± 3.25, other dieoff = 14.57 ± 3.54). The majority (88%) of the herds in the pneumonia-induced-dieoff category experienced outbreaks of disease and drastic declines in population size near peak survey numbers (see Results). Thus, to compare demographic attributes of herds in the pneumonia-induced-dieoff and other-dieoff categories with those of non-dieoff herds we considered the year where peak numbers were reached to be comparable to the last survey before a dieoff. This enabled comparison of herd dynamics using a fixed point (i.e., population peak vs. 1 year pre-dieoff; year = 0) in time. Owing to the general occurrence of discrete bighorn herds and the largely "closed" nature of herd demographics (Bleich et al. 1990), we assumed that long-term changes (e.g., 5 years) in survey numbers corresponded to actual population changes (i.e., not migrations). We also assumed a negligible effect of translocations; of the 24 herds included in the

[3] A list of sources of data for bighorn sheep herds included in this study may be purchased from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Montreal Road, Ottawa, ON K1A 0S2, Canada.

pneumonia-induced-dieoff category, 1 was supplemented (+18) and 2 were reduced (–18, –72) in the year of the pneumonia outbreak.

To compare the demography of herds in the pneumonia-induced-dieoff and other-dieoff categories with that of herds in the non-dieoff category we measured the annual rate of increase of all age and sex classes, and numbers of rams per 100 ewes and lambs per 100 ewes before and after a population peak or dieoff. For each of the above metrics, we estimated change in each of these by dividing the mean of 2 years post peak or dieoff by the mean of 2 years prior to the peak or dieoff. This calculation was restricted to dieoffs where the "pre-dieoff" or "post-dieoff" years occurred within 3 years of the dieoff or peak, thereby ensuring a more precise estimate of the rate of population change.

Finite rates of increase

To examine differences among herd growth rates we calculated the average annual rate of increase (λ) for each metric before and after the herd peak or dieoff (Johnson 1996). We used interpolation to estimate missing values. For all the above analyses we used MANOVA to test for differences among the various demographic attributes. Significant results obtained using Pillai's trace statistic ($\alpha = 0.05$) were further examined using Tukey's comparisons (SAS Institute Inc. 1996).

Population growth curve analyses

We compared the individual herd growth patterns (i.e., linear, logistic, or exponential) of herds in the pneumonia-induced-dieoff and non-dieoff categories. For the pneumonia-induced-dieoff category, we fit curves to data for all herds that had at least five surveys conducted pre-dieoff (n = 20). This sample was compared with 20 randomly selected herds in the non-dieoff category with the same bighorn subspecies composition (16 Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) herds, 2 desert bighorn sheep (*O. c. nelsoni*) herds, and 2 California bighorn sheep (*O. c. californiana*) herds). Analyses included (*i*) herd growth to the point of dieoff or peak and (*ii*) the entire data set including pre- and post-dieoff/peak periods. For each herd in each category we calculated the Akaike Information Criterion (AIC) for each model fitted and selected the model for which AIC was the smallest. Curves that differed by a AIC value of more than 2 were considered significantly different (Burnham and Anderson 1998).

Weather data and analyses

We compiled monthly and annual precipitation levels for each herd found within the United States, using National Climatic Data Center regional weather data. For 12 herds we were able to determine conclusively that a pneumonia outbreak originated in the herd (i.e., pneumonia was not transmitted from a neighboring herd) and the month and year that the dieoff was initiated. We compared weather patterns for this subsample with those for a similar sample of herds in the non-dieoff category with the same subspecies composition. Herds from the non-dieoff category were selected on a subspecies rather than a regional basis because herds in the same region would likely be subject to similar weather conditions (i.e., non-independent).

We tested for annual and monthly differences in weather patterns among herd categories using the divergence (absolute value) from average (1961–1990) temperature and precipitation as our dependent variable. Annual differences were compared using 5 years of data prior to a dieoff or peak. Monthly temperature and precipitation differences were examined by comparing the month of dieoff with a "random" month for non-dieoff herds, using 12 months of data prior to the dieoff/random month. Random months assigned to herds in the non-dieoff category were the same months as those for the 12 herds included from the pneumonia-induced-dieoff category, with each month randomly assigned to each non-dieoff herd. Absolute values of divergence from average weather values were used in order to maximize the possibility of detecting abnormal weather patterns. Within the pneumonia-induced-dieoff category we noted a qualitative difference between summer or fall outbreaks (August to November) and those from winter or spring (December to April; see Results). Thus, we also tested for differences between herds that experienced dieoffs during these periods and non-dieoff herds. For the latter analysis we used actual weather values (to analyze seasonal effects) 6 months prior to the dieoff. All of the above measures were analyzed via repeated-measures ANOVA, while blocking for year or month (SAS Institute Inc. 1996).

Results

We collected data from 174 bighorn sheep herds ranging in geographical distribution from the southwestern United States to Alaska. These data included herds comprising four bighorn species/subspecies: Rocky Mountain bighorn sheep, California bighorn sheep, desert bighorn sheep, and Dall sheep (*Ovis dalli dalli*). Of these, 99 herds (57%) had at least 2 years of data prior to and post population peak or dieoff, and therefore met our minimum requirements for inclusion in the population analyses (Fig. 1). The majority of herds (61) were found to be in the non-dieoff category (i.e., controls), and consisted primarily of Rocky Mountain bighorns (46%). The majority of herds in the pneumonia-induced-dieoff category (24) also consisted mainly of Rocky Mountain bighorns (83%), while herds in the other-dieoff category consisted primarily of California bighorns (57%). No pneumonia outbreaks were reported for Dall sheep (Table 1).

Of the 24 herds in the pneumonia-induced-dieoff category, 12 (50%) experienced a pneumonia outbreak and population crash in the year of their peak survey number, and 21 (88%) did so within 3 years after their numerical peak. Peak herd sizes prior to a dieoff or peak were not significantly different among non-dieoff (198 ± 83, mean ± 95% CI), pneumonia-induced-dieoff (207 ± 77), and other-dieoff (209 ± 111) categories (ANOVA, $F_{[2,96]} = 0.015$, $P = 0.985$). Peak herd sizes for the non-dieoff category in the western United States (excluding Alaska) were smaller (162 ± 47) than those in Canada and Alaska (343 ± 417), although not significantly so (t test, $t = 0.949$, df = 11, $P = 0.182$). Herds in the pneumonia-induced-dieoff category occurred primarily in northwestern North America, including Idaho (6), Oregon (3), British Columbia (3), Utah (3), Wyoming (3), Washington (2), Montana (2), Alberta 1), and Arizona (1). The majority of herds in the non-dieoff (64%) and pneumonia-induced-dieoff (54%) categories were native, while herds in the other-dieoff category were largely reintroduced (71%). Only herds in the non-dieoff category were more likely to be native (binomial test: expected proportion of native herds = 0.50; n = 61, number of observed native herds = 43, $P = 0.041$).

There was a significant difference in distance to domestic sheep among the three herd categories (Kruskal–Wallis test, $\chi^2 = 6.271$, df = 2, $P = 0.043$). Multiple comparisons indicated that herds in the pneumonia-induced-dieoff category were located significantly closer to domestic sheep allotments than those in the non-dieoff category (24.13 ± 11.54 and 39.61 ± 8.50 km (mean ± 95% CI) for pneumonia-induced-dieoff and non-dieoff herds, respectively; Mann–Whitney U test, $P = 0.014$). Herds in both the pneumonia-

Fig. 1. Numbers and approximate locations of 99 bighorn sheep (*Ovis canadensis*) herds across western North America used in demographic analyses.

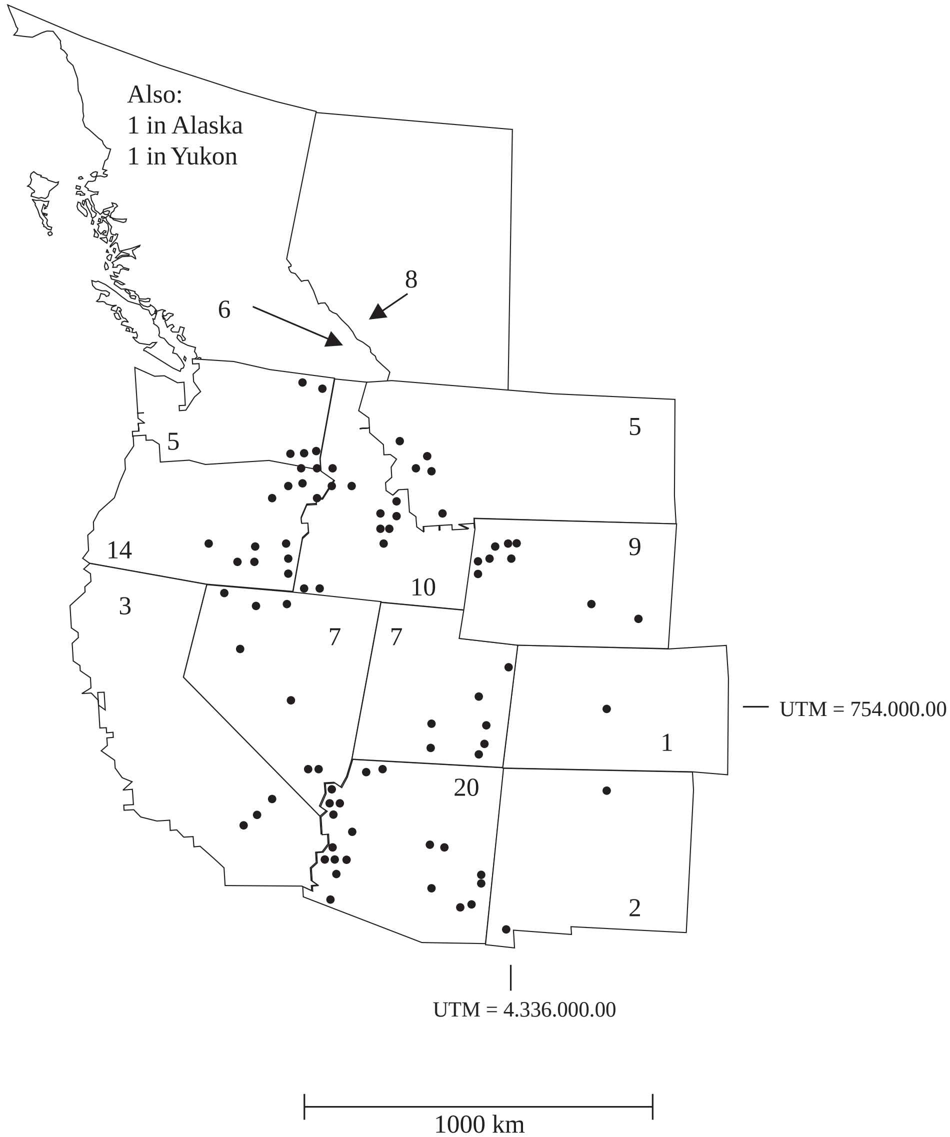


Table 1. Classification of herds according to the percentage of subspecies (Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*), desert bighorn sheep (*Ovis canadensis nelsoni*), California bighorn sheep (*Ovis canadensis californja*), and Dall sheep (*Ovis dalli dalli*)) used in the analyses.

	Non-dieoff herds (61), %	Pneumonia-induced-dieoff herds (24), %	Other-dieoff herds (14), %
Rocky Mountain bighorns	46 (28)	83 (20)	21.5 (3)
Desert bighorns	36 (22)	13 (3)	21.5 (3)
California bighorns	15 (9)	4 (1)	57 (8)
Dall sheep	3 (2)	0 (0)	0 (0)

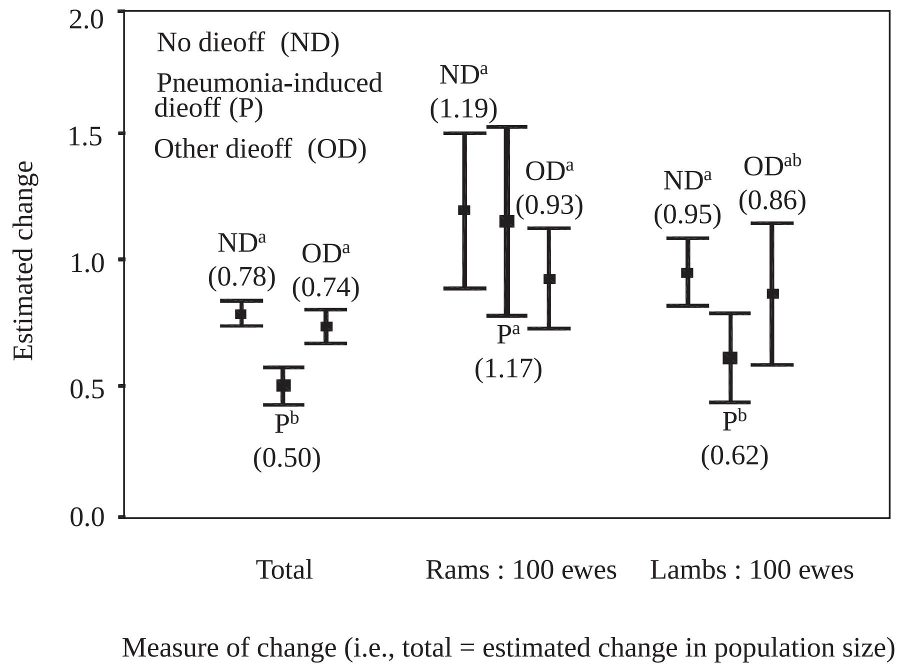
Note: Numbers in parentheses are sample sizes.

induced-dieoff and non-dieoff categories had a high incidence of co-occurrence with cattle (≥70% in all cases) and moderate overlap with goats and llamas (11–33%).

Demographic attributes

No differences were detected among the estimated rates of numerical change (MANOVA, $F_{[18,162]} = 1.811$, $P = 0.188$), annual rates of increase ($F_{[36,144]} = 0.837$, $P = 0.729$), or sex and age ratios ($F_{[12,168]} = 1.590$, $P = 0.099$) for the four subspecies in the non-dieoff category. Thus, all 99 herds were used in the ensuing analyses without consideration of subspecies status. The estimated numerical changes in demo-

Fig. 2. Estimated change (λ; average ± 95% CI) in total population size and age and sex ratios following a peak survey number (for non-dieoff herds) or dieoff (for pneumonia-induced-dieoff or other-dieoff herds). A value of 1.0 represents no change and a value above or below 1.0 represents an increase or a decrease in population size, respectively. Values in parentheses represent average rates of change following a peak number or dieoff. Different lower-case superscripts indicate significant differences (α = 0.05) using Tukey's comparisons.



graphic attributes varied among the three herd categories following a dieoff or peak (MANOVA, $F_{[12,184]} = 3.330$, $P < 0.001$). The average change in herd size was less in the non-dieoff (λ = 0.79 ± 0.05, mean ± 95% CI) and other-dieoff (λ = 0.74 ± 0.07) categories than in the pneumonia-induced-dieoff category (λ = 0.50 ± 0.08), where declines were notably greater (Tukey's comparisons, $P < 0.003$ in each case; Fig. 2). Given the differences between these categories, and the small variation within them, these data suggest that our classification of herds was correct.

Ewe numbers experienced greater reductions in the pneumonia-induced-dieoff category than in the non-dieoff and other-dieoff categories (Tukey's comparisons, $P < 0.004$ in each case), and lamb numbers were more depressed in the pneumonia-induced dieoff category than the non-dieoff category (Tukey's comparisons, $P \leq 0.001$). Within the pneumonia-induced-dieoff category there was a clear trend for annual lamb numbers to be strongly affected by a pneumonia epizootic, while rams and ewes had similar rates of change across herd types (Fig. 3). The decrease in number of lambs per 100 ewes was greater in the pneumonia-induced-dieoff category than the non-dieoff category (Tukey's comparison, $P = 0.018$; Fig. 2).

Finite rates of increase

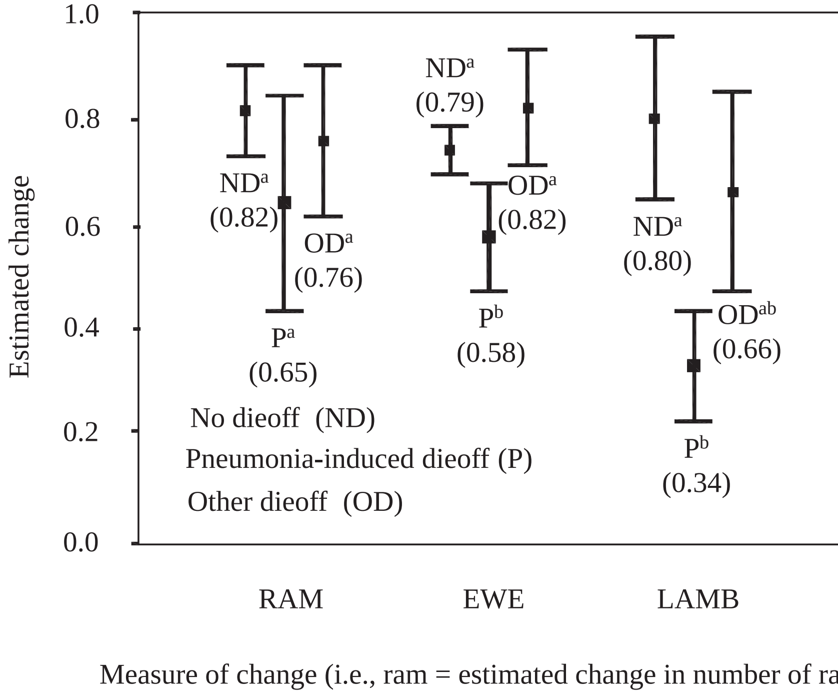
Annual rates of increase were significantly different among the three herd categories (MANOVA, $F_{[24,172]} = 1.822$, $P = 0.015$). After a dieoff or peak, rates of increase for ewes were significantly higher in the non-dieoff category than in both dieoff categories (Tukey's comparisons, $P < 0.012$ in both cases). Although they were not significantly different, our analyses revealed two distinct patterns between bighorn herds that did and did not experience a population decline. Prior to a dieoff or peak, all herd categories were found to be increasing (non-dieoff, λ = 1.44 ± 0.43 (5-year average prior to a dieoff or peak ± 95% CI); pneumonia-induced-dieoff, λ = 1.21 ± 0.15; other-dieoff, λ = 1.19 ± 0.20). Following peak numbers, herds in the non-dieoff category tended to decrease for a 1- to 2-year period and then increase at a lower rate than prior to their peak (λ = 1.05 ± 0.04 (post peak five-year average ± 95% CI)). Conversely, herds in the pneumonia-induced-dieoff and other-dieoff categories decreased for a 1- to 2-year period and did not tend to increase, owing to greater variation in their rates of increase from year to year (pneumonia-induced dieoff, λ = 1.04 ± 0.13 (post-dieoff 5-year average ± 95% CI); other dieoff = 0.97 ± 0.22).

There was a marginally significant difference in numbers of rams per 100 ewes and lambs per 100 ewes among the three herd categories (MANOVA, $F_{[8,188]} = 1.976$, $P = 0.051$). Multiple comparisons indicated that numbers of lambs per 100 ewes post peak or dieoff were higher in the non-dieoff than in the pneumonia-induced-dieoff category (Tukey's comparison, $P = 0.006$). No differences were found among the numbers of rams per 100 ewes. Although not significant, both pneumonia-induced-dieoff and other-dieoff herd categories demonstrated decreasing numbers of lambs per 100 ewes prior to the dieoff, whereas non-dieoff herds demonstrated increasing numbers of lambs per 100 ewes.

Analysis of population growth curves

There were no strong growth patterns among herds in the pneumonia-induced-dieoff and non-dieoff categories. Generally, linear growth curves were a significantly better fit for

Fig. 3. Estimated change (λ; average ± 95% CI) in individual age and sex classes following the peak survey number (for non-dieoff herds) or dieoff (for pneumonia-induced-dieoff or other- dieoff herds). A value of 1.0 represents no change and a value above or below 1.0 represents an increase or decrease in population size, respectively. Values in parentheses represent average rates of change following a peak number or dieoff. Different lower-case superscripts indicate significant differences (α = 0.05) using Tukey's comparisons.



survey data for herds in the pneumonia-induced-dieoff category (i.e., in 10 of 20 cases linear regression was a significantly better fitting model than either the logistic or exponential curve fit) and non-dieoff category (6 of 20 cases) when all years were included in the analyses. When examined to the point of dieoff or peak, the logistic curve best fit growth patterns for herds in the pneumonia-induced-dieoff category (4 of 20 cases), and a linear fit was the most common fit for non-dieoff herds (6 of 20 cases).

Analyses of temperature and precipitation

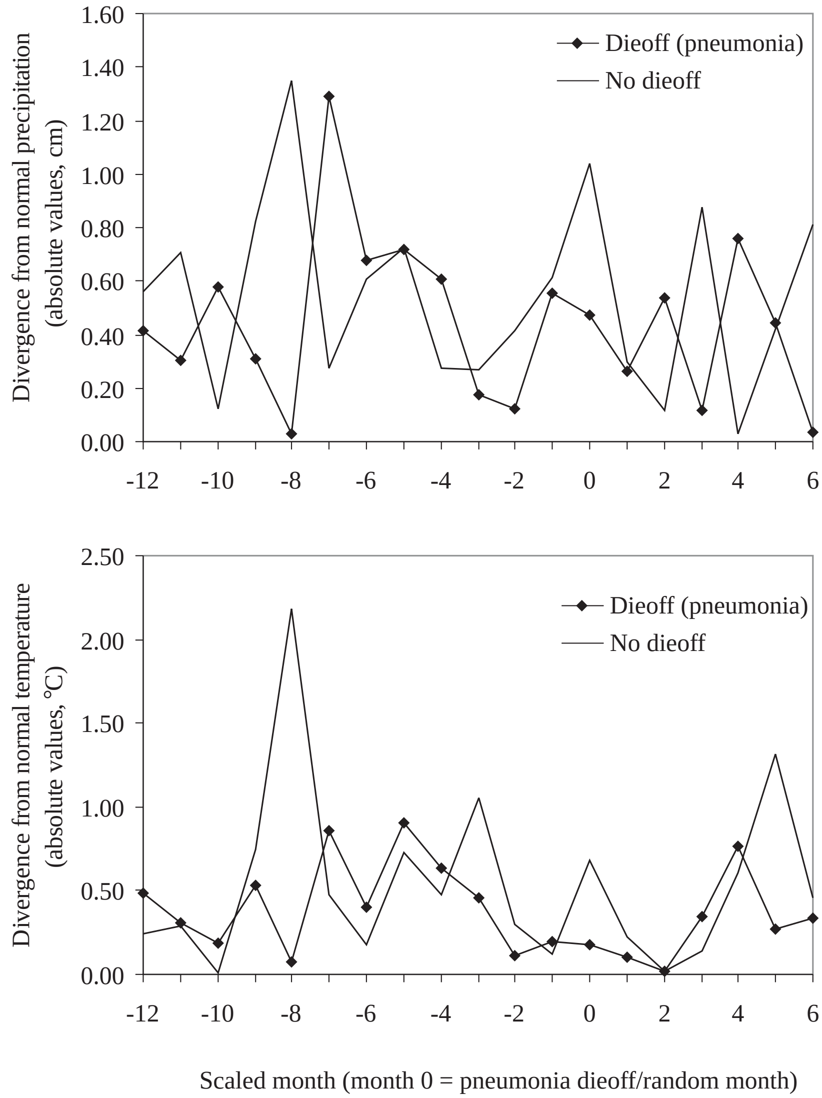
For all weather analyses, weather did not differ over time among dieoff and non-dieoff categories (time × weather interaction, $P \geq 0.161$ in all cases). Thus, only between-herd tests (ANOVA) are reported. Annual precipitation prior to and during the year of a dieoff or peak was similar for the pneumonia-induced-dieoff and non-dieoff categories (ANOVA, $F_{[1,22]} = 0.381$, $P = 0.543$). Results were characterized by large yearly deviations in precipitation 4–5 years prior to a peak or dieoff, and close to average precipitation levels during the peak or dieoff year. Annual temperature followed a similar trend, with herds in the pneumonia-induced-dieoff category experiencing less divergence than those in the non-dieoff category in the dieoff or peak year ($F_{[1,22]} = 0.297$, $P = 0.591$). Herds in the pneumonia-induced-dieoff category also experienced smaller fluctuations and less divergence from normal monthly precipitation levels ($F_{[1,22]} = 0.020$, $P = 0.889$) and temperatures ($F_{[1,22]} = 0.211$, $P = 0.650$) than herds in the non-dieoff category (Fig. 4). When pneumonia outbreaks were separated into late summer – fall (August to November, $n = 6$) and winter–spring (December to April, $n = 6$), we found that summer and fall pneumonia outbreaks occurred in years and months with lower than average precipitation and higher than average temperatures, and winter and spring outbreaks occurred in years and months with higher than average precipitation and lower than average temperatures. However, when the pneumonia-induced-dieoff and non-dieoff categories were compared seasonally, no differences were found between monthly precipitation levels (fall: $F_{[1,10]} = 0.116$, $P = 0.741$: spring: $F_{[1,10]} = 1.280$, $P = 0.284$) or temperatures (fall: $F_{[1,10]} = 0.790$, $P = 0.395$; spring: $F_{[1,10]} = 0.239$, $P = 0.636$).

Discussion

A number of factors have been proposed as contributing to pneumonia outbreaks in bighorn sheep herds, but little research has quantitatively addressed the importance of these in more than a few herds at a given time. Our results indicate that almost 90% of the pneumonia epizootics in this study occurred during or within 3 years of peak survey numbers. To our knowledge, this is the first rangewide study that has documented a widespread, common tendency for bighorn herds to die off at peak numbers. Also, herds found to be in proximity to domestic sheep grazing areas were more likely to experience pneumonia outbreaks than were those farther away. However, we failed to detect significant effects of temperature or precipitation on the timing of an outbreak. These results imply that density-dependent forces and proximity to domestic sheep both contribute importantly to pneumonia epizootics in bighorns, and these two factors may act either sequentially or in concert to promote disease outbreaks.

Declining numbers of lambs per 100 ewes prior to a dieoff further support the conclusion that pneumonia outbreaks are

Fig. 4. Monthly divergence (absolute values) from normal precipitation levels and temperatures for non-dieoff and pneumonia-induced-dieoff herds.



partially brought about by density-dependent factors, as the juvenile cohort is the most strongly affected by density-dependent processes (e.g., Woodgerd 1964; Wehausen et al. 1987; Gaillard et al. 1998). However, numbers of lambs per 100 ewes prior to a dieoff did not vary among the three herd categories. Given this, and the lack of any notable signs of constraint (i.e., herds did not grow logistically), we suggest that demographic effects of pneumonia were likely manifested suddenly, and only occurred during the period of an actual pneumonia outbreak rather than before a dieoff. This is typical of ungulates with a broad diet, such as bighorn sheep (Daily et al. 1984), which only show signs of density dependence once they reach a threshold density (Fowler 1987; Sinclair 1989; McCullough 1990). Further, although high herd numbers may play a vital role in pneumonia outbreaks, they may only act to facilitate a dieoff (directly or indirectly) under certain conditions (e.g., proximity to domestic sheep); the finding that the majority of herds in these analyses reached peak numbers but did not experience a dieoff supports this reasoning.

The principal means by which density-dependent forces may affect bighorns' susceptibility to pneumonia include inducing malnutrition or stress through food limitation, competition for mates, or emigration (Festa-Bianchet 1988). Both malnutrition and stress are known to affect animal immunity (Bundy and Golden 1987; Burkolder and Swecker 1990; Crompton 1991; Ullrey 1993; Solomons and Scott 1994), which implies that bighorns from high-density populations simply may be less capable of controlling otherwise benign infections. Elsewhere (e.g., Murray et al. 1997) it has been shown experimentally that food limitation can increase animals' susceptibility to parasitism and its effects on survival, probably through immunosuppression. As in previous individual dieoffs (e.g., Coggins 1988), we found lambs to be most susceptible to a pneumonia outbreak, with reduced lamb production continuing for at least 5 years after the dieoff. As expected, our results suggest that the immune system of lambs is compromised to a greater degree than that of ewes or rams during and following a dieoff.

Alternatively, pneumonia outbreaks may occur during population peaks because of the effects of high density on movement and dispersal. Indeed, it is plausible that bighorn herds occupy larger ranges during population peaks, and thus may be more likely to contract *Pasteurella* spp. from other bighorn herds or even from domestic sheep herds. Our finding that herds in the pneumonia-induced-dieoff category were located significantly closer to domestic sheep grazing areas than herds in the non-dieoff category supports the contention that domestic sheep are a common source of infection with lethal strains of *Pasteurella* spp. (see also Goodson 1982). Festa-Bianchet (1986) found that rams in Alberta can range over a wide area (up to 48 km), even in the presence of an abundance of ewes and the apparent absence of food limitation or excessive stress. It is likely that such distances would only increase in the presence of elevated sheep numbers (i.e., presaturation dispersal; Lidicker 1976; Krebs 1978), thereby increasing the likelihood of contact with infected individuals and transmission of disease. This hypothesis is also consistent with the observed higher rates of dispersal in rapidly increasing bighorn populations before they reach carrying capacity (Singer et al. 2000). However, it should be noted that high rates of presaturation dispersal in bighorns are not ubiquitous (e.g., Geist 1971; Jorgenson et al. 1997), which implies that probably not all pneumonia outbreaks are initiated by altered movement patterns at high densities.

Our ability to predict the onset of an epizootic on the basis of the population characteristics of herds in the pneumonia-induced-dieoff category was limited. Some herds experienced dieoffs while at relatively high numbers, while herds in the non-dieoff category also experienced similar peak numbers without succumbing to a dieoff. Furthermore, no differences were found among most of the various demographic attributes that were measured in the dieoff and non-dieoff categories. Our results agree with previous findings that age ratios are notoriously poor predictors of future population dynamics (Caughley 1974; Festa-Bianchet 1992) and thus should be used with caution. Rather, careful monitoring of bighorn populations that show increasing numbers and also are in proximity to domestic sheep may be the best indicator of the likelihood of a pneumonia outbreak.

Our results also suggest that native herds are less likely to experience pneumonia-related disease problems. In light of the varying success of bighorn sheep transplants (Risenhoover et al. 1988; Bailey 1990; Berger 1990), it is possible that these factors (reintroductions/source herd) play a role in the onset of an epizootic. However, given that reintroduced herds are almost always placed in areas from which previous sheep herds have been extirpated, it may be that areas, rather than the herds themselves, are susceptible to a lethal outbreak of pneumonia. This could be caused by a number of factors, such as proximity to domestic sheep grazing areas or less available habitat that exacerbates the effects of higher sheep numbers. The observation that dieoffs have occurred within some reintroduced herds, but not others from the same source population, supports this hypothesis. Likewise, Singer et al. (2000) suggest that continuous habitat and connectivity between other herds and (or) seasonal ranges are factors crucial to successful bighorn transplants.

The finding that Rocky Mountain and California bighorns dominated the pneumonia-induced-dieoff and other-dieoff categories, respectively, should not be taken to mean that these subspecies are more susceptible to a particular type of dieoff. Instead, we suggest that the cause is most likely the areas where these subspecies occur. Rocky Mountain bighorns may simply be located in areas that contain more domestic sheep allotments, while in desert areas, bighorns occur in areas that are more susceptible to factors such as drought (Wehausen 1992). Alternatively, differences may also be due to the directives of management agencies (e.g., the State of California did not intensively monitor sheep herds until they became a game species).

Our failure to detect differences in weather patterns between the pneumonia-induced-dieoff and non-dieoff categories may imply the absence of such effects. However, it should be noted that our small sample provided low statistical power and thus increased the likelihood of a Type II statistical error. We noted qualitatively that herds tended to die off under more extreme weather conditions. It has been suggested that harsh winter weather conditions play a role in the onset of a pneumonia epizootic (Festa-Bianchet 1988; Ryder et al. 1992), and it seems plausible that similar responses to summer weather extremes (e.g., drought) may also exist. It is likely that weather extremes could affect bighorn susceptibility to pneumonia directly by compromising immunity through food shortage or stress, or indirectly by affecting infection/transmission rates through contact with infected domestic or wild sheep, or through altered social contact.

In summary, numerous factors contribute to pneumonia epizootics and their associated dieoffs in bighorns. However, our results suggest that bighorn herds are rendered vulnerable to pneumonia principally through density-dependent factors, as well as through horizontal transmission of *Pasteurella* spp. from domestic sheep serving as reservoir hosts. Future studies should evaluate the potential link between density dependence, available habitat, and susceptibility to pneumonia and harsh weather conditions and pneumonia outbreaks.

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