

Electronic Supplementary Information: Costs and benefits of group living with disease:

A case study of pneumonia in bighorn lambs (*Ovis canadensis*)

Kezia R. Manlove, E. Frances Cassirer, Paul C. Cross, Raina K. Plowright & Peter J. Hudson

Supplementary figures

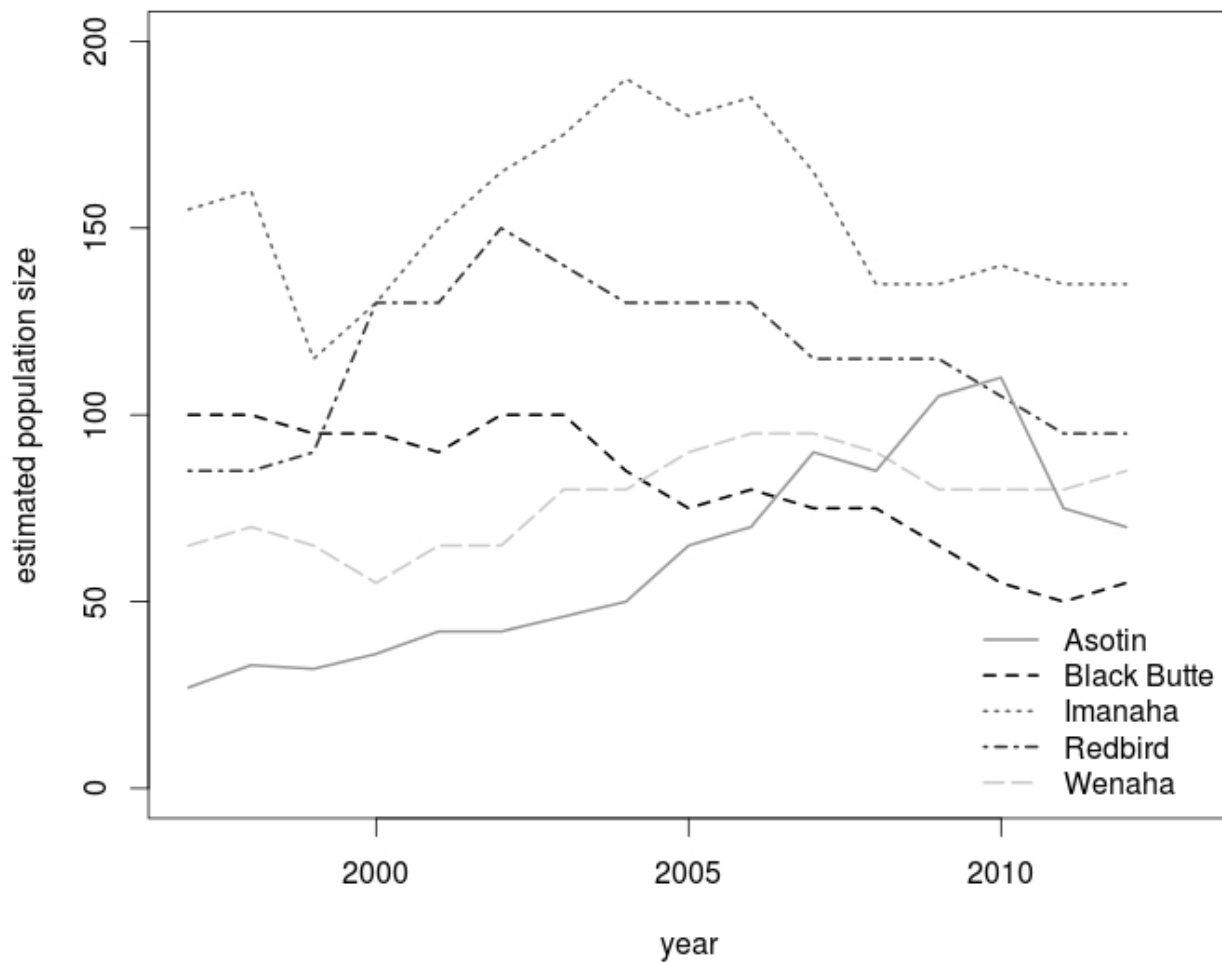


Figure S1. Hells Canyon population sizes over the duration of the study. Populations do not follow consistent trajectories through time, thus we treated disease severity in years following pathogen introduction as independent.

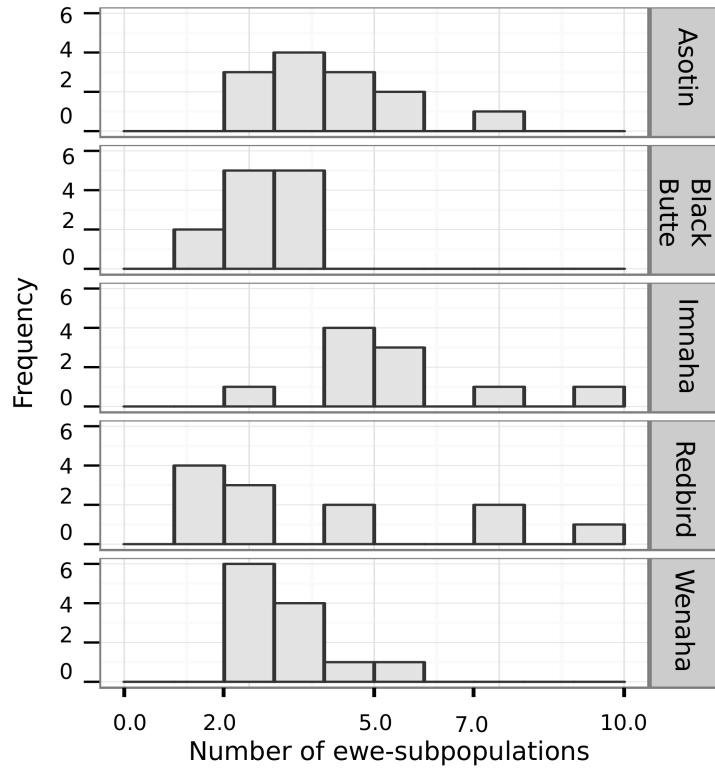


Figure S2. Distribution of number of ewe-subpopulations (“components”) observed for each population included in this study.

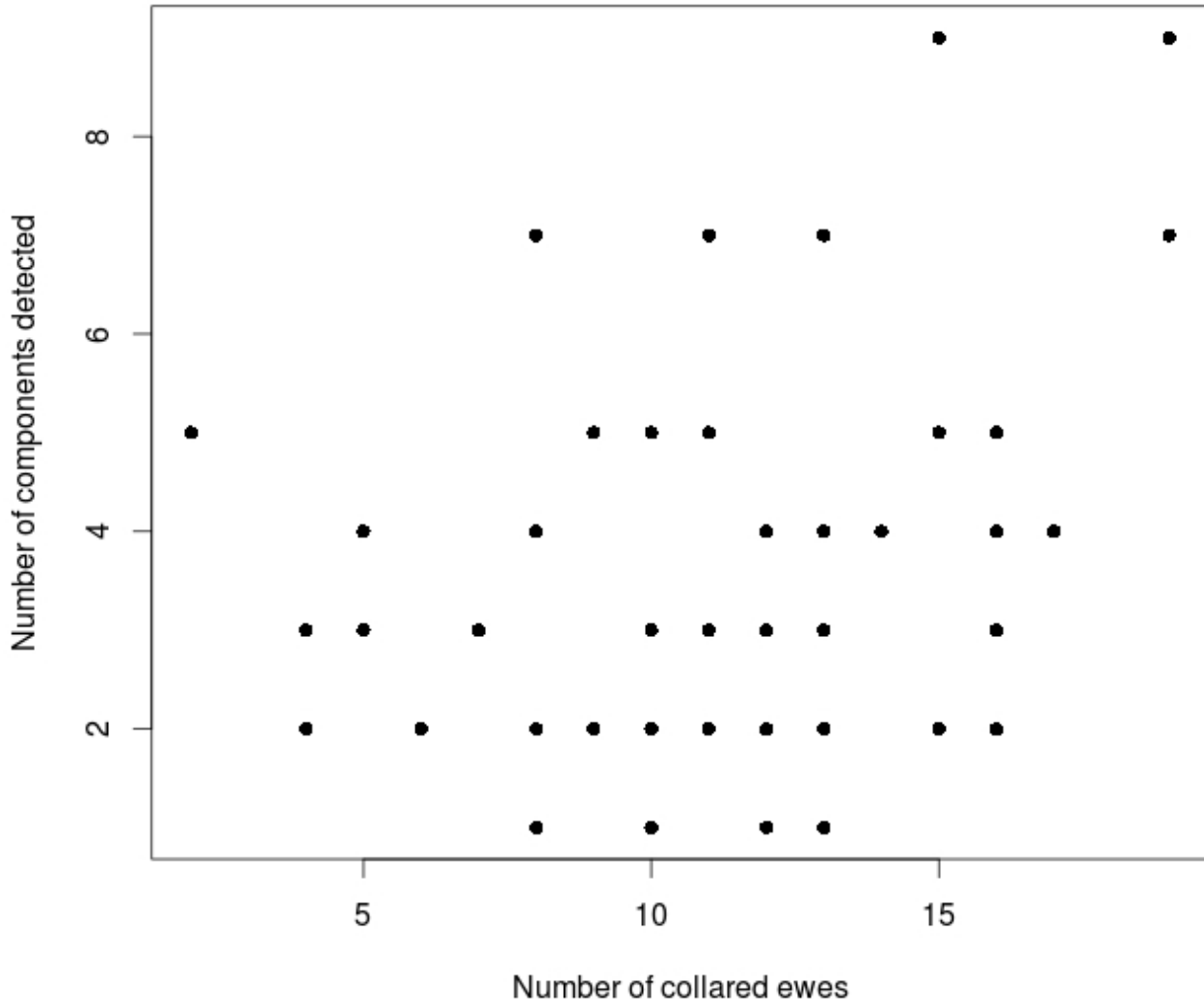


Figure S3. Number of radiocollared ewes by number of ewe-subpopulations (“components”) detected in a given population-year.

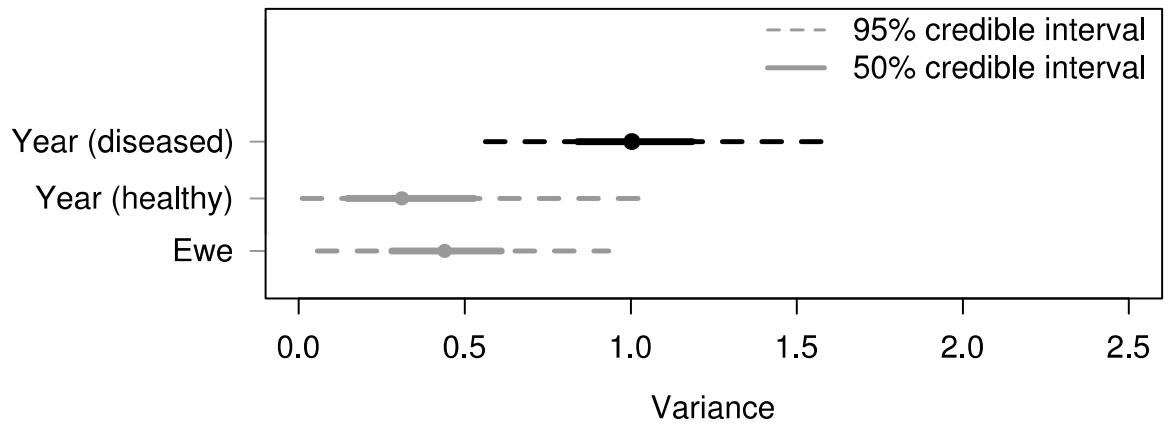


Figure S4. Variance components when ewe-group was excluded from the model. Note that variance previously attributed to ewe-group is now attributed to population-year (“Year”) in diseased years.

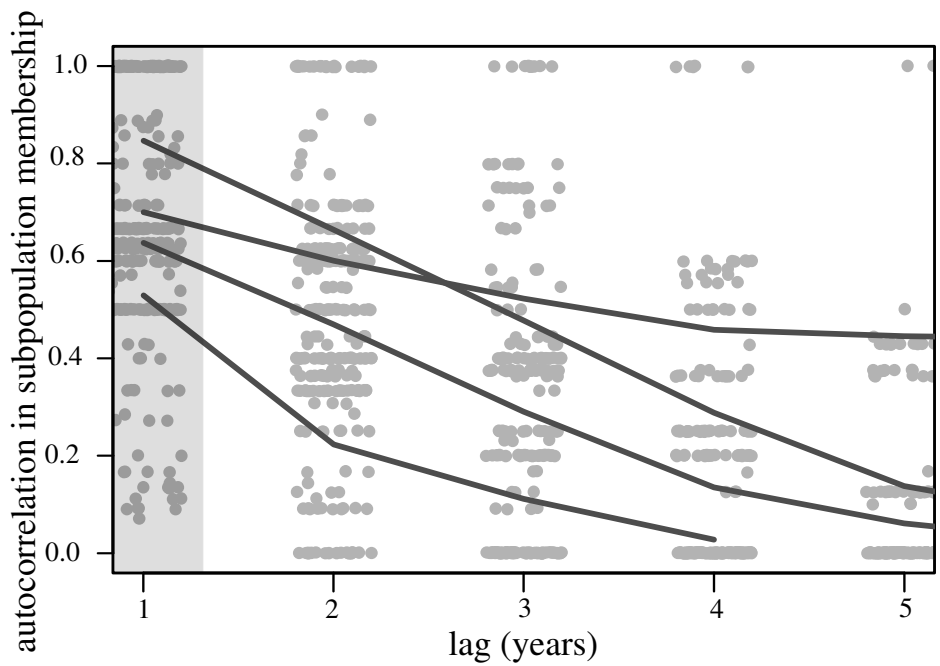


Figure S5. Palla's temporal autocorrelation estimates for summer ewe-subpopulation membership. High autocorrelation corresponds to high overlap in group membership. The x-axis reflects the time lapse between the two years for which group membership is being compared. Points represent all pair-

wise lags between years included in this analysis. We show separate lines for autocorrelation functions in each of our four study populations that experienced lamb disease. The grey box indicates autocorrelation between consecutive years (i.e., “lag-one autocorrelation”).

Supplementary text

1 Ewe social network construction and structures

Ewes were located at least biweekly on the ground or from a fixed wing aircraft, and locations were usually accompanied by visual observation. The median time lag between locations for an individual was six days in the cohorts used in this analysis (electronic supplementary material Table S1). We defined “summer” as the period from May 01 to September 30. This window ranges from birth to weaning, and is the interval during which most disease-induced lamb mortality is detected [1]. We constructed a social contact network of radiocollared individuals for each summer by considering each marked ewe to be a node, and allowing an edge to exist between every pair of marked individuals. We calculated pairwise association indices between all marked animals in the population, and used these association indices as edgeweights linking pairs of marked ewes. This had the consequence of removing edges between pairs of animals that were never observed together. We then used these networks to identify the ewe-subpopulation (Fig. 1C) to which each radiocollared ewe belonged. We defined ewe-subpopulations to be sets of individuals observed at least once together, but never observed with individuals from other subpopulations (i.e., network “components”; Fig. 1C). This definition does not require ewes within a subpopulation to be located with all other ewes in their subpopulation, rather that they be located with at least one other member of their subpopulation at least once. Our weekly sampling intensity allows for the presence of some undetected bridges linking ewe-subpopulations to one another. However, the fact that these bridges were never observed suggests that they were subject to limited activity, lowering their potential impact on disease transmission. The entities that we refer to as “ewe-subpopulations” in the main body of the text are in fact K2-clusters

(i.e., open triplets) in each population-summer's ewe social networks.

2 Bootstraps to test for relationship between number of collars and network structure

We used bootstrap-based approach to test for relationships between number of radiocollared individuals and network structure. Bootstrap-based approaches were chosen since they do not make assumptions about the underlying distributional form of the data, and are therefore robust to departures from normality. To determine whether the number of ewe-subpopulations differed significantly between healthy and diseased years, we sampled with replacement from the full distribution of observed number of components across all population-years. Resampled values were bound to the population-years recorded in the order observed in empirical the dataset, to generate resampled blocks of numbers of components for each population. In each resampled block, we recorded the resampled number of components and the empirically observed population disease status. This comprised a resampled dataset. We then calculated the (resampled) mean number of observed components for each population, and calculated the sum of squared error residuals and sum of squared treatment (e.g., disease status) effects in each bootstrapped dataset. In this way, we created a bootstrapped distribution of sum of squared treatment effects divided by the sum of squared residuals. We replicated this process 1000 times to generate a bootstrapped distribution that we then used as a null distribution in which disease status is independent of number of ewe-subpopulations detected. The final step was to compare the empirically observed sum of squared treatment effects over sum of squared residuals to the null distribution, with the proportion of bootstrapped test statistics in excess of the empirically observed test statistic providing a bootstrapped p-value. We used an identical bootstrap approach to determine whether the number of ewe-subpopulations differed significantly between populations, except in this case treatments were taken to be populations.

3. Temporal autocorrelation in ewe-subpopulation membership

To measure stability of ewe-subpopulation membership across years, we followed the approach taken by Palla et al. [2]. First, we determined groups in consecutive years that had the maximum group membership overlap. For two ewe-subpopulations, A in year t and B in year $t + 1$, we defined “overlap” as

$$C(A, B) = \frac{A \cap B}{A \cup B}$$

where $A \cup B$ represents the ewes contained in either group A or B , and $A \cap B$ is the ewes present in both groups A and B . A ewe-subpopulation A in year t was “matched” with a ewe-subpopulation B in year $t + 1$ when the overlap between subpopulations A and B was greater than the overlap between subpopulation A and any other subpopulation in year $t + 1$. We considered “matched” subpopulations to be essentially the same, with marginal changes through time. We quantified year-to-year subpopulation stability using an approximate autocorrelation [2] defined as

$$C(t) = \frac{|A(t_0) \cup A(t_0+t)|}{|A(t_0) \cap A(t_0+t)|}$$

where $|A(t_0) \cup A(t_0+t)|$ is the number of ewes present in both subpopulation A at time t_0 and in ewe-subpopulation A at time t_0+t and $|A(t_0) \cap A(t_0+t)|$ is the set of all ewes present in either $A(t_0)$, $A(t_0+t)$, or both [2]. High autocorrelation suggested consistent year-to-year ewe-subpopulation membership, whereas low autocorrelation suggests reshuffling of subpopulation membership between years.

All study populations displayed temporal autocorrelation in ewe-subpopulation membership across years (shaded region of Fig. S5), suggesting that ewe social bonds generally persist or are re-established consistently. Although autocorrelation decay rates over time varied among populations, all populations displayed the similar qualitative trend, suggesting that temporal patterns in subpopulation stability do not vary substantially between populations. Perceived changes in ewe-subpopulation

membership occurred primarily when new individuals were collared or died, and occasionally when individuals switched ewe-subpopulations between years.

4 Multilevel Poisson Model

After identifying distinct ewe-subpopulations within each cohort, we examined relationships between number and size of ewe-subpopulations, the daily observed group size within which ewes occurred, and population size. We tested whether the observed number of ewe-subpopulations during the l^{th} study year in the m^{th} population (λ_l depended on population size (as measured by total number of ewes counted in annual aerial surveys) with a hierarchical Poisson model containing a fixed effect for total ewes counted (“TotEwes”), and a random intercept for each population (“pop”). We included an overdispersion term, ϕ , to capture extra-Poisson variation (Agresti 2007). Formally, this model was

$$\log(\lambda_l) = \beta_0 + \beta_1 \text{TotEwes}_{m[l]} + \text{pop}_{m[l]} + \phi_i$$

$$\text{pop}_m \sim N(\mu_{pop}, \tau_{pop})$$

In this model, our inferential focus was on the posterior density associated with the β_1 parameter, which links total counted ewes to the observed number of ewe groups in the population.

Generalized linear mixed model fit by maximum likelihood ['glmerMod']

Family: poisson (log)

Formula: no.components ~ tot.ewes + (tot.ewes | Herd)

Data: popyr.component.tab

AIC	BIC	logLik	deviance
228.9527	239.3404	-109.4763	218.9527

Random effects:

Groups Name	Variance	Std.Dev.	Corr
-------------	----------	----------	------


```

Herd (Intercept) 2.502e-01 0.500164
      tot.ewes    4.867e-05 0.006976 -1.00

```

Number of obs: 59, groups: Herd, 5

Fixed effects:

```

      Estimate Std. Error z value Pr(>|z|)
(Intercept) 0.534958    0.301354   1.775  0.07587 .
tot.ewes    0.013297    0.004593   2.895  0.00379 **

```

5. Piecewise Regression

We fit a piecewise linear regression model to describe how the number of ewe-subpopulations related to median group size. Piecewise regression allows a process to abruptly change forms at some (model-estimated) point along a covariate axis. In this case, we fit median daily group sizes as a function of the number of subpopulations present in each population, and allowed for a possible changepoint in the relationship between daily group size and number of ewe-subpopulations. In this model, λ_k represents the median daily group size observed for individuals in the k^{th} subpopulation in the j^{th} year. Let β_1 be the linear relationship between number of ewe-subpopulations (“NumSubPops”) and median daily group size prior to the changepoint; let U be the changepoint, and let γ be the adjustment to the relationship between number of groups and group size for numbers of groups exceeding the changepoint. Then the changepoint model is

$$\log(\lambda_k) = \beta_0 + \beta_1 \text{NumSubPops}_{j[k]} + \gamma (\text{NumSubPops}_{j[k]} - U) \times \text{step}(\text{NumSubPops}_{j[k]} - U) .$$

Interval estimates for all piecewise regression model coefficients

	Change Point	Initial Slope	Slope Change	Second Slope
2.5%	1.541095	-14.176396	0.1103687	-0.7245282
97.5%	7.111524	-0.227666	14.6360225	3.2145788

6. Group size by population size

We tested whether the median observed ewe group size during the l^{th} study year in the m^{th} population (μ_l) depended on population size (as measured by total number of ewes counted in annual aerial surveys) with a hierarchical linear model containing a fixed effect for total ewes counted (“TotEwes”), and a random intercept for each population (“pop”). Formally, this model was

$$\mu_l = \beta_0 + \beta_1 \text{TotEwes}_{m[l]} + \text{pop}_{m[l]},$$

$$\text{pop}_m \sim N(\mu_{pop}, \tau_{pop})$$

In this model, our inferential focus was on estimates associated with the β_1 parameter, which links total counted ewes to the observed median group size during that population-summer.

Linear mixed model fit by REML ['lmerMod']

Formula: med.grpsz ~ tot.ewes + (1 | Herd)

Data: popyr.component.tab

REML criterion at convergence: 344.3188

Random effects:

Groups	Name	Variance	Std.Dev.
Herd	(Intercept)	0.00	0.000
	Residual	19.15	4.376

Number of obs: 59, groups: Herd, 5

Fixed effects:

	Estimate	Std. Error	t value
(Intercept)	10.40952	1.38748	7.502
tot.ewes	-0.01064	0.02678	-0.397

7. Variance Decomposition

To determine an organizational level of transmission most consistent with observed lamb mortality patterns in Hells Canyon, we decomposed the variance in the proportion of lambs that

survived through September 30th. We compared variation in lamb mortality outcomes at four organizational levels: populations, years within populations (“years”), ewe-subpopulations, and ewes. We took years to be nested in populations because disease severity was not temporally synchronized across all Hells Canyon populations. A nested structure allowed different populations to experience different disease statuses in the same year. Comparisons were based on a variance decomposition performed using a multilevel logistic regression model with random effects for ewes, ewe-subpopulations, years, and populations. Ewe effects were estimated across all years during which a ewe reproduced, regardless of that year’s disease status. For the i^{th} lamb born to the j^{th} ewe in the k^{th} ewe-subpopulation during the l^{th} year in the m^{th} population, this corresponded to the following multilevel model:

$$\log\left(\frac{p_i}{1-p_i}\right) = group_{k|i} + ewe_{j|i} ,$$

$$group_k \sim N\left(year_{l|k}, \tau_{group,PN} \times I(PN\ status)_k + \tau_{group,Healthy} \times (1 - I(PN\ status)_k)\right) ,$$

$$year_l \sim N\left(pop_{m|l} + \delta I(PN\ status)_l, \tau_{year,PN} \times I(PN\ status)_l + \tau_{year,Healthy} \times (1 - I(PN\ status)_l)\right) ,$$

$$ewe_j \sim N(0, \tau_{ewe})$$

$I(PN\ status)$ terms take on the value 0 for years classified as healthy, and 1 otherwise. In general, these indicator terms control the variance estimate to which each observation contributes. Indicator terms were generated separately for each level of the model, but always retain the same meaning: any ewe-group present in a year classified as having pneumonia is assigned an $I(PN\ status)$ term of 1, as is any year classified as having pneumonia.

For our purposes, the critical attributes of this model are the precision parameters, $\tau_{group,PN}$, $\tau_{group,Healthy}$, $\tau_{year,PN}$, $\tau_{year,Healthy}$, and τ_{ewe} , which we inverted to variances following model fitting. Our focus was on the relative size of each component. High variance at a particular level indicated that the proportion of lambs surviving differed between observations at that level, whereas

low variance meant that lamb survival proportions were similar for all units at that level (e.g., Figure 1D). For example, high variance at the ewe-group level meant that lamb survival in some ewe groups was very different than in other groups, whereas low variance suggested all groups experienced similar within-group mortality rates.

JAGS Model Statement

```
model {
  #FEs
  #pop intercepts
  for(i in 1:n.pops){
    alpha[i] ~ dnorm(0, 0.01)
  }

  #pn effect
  delta ~ dnorm(0, 0.01)

  #loop for year-level terms
  for(i in 1:n.years){
    b.year[i] ~ dnorm(alpha[pop.hier[i]] + delta * pn.status[i], tau.year.pn * pn.status[i] + tau.year.he *
he.status[i]) #year effect
  }

  #loop for component-level terms
  for (i in 1:n.compos) {
    b.compo[i] ~ dnorm(b.year[year.hier[i]], tau.compo.pn * compo.pn.status[i] + tau.compo.he *
compo.he.status[i]) #component effect
  }

  #loop for ewe-level terms
  for(i in 1:n.ewes){
    b.ewe[i] ~ dnorm(mu.ewe, tau.ewe) #ewe effect
  }

  tau.compo.he <- pow(sigma.compo.he, -2)
  tau.compo.pn <- pow(sigma.compo.pn,-2)
  sigma.compo.he ~ dunif(0, 10)
  sigma.compo.pn ~ dunif(0, 10)

  tau.year.he <- pow(sigma.year.he, -2)
  tau.year.pn <- pow(sigma.year.pn, -2)
  sigma.year.he ~ dunif(0, 10)
  sigma.year.pn ~ dunif(0, 10)

  mu.ewe <- 0
  tau.ewe <- pow(sigma.ewe, -2)
```

```

sigma.ewe ~ dunif(0, 10)

#binomial likelihood
for(i in 1:n){
  C[i] ~ dbin(p[i], N[i])
  logit(p[i]) <- b.compo[compo[i]] + b.ewe[ewe[i]]
}
}

```

Summary of MCMC output

Quantiles for each variable:

Posterior quantiles for each variable

	2.5%	25%	50%	75%	97.5%
beta.int	-1.93295	-1.4256	-1.2242	-1.0319	-0.5574
delta	1.39940	1.8810	2.1300	2.4010	2.9664
sigma.compo.he	0.02036	0.2117	0.4343	0.7051	1.3149
sigma.compo.pn	0.77227	1.1872	1.4115	1.6576	2.2096
sigma.ewe	0.02115	0.2267	0.4057	0.5935	0.9542
sigma.pop	0.01294	0.1296	0.2798	0.5063	1.4556
sigma.year.he	0.01237	0.1286	0.2792	0.4838	0.9644
sigma.year.pn	0.03304	0.3124	0.5818	0.8666	1.4473

Gelman-Rubin statistics

Gelman-Rubin statistics were <1.03 for all parameters.

8. Variance decomposition without ewe-groups

We conducted a second variance decomposition to examine how variance was attributed when ewe-groups were not included in the model hierarchy. The resulting variance decomposition is shown in Figure S4.

Posterior quantiles for each variable:

	2.5%	25%	50%	75%	97.5%
beta.int	-1.78546	-1.3820	-1.2117	-1.0493	-0.6579
delta	1.33368	1.7362	1.9491	2.1691	2.6217
sigma.ewe	0.01874	0.2060	0.3820	0.5576	0.8810
sigma.pop	0.01051	0.1008	0.2173	0.3987	1.1725

sigma.year.he	0.01011	0.1216	0.2634	0.4487	0.8886
sigma.year.pn	0.55791	0.8280	0.9855	1.1606	1.5660

9. References

1. Cassirer, E.F., Plowright, R.K., Manlove, K.R., Cross, P.C., Dobson, A.P., Potter, K.A. *et al.* (2013). Spatio-temporal dynamics of pneumonia in bighorn sheep. *J. Anim. Ecol*, 82, 518-528.
2. Palla, G., Barabási, A.L. & Vicsek, T. (2007). Quantifying social group evolution. *Nature*, 446(7136), 664–7.

Supplementary tables

Table S1. Attributes associated with all lamb cohorts included in this study.

Herd	Year	Number of ewe-subpopulations detected	Disease status*	Median relocation interval (d)	Total number of ewes**	Population estimate	Median total group size	Number of radiocollared ewes	Summer lamb survival	Median number of ewes per group	Average number of ewes per subpopulation
Asotin	1998	3	Healthy	5.88	11	33	8	5	1	7	4
Asotin	1999	3	Healthy	5.28	15	32	23	5	0.8	9	5
Asotin	2000	2	Healthy	5.88	23	36	21	4	0.75	10	12
Asotin	2001	2	Healthy	5.28	18	42	12	6	0.67	8	9
Asotin	2002	3	Healthy	5.91	23	42	9.5	4	0.75	4	8
Asotin	2003	3	Healthy	7.67	22	46	3	10	0.8	2.5	7
Asotin	2004	4	Healthy	6.13	26	50	8	5	0.8	4	7
Asotin	2005	4	Healthy	10.93	34	65	10	5	0.33	4	9
Asotin	2006	4	Healthy	8.50	30	70	6	8	0.83	3	8
Asotin	2007	5	Healthy	8.05	40	90	4.5	2	0.5	3	8
Asotin	2008	2	Healthy	10.20	48	85	7	8	0.88	5.5	24
Asotin	2009	5	Healthy	8.50	46	105	10	9	0.78	7	9
Asotin	2010	7	Healthy	10.93	40	110	6	8	0.86	5	6
Imnaha	2000	5	Adults	11.77	69	130	8	16	0.71	4	14
Imnaha	2001	4	Healthy	9.00	78	150	9	13	0.6	5	20
Imnaha	2002	4	Lambs	9.56	77	165	9	12	0.6	5	19
Imnaha	2003	4	Adults	11.77	81	175	7	17	0.36	4	20
Imnaha	2004	2	Healthy	6.65	93	190	17	12	0.86	9	47
Imnaha	2005	5	Lambs	8.05	94	180	10.5	11	0.44	6	19
Imnaha	2006	4	All-age	9.28	84	185	10	16	0.69	5	21
Imnaha	2007	5	Lambs (S)	10.93	101	165	9	15	0.5	6	20
Imnaha	2008	9	Lambs (S)	11.77	74	135	7	19	0.46	5	8
Imnaha	2010	7	Lambs	10.20	73	140	6	19	0.36	4	10
Black Butte	1997	3	Lambs	4.14	45	100	10	13	0.63	6	15
Black Butte	1998	3	Healthy	5.28	44	100	10	12	0.67	6	15
Black Butte	1999	2	Lambs	4.19	46	95	12	12	0.56	7	23
Black Butte	2001	2	Lambs	5.28	35	90	8	6	0.25	5	18
Black Butte	2003	1	Adults	4.57	44	100	20	10	0.7	10	44
Black Butte	2004	1	Lambs	3.00	45	85	8	8	0.17	5	45

Table S1 (continued). Attributes associated with all lamb cohorts included in this study.

Herd	Year	Number of ewe-subpopulations detected	Disease status*	Median relocation interval (d)	Total number of ewes**	Population estimate	Median total group size	Number of radiocollared ewes	Summer lamb survival	Median number of ewes per group	Average number of ewes per subpopulation
Black Butte	2005	3	Lambs	3.12	31	75	8	7	0.4	6	10
Black Butte	2006	2	Lambs	6.38	39	80	8	15	0.08	6	20
Black Butte	2007	2	Lambs	10.93	43	75	8	15	0.14	6	22
Black Butte	2008	3	All-age	10.98	38	75	7	16	0	5	13
Black Butte	2009	3	All-age	9.88	29	65	6.5	12	0.1	5	10
Black Butte	2010	2	All-age	10.93	31	55	7	9	0	5	16
Wenaha	1997	3	Lambs	3.00	50	65	9	12	0.22	7	17
Wenaha	1998	3	Lambs	5.46	41	70	9	11	0.14	6	14
Wenaha	1999	2	Lambs	2.86	36	65	12	10	0.29	8	18
Wenaha	2000	2	Adults	4.50	28	55	17	11	1	9	14
Wenaha	2001	5	Lambs	4.79	35	65	6	10	0.25	4	7
Wenaha	2002	2	Healthy	6.66	29	65	12	8	0.8	6	15
Wenaha	2003	3	Healthy	6.00	32	80	9	12	0.88	5	11
Wenaha	2004	3	Lambs	6.80	32	80	9.5	10	0.5	5	11
Wenaha	2005	2	Healthy	8.50	35	90	8	9	0.5	5	18
Wenaha	2006	4	Adults	11.35	31	95	6	16	0.89	4	8
Wenaha	2007	2	All-age (S)	12.75	33	95	5	13	0.25	4	17
Wenaha	2010	2	All-age	9.56	37	80	12	16	0.46	6.5	19
Redbird	1997	1	Healthy	3.06	23	85	17	12	0.32	9	23
Redbird	1998	1	Lambs	3.97	44	85	12	12	0.17	8	44
Redbird	1999	1	Lambs (S)	3.33	46	90	9	12	0.58	5	46
Redbird	2000	1	Healthy	4.14	56	130	23	13	0.75	13	56
Redbird	2001	4	Healthy	4.25	61	130	13	13	0.83	7	15
Redbird	2003	9	Lambs (S)	3.83	77	140	12	15	0.17	9	9
Redbird	2004	7	Lambs	3.48	74	130	12	11	0.3	8	11
Redbird	2006	4	Adults	5.10	65	130	13	14	0.71	8	16
Redbird	2007	7	All-age (S)	10.20	57	115	7	13	0	5	8
Redbird	2008	2	Lambs	10.20	67	115	6	16	0.2	6	34
Redbird	2009	2	Lambs	8.05	59	115	8	16	0.44	6	30
Redbird	2010	2	Lambs	15.30	69	105	5	15	0.11	4	35

* Classifications from Cassirer et al. 2013, Journal of Animal Ecology; “S” indicates suspected disease status

** Counts based on aerial surveys of entire population