



## Research Article

# Modeling Elk-to-Livestock Transmission Risk to Predict Hotspots of Brucellosis Spillover

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**ABSTRACT** Wildlife reservoirs of infectious disease are a major source of human–wildlife conflict because of the risk of potential spillover associated with commingling of wildlife and livestock. In the Greater Yellowstone Ecosystem, the presence of brucellosis (*Brucella abortus*) in free-ranging elk (*Cervus canadensis*) populations is of significant management concern because of the risk of disease transmission from elk to livestock. We identified how spillover risk changes through space and time by developing resource selection functions using telemetry data from 223 female elk to predict the relative probability of female elk occurrence daily during the transmission risk period. We combined these spatiotemporal predictions with elk seroprevalence, demography, and transmission timing data to identify when and where abortions (the primary transmission route of brucellosis) were most likely to occur. Additionally, we integrated our predictions of transmission risk with spatiotemporal data on areas of potential livestock use to estimate the daily risk to livestock. We predicted that approximately half of the transmission risk occurred on areas where livestock may be present (i.e., private property or grazing allotments). Of the transmission risk that occurred in livestock areas, 98% of it was on private ranchlands as opposed to state or federal grazing allotments. Disease prevalence, transmission timing, host abundance, and host distribution were all important factors in determining the potential for spillover risk. Our fine-resolution (250-m spatial, 1-day temporal), large-scale (17,732 km<sup>2</sup>) predictions of potential elk-to-livestock transmission risk provide wildlife and livestock managers with a useful tool to identify higher risk areas in space and time and proactively focus actions in these areas to separate elk and livestock to reduce spillover risk. © 2019 The Authors. *The Journal of Wildlife Management* published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

**KEY WORDS** *Brucella abortus*, *Cervus canadensis*, cross-species pathogen spillover, Greater Yellowstone Ecosystem, habitat selection, human–wildlife conflict, resource selection function, wildlife disease.

The ability to predict pathogen spillover in space and time from reservoirs of infectious diseases remains a persistent challenge in disease ecology (Plowright et al. 2017, White et al. 2018). These reservoirs have the potential to adversely affect the health of wildlife, humans, and domestic animals (Daszak et al. 2000, Cassirer et al. 2018), to negatively influence economic development and activity (Nishi et al. 2006, National Academies of Sciences, Engineering, and Medicine [NASEM] 2017), and to erode public support for

wildlife and conservation efforts (Madden 2004, Haggerty et al. 2018). Despite these threats, there have been relatively few studies that have combined ecological, epidemiological, and behavioral datasets to predict the spatiotemporal dynamics of disease spillover (Plowright et al. 2017, White et al. 2018).

Epidemiological models have typically focused on the temporal components of disease transmission (Diekmann et al. 2012), while disregarding the effect of host movements on host–pathogen dynamics (Dougherty et al. 2018). This simplification of the contact process ignores host behavior, thereby disregarding an essential component of disease transmission dynamics (Zidon et al. 2017, Dougherty et al. 2018). The field of movement ecology (Kays et al. 2015) offers useful tools to help describe and predict heterogeneous disease transmission between hosts, and to pose novel questions about the effects of animal movements on disease dynamics (Dougherty et al. 2018). For diseases with highly mobile wildlife hosts and long periods of potential

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transmission, integrating spatial heterogeneity of host movements into disease models may be particularly important to adequately forecast spillover dynamics (Kilpatrick et al. 2009, White et al. 2018, Merkle et al. 2018). It remains rare and challenging, however, to simultaneously model movement and epidemiological processes because of the difficulties associated with synthesizing movement and disease ecology data streams collected at varying spatial and temporal resolutions and scales (Dougherty et al. 2018). Further complexity frequently arises because of the large amounts of data required for, and the high computational demand associated with, integrated modeling approaches (Dougherty et al. 2018).

Bovine brucellosis, caused by the bacterium *Brucella abortus*, is an important zoonotic disease worldwide that causes chronic infections in wildlife, livestock, and humans (Pappas et al. 2006). Following an extensive eradication program by the United States Department of Agriculture in the last century, brucellosis was nearly eliminated from the United States (Ragan 2002). It still persists, however, in elk (*Cervus canadensis*) and bison (*Bison bison*) populations in the Greater Yellowstone Ecosystem (GYE; NASEM 2017). Brucellosis causes reproductive failures in elk, bison, and cattle, with transmission occurring when individuals physically contact *Brucella abortus* bacteria in aborted fetuses, placentas, or birthing fluids (Cheville et al. 1998). In the GYE, elk are the source of recent livestock infections (Rhyan et al. 2013, Kamath et al. 2016). Although rare, these spillover events are occurring with increasing frequency (Cross et al. 2013, Brennan et al. 2017), and are of substantial concern for livestock producers because of the associated costs of livestock quarantine and trade restrictions (NASEM 2017). Brucellosis appears to be spreading into new elk populations in the GYE, and the seroprevalence is increasing in some elk herds (Brennan et al. 2017, NASEM 2017). Currently, a designated surveillance area within which domestic bison and cattle (livestock) must be tested prior to moving to other regions, keeps the rest of the United States livestock population free of the disease.

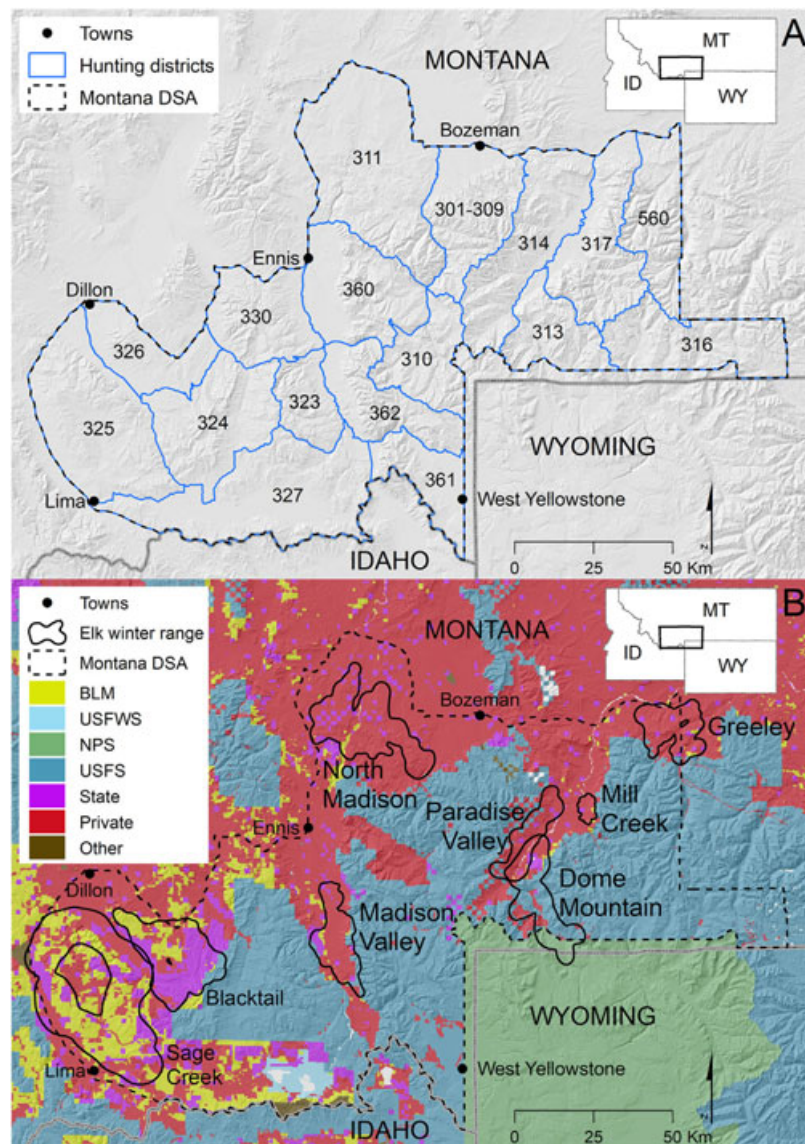
Ecological, epidemiological, and behavioral factors need to align before cross-species pathogen spillover can occur (Plowright et al. 2017). Elk-to-livestock brucellosis transmission involves interactions among seroprevalence, demography and density, distribution, the timing of abortions in elk, and the distribution and density of livestock (NASEM 2017). These dynamic interactions occur over relatively long time-scales and large geographic areas. The transmission period for brucellosis in elk spans >4 months (Cross et al. 2015). During this time, elk in the GYE migrate tens to hundreds of kilometers from winter to summer range (White et al. 2010, Barker 2018).

Previously, Proffitt et al. (2011) developed predictive models of elk space use to estimate the risk of elk and livestock commingling during the brucellosis transmission risk period within a portion of the Montana, USA, designated brucellosis surveillance area (DSA). Since that research was conducted, the Montana Department of Fish,

Wildlife and Parks (MFWP) initiated a multi-year brucellosis surveillance project to collect additional seroprevalence and elk movement data throughout the Montana DSA. Additionally, the seasonal timing of elk abortion events in the GYE (i.e., abortion phenology) was quantified for the first time (Cross et al. 2015). With these new sources of information, it is now possible to develop an integrated model that provides a more comprehensive evaluation of elk-to-livestock brucellosis transmission risk throughout the Montana DSA. We combined elk seroprevalence, elk demography and density, elk distribution, elk abortion phenology, and livestock distribution data to quantify the distribution of elk transmission risk, and determine the spatiotemporal overlap of elk transmission risk with areas of potential livestock presence.

## STUDY AREA

We studied elk in the Montana DSA in southwest Montana. Eighteen Montana elk hunting districts occurred partially or entirely within the DSA, which was 17,732 km<sup>2</sup> in 2016 (Fig. 1A). Since it was first delineated in 2010, the DSA has expanded several times as elk outside the boundaries have tested positive for exposure to *B. abortus*. The DSA was characterized by short, cool summers and long, cold winters, and was a mixture of private, Bureau of Land Management (BLM), United States Fish and Wildlife Service (USFWS), United States Forest Service (USFS), and state government lands. Privately owned lands within the DSA were a mixture of agriculture and residential and exurban development. These private lands were more likely to occur at lower elevations, whereas publicly owned lands were more likely to occur at higher elevations. Elevations ranged from 1,200 m to 3,900 m. Vegetation was characterized by open sage-grassland communities consisting of sagebrush (*Artemisia* spp.), Idaho fescue (*Festuca idahoensis*), and blue-bunch wheatgrass (*Pseudoroegneria spicata*) at lower elevations. At mid elevations, Douglas fir (*Pseudotsuga menziesii*), and lodgepole pine (*Pinus contorta*) forests and herbaceous meadows predominated. Spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) forests and herbaceous meadows dominated at higher elevations. In addition to elk, the large mammal community in the DSA included mule deer (*Odocoileus hemionus*), white tail deer (*Odocoileus virginianus*), pronghorn (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), moose (*Alces alces*), bison (*Bison bison*), wolves (*Canis lupus*), mountain lions (*Puma concolor*), American black bears (*Ursus americanus*), coyotes (*Canis latrans*), and grizzly bears (*Ursus arctos*). Using elk trend counts, we estimated that there were ≥26,800 elk (including ~17,500 adult female elk) living within the DSA in 2016. Within the risk period for brucellosis transmission from elk to livestock, we defined winter (15 Feb–31 Mar; elk on winter range), spring (1 Apr–31 May; elk migrating to summer range), and summer (1 Jun–30 Jun; elk on summer range) seasons based upon elk movement and aggregation patterns.



**Figure 1.** A) Elk hunting districts (HDs; labeled with black text) within the Montana, USA, designated brucellosis surveillance area (DSA; black dashed line). We merged HD 301 and HD 309 in our analyses and the portion of HDs 301-309, 311, 316, and 560 that extend beyond the border of the DSA are not shown. Shading depicts hillshade of elevation. B) Winter ranges of 8 elk herds (labeled with black text) within the Montana DSA where adult female elk were radio-collared from 2005–2015, and the matrix of Bureau of Land Management (BLM), United States Fish and Wildlife Service (USFWS), National Park Service (NPS), United States Forest Service (USFS), state government (State), private (Private), and other (Other) lands in the region. Shading depicts hillshade of elevation.

## METHODS

We captured adult female elk  $\geq 2$  years of age from 8 herds within the DSA by helicopter net-gunning or chemical immobilization during January–March 2005–2015 (Fig. 1B). During initial captures, we collected a blood sample and used pregnancy-specific protein B (PSPB) analysis (BioTracking, Moscow, ID, USA) to determine pregnancy. We radio-collared elk with global positioning system (GPS)-collars that attempted to acquire a location every 0.5, 1, or 2 hours (GPS 3300L, Lotek Wireless, New Market, Ontario, Canada), and we monitored individual elk for 1–5 years. We followed MFWP biomedical protocols for free-ranging cervidae in Montana during capture and handling procedures (Protocol FWP04-2018). Most brucellosis transmission

events in elk occur between 15 February and 30 June (Cross et al. 2015); therefore, we limited our analyses to this time (i.e., risk period).

To predict the risk of brucellosis transmission from elk to livestock within the DSA, we followed a similar framework to Merkle et al. (2018). We estimated the occurrence of adult female elk using resource selection functions (RSFs; Manly et al. 2002); combined our RSF elk occurrence estimates with estimates of adult female elk abundance, seroprevalence, pregnancy rates, and transmission phenology to predict the daily relative risk of abortion events; and estimated the proportion of risk occurring on public and private lands and within private ranchland and federal and state livestock allotments during an average snowfall year (Fig. S1, available

online in Supporting Information). Our approach differed from that of Merkle et al. (2018) by accounting for the potential distribution of livestock and because we used a metric of relative risk and not the number of abortion events to quantify transmission potential. In addition, to predict elk distribution, we used RSFs rather than converting parameterized step-selection functions into integro-difference equations of space use (Potts et al. 2014; Merkle et al. 2017, 2018). We did so because visual evaluations during a previous analysis (N. D. Rayl, U.S. Geological Survey, unpublished data) indicated that RSF space-use predictions matched the observed data better than integro-difference equations of space use for these elk herds. The integro-difference equations frequently predicted elk in areas where they were not observed and failed to predict them in areas where they were observed.

### Resource Selection Function Development

We developed RSFs to characterize the spatiotemporal relationship between the relative probability of female elk occurrence and landscape attributes. Because all of the Montana DSA was potential elk range, and our primary objective was to identify fine-scale spatiotemporal overlap of elk abortion events with areas of potential livestock presence, we used third-order RSFs (selection of patches within individual home ranges [Meyer and Thuiller 2006]) to characterize habitat selection. Because we anticipated resource selection to vary seasonally, we built a separate RSF for each season. In our RSFs, we compared the habitat characteristics of observed locations with an equal number of available locations using a generalized linear mixed model (GLMM) with a binomial distribution, logit link, and individual-year nested within herd as the random intercept. The random intercept accounted for the unbalanced sample sizes among elk-years, and the non-independence of GPS locations and herds (Gillies et al. 2006). We generated available locations by randomly sampling within a 99% contour of a bivariate normal kernel calculated with the reference bandwidth for each elk-year in each season (Worton 1989). We assigned available locations to a specific day randomly drawn with replacement from the distribution of days of the corresponding elk-year-season observed locations. In each season our RSFs took the form:

$$w(x) = \exp(\beta_1 x_{1ijb} + \beta_2 x_{2ijb} + \dots + \gamma_{0j} + \gamma_{0b}) \quad (1)$$

where  $w(x)$  represented the RSF scores;  $\beta_u$  was the selection coefficient for explanatory variable  $x_u$  for the  $i$ th observation,  $j$ th individual-year, and  $b$ th herd;  $\gamma_{0j}$  was the random intercept for the  $j$ th individual-year; and  $\gamma_{0b}$  was the random intercept for the  $b$ th herd.

We used variables that are important predictors of elk occurrence in our RSFs (Proffitt et al. 2011, Merkle et al. 2018): elevation, slope, terrain position index (calculated as the difference between the elevation of a cell and the mean elevation of its nearest 80 surrounding cells), solar radiation during the risk period (30-m resolution, U.S. Geological Survey National Elevation Dataset), distance to motorized

roads (30-m resolution, U.S. Department of Commerce, Bureau of the Census), landcover type (consolidated into 4 categories: forest, shrub, agriculture, grass [reference category]; 30-m resolution, 2011 National Land Cover Database), snow cover (500-m spatial and 8-day temporal resolution, MODIS data; Hall et al. 2002), overall productivity or biomass of a habitat patch each year calculated as the annual integrated normalized difference vegetation index (NDVI; 250-m resolution, MODIS data; Pettorelli et al. 2005), and the phenological stage of a habitat patch calculated as the daily NDVI value of a patch (250-m resolution; scaled between 0 and 1). We assigned daily values of snow cover to each pixel using the pixel value from the 8-day snow cover interval that encompassed that day. To derive daily NDVI values, we followed the methods of Bischof et al. (2012) and Merkle et al. (2016) to construct a smoothed and scaled NDVI time series for each pixel. Merkle et al. (2016) provides additional details for methods.

Before building seasonal RSFs, we conducted preliminary analyses to select functional forms of continuous variables. We tested whether a linear or quadratic functional form for elevation, slope, solar radiation, and phenological stage and whether a linear or pseudothreshold (natural logarithm transformed distance + 1; Prokopenko et al. 2017) functional form for distance to motorized roads was better supported. For the functional forms of each variable in each season, we built univariate GLMMs and determined the form with the most support using Akaike's Information Criterion for small sample sizes (AIC<sub>c</sub>; Burnham and Anderson 2002). We similarly evaluated support for different spatial scales for all non-time-varying variables, except distance to motorized roads (Laforge et al. 2015). For each of these variables, we iteratively calculated moving window averages (at the resolution of the original data) within concentric radii (30, 100, 250, 500, 750, 1,000 m; Ranglack et al. 2017) larger than the resolution of the original data. This resulted in spatial scales of 30, 100, 250, 500, 750, and 1,000 m for all variables except annual integrated NDVI, which we calculated at scales of 250, 500, 750, and 1,000 m. We selected the spatial scale with the most support for each variable in each season by building GLMMs and determining support using AIC<sub>c</sub>. We were unable to evaluate different spatial scales for time-varying variables (snow cover, daily NDVI) because of computational limitations. We tested for collinearity between pairs of covariates prior to building seasonal RSFs and detected no issues (Pearson's correlation coefficient <0.7 for all variables). We also evaluated our RSFs for multicollinearity using the variance inflation factor (VIF; without quadratic terms; Graham 2003), and detected no issues (VIFs for all variables ≤3.04; Dormann et al. 2013).

We used cross-validation procedures to assess the internal accuracy and external applicability of our RSF models. To evaluate the internal accuracy of each seasonal RSF, we used a k-fold cross validation procedure (Boyce et al. 2002). For each iteration of this procedure, we followed Equation (1) to estimate an RSF model built with 80% of the elk data, withholding 20% for evaluation. We then reclassified the available locations of the excluded data into 10 ordinal bins

based on the percentile range of the RSF-predicted scores for those locations from the RSF model estimated with 80% of the data. To evaluate model performance, we calculated the Spearman rank correlation ( $r_s$ ) between the frequency of occurrence of RSF-predicted scores for the withheld used locations and the ranked RSF-availability bins. We repeated this process 100 times.

To assess external applicability, thereby estimating the generalizability of our space-use predictions to unsampled elk herds within the DSA, we iteratively fit seasonal RSFs using data from 7 of 8 sampled herds (3 seasons  $\times$  8 herds = 24 partial RSF models; estimated using Equation (1)). For each partial RSF model, we reclassified the available locations of the excluded herd into 10 ordinal bins based on the percentile range of the partial RSF-predicted scores for those locations. We then calculated the  $r_s$  between the frequency of occurrence of RSF-predicted scores for used locations from the excluded herd and the ranked RSF-availability bins. This allowed us to evaluate the ability of the partial RSF model to predict the space use of the excluded herd.

### Predicting Transmission Risk

We quantified the relative risk of elk abortion events on a daily 250-m grid of the DSA, and determined the spatiotemporal overlap of relative risk with areas of potential livestock presence for an average snowfall year. We downloaded snow water equivalent (SWE) data from 19 SNOTEL sites (U.S. Department of Agriculture, Natural Resources Conservation Service) located within the Montana DSA during all years that we monitored elk (2005–2015). At each site in each year, we calculated the cumulative SWE value from 1 October to 30 April. Because of the variation in cumulative SWE values among sites, we calculated an SWE anomaly for each site in each year. We calculated the cumulative SWE anomaly by subtracting the mean cumulative SWE value from 2005–2015 for individual sites from the cumulative SWE value for each site in each year. We then identified a representative year for average snowfall (2013) from among the years of elk monitoring (Fig. S2).

Resource selection functions produce relative probability values that are proportional to the probability of use (Manly et al. 2002). Therefore, we estimated the predicted relative probability of adult female elk use  $u(x, t)$  per 250-m pixel  $x$ , per time step  $t$  (in days) within each hunting district, as:

$$u(x, t) = \frac{w_{xt}}{\sum_{i=1}^n w_{xi}} \quad (2)$$

where  $i$  = refers to pixels 1 through  $n$  for time step  $t$ , and  $w_{xt}$  is the daily predicted RSF value of the relative probability of use by elk for a 250-m pixel  $x$ . The denominator served as a normalizing constant, ensuring that  $\sum_{i=1}^n x_i$ . We resampled all covariate grids from their original resolution to 250 m by calculating the mean pixel value that fell within the extent of the output 250-m pixel. Following Merkle et al. (2018), we then calculated the relative risk of abortion events  $R_{xt}$  per 250-m pixel  $x$ , per time step  $t$  (in days), as:

$$R_{xt} = u(x, t) \times N_{dt} \times S_d \times y \times p_t \quad (3)$$

where  $u(x, t)$  is the daily predicted relative probability of elk use for pixel  $x$  within hunting district  $d$ ,  $N_{dt}$  is the daily estimated number of female elk in that hunting district  $d$  during time step  $t$ ,  $S_d$  is the average brucellosis seroprevalence estimated for each hunting district  $d$ ,  $y$  is a mean pregnancy rate of 90%, and  $p_t$  is the predicted daily probability of aborting given an individual is seropositive and pregnant during time step  $t$  (Cross et al. 2015). This equation highlights an important issue whereby datasets are collected at different spatial and temporal scales, creating what is referred to as a change in support problem and the related ecological fallacies and modifiable areal unit problem (Openshaw 1984, Gotway and Young 2002). In our analyses, we assumed that seroprevalence ( $S_d$ ) did not vary within a district, pregnancy was constant across all districts, and the timing of abortions did not vary among or within districts. The elk distribution within a district, however, is the product of the overall count within that district (accounting for movement into and out of the district over the season) and the resource selection of elk in that area (Fig. S1). Solving this change of support problem remains an important area of statistical development and is an important hurdle to predicting disease spillover that requires combining many different data sources.

We used data from MFWP to calculate the number of female elk and brucellosis seroprevalence for each hunting district. Each winter, MFWP collects elk survey data on winter range (Fig. S3; see Proffitt et al. 2015 for additional details). We averaged calf:female ratios from the 3 most recent years of survey data to estimate the number of elk calves per 100 adult females  $c$  (this ratio is not estimated every year), and we assumed the number of adult male elk per 100 adult females  $m$  was 10 for all herds (MFWP, unpublished data). We estimated the proportion of adult female elk  $z$  as:

$$z = 1 - (c + m/100 + c + m) \quad (4)$$

We had detailed movement data for 8 collared elk herds. We distributed the estimated number of adult female elk from these sampled herds among the hunting districts of the DSA according to the movement patterns of collared females. Because we lacked movement data for unsampled herds, we assumed that unsampled herds remained within the hunting district where they were counted during winter surveys. We merged hunting district 301 and hunting district 309 into 1 district (i.e., hunting district 301–309) because these districts were treated as 1 unit during winter surveys. We defined  $\mathbf{M}$  as a matrix with  $b$  rows and  $d$  columns, with cells containing the proportion of sampled herd  $b$  (i.e., a herd with GPS location data) located within the portion of elk hunting district  $d$  that was within the boundary of the DSA. To estimate the daily proportion of time each sampled herd was located within each hunting district ( $\mathbf{M}$  cell values), we estimated the time individual collared elk were within the borders of each hunting district in each day, and averaged those values (Fig. S4). We estimated the number of adult

female elk  $f(d, t)$  in the portion of each hunting district  $d$  that was within the boundary of the DSA per time step  $t$  (in days) as:

$$f(d, t) = z_d u_d + \mathbf{M}_t z_b s_b \quad (5)$$

where  $u_d$  is the population estimate of unsampled elk (i.e., herds with no location data from GPS collars) in hunting district  $d$  (Table S1, available online in Supporting Information), and  $s_b$  is the population estimate of sampled elk herd  $b$  located in hunting district  $d$  during time step  $t$  (Table S2). We used data from the most recent surveys available (2016 or 2017) for  $u_d$  and  $s_b$ .

In 2011, MFWP initiated a multi-year brucellosis surveillance project. Personnel from MFWP tested hunter-harvested and research-captured adult female elk from herds in southwest Montana for exposure to *Brucella abortus* as part of this project. Where available, we used the proportion of positive to negative results from these tests during 2011–2017 to estimate the seroprevalence of hunting districts located within the DSA (see MFWP [2015] for details on how serostatus was determined). For hunting districts without data from this project, we used seroprevalence estimates for 2014 estimated from models predicting the trend in seroprevalence over time, which were built using data collected from a combination of hunter-harvested and research-captured adult female elk (Table S3, Fig. S5; Brennan et al. 2017).

We estimated the relative risk of abortion events  $R_{xt}$  per 250-m pixel  $x$ , per time step  $t$  for each hunting district separately, and then summed all hunting districts in time step  $t$  to predict spillover risk across the DSA. We combined  $R_{xt}$  estimates with landownership data to calculate the daily, cumulative, *per capita* daily, and *per capita* cumulative relative risk occurring on private, BLM, USFWS, USFS, and state government lands during the risk period. We did not consider the distribution of livestock within the Montana DSA in these calculations. We then calculated these same metrics for areas with potential livestock grazing (cattle or domestic bison) to quantify risky areas for elk-to-livestock transmission risk on the landscape. We defined areas of potential livestock grazing as private ranchlands in Montana with  $\geq 0.4$  hectares of grazing area (<http://svc.mt.gov/msl/mtcadastral/>, accessed 13 Jun 2017; Proffitt et al. 2011), and federal (USFS, BLM), and state (Wildlife Management Area) grazing allotments in Montana when livestock were potentially present on the allotments during the risk period (Fig. S6). We used turnout dates from BLM and USFS grazing records from 2014 (Wells 2017) and state grazing records from 2017 to determine when livestock were present on federal and state allotments. When transmission risk occurred on allotments during time periods when livestock were not present, we did not include it in our estimates of transmission risk on that grazing type.

### Assessing Uncertainty in Transmission Risk

Ideally, when combining multiple datasets to make spatiotemporal estimates of transmission risk, one would propagate the sampling errors associated with each

underlying parameter. In our case, this is challenging because in some instances we had no formal assessment of sampling error or the necessary data to conduct such an assessment (e.g., elk trend count data). Additionally, we did not evaluate the influence of uncertainty in estimates of  $u(x, t)$  on risk because of computational limitations associated with deriving error estimates for  $u(x, t)$  on a cell-by-cell basis. Therefore, we highlight some of the uncertainties of the individual data streams below but leave the full propagation of errors as an issue for further research.

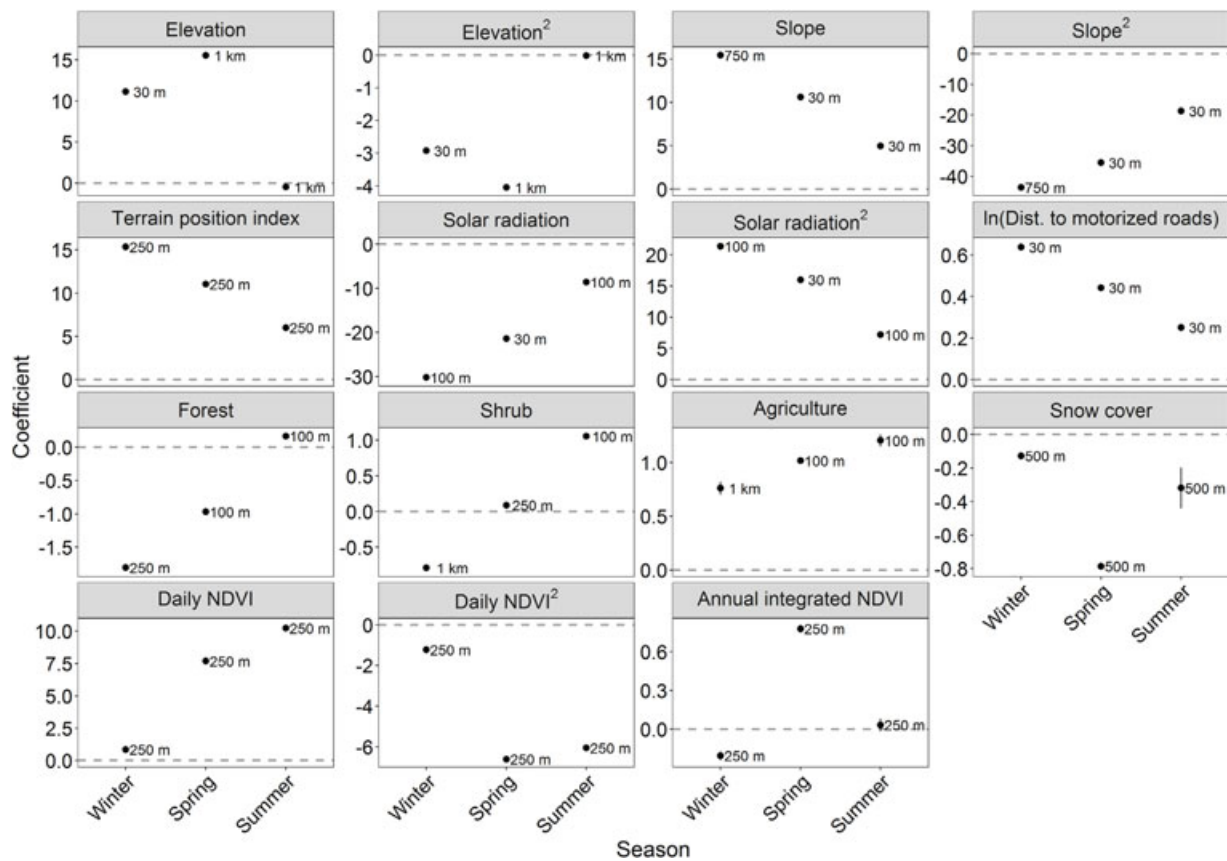
We used elk trend count and age ratio data collected by MFWP to estimate  $N_{dt}$ . These data provided a minimum estimate of the number of adult female elk but were not corrected for visibility bias (Samuel et al. 1987). During aerial surveys in land cover types similar to those encountered in our study area, detection estimates for elk have been estimated to range from as low as 64% (Jarding 2010) to as high as 95% (Anderson et al. 1998). To assess uncertainty associated with visibility bias, we quantified the transmission risk that would have occurred within the DSA during the risk period if we had detected 64% or 95% of elk during our surveys. To investigate uncertainty associated with annual abortion rates, we estimated the transmission risk within the DSA during the risk period using 95% confidence interval estimates for the proportion of seropositive and pregnant female elk that abort (Cross et al. 2015; 95% CI proportion aborting = 0.11, 0.23).

We randomly generated 1,000 seroprevalence estimates for each hunting district to evaluate uncertainty associated with brucellosis seroprevalence data. We used independent Bernoulli trials to generate seroprevalence estimates for hunting districts with data collected during the multi-year brucellosis surveillance project. For hunting districts without seroprevalence data from this project, we used 1,000 random draws from the predictive posterior distributions of seroprevalence in 2014 from Brennan et al. (2017). For each seroprevalence estimate, we calculated the transmission risk within the DSA during the risk period and report the 95% range of this risk. We conducted all analyses in Program R version 3.3.1 (R Development Core Team 2016), using lme4 to fit GLMMs.

## RESULTS

Our risk period dataset consisted of 223 elk monitored from February 2005 to June 2015 (280 elk-years, 1,475,613 locations). In our preliminary analyses of resource selection, we found stronger support in all seasons for quadratic functional forms for elevation, slope, solar radiation, and phenological stage, and a pseudothreshold functional form for distance to motorized roads. Patterns of resource selection and spatial scales of explanatory covariates of adult female elk varied among seasons (Fig. 2, Tables S4–6; Figs. S7–12). In general, adult female elk selected areas at low to moderate elevations on moderate slopes, with higher terrain position index (i.e., on ridges) and low to high solar radiation. Elk avoided motorized roads and snow cover and selected agricultural landcover and intermediate values of daily NDVI (i.e., surrogate for phenology stage). Patterns of





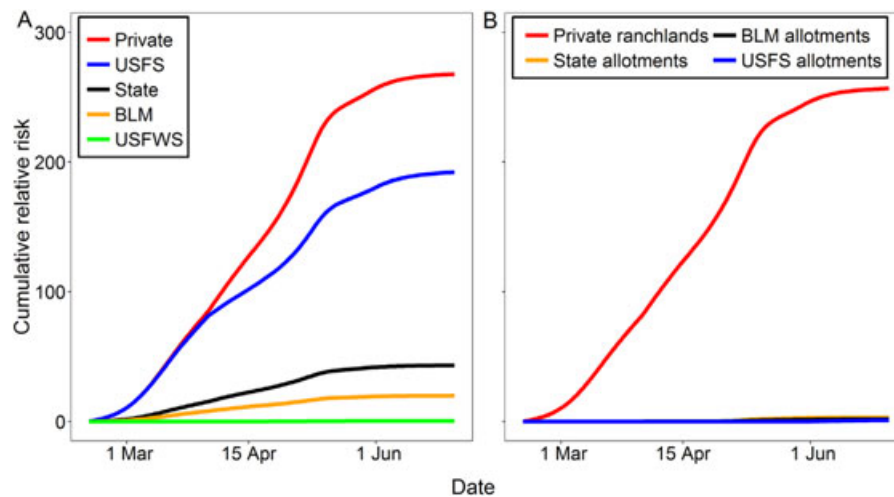
**Figure 2.** Estimated coefficients and 95% confidence intervals from resource selection functions for adult female elk sampled from 2005–2015 during winter (15 Feb–31 Mar), spring (1 Apr–31 May), and summer (1 Jun–30 Jun), southwest Montana, USA. The scale for each variable is given to the right of each estimated coefficient. The dashed line in each panel represents an estimated selection coefficient of zero. The 95% confidence intervals are too small to be visible for most coefficients, and distance (Dist.) and normalized difference vegetation index (NDVI) are abbreviated in the panel labels.

selection for forest landcover, shrub landcover, and annual integrated NDVI (i.e., surrogate for patch quality or biomass) changed among seasons; female elk selected forest landcover only during summer, shrub landcover during spring and summer, and annual integrated NDVI only during spring. The internal predictive accuracy of our RSFs was strong. The average  $r_s$  from 100 repetitions of our 5-fold cross validation procedure was 1.00 (range = 1.00–1.00) in winter, 1.00 (range = 1.00–1.00) in spring, and 1.00 (range = 1.00–1.00) in summer. The ability of our partial RSFs to predict the space use of excluded herds was also strong. The average  $r_s$  for our 24 partial RSFs was 0.98 in winter (range = 0.94–1.00), 0.99 in spring (range = 0.95–1.00), and 0.95 in summer (range = 0.88–1.00; Fig. S13).

Within the risk period during an average snowfall year, we estimated that 51% of the relative risk of abortion events inside the Montana DSA occurred on private lands (comprising 35% of land in the DSA), 37% on USFS lands (comprising 47% of land in the DSA), 8% on state lands (comprising 8% of land in the DSA), 4% on BLM lands (comprising 8% of land in the DSA), and <1% on USFWS lands (comprising 1% of land in the DSA; Fig. 3A). When we limited our analyses to include only areas with potential livestock presence, however, we found that 98% of the relative risk of abortion events occurred on private ranchlands

(comprising 31% of land in the DSA), 1% on state livestock allotments (comprising 1% of land in the DSA), 1% on BLM livestock allotments (comprising 4% of land in the DSA), and <1% on USFS livestock allotments (comprising 5% of land in the DSA; Fig. 3B). We calculated the percentages of land in the DSA that were comprised of allotments (provided above in parentheses) only for allotments where livestock was present at some point during the risk period.

The relative risk of abortion events on private ranchlands (private land with potential livestock presence) represented 49% of the total relative risk that occurred during an average snowfall year within the Montana DSA. Across elk hunting districts, there was a large amount of variation in the density of relative risk occurring on private ranchlands, ranging from an estimated density of <0.001/km<sup>2</sup> in hunting district 316 to 0.091/km<sup>2</sup> in hunting district 362 (Fig. S14A). Across hunting districts, we also identified variation in the *per capita* relative risk posed by individual adult female elk on private ranchlands. During the risk period, we estimated that the relative risk posed by an average adult female elk on private ranchlands was 0.002 in hunting district 301–309, whereas it was 0.040 in hunting district 317 (Fig. S14B). Differences in the monthly density of relative risk on private ranchlands among hunting districts were consistent across time during the risk period (Fig. S15).



**Figure 3.** Daily predicted cumulative relative risk of abortion events during an average snowfall year from adult female elk sampled from within the Montana, USA, designated brucellosis surveillance area (DSA) during the brucellosis transmission risk period (15 Feb–30 Jun) occurring on A) private (Private), United States Forest Service (USFS), state government (State), Bureau of Land Management (BLM), and United States Fish and Wildlife Service (USFWS) lands, and on B) livestock grazing lands (private ranchlands and state and federal livestock allotments) when livestock were potentially present. Elk trend counts from 2016–2017 were used to estimate the number of elk within the DSA.

We estimated that 4% of transmission risk within the DSA occurred during February, 32% during March, 29% during April, 30% during May, and 5% during June (Fig. 4, Figs. S16–21). Uncertainty associated with just the visibility bias during aerial surveys would increase the estimated relative risk of abortion events by 5% to 56% (assuming 95% and 64% visibility, respectively). Uncertainty associated with only the annual probability of aborting or with seroprevalence estimates would create 95% credible intervals of relative risk that varied by –31% to 44% and by –17% to 18% around our estimate, respectively.

## DISCUSSION

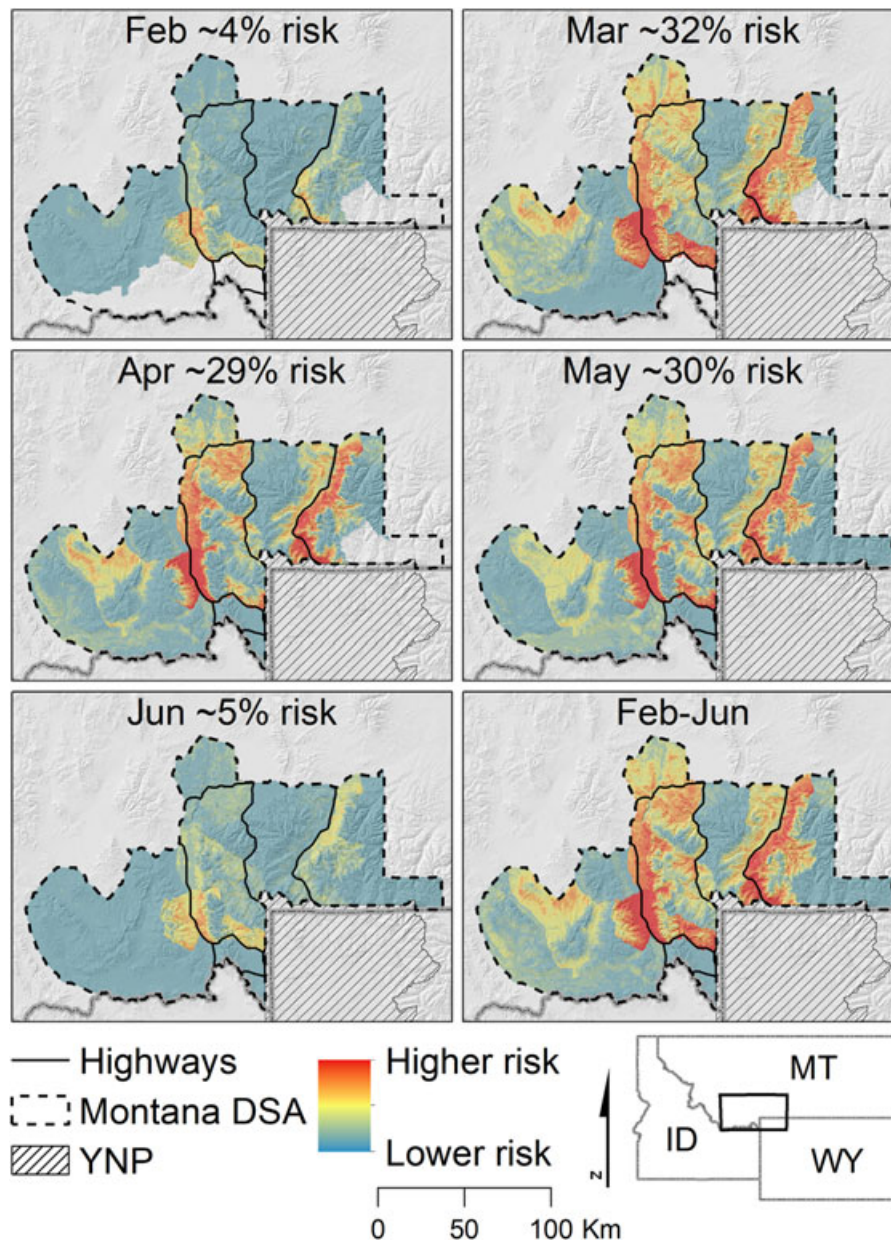
To date, few studies have attempted to synthesize ecological, epidemiological, and behavioral datasets to predict cross-species pathogen spillover (Plowright et al. 2017, Dougherty et al. 2018). When such work has occurred, it has typically been at coarse resolutions, and has relied on a number of parameters that are poorly estimated or incompletely known. We used 1 approach to combining information on host movement, distribution, density, prevalence, and the timing of disease transmission to assess the potential for cross-species pathogen spillover. We built upon the work of Merkle et al. (2018), and developed a fine-resolution (250-m spatial, 1-day temporal), large-scale (17,732 km<sup>2</sup>) disease transmission risk model that accounted for most of the measurable components of elk-to-livestock brucellosis transmission risk.

There were several components of transmission risk that we were unable to consider in our model, however, because we lacked the necessary data to do so. Specifically, we did not account for contact rates of livestock with infected fetuses, how often that contact results in infection, the environmental persistence of *B. abortus*, or potential immune responses in elk or livestock that might prevent infection. Aune et al.

(2012) reported that brucellosis bacteria can persist on fetal tissues and soil or vegetation for 21–81 days depending on month, temperature, and exposure to sunlight, but that there was only a 0.05% chance of brucellosis surviving beyond 26 days. We expect that few aborted fetuses will persist on the landscape for that long, however, because they will likely be removed by scavengers much more quickly (Cook et al. 2004). We do not currently have estimates of fetal scavenging rates for our study area, but ongoing work to estimate the persistence of fetuses will allow us to incorporate these estimates into our framework in the future. Finally, we did not account for potential shifts in habitat selection by adult female elk that may have occurred prior to or during parturition. We think this likely had little influence on our results, however, because the majority of sampled elk were pregnant; therefore, any behavioral shifts that may have occurred should have been incorporated into our RSFs.

Our results suggested that the risk of disease spillover within the Montana DSA was greatest on private ranchlands, with only approximately 2% of total risk occurring on state or federal grazing allotments when livestock were present on these allotments (Fig. 3B). Within the DSA, areas that we predicted were at higher risk for elk abortions in livestock grazing areas were concentrated along the Madison Valley in the west (hunting districts 323, 330, 360, 362), and the Paradise Valley (hunting districts 313, 314, 317) in the east (Fig. 4, Figs S16–21). This is in rough agreement with where livestock herds have been affected by brucellosis (Brennan et al. 2017). High levels of predicted spillover risk within these valleys were influenced by a combination of high disease prevalence, large herd size, and the occurrence of a significant number of private ranchlands. The 5 hunting districts with the highest estimated seroprevalence all occurred within these valleys, and these valleys also contained the 2 largest elk herds in the DSA (Tables S1–S3).





**Figure 4.** Predicted relative risk of transmission events during an average snowfall year by adult female elk within the boundary of the Montana, USA, designated brucellosis surveillance area (DSA) during each month of the brucellosis transmission risk period (15 Feb–30 Jun). We produced monthly estimates by summing estimates of the daily relative risk of abortion events during all days of the month. Shading depicts hillshade of elevation. Yellowstone National Park (YNP) is shown with cross-hatching.

During winter, elk select for flat grasslands in windswept areas with more available forage (Gude et al. 2006, Proffitt et al. 2010), which brings them onto private ranchlands in valley bottoms. Across the DSA, the largest wintering groups of elk tend to occur on flat grasslands in valley bottoms (where private land dominates) in areas with high elk population density (Proffitt et al. 2015). Over the last several decades elk have become more concentrated in larger groups on the Madison Valley bottom (Proffitt et al. 2012). Similarly, over the last 15 years, the proportion of the Northern Yellowstone herd wintering outside of Yellowstone National Park in the Paradise Valley has increased (White et al. 2010, 2012). The area of private land in

irrigated alfalfa in these valleys has increased over the last decade (Haggerty et al. 2018), which reduces the propensity of elk to migrate off of these winter ranges in spring (Barker 2018).

Traditional methods of disease control, such as vaccination, culling, and test and slaughter, are unlikely to be effective, politically feasible, or logistically possible to implement on wide-ranging elk populations (Bienen and Tabor 2006, Kilpatrick et al. 2009). Thus, the primary strategy for managing brucellosis transmission risk between elk and livestock is to prevent commingling. This may be achieved by hiring herders to disperse or redistribute elk, by holding dispersal hunts during the transmission risk period, by

fencing or removing haystacks and other attractants, or by improving available forage on public lands (Bienen and Tabor 2006). Our results clearly indicate that commingling between elk and livestock carries very different levels of spillover risk, depending on when and where that commingling occurs (Fig. 4). Thus, our predictions can be used by wildlife managers to prioritize when and where to implement these actions. Additionally, prior to the abortion period, wildlife or livestock managers can proactively work with livestock producers to develop grazing regimes and feeding locations that minimize livestock presence in pastures predicted to have high transmission risk. Similarly, our predictions can be used to focus disease monitoring and research efforts in high risk areas. In turn, data collected during these future efforts can be used to evaluate management efficacy and improve our predictions.

Individual female elk posed different *per capita* levels of brucellosis transmission risk because of differences in seroprevalence, movement patterns, and landownership among hunting districts. For example, we predicted that on a per individual basis 1 female elk in hunting district 317 generated 4 times more risk on private ranchlands than one in hunting district 313 (Fig. S14B). Hunting districts with the highest *per capita* risk of brucellosis transmission from elk to livestock on private ranchlands were not always the hunting districts with the highest densities of relative risk on private ranchlands (Fig. S14). For most management interventions, the greatest overall reduction in risk will likely be achieved by focusing on hunting districts with the highest density of relative risk. Currently, there is no limit on the number of elk that can be targeted during management interventions in Montana. If logistical, financial, or social constraints limit the number of elk that can be targeted in the future, however, it may be useful for managers to consider both risk metrics (*per capita*, density) when designing mitigation strategies.

We expanded upon the work of Merkle et al. (2018) by incorporating spatiotemporal data of livestock distribution into our modeling framework. In doing so, we demonstrated the importance of considering livestock distribution during investigations of elk-to-livestock brucellosis spillover. By itself, the distribution of relative risk across landownership types did not provide an accurate picture of the distribution of transmission risk. For example, we estimated that 51% of relative risk occurred on private lands, and 37% occurred on USFS lands (Fig. 3A). When we considered the spatiotemporal distribution of livestock, however, we found that elk-to-livestock transmission risk was primarily concentrated on private ranchlands, with 98% of relative risk on livestock grazing lands occurring on private ranchlands (Fig. 3B). However, we lacked detailed data on the spatiotemporal distribution of livestock on private ranchlands. As a result, we most likely overestimated risk on private ranchlands because we assumed that livestock were always present on this grazing type. Further, we were unable to account for the number of livestock and the chance that livestock may be infected by a given elk fetus, so our gradient of risk may be only weakly correlated with the occurrence of actual spillover

events. Nonetheless, our results are reflective of differences in transmission risk posed by elk across the landscape.

The current stocking dates for livestock on state and federal allotments within the Montana DSA appear to be effective at limiting commingling of elk and livestock during the risk period. Recently, however, Kamath et al. (2016) estimated that the distribution of brucellosis in elk in the GYE is expanding at 3–8 km/year and that the rate of expansion appeared to increase over time. Outside the northern boundary of the Montana DSA, the density of BLM allotments that are stocked with livestock during the risk period is much higher. If brucellosis continues to expand this may become an important issue.

Within the DSA, uncertainty associated with the timing of abortions had the largest influence on the relative risk of abortion events. The model of abortion phenology we employed was developed in Wyoming by Cross et al. (2015) using data from vaginal implant transmitters deployed in 575 elk from 2006–2014. It is unlikely that a similar dataset will be replicated soon because of the high cost and logistical demands required to assemble a sample of similar or greater size. Therefore, it may be unrealistic to target abortion phenology in data collection and surveillance strategies to attempt to minimize uncertainty in risk predictions. Instead, developing a model to correct for visibility bias (Samuel et al. 1987) during aerial surveys, the second largest contributor to uncertainty, might be a more feasible way to reduce overall uncertainty. Increased efforts to refine brucellosis serology estimates might also help to reduce overall uncertainty. Additionally, as computational capacity increases in the future, it may be useful to account for the unknown uncertainty associated with space-use predictions. Further research is needed, however, to assess whether reductions in uncertainty are useful for focusing efforts aimed at reducing transmission risk (i.e., assessing whether or not reductions in uncertainty alter predicted differences in risk among areas).

Because management decisions for elk in areas with brucellosis in Montana are made annually, our modeling approach could be used in the design of an adaptive management program whereby uncertainty in predictions could be reduced over time (Walters 1986). The value of this approach, versus annual state-dependent decision making, depends on the extent to which the uncertainty we documented affects wildlife managers' choice among the portfolio of elk distribution management options available. Expected value-of-information analyses could be used to estimate the extent to which the brucellosis management program for elk could be improved by implementation of adaptive management to reduce uncertainty in the risk of elk-to-livestock transmission (Runge et al. 2011).

The risk of transmission events from elk involves complex interactions among the demographic, seroprevalence, and space use patterns of elk, as well as the timing of abortion events (NASEM 2017). Our dataset did not permit us to account for these interactions equally across the DSA, however. We had detailed movement data for some elk herds, which allowed us to distribute the estimated number of adult female elk from those herds among the hunting

districts of the DSA according to the movement patterns of collared females. Conversely, in hunting districts without movement data, we had to assume that the number of female elk was static throughout the risk period (unless sampled herds moved into these hunting districts). This likely biased our estimates high in some hunting districts (e.g., hunting district 323) because elk likely departed the district during the risk period. In other hunting districts, there was likely little movement outside of the district (e.g., hunting district 301), so we expect that this issue likely had little effect. During future collaring efforts, it may be beneficial to target hunting districts without recent movement data where elk-to-livestock brucellosis transmission risk estimates are high (e.g., hunting districts 323 and 360; Fig. S14).

Across disciplines, synthesizing data collected at different spatial scales is challenging (Gotway and Young 2002). We collected brucellosis seroprevalence data at the scale of the hunting district from hunter-harvested and research-captured adult female elk. Because most of our seroprevalence estimates could not be coupled with individual elk herds, we could not adjust seroprevalence estimates according to the movement patterns of collared females. Among hunting districts, we observed a large amount of variation in transmission risk (Figs. S14A, S16–21). We are confident that much of this variation was due to true biological differences among hunting districts. We are aware, however, that some of this variation was likely artificially introduced because of the scale at which our seroprevalence data were collected. For example, abrupt changes in the predicted risk of abortions along some hunting district borders (e.g., border of hunting district 323 and 330; Figs. S16–21) likely did not represent biological reality on the ground.

## MANAGEMENT IMPLICATIONS

In Montana, management decisions for elk in the DSA are made annually by the Montana Fish and Wildlife Commission and are guided by a structured decision making framework (MFWP 2013). A fundamental objective of this management program is to minimize the risk of brucellosis transmission from elk to livestock. Management actions to achieve this objective are focused on hazing, hunting, and other actions to disperse or redistribute elk. Our integrated modeling approach was designed to feed directly into this management program as a tool to prioritize when and where to implement these interventions. Our results suggest that brucellosis transmission risk from elk to livestock in Montana is greatest from March through May on private ranchlands. Focusing management activities on private ranchlands during March through May will likely reduce disease spillover opportunities. Managers could also use our results to provide quantitative predictions of the expected reduction in transmission risk that might follow from a set of elk distribution management actions employed in a given year. Such predictions and assessments should be conducted in the context of similar evaluations for other fundamental objectives related to stakeholder acceptance of management actions and costs of implementation (Metcalf

et al. 2017). Additionally, we suggest that wildlife or livestock managers and livestock producers collaboratively gather data on the distribution of livestock on private ranchlands during the brucellosis transmission risk period. These data could then be used to refine estimates of where transmission events from elk to livestock are most likely to occur on private ranchlands.

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