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Spatio-temporal dynamics of pneumonia in bighorn sheep

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Summary

1. Bighorn sheep mortality related to pneumonia is a primary factor limiting population recovery across western North America, but management has been constrained by an incomplete understanding of the disease. We analysed patterns of pneumonia-caused mortality over 14 years in 16 interconnected bighorn sheep populations to gain insights into underlying disease processes.

2. We observed four age-structured classes of annual pneumonia mortality patterns: all-age, lamb-only, secondary all-age and adult-only. Although there was considerable variability within classes, overall they differed in persistence within and impact on populations. Years with pneumonia-induced mortality occurring simultaneously across age classes (i.e. all-age) appeared to be a consequence of pathogen invasion into a naïve population and resulted in immediate population declines. Subsequently, low recruitment due to frequent high mortality outbreaks in lambs, probably due to association with chronically infected ewes, posed a significant obstacle to population recovery. Secondary all-age events occurred in previously exposed populations when outbreaks in lambs were followed by lower rates of pneumonia-induced mortality in adults. Infrequent pneumonia events restricted to adults were usually of short duration with low mortality.

3. Acute pneumonia-induced mortality in adults was concentrated in fall and early winter around the breeding season when rams are more mobile and the sexes commingle. In contrast, mortality restricted to lambs peaked in summer when ewes and lambs were concentrated in nursery groups.

4. We detected weak synchrony in adult pneumonia between adjacent populations, but found no evidence for landscape-scale extrinsic variables as drivers of disease.

5. We demonstrate that there was a >60% probability of a disease event each year following pneumonia invasion into bighorn sheep populations. Healthy years also occurred periodically, and understanding the factors driving these apparent fade-out events may be the key to managing this disease. Our data and modelling indicate that pneumonia can have greater impacts on bighorn sheep populations than previously reported, and we present hypotheses about processes involved for testing in future investigations and management.

Key-words: bacterial pneumonia, livestock-wildlife interface, Markov model, time series

Introduction

Over the past 20 years, considerable advances have been made in understanding the spatio-temporal patterns of disease persistence and fade-out following invasion into susceptible host populations. Infections that generate

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rapid mortality such as Ebola virus, burn through susceptible populations until there are no more hosts and effectively die out (Sanchez *et al.* 2001). Infections with a strong immunizing effect, such as measles in England and Wales, persist in populations and exhibit biannual epidemic peaks that coincide with the birth and aggregation of sufficient susceptibles (Bjørnstad & Grenfell 2008). The dynamics of strong immunizing or fatal infections can leave a distinct spatio-temporal signature, although an infection that results in predictable disease in one instance, may appear almost chaotic in another setting; for example, contrast the dynamics of measles in the UK and Niger (Ferrari *et al.* 2008). Describing these spatio-temporal patterns can reveal underlying processes and this approach can be especially important in understanding infections that have recently invaded a population where the transmission routes or aetiological agents are not clear (Cleaveland *et al.* 2007). In this article, we examine the spatio-temporal dynamics of pneumonia in bighorn sheep, where the disease has been described for at least 80 years (Rush 1927), but debate continues about the identities and roles of causal agents, and disease remains an important factor limiting recovery of populations.

Bighorn sheep (*Ovis canadensis*) are social, sexually dimorphic ungulates. The species commonly occurs in spatially structured, demographically independent, interconnected populations in steep, rugged terrain. Males and females pursue different life-history strategies (Bleich *et al.* 1996; Rubin, Boyce & Caswell-Chen 2002). Interactions between the sexes are concentrated around the breeding season which is relatively short in northern latitudes and high altitudes (Bunnell 1982; Thompson & Turner 1982; Bleich, Bowyer & Wehausen 1997; Valdez & Krausman 1999). Seasonal breeding also governs contact patterns between age classes, and each year a pulse of neonates is reared in female-juvenile nursery groups. Outside the breeding season, mature males and females generally occur in male-only, female-only or female-offspring associations. Males are more mobile and more likely than females to contact conspecific hosts in adjacent populations, or potential disease reservoirs such as domestic sheep (Bleich, Bowyer & Wehausen 1997; Rubin *et al.* 1998; DeCesare & Pletscher 2006).

Pneumonia is a significant factor limiting the distribution and abundance of bighorn sheep (Gross, Singer & Moses 2000; Cassirer & Sinclair 2007; Boyce *et al.* 2011). The disease is associated with infection by directly transmitted bacteria, principally thought to be *Mycoplasma ovipneumoniae* and *Mannheimia haemolytica*, but, as is often the case with pneumonia, the precise aetiology remains unclear (Foreyt, Snipes & Kasten 1994; Besser *et al.* 2008, 2012b; Dassanayake *et al.* 2009, 2010). Initially, infection probably originates in domestic sheep, but once it has spilled over into bighorn sheep populations it is most likely maintained in the population and spread by bighorn sheep. Bighorn sheep appear highly susceptible to infection from domestic sheep: nearly all (98%) of a total of 90 bighorn sheep that were co-pastured with domestic

sheep in 11 experimental commingling studies conducted between 1979 and 2009 died of pneumonia within 100 days, while the domestic sheep remained healthy (summarized in Besser *et al.* (2012a)). Although these captive experimental results support field observations by naturalists and field biologists (Grinnell 1928; Shillenger 1937; Goodson 1982; George *et al.* 2008), they do not replicate the range of demographic variation in pneumonia events observed under natural conditions. Pneumonia described in free-ranging bighorn sheep populations includes acute die-offs with wide ranges in all-age mortality (10–90%), chronic or sporadic low levels of adult mortality, and annual or sporadic epizootics with high mortality rates restricted to juveniles from 1 to many (>20) years following all-age outbreaks (Rush 1927; Jorgenson *et al.* 1997; Aune *et al.* 1998; Enk, Picton & Williams 2001; Hnilicka *et al.* 2002). The aim of this paper was to use empirical data to describe these mortality patterns in detail and to develop hypotheses about the underlying processes involved. Indeed, a lack of data has so far constrained models of pneumonia dynamics in bighorn sheep (Hobbs & Miller 1992; Gross, Singer & Moses 2000; Clifford *et al.* 2009; Cahn *et al.* 2011). Our objective was to develop an understanding of the disease that will ultimately aid in identifying and assessing intervention options.

Materials and methods

STUDY AREA

We studied bighorn sheep in a 22 732 km² area encompassing Hells Canyon of the Snake River in the Blue Mountain and Columbia Plateau ecoregions of Idaho, Oregon and Washington (−117.875°, 46.500° to −116.250°, 44.750°, Fig. 1). Bighorn sheep occupy three climate zones within this diverse area from lowest to highest elevation: Snake River, Blue Mountains and Wallowa Mountains. The low elevation Snake River canyon is warm and dry with temperatures averaging 17.6 °C at Lewiston, ID. Average annual precipitation of 31.4 cm occurs fairly evenly year-round except during the months of July and August. The adjacent uplands including the Blue Mountains in Washington, are cooler and wetter with average temperatures of 10 °C in Pomeroy, Washington (WA) and average annual precipitation of 61 cm at Asotin, WA and 66 cm in Pomeroy. The upper elevations in the Wallowa and Seven Devils mountains receive annual precipitation of up to 205 cm, over two-thirds of which occurs as snow. Temperature averages 7 °C at the base of the Wallowa Mountains in Enterprise, OR and annual precipitation averages 76 cm. Seasonal temperature patterns in all three climate zones are similar, with highs in July and August and lows in December and January (Johnson & Simon 1987; Western 2008).

Bighorn sheep are native to Hells Canyon, but were extirpated by 1945, probably through a combination of unregulated hunting, competition with livestock for forage and diseases introduced from domestic sheep (Smith 1954; Johnson 1980; Coggins & Matthews 1996). From 1971 to 1995, wildlife agencies in Idaho, Oregon and Washington translocated a total

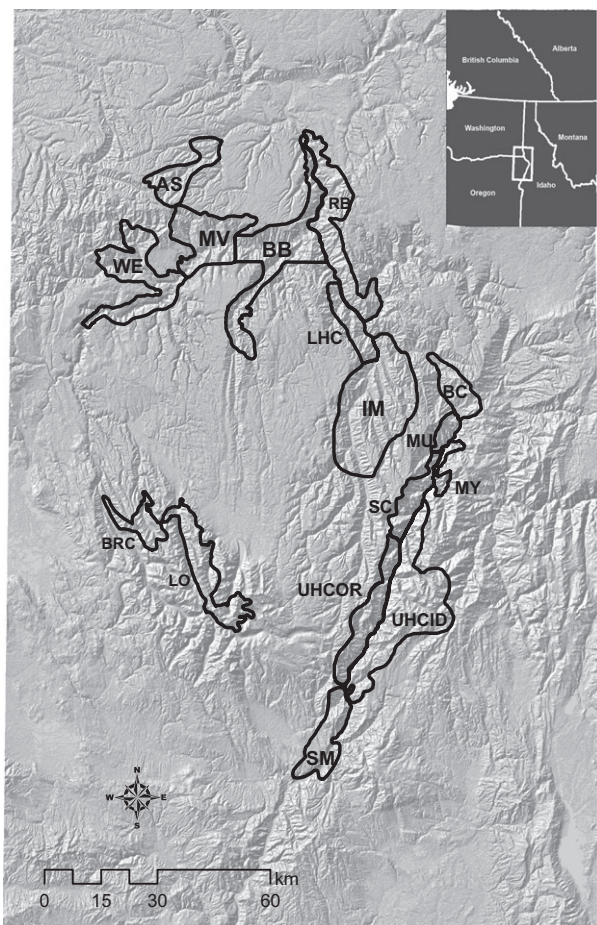


Fig. 1. Distribution of the 16 bighorn sheep populations in the Hells Canyon metapopulation, Idaho, Oregon and Washington. AS = Asotin; WE = Wenaha; BB = Black Butte; BC = Big Canyon; BRC = Bear Creek; IM = Imnaha; LHC = Lower Hells Canyon; LO = Lostine; MU = Muir; MV = Mountain View; MY = Myers Creek; RB = Redbird; SC = Upper Saddle Creek; SM = Sheep Mountain; UHCID = Upper Hells Canyon, Idaho; UHCOR = Upper Hells Canyon, Oregon.

of 329 bighorn sheep into Hells Canyon and moved 79 within the metapopulation, establishing 12 interconnected populations prior to our study (Figure S1). Another four populations were established and one population supplemented with translocations 1997–2005, during our study. Populations were delineated by movement patterns of females (Rubin *et al.* 1998). Females rarely move between populations whereas males may move seasonally or disperse among populations. Periodic pneumonia outbreaks were documented prior to this study, although monitoring was sporadic and most pneumonia events were documented following reports of sick and dying sheep. Over the same time period, domestic sheep grazing declined dramatically. However, reduced numbers of domestic sheep and goats continue to graze intermittently on public and private lands. Active management is ongoing to prevent contact between species: 22 bighorn sheep, five domestic goats and three domestic sheep were removed from areas where there was risk of contact during the study, nonetheless, some potential for disease transmission from domestic sheep and goats existed for all bighorn sheep populations throughout the study.

MONITORING

In 1995 and 1996, all-age pneumonia outbreaks occurred in five populations in the northern part of the project area (Cassirer *et al.* 1996). In 1997, we started monitoring movements and survival of radio-collared bighorn sheep in three of these populations (Redbird, Black Butte and Wenaha) as part of an unsuccessful vaccination trial to improve lamb survival (Cassirer *et al.* 2001). We collared animals in additional populations in 1998, 1999, 2000, 2006 and 2010 including animals that were translocated and, as animals left the study due to death or were censored due to radio failure, we replaced them by collaring new individuals.

State wildlife agencies have conducted periodic ground and aerial surveys since initial reintroductions in 1971. Between 1997 and 2010, annual helicopter surveys were conducted between February and April. Visibility of sheep is high (87%), as determined by detection of radio-collared animals (Idaho Fish and Game data) and population estimates were derived by combining helicopter counts with observations from ground and observations from fixed-wing monitoring of radio-collared animals. Most lambs were born in May and we conducted our population analyses on a biological year, May–April. Annual exponential rate of population increase was calculated as $r = \ln(N_t/N_{t-1})$. During this period, 735–900 bighorn sheep were estimated to occur within the metapopulation. Estimated population sizes ranged from 5 to 190, with a median of 35.

We calculated annual adult survival by sex as the proportion alive in May that survived to the following May in populations with at least five radio-collared animals. Summer lamb survival was the proportion of known offspring of radio-collared ewes that survived until October (approximately to weaning). We classified a female as having a lamb when she was observed alone with, or nursing a lamb. We assumed lambs were dead when the female was no longer associating with a lamb. We located dead lambs through visual observation. We defined recruitment as the ratio of lambs to ewes recorded in the annual February–April surveys.

We located radio-collared sheep at least bi-weekly from the ground or from fixed-wing aircraft. We located females up to several times per week during lamb-rearing to monitor productivity and lamb survival. Radiocollars were equipped with a motion-sensitive switch. When no movement was detected for 4 h, the switch was activated and we conducted an investigation on site and collected the entire carcass or tissue samples for analysis at the Washington Animal Disease and Diagnostic Laboratory (WADDL), Washington State University, Pullman. On the basis of site investigations and necropsy results, we classified causes of death as disease, predation, accident or injury, human-caused or unknown. We censored animals that died within 30 days of capture and animals translocated to Hells Canyon did not enter the study until the start of the biological year following translocation (2–4 months following release).

PATHOLOGY

We based diagnoses of pneumonia on gross and histological examination of lung tissue at WADDL. Gross features used to diagnose pneumonia included consolidation, presence of lung adhesions, abscesses, bronchiectasis or pleuritis. Affected areas of the lung were characterized by tissue colour, consistency and ability to float in formalin. Histological features of acute pneumonia included fibrin and oedema, increased presence of pulmonary macrophages, neutrophils, necrotic neutrophils,

necrosis, haemorrhage and bacterial colonies in lung tissue. Chronic pneumonia was characterized by the presence of fibrosis, abscesses or bronchiectasis. Bronchiolar epithelial hyperplasia and peribronchiolar lymphocytic infiltrates in the absence of fibrosis or abscessation was designated as subacute pneumonia. Severity (mild, moderate or severe) was based primarily on the percentage of both right and left lung fields affected on gross examination. Severity assessed by histopathology was based on the total percentage of affected tissue on individual sections of lung. Five to 15% total affected lung or tissue was considered mild, > 15–50% was moderate and > 50% was severe.

HEALTH STATUS

We used confirmed and suspected (for lambs) pneumonia-caused mortalities to characterize the seasonality, duration and intensity of four types of pneumonia events by population and year: (i) all-age pneumonia, (ii) secondary all-age pneumonia, (iii) adults only, and (iv) lambs only. We classified a population-year as healthy if animals were radiocollared in the population, but we did not detect any pneumonia in adults or detect or suspect pneumonia in lambs as described in the results.

ANALYSIS

We used Mann–Whitney's *U* test and Wilcoxon's Rank Sum (Siegel & Castellan 1988) to compare median survival rates of adults and juveniles and population growth by health class due to lack of normality in the data (Shapiro-Wilks test $P < 0.0001$). We analysed seasonal patterns in lamb survival to weaning by translocation status and climate zone with Kaplan–Meier estimates and log-rank tests (Kaplan & Meier 1958).

We fit Bayesian survival models to analyse the effect of pneumonia on the daily mortality risk from birth to 140 days in lambs. Starting at day 0 (birth), we used a piecewise-constant hazard approach where the instantaneous daily mortality hazard, $h(a)$, was assumed to be constant for each day. Daily hazard estimates were smoothed using a first order conditional autoregressive approach, $h(a) = \exp(\beta + \gamma(a))$, where β is a global intercept with an improper flat prior distribution and $\gamma(a)$ was specified using the `car.normal` function in WinBUGS assuming a $Uniform(0,10)$ hyperprior on σ , and τ , the `car.normal` precision parameter, set equal to $\frac{1}{\sigma^2}$ (Besag, York & Mollie 1991; Heisey *et al.* 2010). We used Markov chain Monte Carlo methods to generate separate posterior distributions for daily mortality hazards by health class (pneumonia or healthy). We ran three Markov chains for 100 000 iterations, discarded the first 50 000 steps, and thinned the remaining steps so that our posterior included every 10th iteration. The Markov chains readily converged (Gelman-Rubin statistic ≤ 1.13 for healthy years, and ≤ 1.02 for pneumonia-years). Further details are provided in Appendix S1.

To identify significant seasonal clustering in adult pneumonia mortalities, we fit a logistic regression model to a series of seasons. The response was a binomial equal to the proportion of adult pneumonia mortalities occurring in that season weighted by month, and the predictor was a binary season indicator for 'summer' or 'winter'. We varied the months categorized as summer by starting with the lamb-rearing months, May–August, and classifying all other months as 'winter' and systematically extended the endpoints of the summer season. We present the grouping that showed the greatest difference between seasons.

In populations where we documented pneumonia during the study (we excluded the healthy Asotin and Upper Saddle Creek populations), we used health status in the current year (a categorical predictor taking on separate values for all-age pneumonia, adult-only pneumonia, lamb-only pneumonia or healthy, with healthy as the baseline) as a predictor for future pneumonia (coded as 0 if the next year was healthy, and 1 otherwise). To test for differences among translocated and resident populations, logistic regression models were of the form, $\frac{\pi(x)}{1-\pi(x)} = e^{\alpha_i + \beta X_i}$ where e^{α_i} is the odds of pneumonia this year given last year's health status and $e^{\beta X_i}$ is the multiplicative adjustment to these odds accounting for the population's translocation status, X_i (an indicator taking on the value 0 for resident populations and 1 for translocated populations). We used Firth's bias-reduction technique for complete separation (Firth 1993) because we always observed pneumonia the year following all-age pneumonia.

We estimated annual transition probabilities between pneumonia classes for populations that had experienced epizootics by building a matrix from the frequency of transitions between classes during the study. Since the transition matrix was regular and irreducible (any state could potentially transition to any other state), we derived the stationary distribution by repeatedly multiplying the probability transition matrix by itself until row values converged (*c.* 15 iterations) (Taylor & Karlin 1998).

To assess the evidence for spatial synchrony of pneumonia, we used logistic regression to evaluate the influence of pneumonia status in neighbouring populations on a population's odds of pneumonia. We calculated centroids of 95% contours of fixed kernel home ranges of radiolocations of resident animals by population in Hawth's Tools (Beyer 2004) and ArcMap 9.3 (ESRI 2008). We defined a population's neighbours to be all populations with centroids within a designated Euclidean distance (from 10 to 70 km) of the population of interest. Pneumonia in neighbours was a categorical predictor that took on the value 1 if any neighbouring population had pneumonia in the year of interest, and 0 otherwise. We included years when pneumonia was known to be present in the neighbourhood, even if some neighbours were not sampled. We recognize that our probability of detecting pneumonia was less than 1, so we excluded data points (range from 26 to 53% of points at each distance category) where no pneumonia was detected in neighbours, but not all neighbours were sampled. Since a population's pneumonia status in year $t-1$ altered its pneumonia odds in year t , we included last year's pneumonia status in both the population of interest and the neighbouring populations as predictors in the models. To evaluate the effect of translocations, we added an indicator variable for translocated populations in the neighbourhood.

Data were analysed in the R statistical computing environment (R Development Core Team, 2008) through the `lme4` (Bates, Maechler & Dai 2008) and `logistf` (Pioner *et al.* 2006) packages. The lamb mortality hazard model was fit in WinBUGS version 1.4 (Lunn *et al.* 2000) through R version 2.13.0 using the `R2WinBUGS` package (Sturtz, Ligges & Gelman 2005).

Results

PNEUMONIA IN ADULTS

Between 1997 and 2010, 477 bighorn sheep were radiocollared (313F, 164M) in 14 populations (Fig. 1) and monitored for a total of 141 population-years (1–14 years

per population). On average, 117 radio-collared adults (range 35–146) were monitored each year, with a median of 24% (range 5–100%) of adults collared in each study population (Table S1). This included 339 resident sheep monitored for 1220 sheep-years. Another 104 sheep translocated to Hells Canyon from presumably healthy populations in British Columbia, Alberta and Montana 1997–2002, and 34 sheep that were moved within the Hells Canyon metapopulation 1999–2005 were monitored for a total of 459 sheep-years. The translocations established the Big Canyon, Muir Creek, and Myers Creek and Saddle Creek populations, and supplemented existing populations at Asotin, Upper Hells Canyon Oregon, Lostine and Bear Creek (Table S1 and Figure S1).

We determined a cause of death for 179 of 264 radio-collared bighorn sheep (94M, 170F) that died and 53 (30%) were diagnosed with bacterial pneumonia (17M, 36F). We also found 12 (8M, 4F) unmarked dead adult sheep that were diagnosed with bacterial pneumonia. Pneumonia-caused mortality of radio-collared sheep was 27% (28 of 104) of translocated animals and 7% of radio-collared resident animals (25 of 339, $\chi^2 = 28.87$, 1 d.f., $P < 0.01$).

PNEUMONIA IN LAMBS

We submitted 129 unmarked dead lambs from 14 populations for necropsy and euthanized 11 live lambs in four populations. We determined a cause of death for 104 lambs and 92 (88%) were diagnosed with pneumonia including 9 of 11 euthanized lambs (Besser *et al.* 2008). Although juveniles of all ages died from pneumonia, most mortality was prior to weaning, between 4 and 14 weeks of age (Fig. 2). We found no differences in the summer survival distribution functions of lambs in years with pneumonia among the Snake River, Blue Mountains and Wallowa Mountains climate zones ($\chi^2 = 0.1$, 2 d.f.,

$P = 0.97$) or between lambs of translocated and resident ewes ($\chi^2 = 1.5$, 1 d.f., $P = 0.23$).

Due to the difficulty of detecting freshly dead unmarked lambs in a large, relatively inaccessible and rugged landscape, we assigned a class of 'suspected pneumonia' in lambs based on (1) the distinct temporal signature of documented pneumonia-induced mortality in 37 lamb-only or secondary all-age population-years (Fig. 2); and (2) observations of clinical signs of pneumonia including lethargy, coughing, nasal discharge and discovery of intact dead lambs that were too autolysed for diagnosis. We were conservative in assigning the suspected class of pneumonia to lambs. Median summer lamb survival and recruitment (lamb : ewe ratio) were higher or did not differ in population-years with documented vs. suspected pneumonia (Fig. 3).

HISTOPATHOLOGY

Lung lesions observed at necropsy included acute fibrinous bronchopneumonia and pleuritis, sub-acute broncho-interstitial pneumonia with lymphocytic cuffing of airways and bronchiolar hyperplasia, and chronic pneumonia with fibrosis and abscessation. Acute lesions were observed in approximately half of the mortalities regardless of age class (30 of 65 adults and 33 of 66 lambs). Chronic lesions were present in about half (33) of the adult mortalities compared with about a quarter of the lambs (15). Sub-acute lesions were more common in lambs ($n = 18$, 27%) than in adults ($n = 2$, 3%).

SEASONAL PATTERNS

There was no difference between sexes in monthly patterns of pneumonia-caused adult mortality ($\chi^2 = 6.77$, d.f. = 11, $P = 0.82$). In both sexes, the odds of pneumonia-caused mortalities were almost three times higher between October and February than during the rest of the year (odds ratio 2.85, 95% CI 1.7–4.8, $P < 0.0001$). The seasonal pattern was driven by mortalities with acute lesions (odds ratio 4.29, 95% CI 1.7–10.9, $P = 0.002$). Deaths of animals with chronic lesions were more evenly distributed across seasons (odds ratio 1.9, 95% CI 1.0–4.0, $P = 0.05$). No acute pneumonia was detected in adults between May and July, the period when most (80%) pneumonia mortalities were detected in lambs. Peak pneumonia mortalities in lambs at 1–3 months of age corresponded to the period when ewes congregated in nursery groups and mortalities associated with pneumonia in adults peaked during the breeding season when mixed sex group sizes were largest (Fig. 4).

TEMPORAL AND SPATIAL PATTERNS

Pneumonia was detected or suspected in 33–77% of the study populations each year. Two populations remained healthy throughout the study: Asotin and Saddle

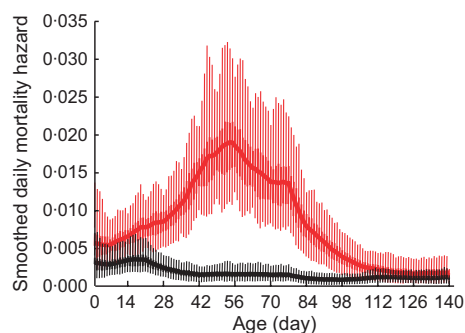


Fig. 2. Daily mortality hazard from 0 to 140 days of lambs born to radio-collared ewes in population-years where no pneumonia was documented (in black, 267 lambs) and where pneumonia was diagnosed (in red, 262 lambs). Solid line is the smoothed daily hazard, dark and light bars represent 50% and 95% credible intervals from a conditional autoregressive model. The 95% credible intervals for lamb hazards in pneumonia and healthy population-years did not overlap between the ages of 27 and 101 days.

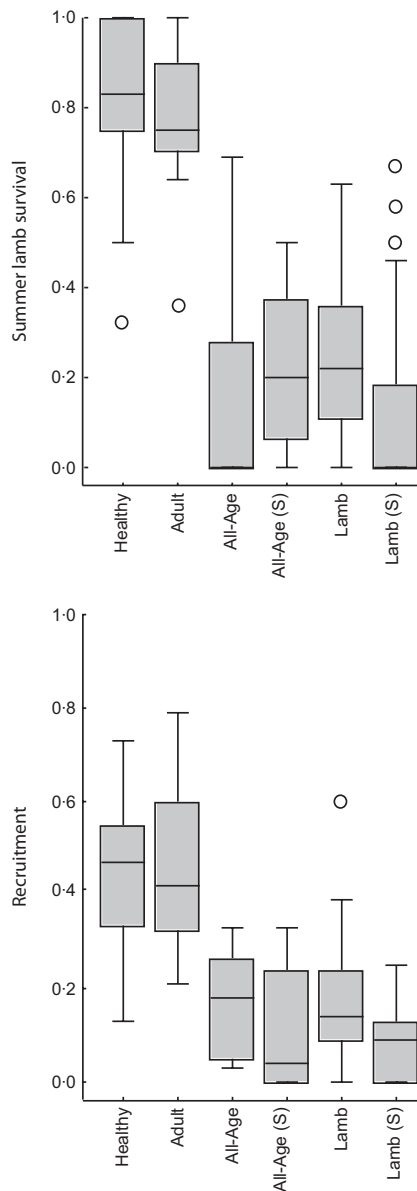


Fig. 3. Summer lamb survival and recruitment in healthy, adult-only, all-age and lamb pneumonia-years vs. suspected all-age or lamb pneumonia-years. The horizontal line denotes the median, the box encloses 50% of the observations and the whiskers show the 2.5th and 97.5th percentiles. Median summer lamb survival and recruitment did not differ significantly between all-age pneumonia population-years when pneumonia was detected in both adults and lambs and population-years when pneumonia was detected in adults and suspected in lambs ($W \leq 48$, $P > 0.10$).

Creek (Fig. 5). Survival and population growth patterns differed significantly among age-structured health classes, indicating that pneumonia was a dominant and additive source of mortality (Table 1).

Pneumonia restricted to lambs (lamb-only) was the most frequent class of pneumonia observed, and populations usually remained stable (Table 1). Pneumonia in both adults and lambs simultaneously (all-age) occurred in translocated populations in biological years 2000, 2002

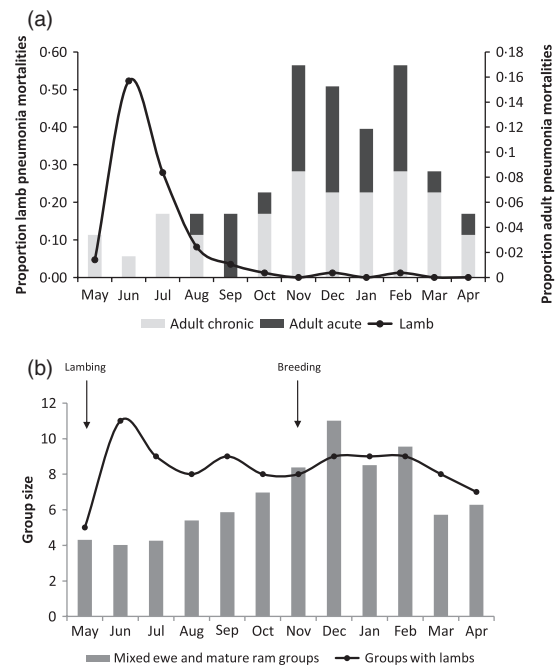


Fig. 4. Seasonal patterns of pneumonia and life-history events. (a) Monthly distribution of pneumonia mortalities detected in adults and lambs. (b) Median group sizes of groups with lambs and ewe-mature ram groups by month.

and 2003. This accounted for 68% (19 of 28) of the pneumonia mortalities in translocated animals and resulted in immediate population declines. Secondary all-age pneumonia events occurred in both resident and translocated sheep in populations that had previously experienced all-age outbreaks. These events were characterized by summer pneumonia outbreaks in lambs followed by lower rates of pneumonia-induced mortality in adults. Pneumonia in adults only was an infrequent, usually low mortality event (Table 1).

We observed high survival and stable to increasing populations in population-years classified as healthy, even in populations with a previous history of pneumonia. However, once pneumonia invaded a population, healthy periods were usually of short duration (median 1 year, range 1–3 years, Table 1, Fig. 5).

Median Euclidian distance between population centroids was 67 km with a range from 1 (populations separated by the Snake River) to 156 km (Fig. 5). We detected no significant differences in probability of pneumonia relative to distance to neighbouring populations with pneumonia. There was a slight, but insignificant increase in probability of adult or all-age pneumonia-years in populations centred 20 km or less apart ($\beta_{\text{NeighbourPN}} = 0.97$, $SE = 0.76$, $P = 0.20$) and no spatial correlation of pneumonia in lambs (Figure S2). Adding a 1-year lag or an indicator for the presence of translocated populations in the neighbourhood did not alter this result ($P > 0.32$).

We found a significant predictive effect of current pneumonia class on health status of the population the follow-

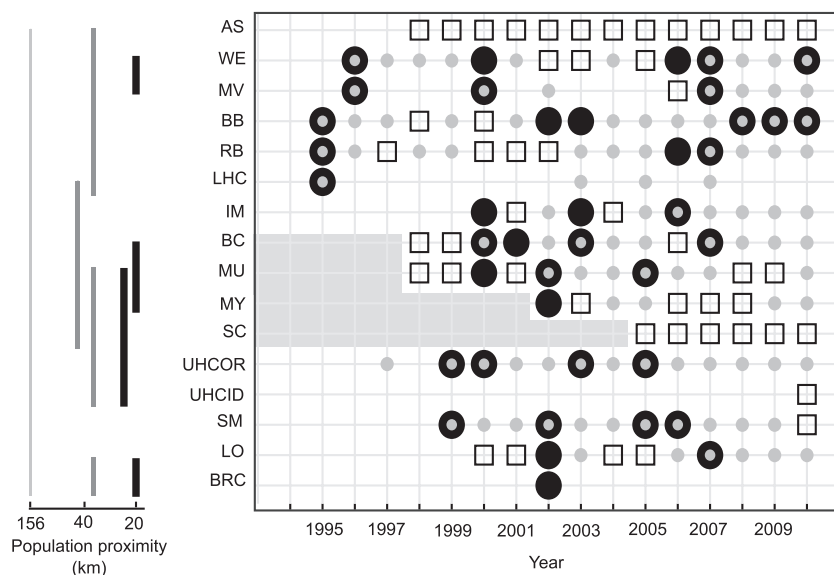


Fig. 5. Fourteen year time series of pneumonia classes in 16 populations in the Hells Canyon bighorn sheep metapopulation 1995–2010. Black circles represent documented pneumonia in adults, small grey dots represent documented or suspected pneumonia in lambs, open squares indicate no pneumonia detected or suspected. White background with no symbols indicates no data. Grey background indicates years prior to establishment of population through translocation. Vertical lines to the left of the plot connect population centroids at three distance scales. All population centroids were within 156 km or less. AS = Asotin; WE = Wenaha; MV = Mountain View; BB = Black Butte; RB = Redbird; LHC = Lower Hells Canyon, Oregon; IM = Imnaha; BC = Big Canyon; MU = Muir; MY = Myers Creek; SC = Upper Saddle Creek; UHCOR = Upper Hells Canyon, Oregon; UHCID = Upper Hells Canyon, Idaho; SM = Sheep Mountain; LO = Lostine; BRC = Bear Creek.

ing year. Continued pneumonia, usually in lambs, was most likely following all-age and secondary all-age (98%) or lamb-only pneumonia-years (83%). The probability of a pneumonia-year following adult-only and healthy years was similar (63% and 62%, respectively, $P = 0.98$), and pneumonia was significantly less likely after healthy years than all-age or lamb pneumonia-years ($P \leq 0.05$, Table 2).

We used the observed frequency of transitions between health classes to develop a transition matrix (Table 2) with Markov properties: there were a finite number of health classes (or states), health class in the current year was dependent on health in the previous year, and any health class could transition to any other health class. Thus, we could predict the stationary distribution of health classes. Assuming transition probabilities among health classes remain constant, pneumonia is predicted in 81% of populations annually: lamb-only pneumonia 57%, all-age and secondary all-age pneumonia combined 17%, adult-only pneumonia 7%. To further illustrate the dynamics of pneumonia-induced mortality, we combined the stationary distribution with mortality and transition rates (Tables 1 and 2) for a visual representation of the impact of disease over time (Fig 6).

Discussion

Analysis of a 14-year time series of pneumonia in 16 interconnected bighorn sheep populations revealed that

age-structured classes of pneumonia and healthy years had markedly different demographic impacts on populations. All-age pneumonia was consistently associated with population declines, but ultimately, lambs carried the greatest burden of disease. Rates of pneumonia-induced mortality in lambs can vary significantly by population and year, but on average, pneumonia in lambs had an even greater impact than previously reported (Clifford *et al.* 2009; Cahn *et al.* 2011). Recurring annual pneumonia epizootics in lambs may pose the greatest threat to population recovery, and when accompanied by high adult survival, the true consequences of disease may not be realized until senescent adults die and are not replaced.

While pathogen invasion, reinvasion, persistence and fade-out can't be confirmed in the absence of known disease agents, we can evaluate evidence for these processes to develop hypotheses for future investigation. High initial all-age mortality, when compared with subsequent adult mortality in translocated and resident populations is consistent with invasion of pathogens into groups of apparently naïve individuals. Pneumonia in lambs after all-age events must be due to infection from carrier ewes as lambs have little contact with other potential sources of pathogens prior to weaning (Festa-Bianchet 1991; Bleich, Bowyer & Wehausen 1997). Lamb pneumonia outbreaks have also been described in captivity with similar conclusions (Foreyt 1990; Ward *et al.* 1992; Cassirer *et al.* 2001). Pneumonia in lambs is thus a good indication of

Table 1. Demographic characteristics of health classes in 14 Hells Canyon bighorn sheep populations, 1997–2010. Data reported as median (range). Years where no adults were radiocollared were excluded from analyses

Outbreak class	<i>n</i>	<i>n</i> pneumonia cases confirmed	Consecutive years	Population growth (<i>r</i>)	Ewe survival ^{a†}	Ram survival ^{a†}	Summer lamb survival	Spring lamb:ewe ratio
All-age	3	28 Adult	1 (1, 1)	-0.34 (-0.42, -0.28)	0.50 (0.29, 0.57)	NA	0.71 (0.29, 0.88)	0.13 (0.06, 0.17)
Secondary all-age	16	(20 Adult, 27 Lamb)	1 (1, 1)	0 (-0.17, 0.03)	0.82 (0.60, 1)	0.75 (0.67, 1)	0.10 ^b (0, 0.69)	0.05 ^b
Adult only	11	14	1 (1, 2)	0.03 (-0.17, 0.16)	0.83 (0.67, 1)	0.74 (0.67, 0.83)	0.75 (0.36, 1)	0.42 (0.21, 0.79)
Lamb only	62	65	2 (1, 4)	0 (-0.69, 0.22)	0.93 (0.56, 1)	0.83 (0.60, 1)	0.20 ^b (0, 0.67)	0.14 ^b (0, 0.60)
Healthy	49	0	1 (1, 13)	0.12 (-0.03, 0.37)	0.93 (0.71, 1)	0.90 (0.71, 1)	0.83 (0.33, 1)	0.47 (0.13, 0.73)

^aSurvival of radio-collared ewes and rams in years where *n* = 5 or more.

[†]Survival in years with documented pneumonia in lambs (*n* = 8 secondary all-age, *n* = 33 lamb-only).

infection and pathogen shedding in ewes. The absence of pneumonia-induced mortality or clear symptoms in these ewes during outbreaks in lambs confirms that they have either developed resistance or perhaps tolerance of the pathogen(s) that are lethal to their offspring (Råberg, Graham & Read 2009). Reasons for more frequent fade-out following years with pneumonia restricted to adults remains unclear, but could be explained by differences in pathogens, host immunity or transmission rates.

Our study confirms previously reported accounts of seasonality of pneumonia deaths in bighorn sheep, a pattern commonly observed in infectious diseases of humans and wildlife (Spraker *et al.* 1984; Aune *et al.* 1998; Enk, Picton & Williams 2001; Altizer *et al.* 2006; Cassirer & Sinclair 2007). Age-specific seasonal patterns in pneumonia mortality corresponded to breeding and lamb-rearing: life-history events that are accompanied by especially intensive and concentrated social interactions. The distinct seasonality of adult pneumonia mortality observed in wild populations is not observed in captive experimental bighorn and domestic sheep commingling trials where bighorn sheep die of pneumonia regardless of season. Seasonal physiological or environmental factors are therefore probably less important in precipitating pneumonia epizootics than the timing of pathogen introduction, pathogen virulence and exposure to infections (contact rates). The lack of synchrony of disease events across populations and the absence of an effect of climate on lamb survival during pneumonia-years also suggest that weather or other landscape-scale extrinsic variables (Grenfell *et al.* 1998; Cattadori, Haydon & Hudson 2005), are unlikely to be important drivers of pneumonia in Hells Canyon.

In lambs, most pneumonia-induced mortality occurred between 1 and 3 months of age, a period that coincided with aggregation in nursery groups. Lamb-to-lamb contact may be an important route of infection as happens in many directly transmitted human 'childhood diseases'; thus, the synchrony in parturition and subsequent concentration of ewes during lamb-rearing which is typical in northern latitudes, could contribute to the timing and high rates of mortality. This period also coincides with the age when passively acquired immunity is probably waning in lambs (Rajala & Castrén 1995), which would further promote transmission and mortality.

By analysing long-term monitoring data to elucidate disease processes from patterns of mortality, we have diverged from studies of bighorn sheep pneumonia that focus on identifying the primary causal agent. The benefits of such a study were that we were able to examine demographic patterns at comparatively large spatial and temporal scales, allowing us to make inferences about processes such as disease introduction, persistence and fade-out. However, the weakness in our approach is an inability to track a known pathogen and directly measure transmission (i.e. infection may occur long before mortality); no opportunity to verify pathogen absence during healthy years;

Table 2. Temporal pattern of pneumonia within affected populations: annual probabilities of transition among health states and annual probability of any pneumonia. Populations that remained healthy throughout the study, population-years before the initial observation of pneumonia, and years where no adults were radiocollared were excluded from analyses (Fig. 5 and Table S2)

Initial state	<i>n</i>	Transition state				Probability of any pneumonia following initial state (95% CI; <i>P</i> -value relative to healthy state)
		All-age ^a	Healthy	Adult	Lamb	
Healthy	24	0.13	0.33	0.08	0.46	0.62 (0.4, 0.8)
All-age ^a	17	0.18	0.00	0.06	0.72	0.97 (0.8, 1; <i>P</i> < 0.01)
Adult	11	0.18	0.36	0.09	0.36	0.63 (0.3, 0.9; <i>P</i> = 0.98)
Lamb	54	0.15	0.19	0.07	0.59	0.82 (0.6, 0.9; <i>P</i> = 0.05)

^aAll-age and secondary all-age classes combined.

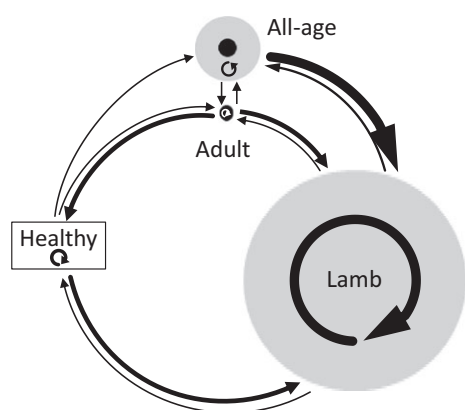


Fig. 6. Long-term patterns of pneumonia mortality in bighorn sheep populations experiencing epizootics, Hells Canyon 1997–2010. Stationary distribution of four age-structured population health classes (all-age includes secondary all-age) and the probabilities of staying within a class or transitioning out. Pneumonia classes are circles scaled by relative frequency multiplied by median death rates of ewes (black) and/or lambs (grey) in the class. The healthy class is not scaled. The thickness of arrows between classes is proportional to transition probabilities (Table 2).

and no possibility to monitor genetic variation in the pathogen over time. Given these limitations, as well as the usual constraints of marking and monitoring animals in the field, a primary concern is an imperfect detection probability for pneumonia, which could lead to overestimating healthy population-years. However, the likelihood of detecting pneumonia was not correlated with the intensity of monitoring as measured by the proportion of the population that was radiocollared (median in suspected and detected pneumonia-years = 0.22; in healthy years = 0.28, $U = 3331.5$, 1 d.f., $P = 0.09$, Tables S1 and S2), or the frequency of locations (median locations per animal per year in suspected and detected pneumonia-years = 30; in healthy years = 32; $U = 2427.5$, 1 d.f., $P = 0.45$). Therefore, there was no bias towards monitoring populations with pneumonia and, despite potentially misclassifying some lower mortality pneumonia events, we still detected significant differences in population dynamics between several different classes of pneumonia and healthy years. Survival and population growth were also similar in years

classified as healthy in populations with and without a history of pneumonia, suggesting that healthy years, with true absence of disease-related mortality (but not necessarily true absence of infection), did occur, even in populations with previous pneumonia, and these classifications are useful and appropriate for describing the system.

Our observations concur with many of the results of previous studies, but also raise questions about disease models that assume all-age pneumonia outbreaks followed by lamb mortality at a constant or declining rate for a period of usually 1–6 years (Gross, Singer & Moses 2000; Clifford *et al.* 2009; Cahn *et al.* 2011). We observed that pneumonia persisted within populations (or was periodically reintroduced) consistently longer than previous models have assumed, and, as indicated by the Markov model stationary frequency distribution, continued to affect all-age classes, not just lambs. The consequence is that all-age pneumonia events can result in sporadic or chronic, long-term reduction of survival of both adult and juvenile age classes. The disparity between our findings and previous studies may be due to the greater sampling intensity, duration and spatial scale of our study. Furthermore, whereas initial invasion associated with high rates of mortality is fairly easy to detect, the end of an epizootic is not always clear. Previously published models assume that low mortality or healthy years represent the pathogen extinction and the end of the epizootic. However, if disease in a long-lived animal like bighorn sheep is accompanied by latent periods and low rates of mortality in chronically infected animals, absence of mortality may not reflect absence of pathogens. Long-term dynamics could be a function of changes in immune status in individuals and include stochastic events common to small populations, such as dispersal, colonization, recruitment, death, intermittent pathogen shedding or lambing status of asymptomatic carriers.

By analysing long-term patterns, we have generated hypotheses about the disease processes associated with pneumonia epizootics in bighorn sheep. As with other diseases with high levels of heterogeneity, these processes are probably affected by a number of factors, including previous exposure of hosts, pathogen dose or virulence, and spatial structuring and contact rates in host popula-

tions (Grassly & Fraser 2008; Salkeld *et al.* 2010; Wendland *et al.* 2010; Jesse & Heesterbeek 2011). On the basis of the patterns we observed, the disease appears to be an infection that, in some ways is similar to measles and other immunizing diseases in humans in that it spreads through all-age classes during invasion, but subsequently mainly affects susceptible juveniles. However, in contrast with measles, pathogens apparently persist, occasionally causing fatal pneumonia in previously exposed adults, and the variable lung lesions and associated bacteriology suggest a polymicrobial aetiology, thus secondary pathogens may play a role in severity and recurrence (Besser *et al.* 2012b). The course of the disease may also be affected by the timing of pathogen invasions relative to contact rates associated with seasonal breeding and parturition. The importance of between-population transmission and recurrent infection from domestic sheep deserves additional investigation as do the conditions that lead to disease and pathogen fade-out.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Lamb mortality hazard analysis.

Figure S1. Demographic histories of Hells Canyon bighorn sheep populations.

Figure S2. Spatial synchrony of pneumonia-years across populations.

Table S1. Number and proportion of adult bighorn sheep radio-collared in each population by year and translocation status.

Table S2. Health classification of population-years (141) used to estimate demographic characteristics and transition probabilities of pneumonia and healthy years in Hells Canyon, 1997–2010.

Appendix S1. Lamb mortality hazard analysis

We estimated the daily mortality hazard for lambs, H_a , where a is the age of each lamb in days. We used age as the baseline hazard but our results would be very similar using the day of the year as the baseline because birthdates are highly seasonal, with 95% of all births occurring within a 16-day window. The cumulative baseline hazard, $H(a)$ is:

$$H(a) = \sum_{s=1}^a \exp(\beta + y(s))$$

where β is a global intercept, and $y(s)$ is the hazard adjustment for individuals of age s . The daily hazard, $h(a)$, which is the primary inferential focus of this analysis referred to in the manuscript, is the above expression evaluated at a single value of s . This model draws inference about the hazard at a given point in time, t , by using information from both t and the two adjacent time points, $A=\{t-1, t+1\}$, which comprise t 's neighborhood:

$$y_t | y_A \sim N\left(\frac{1}{2} \sum_{j \in A} \beta_j, \frac{\sigma_s^2}{2}\right)$$

The smoothing is integrated into the model through WinBUGS' `car.normal` function. This function relies on a precision parameter, τ , which is calculated as $\frac{1}{\sigma^2}$, where σ is given a $U(0,10)$ hyperprior. We used MCMC techniques to create posterior distributions of daily mortality hazards for healthy and pneumonia years. Three chains were run for each scenario (pneumonia and healthy). Each chain ran for 50000 steps, following a 50000 step burn-in. We estimated the difference in daily mortality hazards between pneumonia and healthy years by subtracting the posterior daily mortality hazard associated with step i of healthy-year chain j from the posterior daily mortality hazard of the step i in pneumonia-year chain j .

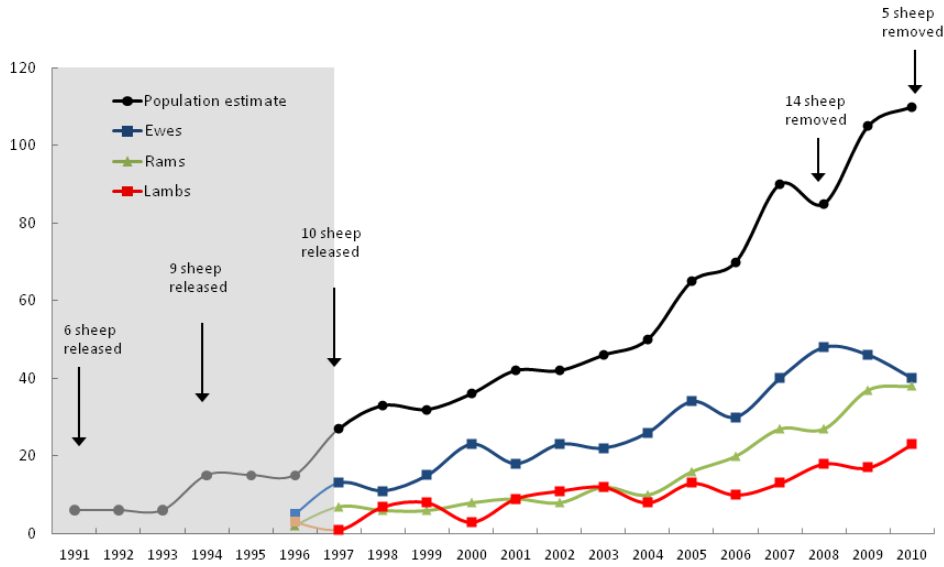
Priors and assignment procedures for all parameters in the intrinsic conditional autoregressive model

Model characteristic	Parameter	Prior Distribution	Implementation
Grand intercept hazard	β	Improper uniform	<code>dflat()</code>
Unconditional temporal random effects	σ	Uniform	<code>dunif(0,10)</code>
Temporal random effects conditioned on temporal neighborhood	ρ	Intrinsic conditional autoregressive dependent on hazard in neighborhood	<code>car.normal</code>

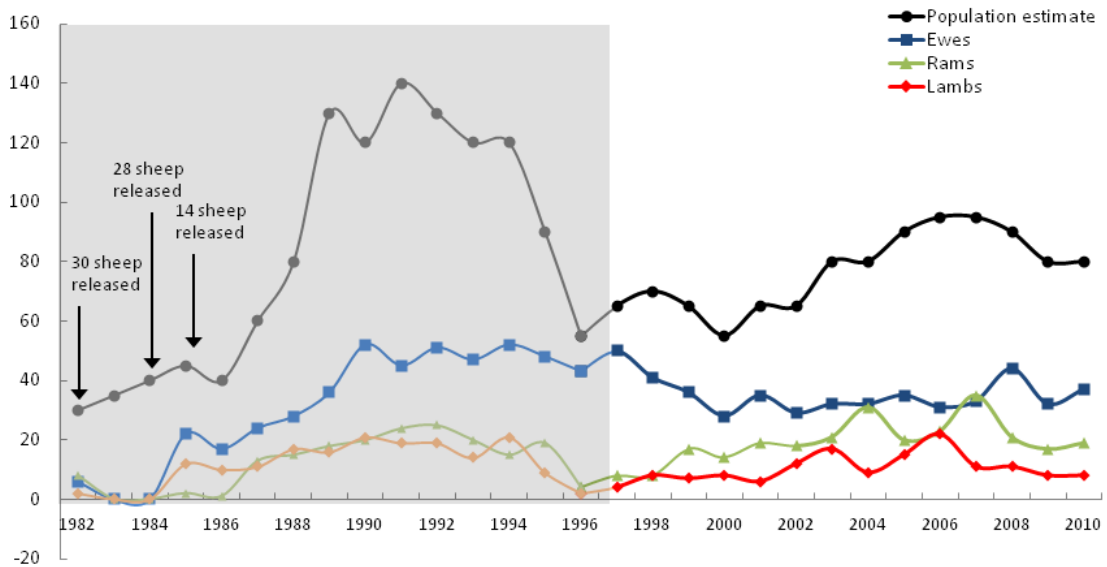
Precision parameter for the ICAR prior	τ	----	$\frac{1}{\sigma^2}$
Instantaneous daily hazard	$h(a)$	----	$Exp(\beta + y(a))$

Figure S1. Population dynamics and translocation histories of 16 Hells Canyon bighorn sheep populations, 1971 – 2010. Radio-collared sheep were monitored during periods without shading.

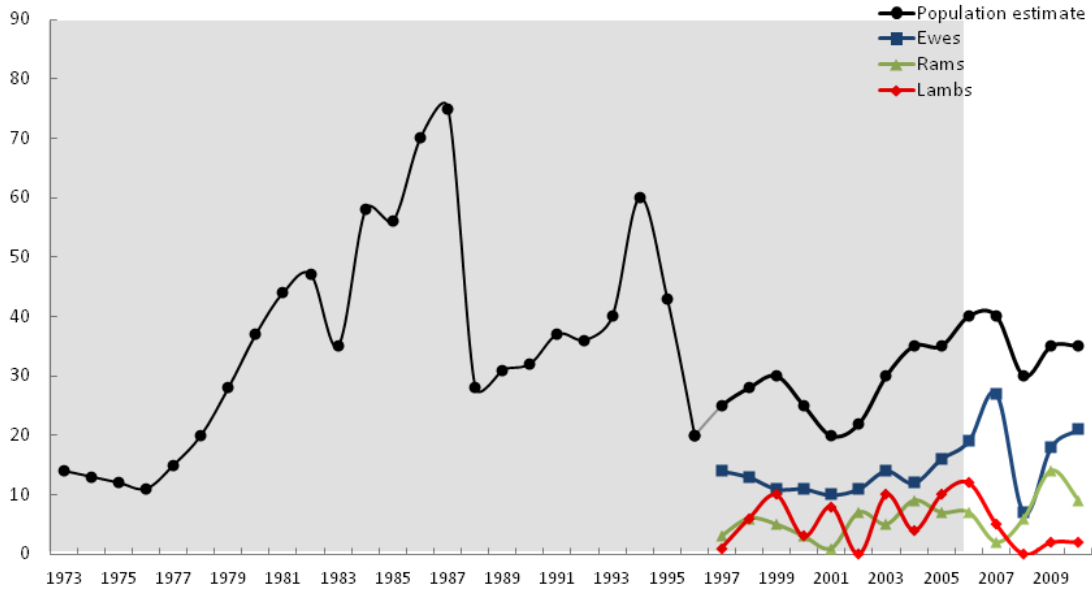
Asotin



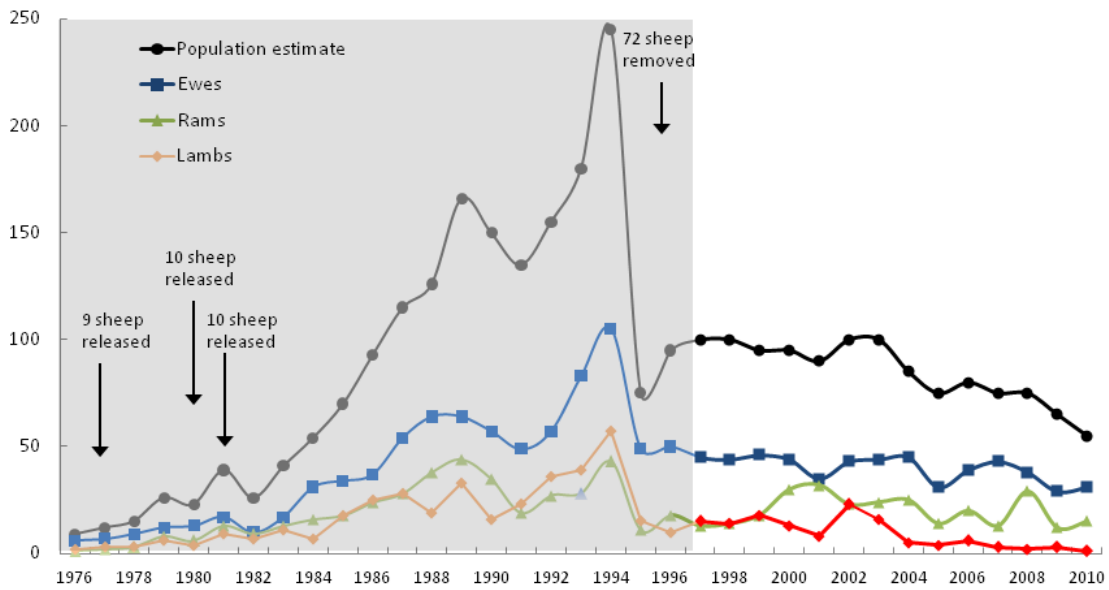
Wenaha



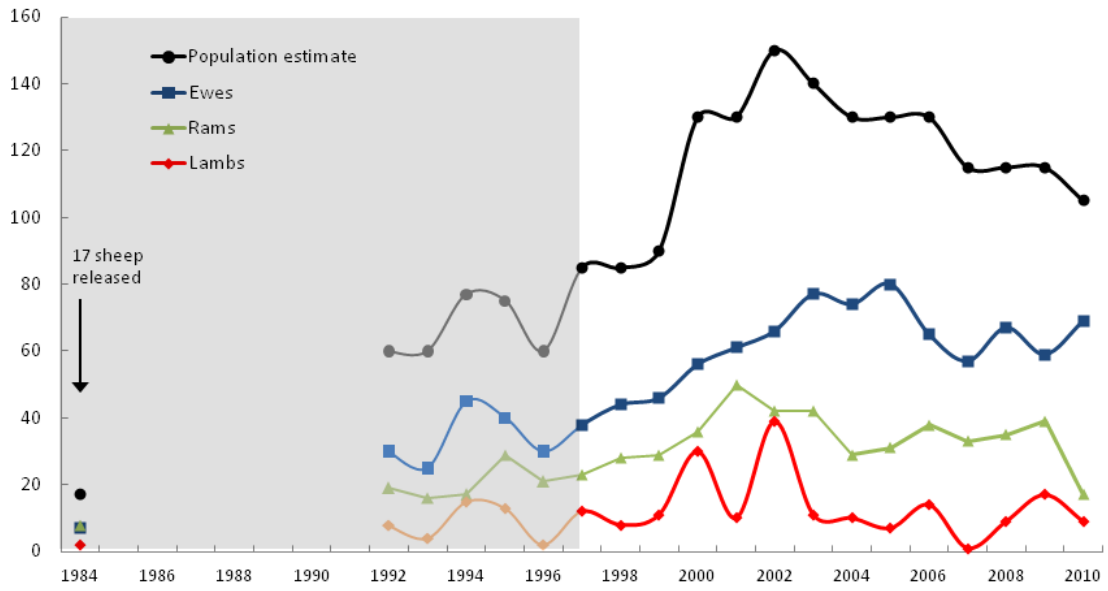
Mountain View



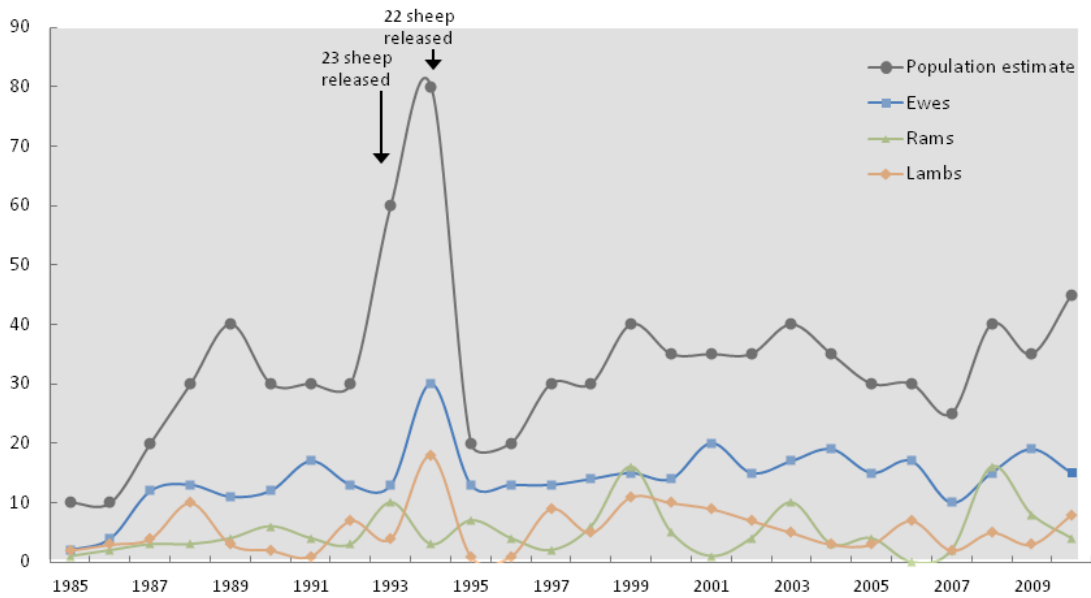
Black Butte



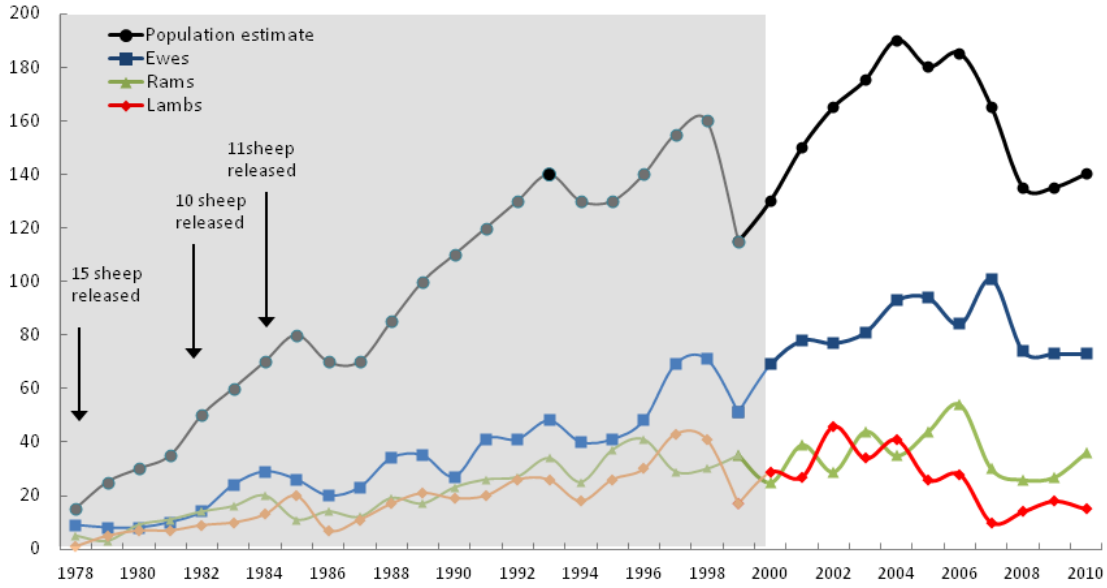
Redbird



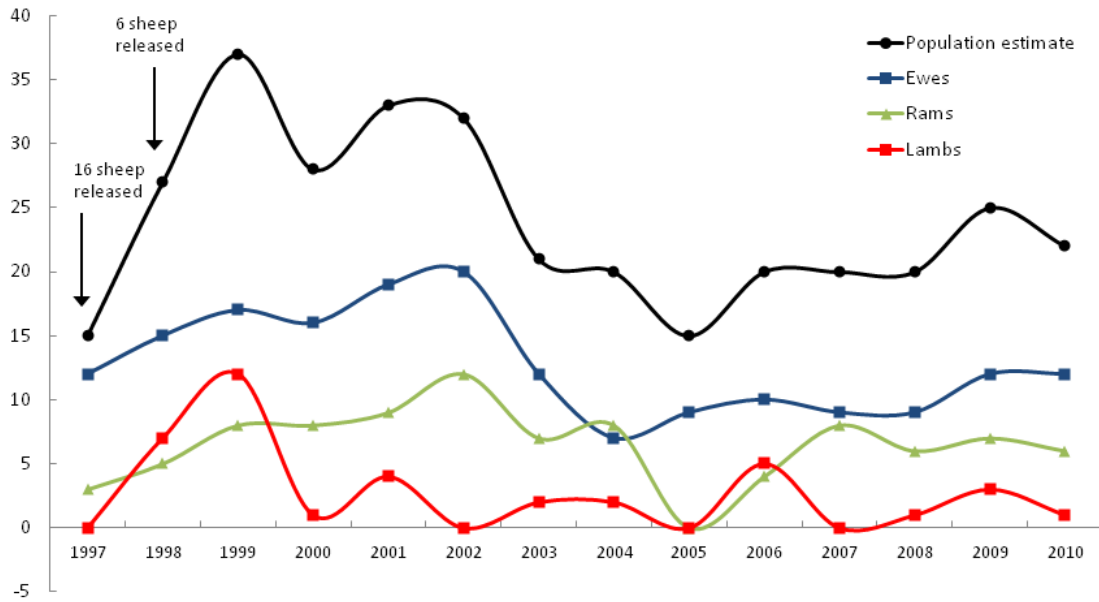
Lower Hells Canyon



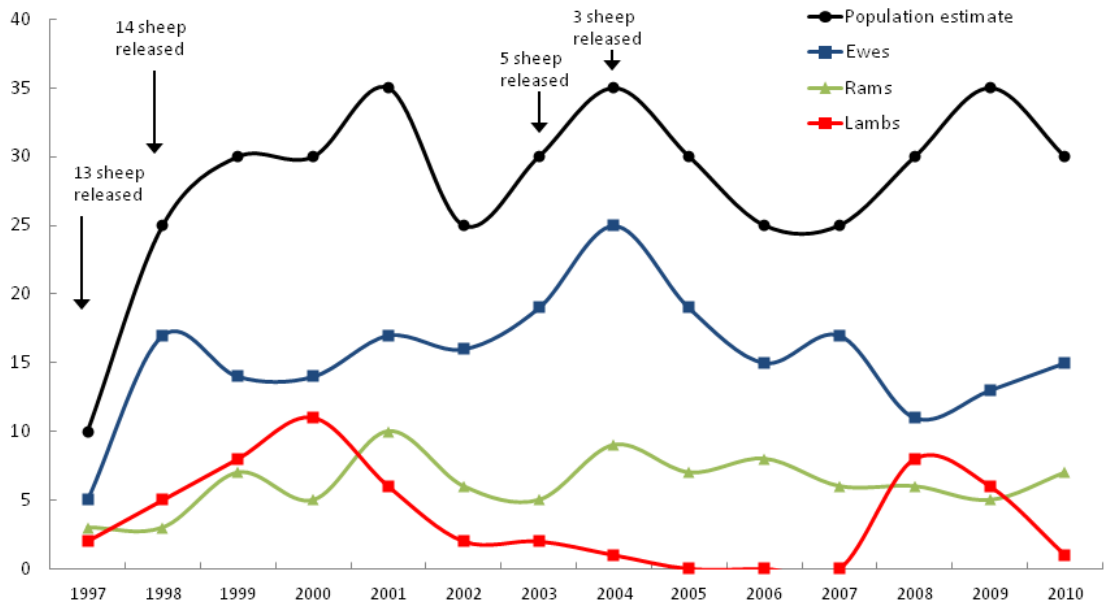
Imnaha



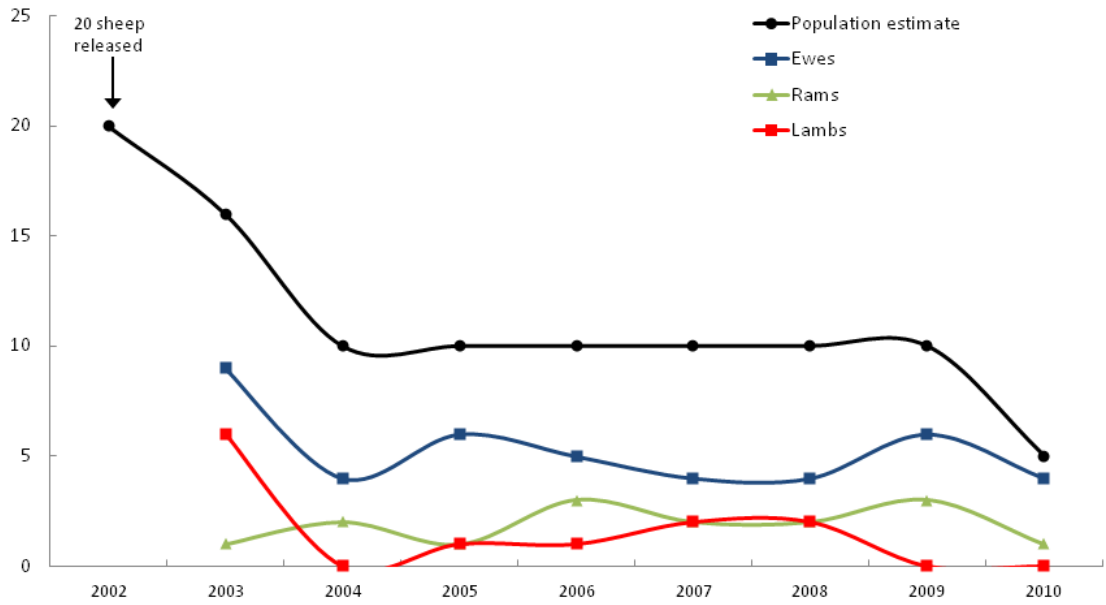
Big Canyon



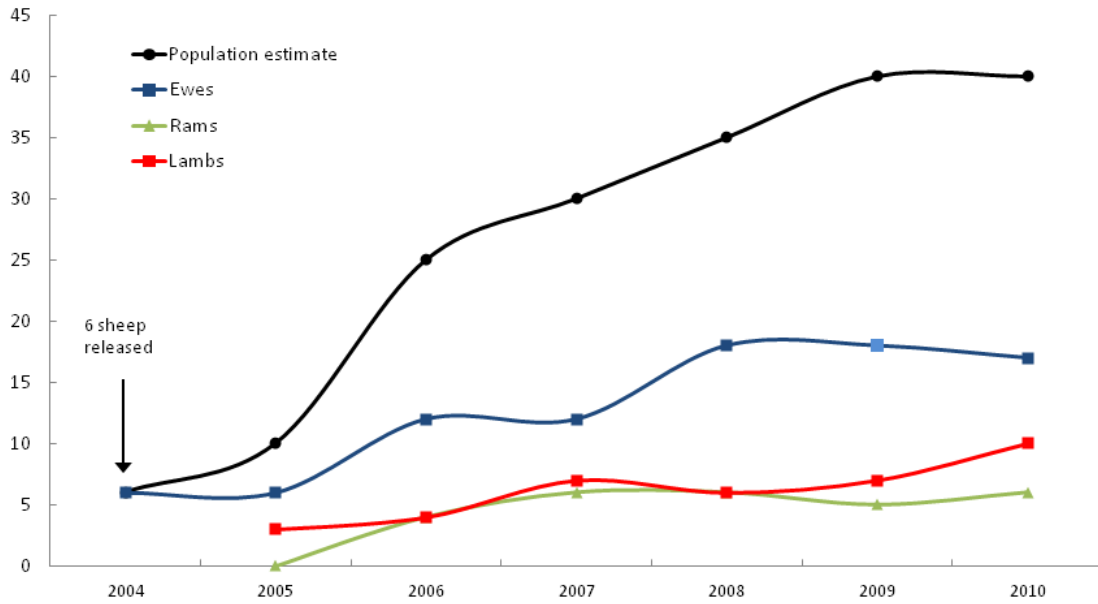
Muir Creek



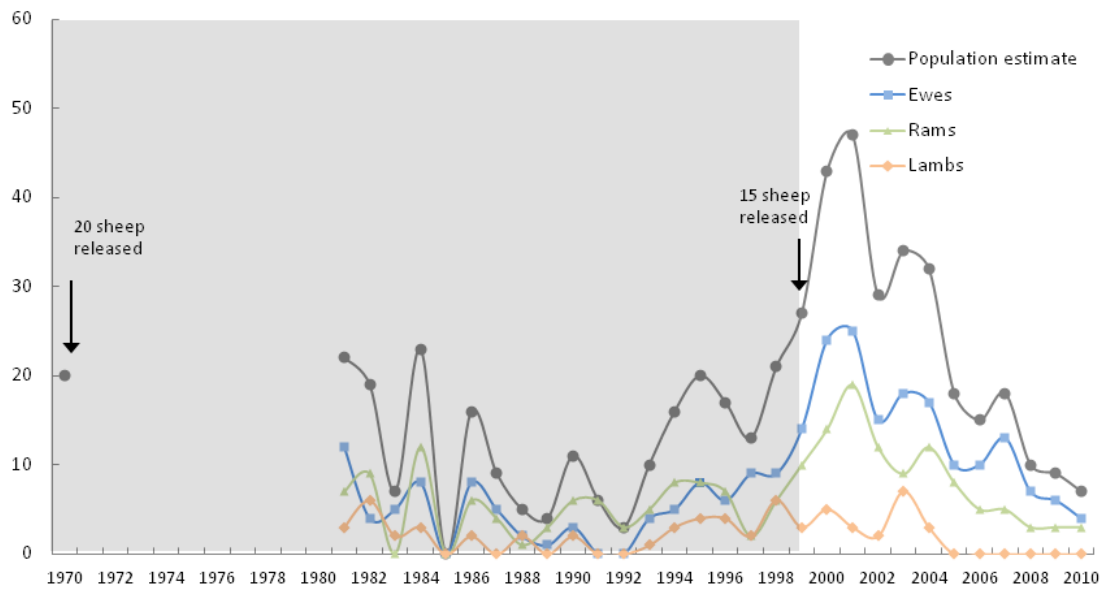
Myers Creek



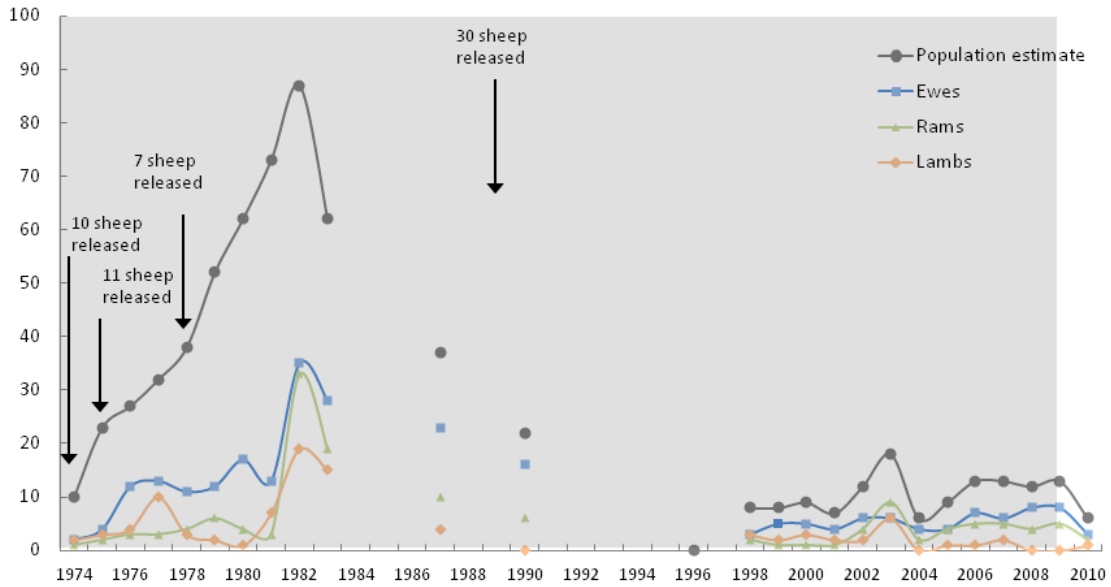
Saddle Creek



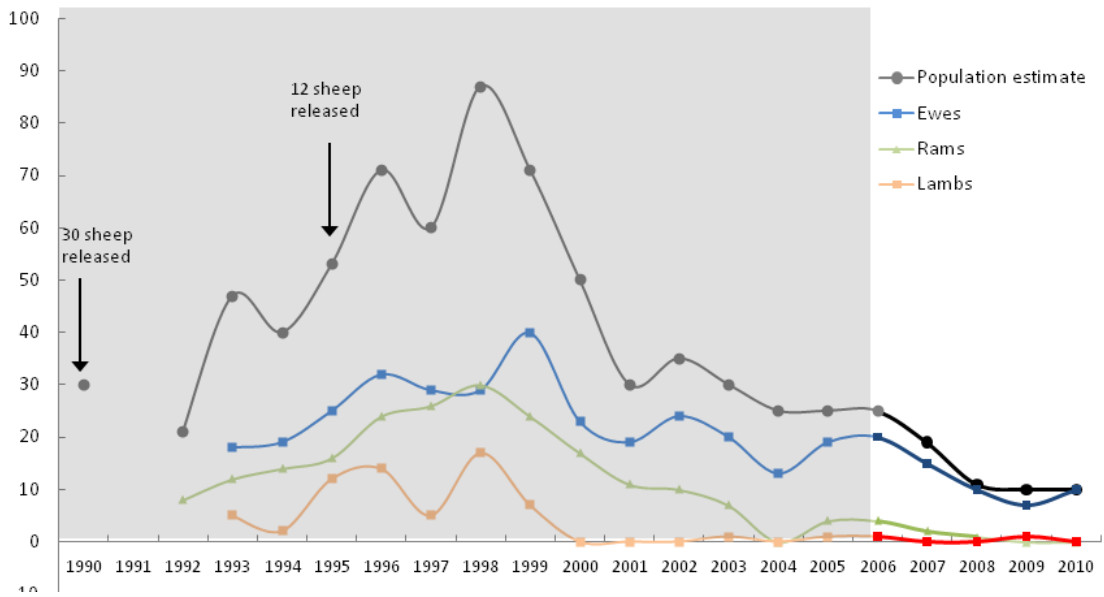
Upper Hells Canyon Oregon



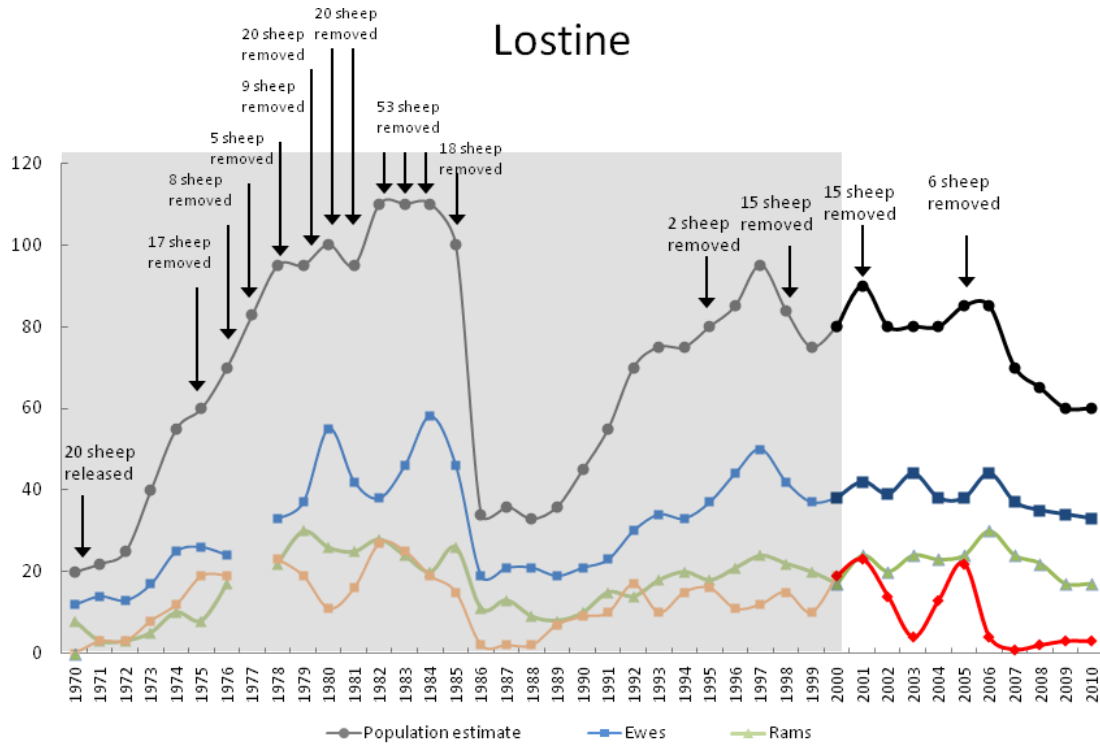
Upper Hells Canyon Idaho



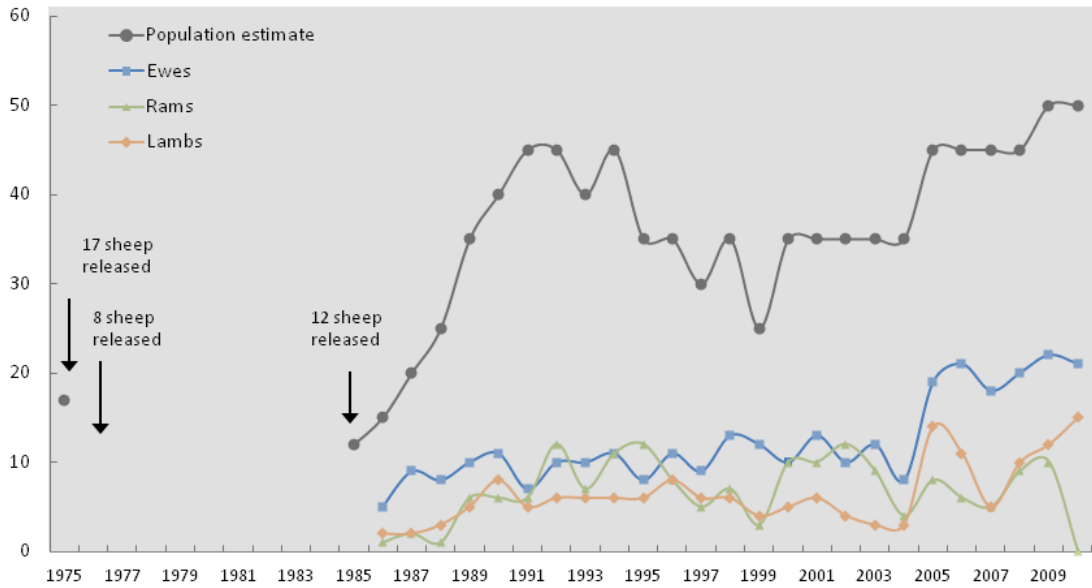
Sheep Mountain

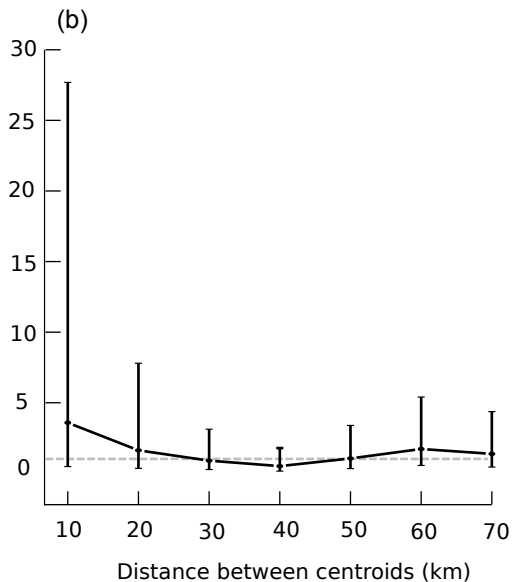
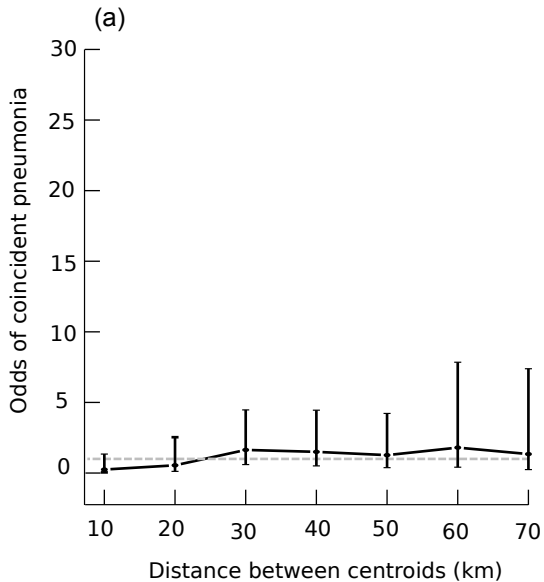


Lostine



Bear Creek





AS		9 0.35	8 0.33	6 0.18	6 0.18	5 0.16	17(4) 0.50	15(4) 0.36	12(2) 0.23	19 0.32	14 0.18	26 0.39	23 0.26	18 0.21
WE	11 0.18	10 0.16	10 0.17	17 0.36	12 0.20	12 0.23	20 0.32	17 0.24	15 0.20	21 0.29	20 0.24	12 0.15	11 0.15	21 0.29
MV										8 0.29	8 0.23	5 0.17	5 0.15	9 0.27
BB	12 0.14	12 0.14	12 0.16	12 0.15	10 0.12	8 0.10	13 0.15	9 0.11	7 0.10	20 0.27	20 0.28	24 0.33	20 0.32	13 0.24
RB	12 0.16	12 0.16	12 0.15	18 0.18	18 0.15	15 0.14	21 0.16	16 0.13	12 0.10	20 0.17	15 0.13	19 0.18	17 0.17	18 0.21
LHC														
IM				20 0.20	16 0.13	16 0.13	21 0.15	15 0.10	13 0.08	21 0.13	23 0.15	24 0.20	14 0.12	25 0.20
BC		14 0.70	20 0.80	19 0.70	12 0.41	11 0.34	9 (8) 0.47	3 0.17	2 0.13	2 (1) 0.13	4 0.20	3 0.16	1 0.05	6 0.29
MU		10 0.50	18 0.82	16 0.84	10 0.34	10 0.43	9 0.32	8 0.24	10 0.33	7 0.28	6 0.24	4 0.18	3 0.10	5 0.17
MY						12 1	10 0.80	8 0.70	4 0.44	4 0.44	3 0.38	3 0.25	2 0.20	4 0.80
SC									5 0.83	5 0.24	5 0.22	5 0.17	5 0.14	5 0.17
UHC OR			16 0.44	16 0.20	12 0.30	16 0.44	11 0.37	9 0.31	9 0.36	7 0.35	6 0.28	4 0.16	2 0.13	6 (2) 0.40
UHC ID														4 0.44
SM										9 0.38	8 0.42	6 0.	5 0.71	5 0.50
LO				21(1) 0.34	23(2) 0.34	23(2) 0.35	22(2) 0.29	22(2) 0.33	21(2) 0.33	25(2) 0.31	20(2) 0.29	20(2) 0.32	19(2) 0.33	19(2) 0.33
BRC						1 0.05								
Total	35	67	95	118	107	116	135	108	97	146	130	132	118	135
	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010

Table S1. Number and proportion of adult bighorn sheep radiocollared in each population by year and translocation status. Resident sheep were monitored in unshaded years, translocated animals were monitored in shaded years. Dark gray indicates all radio-collared animals in the population were translocated, light gray indicates a mix of translocated and resident sheep with the number of radio-collared translocated animals in parentheses. BC, MU, and MY populations were started during the study and initially all adults in these populations were translocated. AS – Asotin, WE – Wenaha, MV – Mountain View, BB – Black Butte, RB – Redbird, LHCOR – Lower Hells Canyon, Oregon, IM – Imnaha, BC – Big Canyon, MU – Muir, MY – Myers Creek, SC – Upper Saddle Creek, UHCOR – Upper Hells Canyon, Oregon, UHCID – Upper Hells Canyon, Idaho, SM – Sheep Mountain, LO – Lostine, BRC – Bear Creek.

AS			H	H	H	H	H	H	H	H	H	H	H	H	H	
WE		L	L	L	A	L	H	H	L	H	A	aa-S	L-S	L-S	aa	
MV											H	aa	L	L	L	
BB		L	H	L	H	L	A	A	L	L	L	L	aa	aa	aa	
RB		H	L	L-S	H	H	H	L-S	L	L	A	aa-S	L	L	L	
IM					A	H	L	A	H	L	aa	L-S	L-S	L	L	
BC			H	H	AA	A	L	AA	L	L-S	H	aa	L	L	L	
MU			H	H	A	H	AA	L	L-S	aa-S	L-S	L	H	H	L-S	
MY							A	H	L	L-S	H	H	H	L-S	L-S	
SC										H	H	H	H	H	H	
UHC ID																H
UHC OR					aa-S	aa-S	L-S	L-S	aa-S	L-S	aa-S	L-S	L-S	L-S	L-S	L-S
SM											aa	L	L-S	L	H	
LO					H	H	A	L-S	H	H	L-S	aa-S	L-S	L-S	L	
	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010

Table S2. Health classification of population-years (141) used to estimate demographic characteristics and transition probabilities of pneumonia and healthy years in Hells Canyon, 1997 – 2010. AA = all-age pneumonia n = 3; aa = secondary all-age pneumonia, n = 16 ; A = adult, n = 11; L = Lamb, n = 62; H = Healthy, no pneumonia detected, n = 49.

The letter S following aa (n = 9) or L (n = 26) indicates pneumonia in lambs was suspected based on clinical signs, high rates of summer mortality, and/or observation of intact dead lambs. In the absence of S (suspected), pneumonia in lambs was confirmed by laboratory diagnosis. All pneumonia in adults was confirmed by laboratory diagnosis.