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Research Article

Effects of Elk Density on Elk Aggregation Patterns and Exposure to Brucellosis

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ABSTRACT Increasing elk (*Cervus elaphus nelsoni*) populations across the West in response to increased demand for recreational and hunting opportunities may have negative, unintended consequences for disease transmission risk. Historically, free-ranging elk populations were not thought to sustain brucellosis (*Brucella abortus*), but recent studies suggest increasing elk densities may result in free-ranging elk serving as maintenance hosts for the disease. We evaluated spatial variation in elk density, group sizes, and adult female brucellosis seroprevalence in 39 elk management districts in the Greater Yellowstone Ecosystem using a Bayesian approach. We used modeled relationships to estimate the effects of reducing elk density by 10–90% on grouping patterns and seroprevalence rates. Reducing the density of the 3 highest density elk herds by 10%, 50%, and 90% was predicted to result in a 9%, 39%, and 59% decrease in mean group size, whereas reducing the density of the 3 lowest density elk herds was predicted to result in only a 0%, 0.7%, and 1.3% decrease in mean group size. We estimated seroprevalence rates of 0.01–0.27 across management districts, and seroprevalence increased as elk density increased. For the 7 of 39 management districts with >10% estimated seroprevalence, 10%, 50%, and 90% reductions in elk density resulted in predicted mean seroprevalence reductions of 2%, 7%, and 9%, respectively. For the 14 management districts with ≤1% estimated seroprevalence, 10%, 50%, and 90% reductions in elk density resulted in no measurable change in predicted mean seroprevalence. Our results suggest that elk density has an important effect on elk group sizes, which may influence the risk of brucellosis transmission and resultant exposure rates. Manipulating elk density may in turn affect brucellosis seroprevalence rates. However, debate among the diverse stakeholders involved in elk management on the effectiveness of reducing density, group sizes, and brucellosis exposure rates in elk, relative to other interests and objectives, is necessary prior to manipulation of elk density for this purpose. © 2015 The Wildlife Society.

KEY WORDS Bayesian, *Brucella abortus*, brucellosis, density, elk management, Montana, wolf risk.

As a worldwide disease that may induce abortions in livestock, brucellosis can result in extensive economic losses to livestock producers (Beinen and Tabor 2006, Seleem et al. 2010). Although the disease may be managed in livestock through vaccinations (Cheville et al. 1996, Yang et al. 2013), potential reintroduction from wildlife populations can undermine these efforts. In the Greater Yellowstone Ecosystem (GYE), elk (*Cervus elaphus*) and bison (*Bison bison*) are the primary wildlife reservoirs of brucellosis, and recently elk have been implicated as the source of multiple brucellosis transmissions to livestock (Rhyan et al. 2013). Brucellosis is primarily transmitted via ingestion of infected placentas and aborted fetuses (Thorne et al. 1978, Cheville et al. 1998), with elk transmission risk being highest during late pregnancy from February to June (Roffe et al. 2004). Seroprevalence of antibodies to *Brucella abortus*, the bacteria causing brucellosis, varies among elk herds in the GYE and is increasing in some free-ranging elk herds (Cross et al. 2010*a*).

Developing a better understanding of the factors that influence the rate of pathogen transmission is a central issue in ungulate management across the GYE. Historically, low brucellosis seroprevalence in free-ranging elk herds suggested that the disease was not self-sustaining in herds not associated with feeding programs (Cheville et al. 1998). However, more recent studies suggest that increases in elk density and the size of large elk aggregations may result in free-ranging elk functioning as maintenance hosts for brucellosis in new regions of the GYE (Cross et al. 2010*a*, *b*). Elk-to-elk transmission events may be more likely in larger elk aggregations because of increased per capita contact rates and increased duration of contacts (Cross et al. 2013). In the northern portion of the GYE, this may result in free-ranging elk herds that traditionally had low levels of

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brucellosis exposure sustaining or increasing levels of exposure through elk-to-elk transmission. If increasing elk density or size of large elk aggregations, or both, are leading to increased risk of elk-to-elk transmission (Cross et al. 2013), efforts to better understand spatio–temporal variations in elk densities and aggregation patterns are needed. This would allow managers to structure brucellosis surveillance efforts and inform efforts aimed at reducing the risk of elk to livestock transmission by affecting elk-to-elk transmission and exposure rates.

Management efforts to affect brucellosis dynamics in wildlife are currently hampered by uncertainty in the nature of the relationship between elk density and pathogen transmission. If the density–transmission relationship is non-linear, efforts to reduce elk density may have little impact on transmission dynamics (Dobson and Meagher 1996). Further, if transmission dynamics are driven by the size and occurrence of large elk aggregations (Cross et al. 2013), the relationship between elk density, other landscape attributes, group size, and prevalence of large elk aggregations in the population needs to be better understood. Management efforts to reduce elk density may have little impact on transmission dynamics if group size, and in particular the formation of large elk aggregations, is driven primarily by landscape attributes of elk winter and spring ranges rather than overall population density or other factors. Behavioral changes associated with wolf (*Canis lupus*) predation risk have the potential to affect elk aggregation sizes, and elk aggregation sizes may increase or decrease with variations in predation risk (Hebblewhite and Pletscher 2002, Creel and Winnie 2005, Gude et al. 2006, Proffitt et al. 2012). To determine the relative influence of landscape factors, which are largely outside of management control, and population or risk factors, which are within management control, it is important to both broadly understand factors affecting average elk aggregation sizes across large, heterogeneous landscapes, as well as identify factors contributing to the formation of large elk aggregations. Increasing elk densities may be linked to the formation of large groups (Hebblewhite and Pletscher 2002, Cross et al. 2010*a*, Proffitt et al. 2012); however, at the population level, effects of wintering elk density on aggregation patterns and exposure to seroprevalence has not be evaluated.

We investigated effects of elk density, wolf predation risk, landscape factors, and weather on elk aggregation patterns across the GYE to determine the extent to which factors under management control affect aggregation behaviors. We used a Bayesian spatial seroprevalence model to estimate elk management-district-specific rates of brucellosis seroprevalence and evaluate the effect of elk density on estimated brucellosis seroprevalence (Heisey et al. 2010). We simulated the effects of reducing elk density on aggregation behaviors and seroprevalence rates.

STUDY AREA

We documented elk aggregation behaviors from 27 wintering elk herds in or adjacent to the southwest Montana brucellosis designated surveillance area (DSA) for livestock (Fig. 1). We estimated management-district-specific brucellosis seroprevalence rates using serology data collected from 39 elk management districts in or adjacent to the DSA in southwestern Montana. Elk density and winter range areas were known for 27 of these 39 management districts. Detailed descriptions of individual herd ranges and management districts, including land ownership, vegetation, and harvest regulations, are found in the State of Montana Elk Management Plan (fwp.mt.gov/hunting/elkplan).

METHODS

Data Collection

We collected elk survey data annually on each winter range using fixed-wing aircraft during December and April of 2006 through 2011. Most surveys occurred during January–March, and we strived to survey each herd within the same 2-week period across years. We timed surveys during the portion of winter with optimal snowpack conditions to maximize elk sightability. We included data only from surveys that observers considered high quality and complete. During each survey, we recorded elk group size, location, sex, and age composition information. We defined groups as aggregations of animals with no more than 100 m between individuals. We censored bull groups to reduce variations in aggregation behaviors associated with behavioral differences between male and female animals, and because brucellosis is transmitted by female animals. We classified elk into distinct wintering herds based primarily on movement data collected from radiocollared individuals. In the few areas where no movement data existed, we classified elk into distinct wintering herds based on knowledge of the local biologist and the State of Montana Elk Management Plan.

Wolves were distributed across the entire study area. We estimated wolf numbers and distribution through a combination of radiocollaring efforts, ground tracking observations, and observations from landowners. We estimated the number of wolves and approximate spatial distribution of each pack annually based on repeated aerial-survey and ground monitoring efforts. We obtained data from Montana Fish, Wildlife and Parks annual reports (http://fwp.mt.gov/fishAndWildlife/management/wolf/default.html; Sime et al. 2008, 2009, 2010, 2011), which represented minimum counts rather than true population estimates. We assumed all packs were detected because the area is intensively monitored for wolf activity by multiple agencies as well as landowners.

We collected brucellosis seroprevalence data during 2001–2013 from hunter–harvested elk and animals captured for research purposes. We used samples collected only from female elk >1.5 years old. Elk were aged based on tooth eruption patterns (Hamlin et al. 2000). Because hunter–harvested samples were collected from elk on their fall ranges rather than winter ranges, the relationship between harvest location and wintering herd unit was not always known. Therefore, we estimated seroprevalence at the management district level rather than the finer scale of the herd unit because management districts generally capture both fall and

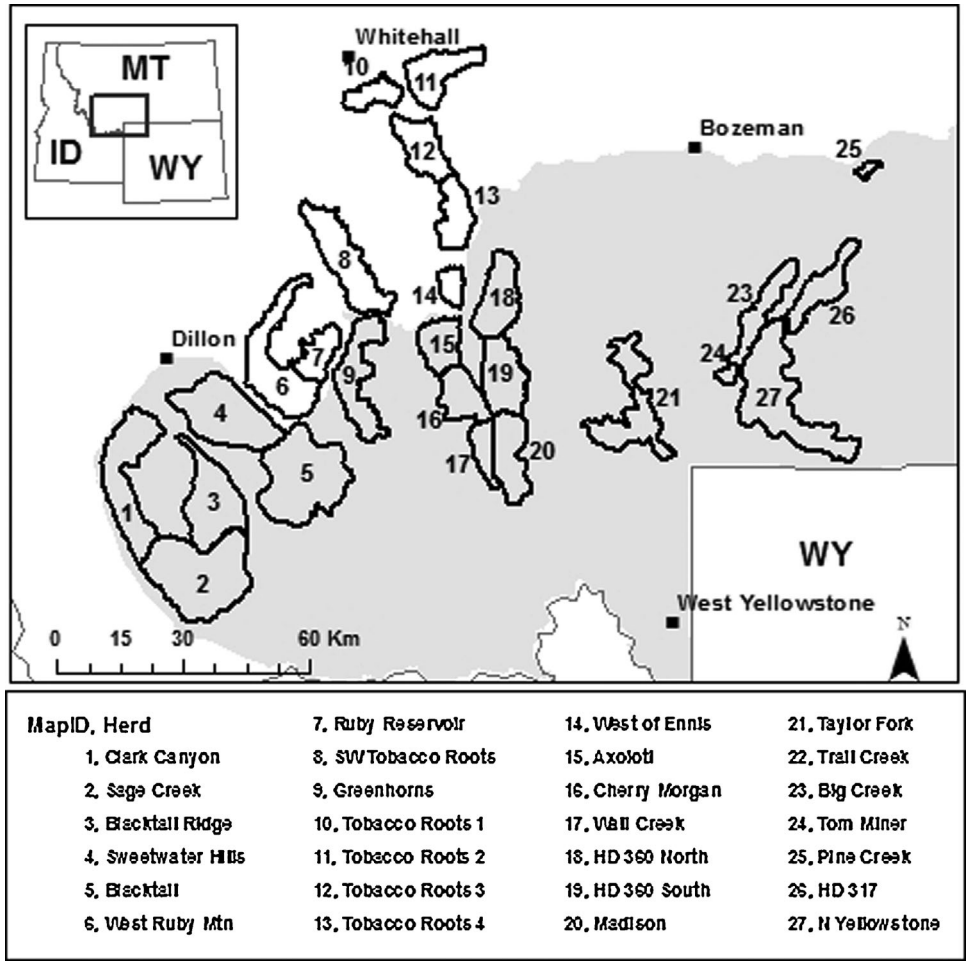

Figure 1. Map of the study area showing the boundaries of elk wintering ranges for 27 herds in and around the Montana brucellosis designated surveillance area (light gray) included in the analysis of elk density and group size during 2006–2011 and brucellosis seroprevalence during 2001–2013.

winter ranges. We initially screened blood serum for *B. abortus* antibodies using a panel of tests that included the rivanol precipitation, fluorescent polarization, and the *B. abortus* antigen rapid card or standard plate agglutination test. We further tested samples testing positive to any one of these tests using the buffered acidified plate antigen and complement fixation tests.We made serologic classifications according to the United States Department of Agriculture (USDA) Animal and Plant Health Inspection Service Uniform Methods and Rules for brucellosis in Cervidae (USDA 2003).

Elk Aggregation Patterns

Using data collected from 27 elk herds during December–April of 2006–2011, we evaluated the effects of landscape attributes, wolf risk, weather, and elk density on 2 metrics of elk aggregations: mean group size and the proportion of the herd that occurred in large groups (≥300 animals; Cross et al. 2010*a*). We also evaluated the effects of elk herd density on the size of the largest elk groups (99th quantile of the group size distribution). We evaluated 3 landscape attributes potentially affecting elk aggregations: vegetation cover type (e.g., grasslands, shrublands, forested areas), elevation, and percent of winter range comprised of grasslands. In this analysis, grasslands cover type included irrigated croplands. We used the national land cover dataset (http://www.mrlc.gov/), which had a 30-m resolution, to identify vegetation cover types. We also used this dataset to calculate the percentage of grasslands within each winter range. We estimated elevation from a 30-m digital elevation map.

We evaluated 1 metric of wolf predation risk and 1 metric of weather potentially affecting elk aggregations: the wolf:1,000 elk ratio and average daily snow water equivalence (SWE). We estimated a wolf:1,000 elk ratio for each winter range each year. Precise estimates of wolf territories and numbers were not available, so our estimates of wolf:1,000 elk ratio represent a coarse-scale metric contrasting level of wolf predation risk across herds and years. We used estimates of wolf numbers on 31 December each year and applied these estimates to the elk data collected during the following January–March. We estimated the number of wolves per winter range as the total number of wolves in each known pack with a range documented to overlap any portion of the elk winter range. We used the herd-specific annual elk count as our metric of elk population size. In some areas, an individual wolf pack overlapped multiple elk winter ranges.

In this case, we calculated the wolf:1,000 elk ratio using the sum of the annual elk counts on each of the elk winter ranges. We calculated wolf:1,000 elk ratios in this manner for wolf packs using multiple elk winter ranges in the Gravelly Mountains and the Gallatin–Madison Mountains.

We estimated an average daily SWE value for the GYE based on data collected at 5 different snow water telemetry sites across the area (West Yellowstone [2,230 m], Lick Creek [2,090 m], Short Creek [2,135 m], Lakeview Ridge [2,257 m], Beaver Creek [2,394 m]). Although snow-sampling sites were located in higher elevation areas than wintering elk, we assumed that average patterns of SWE accumulation at the high elevation sites would capture the variation in snowpack across years of the study. We considered this estimate of average daily SWE to be an annual index of winter severity.

We evaluated 1 metric of elk population management: elk density on the winter range. We defined the spatial extent of each elk winter range based on all winter elk observations during the past 5 years. Observations included both information from the annual survey data and radiocollar data. We expected survey data going back 5 years to capture a range of variation in winter elk distributions across a variety of snowpack conditions. For each elk herd, we calculated an average elk density on the winter range as the total annual elk counted per unit area of the winter range (elk/km^2), averaged across the 5-year period. Because elk counts were not true population estimates, and the exact extent of the winter use area likely varied across the winters, we considered the elk density metric an approximation of average density associated with a particular elk herd. Because we screened data to censor elk counts with poor sightability, the elk density metric should reliably capture variations among herds.

Prior to developing our candidate models, we screened covariates for correlations and excluded pairs with Pearson's correlation coefficients correlations $|r| \geq 0.6$ from entering the same model. We developed a total of 13 a priori candidate models representing the potential effects of the above covariates on elk group sizes based on previous literature (Creel and Winnie 2005, Gude et al. 2006). We used a generalized linear mixed modeling approach to evaluate competing hypotheses regarding variations in group size. We natural log-transformed group size to create a normally distributed response variable. We standardized coefficients to allow for comparison of effect sizes. Landscape attributes, SWE, and elk herd density were each continuous covariates that we treated as fixed effects. Because the dataset included group size data collected from 27 different elk herds, we treated herd as a random effect. We evaluated competing models that included the random effect of herd and estimated parameters using restricted maximum likelihood (Zuur et al. 2009). We fit models in program R version 2.12.1 (R Core Team 2011) using an extension package for linear and nonlinear mixed effects models (nlme; Pinheiro et al. 2010). Additionally, because the upper ends of the group size distribution may be particularly important for disease transmission risk (Cross et al. 2010*a*), we used a quantile regression model to estimate effects of elk herd density on the upper end of the group size distribution.

We evaluated 11 a priori models assessing the probability that an elk group was large ($\geq$300; Cross et al. 2010*a*) given the environmental conditions using a logistic model. We standardized coefficients to allow for comparison of effect sizes. Because the response variable represented a group within herd-years, which resulted in a smaller sample size, our candidate a priori model set included only 1- and 2-predictor models. We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to rank competing models and Akaike model weights (w_i) to address model-selection uncertainty. For model interpretation, we estimated the odds of a large group occurring under different covariate combinations (Jacques et al. 2014).

We predicted the effects of reducing elk density by 10%, 50%, and 90% on group sizes and the proportion of the herd aggregated in large groups using the top-ranked models and holding all other covariates at their mean value. We then calculated the absolute reduction (i.e., the change in the probability that an elk is seropositive) in group size and proportion of the herd in large groups associated with density reductions.

Spatial Seroprevalence Model

We fit a Bayesian spatial seroprevalence model to estimate rates of brucellosis seroprevalence in each elk management district (Heisey et al. 2010). We had limited sampling data available for some districts. The spatial seroprevalence model enabled estimates to be generated for these districts in spite of limited or missing sample data. Further, because elk are free ranging across the study area and interchange occurs among herds, the spatial seroprevalance model reflected the process of elk movement across the landscape by estimating spatial covariance among adjacent units. We used a Bayesian approach because this type of analysis is more tractable in such a framework (Heisey et al. 2010).

We followed the model and coding of Heisey et al. (2010), except we had only 1 age class of elk because we were not interested in cohort effects or changes over time. Our response variable was the management district seroprevalence level, γ_{ij}, for individual elk i in management district j. We used a log-linear hazard model to relate management district seroprevalence to covariates. Our model included spatial covariance using a conditional autoregressive model at the individual animal level and a random effect across districts (Heisey et al. 2010). For the spatial relationships, we considered neighbors to be any 2 adjoining management districts, regardless of the length of the adjoining border.

We included 2 fixed covariates on prevalence: winter elk density (density) and season of sample collection (season). To calculate elk density at the management district level, we counted all elk within the management district boundary and divided by the total area of all winter ranges within the management district. We used the overall mean elk density for the 12 management districts lacking density information. We measured density as the number of elk per km^2 of winter range in a district. A previous study found samples collected

late in pregnancy (Jan–Mar) may be more likely to test positive than samples collected early in pregnancy (Cross et al. 2010*b*), potentially because of the association between brucellosis and late pregnancy. Therefore, we defined the season of sample collection as an indicator variable contrasting samples collected in fall (Sep–Dec) and samples collected in winter (Jan–Mar).

We fit the model in OpenBUGS version 3.2.2 (Spiegelhalter et al. 2012). We ran three chains of 100,000 iterations each of the Markov chain Monte Carlo (MCMC) with the first 10,000 removed for burn-in. We assessed goodness of fit by visually comparing the observed seroprevalence estimates (binomial estimates) to modeled estimates of seroprevalence for each district.

We used predicted estimates from the posterior distribution of seroprevalence rates to evaluate the potential effect of reducing elk density. We reduced density in 10% increments from 10–90%. We predicted reductions in elk density in management districts within the MCMC analysis to account for the spatial dependence and sampling covariance in the model. We calculated the absolute reductions in seroprevalence associated with density reductions.

RESULTS

We observed 919 elk groups from 27 elk herds between December and April of 2006 through 2011. We sampled 104 elk herd-years. Elk group sizes ranged from 1 to 2,610 and the median group size was 28. The proportion of each herd in large groups ranged from 0.00 in 60 herd-years to >0.95 in 3 different herd-years. Elk winter range density varied from 0.1 to 30.8 elk/km^2 among management districts, and median density was 3.9 elk/km^2 (Fig. 2). We located 132 elk groups in grasslands, 158 groups in forested cover, and 629 groups in shrublands. The amount of grasslands per winter range varied from 4.6% at Clark Canyon to 56.4% at HD 317 ($\bar{x} = 21.4$, SD = 13.0). Elevation ranged from 1,340 to 2,590 m ($\bar{x} = 1923$ m, SD = 226). Snow water equivalence ranged from 10.4 to 33.7 cm ($\bar{x} = 21.5$, SD = 5.7). The wolf:1,000 elk ratio ranged from 0 to 21.2 ($\bar{x} = 4.03$, SD = 4.8).

Group Sizes

The highest-ranked model explaining variation in elk group sizes included the covariates cover type, SWE, elevation, and elk density ($w_i = 0.94$; Fig. 2). Group sizes were similar between grasslands and shrublands ($\hat{\beta} = -0.13$, 95% CI = −0.41, 0.15), and between grasslands and forests ($\hat{\beta} = -0.30$, 95% CI = −0.65, 0.05). Group size increased as elk density increased ($\hat{\beta} = 0.21$, 95% CI = 0.06, 0.35). Group size increased as elk density increased ($\hat{\beta} = 0.21$, 95% CI = 0.06, 0.35). Across the range of elk densities observed, mean group size in grasslands was predicted to increase from 34 (95% CI = 24, 50) on a low elk-density winter range to 103 (95% CI = 52, 205) on a high elk-density winter range when estimates of other covariates were held at their mean. Mean group size in forested areas was predicted to increase from 26 (95% CI = 18, 37) on a low elk-density winter range to 77 (95% CI = 38, 155) on a high elk-density winter range (estimates with other covariates held at their mean). Mean group size increased as SWE decreased ($\hat{\beta} = -0.12$, 95% CI = −0.22, −0.01) and elevation decreased ($\hat{\beta} = -0.43$, 95% CI = −0.55, −0.31). When SWE was low, the predicted mean group size in grasslands was 56 (95% CI = 38, 80) and when SWE was high, the predicted mean group size decreased to 35 (95% CI = 23, 52; estimates created using min. and max. SWE values and holding other covariates at their mean). The second-ranked model also received some model support ($w_i = 0.05$) and included each of the covariates in the top model except elk density. Standardized coefficient estimates for cover type, SWE, and elevation were stable in the top 2 models. Other competing models were not well supported by the data ($w_i < 0.01$ or $\Delta AIC_c \geq 5.0$).

Based on predictions from the highest-ranked model, reducing the density of the three highest density elk herds by 10%, 50%, and 90% resulted in an average decrease in mean group size of 9%, 39%, and 59%, respectively (Table 1). Given a 90% reduction in elk density, mean group size in 2 of the 3 highest density herds was predicted to remain above the median group size of all groups in all the elk herds included in our analysis (Table 1). Reducing the density of the 3 lowest density elk herds by 10%, 50%, and 90% resulted in an average decrease in mean group size of 0%, 0.7%, and 1.3%, respectively (Table 1).

The quantile regression results indicated that median group size did not vary with elk density, but the 95th and 99th quantile of the group size distribution increased as elk density increased (Fig. 3). The slope of the 95th ($\hat{\beta} = 41.5$, 95% CI = 23.6, 54.2) and 99th ($\hat{\beta} = 96.8$, 95% CI = 94.7, 110.7) quantile regression line was greater than the slope of the ordinary least squares regression line ($\hat{\beta} = 8.8$, 95% CI = 6.5, 11.2).

Proportion of Herd in Large Groups

The highest-ranked model explaining the probability a group was large (>300) included elk density and percent grasslands ($w_i = 1.0$; Fig. 2). Based on comparison of the standardized coefficients, the effect of elk density 95th ($\hat{\beta} = 0.48$, 95% CI = 0.47, 0.50) was stronger than the effect of percent grassland ($\hat{\beta} = 0.33$, 95% CI = 0.32, 0.35). The estimated odds of elk occurring in large groups increased 7.2% (95% CI = 6.9, 7.4) for every 1-unit increase in elk density (elk/km^2) on the winter range. The estimated probability of elk occurring in a large group on a low-density (0.1 elk/km^2) elk winter range was 0.349 (95% CI = 0.349, 0.350) and increased to 0.813 (95% CI = 0.804, 0.827) on a high-density (30.8 elk/km^2) winter range. The estimated probability of elk occurring in a large group on a winter range with a low (4.6%) percentage of grasslands was 0.346 (95% CI = 0.343, 0.350) and increased to 0.663 (95% CI = 0.660, 0.667) on a winter range with a high (56.4%) percentage of grasslands (estimates created using the mean elk density).

Based on predictions from the highest-ranked model, reducing the density of the highest density elk herd by 10%, 50%, and 90% reduced the probability of elk occurring in a large group from 0.874 (95% CI = 0.867, 0.883) to 0.850 (95%

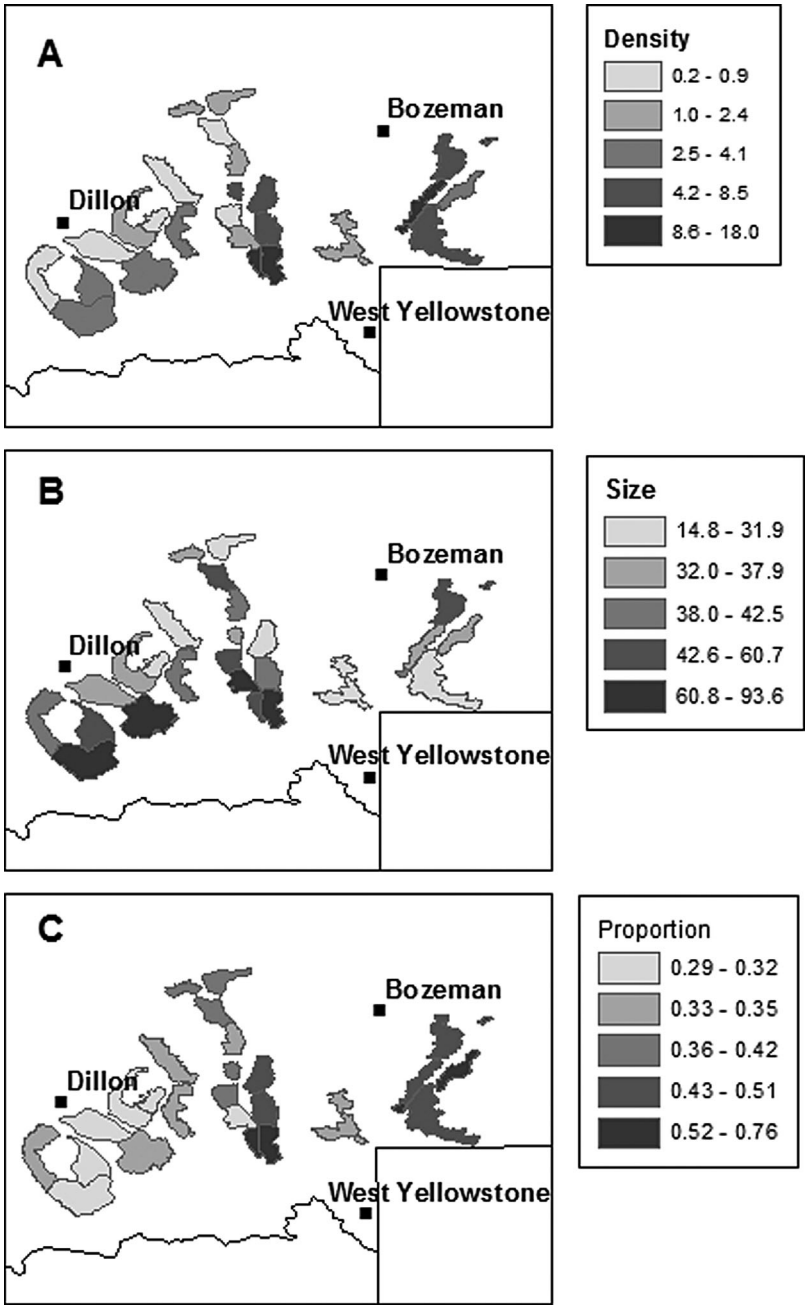

Figure 2. Estimated elk density (elk/km^2, Panel A), predicted mean group size (Panel B), and predicted proportion of the population occupying large groups (Panel C) for 27 elk herds in the southwestern Montana portion of the Greater Yellowstone Ecosystem. Elk density is estimated from annual survey data collected during 2006–2011. The predicted group size and proportion of the herd in large groups is generated from the top-ranked models.

CI = 0.741, 0.859), 0.708 (95% CI = 0.701, 0.717), and 0.511 (95% CI = 0.510, 0.513), respectively. Reducing the density of the second highest density (23.2 elk/km^2) elk herd by 10%, 50%, and 90% reduced the probability of elk occurring in a large group from 0.811 (95% CI = 0.803, 0.821) to 0.786 (95% CI = 0.777, 0.795), 0.658 (95% CI = 0.652, 0.665), and 0.503 (95% CI = 0.502, 0.504), respectively.

Spatial Seroprevalence Model

We tested 2,058 blood samples from individual elk collected in 39 management districts for exposure to brucellosis. Six hundred and sixteen samples were collected during the winter and the remainder during the fall. One hundred and eighty seven samples from 15 districts tested positive and the remainder tested negative (Table 2). The observed raw seroprevalence rate estimates varied from 0.00–0.28 across the 39 districts.

The model predicted seroprevalence rates varied from 0.01 to 0.27 across management districts (95% credible interval range = 0.00, 0.42; Table 2, Fig. 4). The median estimated seroprevalence rate for all districts was 0.05 (95% CI = 0.03, 0.07). Overall unit-to-unit variability was 24× higher than spatial variance ($\sigma_b = 1.21$, $\sigma_s = 0.05$). Observed and estimated district-level seroprevalence rates were similar,

Table 1. Estimated density of the 3 highest and 3 lowest density elk herds in the southwest Montana study area during 2006–2011, and estimated mean elk group size across a range of simulated elk herd reductions. The 95% confidence interval is denoted parenthetically below the mean group size estimate.

		Group size after density reduction			
Herd	**Density (elk/km2)**	**0% reduction**	**10% reduction**	**50% reduction**	**90% reduction**
Wall Creek	30.4	98.2 (46.0, 210.3)	88.1 (44.5, 174.8)	57.1 (39.1, 83.5)	36.9 (34.2, 39.9)
Tom Miner	27.2	58.9 (30.0, 116.3)	53.4 (29.0, 98.6)	36.2 (25.8, 50.9)	24.5 (22.9, 26.3)
HD 362	25.2	118.2 (63.1, 221.7)	108.0 (61.4, 190.3)	75.4 (55.1, 103.3)	52.6 (49.4, 56.1)
Axolotl	0.49	43.4 (42.9, 44.0)	43.4 (42.9, 43.9)	43.1 (42.8, 43.3)	42.8 (42.7, 42.8)
Sweetwater	0.35	38.0 (37.6, 38.3)	37.9 (37.6, 38.2)	37.7 (37.6, 37.9)	37.5 (37.5, 37.6)
Ruby Reservoir	0.29	19.0 (18.9, 19.1)	19.0 (18.9, 19.1)	18.9 (18.8, 19.0)	18.8 (18.8, 18.8)

indicating an adequate goodness of fit (Table 2). In several cases, districts with no observed seroprevalence had an estimate prevalence >0; however, in each of these cases the credible interval on estimated seroprevalence included 0 (Table 2). Seroprevalence was positively related to elk density ($\beta_1 = 0.09$, 95% CI = 0.02, 0.19). There was no relationship between seroprevalence and season of sample collection ($\beta_2 = -0.06$, 95% CI = −0.53, 0.37), indicating that samples from within a given management unit collected during fall and winter were equally likely to test positive.

Reducing elk density resulted in decreased estimates of seroprevalence (Table 2, Fig. 5). For the 7 units with >10% estimated seroprevalence, a 10% reduction in elk density resulted in an average 2% reduction in seroprevalence. Similarly, a 50% reduction resulted in an average 7% reduction and a 90% reduction resulted in an average 9% reduction in seroprevalence. However, the precision of the predicted effects of density reductions on seroprevalence is low, and in some cases credible intervals for seroprevalence estimates corresponding to 10% and 90% density reductions overlap.

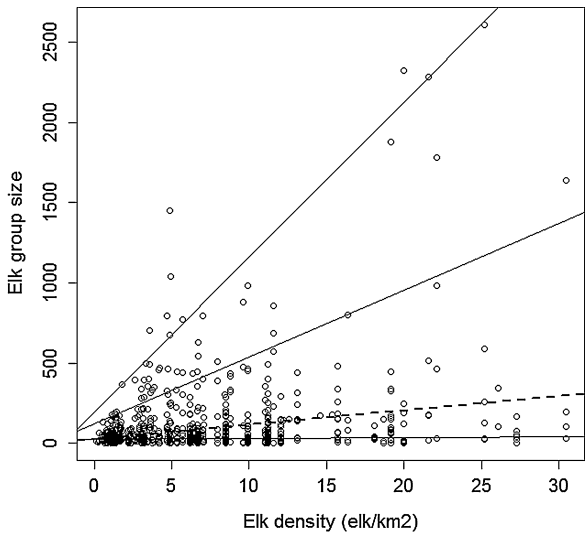

Figure 3. Scatterplot of elk group size and elk density for a sample of 919 elk group observations in the Greater Yellowstone Ecosystem during 2006–2011. We show the 50th (bottom line), 95th (middle line), and 99th (top line) quantile regression lines (solid lines) and the least squares estimate of the conditional mean function (dashed line).

DISCUSSION

We documented wide spatial variation in elk densities and found density affected elk aggregation patterns and brucellosis seroprevalence. As density increased, elk group size increased, the size of the largest groups increased, and the proportion of herds in large groups increased. This suggests that density may increase elk exposure to brucellosis by aggregating elk into larger groups where elk-to-elk contact rates and disease transmission risk is increased (Cross et al. 2013). These aggregation behaviors and the formation of large groups may be particularly important in the dynamics of elk-to-elk brucellosis transmission because in many areas, infected fetuses remain on the ground only for short periods of time because of the presence of scavengers (Maichak et al. 2009, Aune et al. 2012). Therefore, transmission may be driven by localized density and size of elk groups rather than density within the entire management district.

Vegetation characteristics of the winter range, such as cover type and the proportion of grasslands, also affected elk aggregations. Winter ranges characterized by a higher proportion of grasslands had a higher proportion of the herd aggregated into large groups, suggesting that elk in grassland-dominated winter ranges may be particularly at risk of elk-to-elk transmission. Elk densities could potentially be manipulated to reduce the size of elk aggregations. However, on winter ranges with a higher proportion of grasslands, effects of reducing elk densities on reducing disease transmission risk may be small if animals remain likely to aggregate in larger groups.

The effect of predation risk on elk aggregation patterns has received considerable attention and has showed habitat-specific elk aggregation (or disaggregation) responses to predation risk (Hebblewhite and Pletscher 2002; Creel and Winnie 2005; Gude et al. 2006; Proffitt et al. 2009, 2012). However, we found no evidence that landscape-level variations in wolf predation risk affected elk aggregation patterns. Our results contrast the site-specific studies within our larger study area that documented effects of predation risk on elk aggregation patterns, most of which evaluated finer-scale spatial or temporal variations in wolf predation risk (Creel and Winnie 2005; Gude et al. 2006; Proffitt et al. 2009, 2012). The coarse-scale metric of wolf risk we evaluated may have failed to detect fine-scale elk aggregation responses to predation risk, or at the winter range–scale,

Table 2. Summary statistics and estimated rates of adult female elk exposure to *Brucella abortus* in 39 elk management districts in southwest Montana. Elk density averaged over 2006–2011 (density, measured as elk per km^2) was included as a covariate of seroprevalence. The number of brucellosis serology samples screened per management district (district) is shown along with the observed binomial (observed) and model-estimated brucellosis seroprevalence (estimated). The median and 95% credible intervals (LCL, UCL) for estimated seroprevalence is shown, as well as estimated median seroprevalence across a range of simulated elk herd density reductions.

			Prevalence				Seroprevalence after density reduction				
District	Density	*n*	Observed	Estimated	LCL	UCL	10%	30%	50%	70%	90%
250	5.9	42	0.00	0.01	0.00	0.05	0.01	0.01	0.01	0.01	0.01
270	20.7	38	0.00	0.02	0.00	0.09	0.02	0.01	0.01	0.00	0.00
300	3.2	46	0.00	0.01	0.00	0.05	0.01	0.01	0.01	0.01	0.01
301	2.7	2	0.00	0.02	0.00	0.16	0.02	0.02	0.02	0.02	0.01
302	1.7	19	0.00	0.01	0.00	0.07	0.01	0.01	0.01	0.01	0.01
309		1	0.00	0.02	0.00	0.28	0.02	0.02	0.02	0.02	0.01
310	2.6	1	0.00	0.02	0.00	0.19	0.02	0.02	0.02	0.02	0.02
311	13.2	114	0.17	0.16	0.10	0.25	0.14	0.11	0.09	0.07	0.06
312		6	0.00	0.02	0.00	0.15	0.02	0.02	0.01	0.01	0.01
313	12.6	285	0.13	0.12	0.09	0.17	0.11	0.09	0.07	0.06	0.04
314	11.0	240	0.05	0.05	0.03	0.09	0.05	0.04	0.03	0.03	0.02
315		28	0.00	0.01	0.00	0.07	0.01	0.01	0.01	0.01	0.01
317	6.0	21	0.19	0.13	0.04	0.30	0.12	0.11	0.10	0.09	0.08
319	7.6	1	0.00	0.03	0.00	0.24	0.02	0.02	0.02	0.02	0.01
320	2.4	85	0.00	0.01	0.00	0.03	0.01	0.01	0.01	0.01	0.01
321		5	0.00	0.02	0.00	0.16	0.02	0.01	0.01	0.01	0.01
322	1.1	12	0.00	0.01	0.00	0.08	0.01	0.01	0.01	0.01	0.01
323	30.8	36	0.28	0.27	0.15	0.42	0.21	0.12	0.07	0.04	0.02
324	10.5	26	0.12	0.09	0.02	0.22	0.08	0.06	0.05	0.04	0.04
325	3.3	101	0.05	0.04	0.02	0.10	0.04	0.04	0.04	0.04	0.03
326	0.1	107	0.14	0.13	0.07	0.24	0.13	0.13	0.13	0.13	0.13
327		20	0.05	0.04	0.00	0.14	0.03	0.03	0.03	0.02	0.02
328	2.5	8	0.00	0.01	0.00	0.10	0.01	0.01	0.01	0.01	0.01
329	1.5	57	0.00	0.01	0.00	0.04	0.01	0.01	0.01	0.01	0.01
330	4.5	16	0.00	0.01	0.00	0.09	0.01	0.01	0.01	0.01	0.01
331	1.7	24	0.00	0.01	0.00	0.06	0.01	0.01	0.01	0.01	0.01
332	0.4	95	0.04	0.03	0.01	0.08	0.03	0.03	0.03	0.03	0.03
333	1.3	14	0.00	0.01	0.00	0.08	0.01	0.01	0.01	0.01	0.01
340		2	0.00	0.02	0.00	0.23	0.02	0.02	0.02	0.01	0.01
360	4.1	186	0.11	0.10	0.06	0.15	0.10	0.09	0.08	0.08	0.07
361		18	0.11	0.07	0.01	0.23	0.07	0.06	0.05	0.04	0.03
362	23.2	306	0.18	0.18	0.14	0.23	0.15	0.10	0.06	0.04	0.03
370		1	0.00	0.02	0.00	0.29	0.02	0.02	0.02	0.02	0.01
380		2	0.00	0.02	0.00	0.23	0.02	0.02	0.02	0.02	0.01
393		62	0.00	0.01	0.00	0.04	0.01	0.01	0.01	0.01	0.01
520		14	0.00	0.01	0.00	0.10	0.01	0.01	0.01	0.01	0.01
560	3.9	12	0.00	0.01	0.00	0.09	0.01	0.01	0.01	0.01	0.01
570		1	0.00	0.02	0.00	0.28	0.02	0.02	0.02	0.01	0.01
575		4	0.00	0.02	0.00	0.18	0.02	0.02	0.01	0.01	0.01

variations in the level of predation risk may have little consistent impact on elk aggregation patterns.

In addition to affecting elk aggregations, elk management district density was positively related to levels of elk exposure to brucellosis. As predicted, the coefficient for the effect of elk density on seroprevalence was positive, and the 95% credibility interval did not span 0. Similar increases in seroprevalence have been reported in the southern GYE, with areas of higher elk density having higher levels of brucellosis exposure than areas with lower elk density (Cross et al. 2010*a*).

The spatial seroprevalence model suggests that elk in areas outside of the brucellosis DSA may have low levels of brucellosis exposure, and this result has important consequences for brucellosis surveillance and management efforts. However, the credible intervals included 0, highlighting the potential that the disease may not be present outside of the DSA. Binomial estimates in most of these districts were based on small sample sizes, and sampling effort may have been inadequate to detect the disease if it was present. The spatial seroprevalence model used the limited data together with the spatial covariance structure to estimate seroprevalence rates, and estimates were >0%. Although the spatial seroprevalence model predicted low levels seroprevalence in the districts along the outer boundary of the DSA, the distinction between no disease exposure and low levels of exposure has important consequences for elk management actions and livestock production. Additional disease surveillance and testing would confirm disease presence, and the estimated rates of seroprevalence may be useful in targeting surveillance in areas where exposure is most likely.

The DSA was created to meet a federal requirement for states with *Brucella abortus* in wildlife populations. These 3 states must develop and implement a brucellosis management plan for livestock to keep the entire state from being downgraded from a brucellosis "Class Free" status, which has

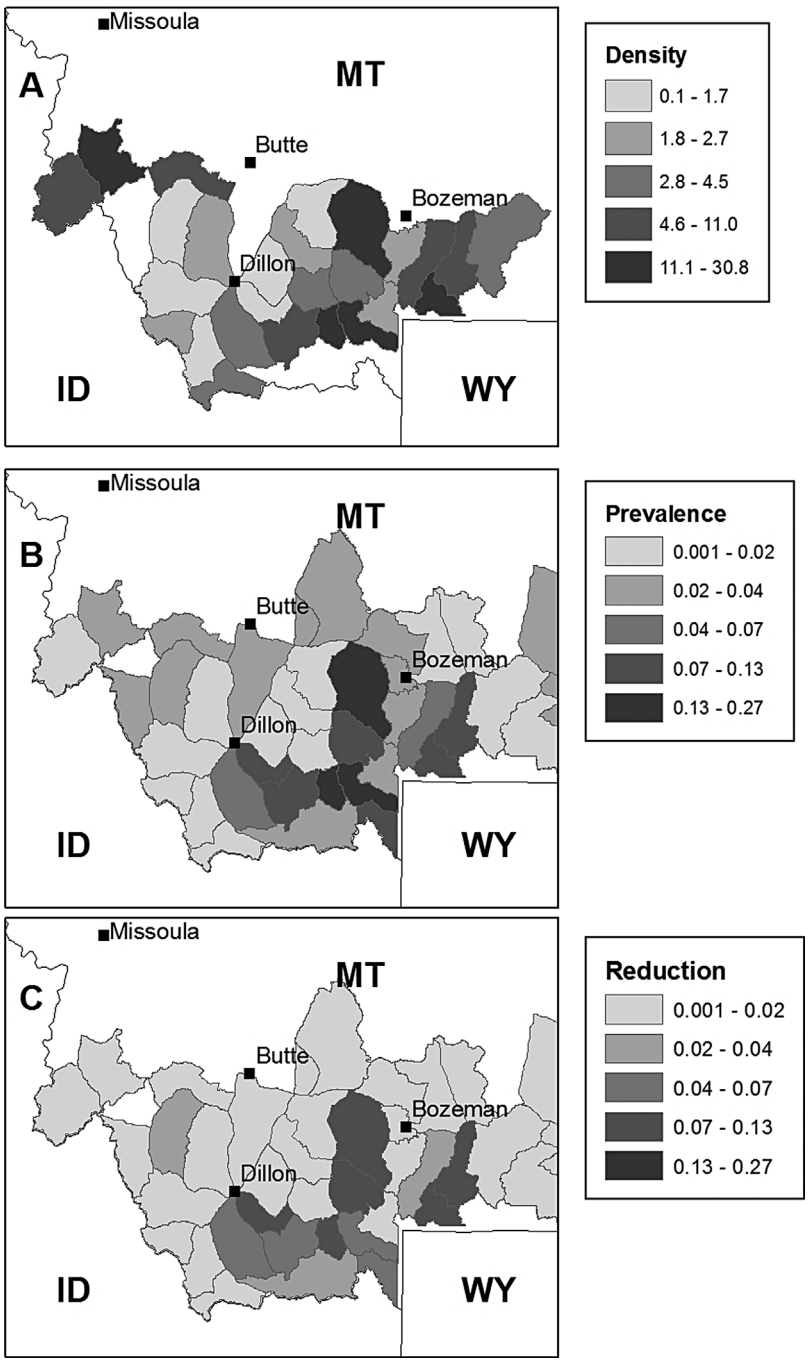

Figure 4. The estimated elk density (elk/km^2, Panel A), elk brucellosis seroprevalence (Panel B), and elk brucellosis seroprevalence estimated assuming a 50% reduction in elk density (Panel C) in 39 southwestern Montana elk management districts in during 2001–2013.

negative consequences for livestock producers. The boundaries of the DSA are based on where brucellosis is found in wildlife, and livestock producers within the DSA are subjected to increased testing, vaccination, and handling costs (Montana Department of Livestock 2011). Livestock exposure to brucellosis as a result of elk-livestock transmission outside the DSA erodes confidence in that management plan. Therefore, any level of elk to livestock transmission risk outside of the DSA has important social consequences for livestock producers. Although our seroprevalence model does predict some level of risk outside of the DSA, the spatial covariance driving these estimates is low and disease exposure beyond the DSA boundary has not been confirmed with field testing to date. Unit-specific binomial estimates may accurately characterize seroprevalence, particularly if large samples of adult female elk are tested. Surveillance efforts should be designed with sample sizes adequate to detect disease presence. To determine the spatial extent of brucellosis, expansion of targeted surveillance efforts along the outer edge of the DSA is warranted.

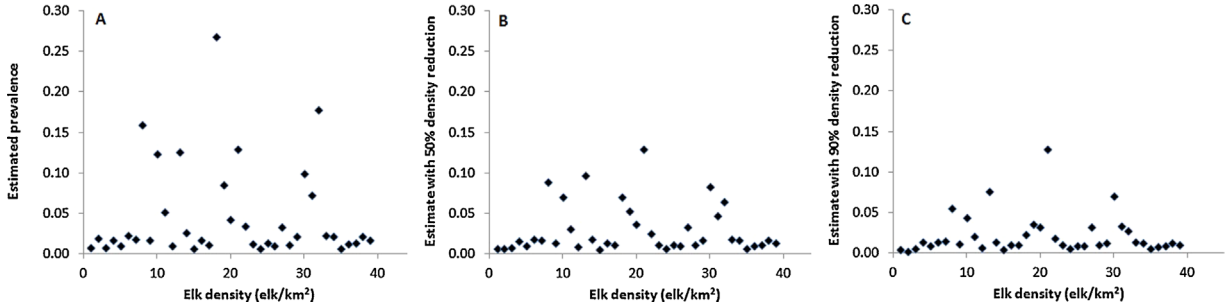

Figure 5. The estimated rates of adult female elk exposure to *Brucella abortus* (estimated prevalence) and density of wintering elk across a range of simulated elk density reductions in southwest Montana based on data collected in 2001–2013. Panel A shows estimated prevalence under current conditions, Panel B shows estimated prevalence given a 50% reduction in elk density, and Panel C shows estimated prevalence given a 90% reduction in elk density.

MANAGEMENT IMPLICATIONS

Although our results show that increasing elk density may result in increased elk aggregations and seroprevalence, the predicted reductions in elk density from our models suggest that reducing elk density may not be an effective management approach to reduce elk exposure to brucellosis because the degree to which elk density would need to be reduced is unlikely to be socially acceptable. Previous work has suggested that elk become maintenance hosts for brucellosis as a result of large aggregations once a threshold is exceeded (Cross et al. 2010*a*). If brucellosis does persist at some population threshold within wild elk, this could have important implications for disease transmission. However, there is currently no empirical evidence that a threshold exists, or an empirical estimate of what that threshold may be. Our modeling predicts relatively large reductions in elk density are likely needed to produce measureable impacts on seroprevalence. However, reductions of this magnitude are unlikely to be compatible with other objectives related to elk management and conservation. We suggest that managers consider addressing disease containment in addition to reduction of exposure rates, perhaps by focusing aggregation management controls such as hazing or hunting in high-density populations where seroprevalence is still at a relatively low level.

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