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Elk distribution and spatial overlap with livestock during the brucellosis transmission risk period

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Summary

1. The presence of *Brucella abortus* within free-ranging wildlife populations is an important conservation and management issue because of the risk of brucellosis transmission between wildlife and livestock. Predicting wildlife distributions is necessary to forecast wildlife and livestock spatial overlap and the potential for brucellosis transmission.

2. We used Global Positioning System data collected from telemetry-collared female elk *Cervus elaphus* to develop resource selection function (RSF) models during the brucellosis transmission risk period (the abortion and calving periods). We validated extrapolation of predictive models at two nearby elk ranges within the Greater Yellowstone Ecosystem. Additionally, we integrated extrapolated RSF maps and domestic livestock distributions to estimate the relative probability of elk and livestock commingling during the brucellosis transmission risk period.

3. The top-ranked model predicted that areas selected by elk had a lower probability of wolf *Canis lupus* occupancy, were privately owned and south facing, and had steeper slopes, lower road densities and higher Normalized Difference Vegetation Index (NDVI). Elk selected forests and shrublands over grasslands; however, the strength of selection decreased as snowpack increased. Elk selection for privately owned lands may lead to spatial overlap with livestock and increase the risk of elk and livestock intermingling. Furthermore, if both elk and livestock concentrate in areas of higher NDVI, increased spatial overlap may occur in these areas.

4. Predictive accuracy was highest in the study area where the model was developed. When compared to the model development area, predictive accuracy of extrapolated RSF maps was similar or better in one of the elk ranges and lower in the other elk range.

5. *Synthesis and applications*. Extrapolated RSF and spatial overlap maps can provide a foundation for identifying the highest risk areas of elk and livestock spatial overlap during the brucellosis transmission risk period. However, the predictive accuracy of the models is limited when applied to different areas. Site-specific models of spatial overlap would therefore be needed to provide the most accurate estimates of elk and livestock spatial overlap during the transmission risk period. The degree to which spatial overlap may lead to actual transmission risk needs to be investigated as this is not yet known and could have important implications for managing transmission risk.

Key-words: *Brucella abortus*, brucellosis, *Cervus elaphus*, Greater Yellowstone Ecosystem, Montana, resource selection, wildlife disease

Introduction

Wildlife reservoirs of infectious diseases present challenges for the protection of domestic animal and human health worldwide (Caron, Cross & Du Toit 2003; Fouchier *et al.* 2004; Nishi, Shury & Elkin 2006). Transmission of avian influenza, bovine tuberculosis and brucellosis from wildlife to domestic animals has highlighted concerns regarding wildlife reservoirs of infectious diseases (Cheville, McCullough & Paulson 1998; Donnelly *et al.* 2003). In the Greater Yellowstone Ecosystem

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(GYE), elk *Cervus elaphus* and bison *Bison bison* are the primary wildlife reservoirs of brucellosis. The potential for these native ungulates to transmit brucellosis to livestock raises concern for livestock health and the economic sustainability of the ranching industry, as well as for social tolerance towards wildlife and wildlife conservation (Thorne & Herriges 1992; Bienen & Tabor 2006; Kilpatrick, Gillin & Daszak 2009). Brucellosis is likely to have been first introduced into the GYE bison and elk populations by cattle in the early 1900s (Meagher & Meyer 1994). Recently, free-ranging elk have been implicated as the source of multiple brucellosis transmissions to cattle due to the lack of contact between the infected cattle herds and bison (Beinen & Tabor 2006). The subsequent losses of Wyoming, Idaho and Montana's brucellosis free status, and economic losses associated with these events, highlight the need for brucellosis risk management plans that reduce elk and livestock commingling and potential transmission risk (Wyoming Brucellosis Coordination Team 2005).

Transmission of brucellosis within and between wildlife and livestock may occur when individuals lick or ingest contaminated foetuses, placentas or birthing fluids (Cheville, McCullough & Paulson 1998). Infected individuals may experience late-term abortions or carry foetuses full term; therefore transmission risk occurs during late pregnancy and the calving period. Seroprevalence of antibodies to *Brucella abortus*, the bacteria causing brucellosis, varies among elk herds in the GYE and has recently increased in some free-ranging elk herds (Cross *et al.* 2010). Herds associated with feeding programmes in the southern GYE have 7–37% seroprevalence (Smith & Anderson 2001; Cross *et al.* 2007). Northern GYE herds not associated with feeding programmes have 1–4% seroprevalence (Barber-Meyer, White & Mech 2007; Proffitt, White & Garrott 2010), however, recent evidence suggests that seroprevalence is increasing (Cross *et al.* 2010). The lower seroprevalence in free-ranging northern herds may be the result of exposed or infected immigrants from herds with higher seroprevalence, or may be the result of within herd elk-to-elk transmission (Cross *et al.* 2010). Regardless of the source, transmission risk between free-ranging elk and livestock exists and a better understanding of the factors facilitating commingling between elk and livestock is necessary to inform brucellosis risk management plans (Cheville, McCullough & Paulson 1998).

The ability to predict spatio-temporal variations in elk distributions coupled with knowledge of ranching practices within the GYE will allow managers to identify areas of highest elk and livestock spatial overlap and implement actions in those areas aimed at minimizing the risk of elk and livestock commingling and potential for brucellosis transmission. Previous studies provide insights into landscape attributes and other factors that affect elk resource selection (McCorquodale 2003; Creel *et al.* 2005; Mao *et al.* 2005). However, important factors affecting resource selection during the brucellosis risk period have not been quantified, therefore predictions of elk distributions during the risk period are imprecise. Furthermore, the applicability of resource selection models developed at individual study sites to the larger landscape also is largely unknown. We investigated elk resource selection during the brucellosis transmission period and used extrapolated resource selection function (RSF) maps to quantify potential elk and livestock commingling in the northern GYE.

Materials and methods

DATA COLLECTION

Data used to develop models were collected from 2005 to 2006 in the Madison Valley, Montana, USA (Fig. 1). A total of 49 adult female (> 1 year old) elk were selected and captured on the Madison Valley winter range. All animals were chemically immobilized by helicopter darting on 15 February 2005 and 18 February 2006 and fitted with Global Positioning System (GPS) collars (Model GPS3300L; Lotek, Newmarket, ON, Canada) programmed to record locations every 30 min. Different individuals were collared in 2005 and 2006, and individual animals were collared for a maximum of 1 year. Animal capture was conducted through Montana Fish, Wildlife, and Parks Animal Use and Care permits 2–2005, 3–2006, 7–2007 and 3–2008. We censored all locations with positional dilution of precision (PDOP) > 10 because such locations often include location errors of ≥50 m (D'eon & Delparte 2005). During this period, the Madison Valley served as a winter range for a migratory herd of *c.* 5000 elk. Wintering area lands are primarily large tracts of private ranchlands grazed by livestock and surrounded by National Forest, Bureau of Land Management and state-owned lands. Elevations range from 1670 to 3064 m. The valley bottom is primarily a mixture of bunchgrass-dominated grasslands (*Festuca idahoensis* and *Pseudoroegneria spicatum*) with xeric shrubland (*Artemesia* sp.), grassland hills and

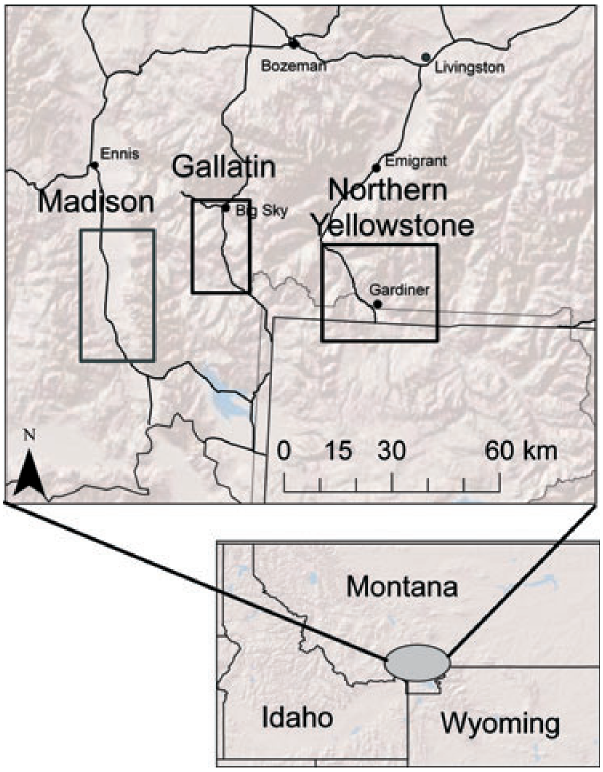

Fig. 1. The study area was located in the northern portion of the Greater Yellowstone Ecosystem.

coniferous forests on the slopes above. The valley is heavily windswept during winter, often leaving the open, low-elevation benches and higher elevation ridges largely snow-free. Standing snow depths in areas with woody vegetation often exceeded 40 cm, while depths in grasslands rarely exceeded 10 cm (Gude *et al.* 2006). Large elk groups (> 1000) frequent these windswept grasslands during winter and spring (Proffitt *et al.* 2009). In 2005, one pack of three wolves *Canis lupus* and in 2006, one pack of six wolves was documented using this area. Spring and summer ranges for this elk herd include mountainous National Forest lands to the south and east of the wintering area, as well as the western edge of Yellowstone National Park.

Ancillary study areas used to extrapolate and validate models included the Gallatin Canyon and Northern Yellowstone. Data from 18 adult female elk in the Gallatin Canyon were collected during 2002–2004 (Creel *et al.* 2005). Individual animals were collared for *c.* 1 year. Wintering area lands are primarily National Forest, with State and private lands interspersed. The valley bottom is primarily xeric shrubland (*Artemesia* sp.) and grassland (*F. idahoensis* and *P. spicatum*), with small riparian zones, coniferous forest and small meadows on the slopes above. Data from 45 adult female elk in the Northern Yellowstone were collected during 2007–2009. Individual animals were collared for *c.* 1 year. Wintering area lands are primarily National Forest, with State and private lands interspersed. The valley bottom is primarily grassland (*F. idahoensis* and *P. spicatum*), with small riparian zones, xeric shrubland (*Artemesia* sp.) and coniferous forest on the slopes above.

MODEL DEVELOPMENT

We used only data collected during the brucellosis risk period to develop predictive resource selection models. We defined the risk period as 15 February–15 June which corresponded to the late-term abortion and calving periods. We censored data within 72 h of capture. The Madison Valley data set was used for model development and prediction, and a different sample of Madison Valley data as well as data collected from the Gallatin Canyon and Northern Yellowstone study areas were used for model validation. To investigate factors affecting elk resource selection, we compared used locations recorded from GPS collars to randomly generated available locations. We randomly selected one record from each animal each day and treated these locations as our set of used locations. To create a sample of available locations, we estimated an 8·75 km circular buffer around each used point and randomly generated available locations from within this buffer. The size of the buffer defining potentially available locations corresponded to the 95th percentile of daily Euclidian distance travelled during the period of study. We calculated this distance by randomly selecting one used location per animal per day and calculating the Euclidian distance between consecutive daily locations. For each used point, we randomly selected 20 available locations from within this 8·75 km buffer. We did not select random points from within the entire study area because it included both winter and calving ranges, and all locations within the study area were not available to elk at all times of the study.

We evaluated five landscape attributes potentially affecting resource selection: vegetation cover, elevation, slope, aspect and cover openness (Unsworth *et al.* 1998; Mao *et al.* 2005; Messer *et al.* 2009). We used GIS to estimate these attributes for each used and available location. The 2001 national land cover data set, which had a 30-m resolution (http://www.mrlc.gov/), was used to classify vegetation cover, and consolidated vegetation into four categories: deciduous forest, coniferous/mixed forest, shrublands and grasslands (which included pasturelands). We also calculated openness as the percentage of non-forested area within a 400-m radius (Mao *et al.* 2005). We estimated elevation from a 30-m Digital Elevation Map (DEM), and derived slope and aspect in degrees from the DEM. We classified aspect as southerly (134–224°) or not-southerly (225–360° or 0–135°).

We evaluated two time-varying seasonal covariates representing potential effects of snowpack and vegetation on resource selection: snow water equivalence (SWE) and Normalized Difference Vegetation Index (NDVI). Snow water equivalents integrates the depth and density of snowpack into a measure of the amount of water contained within the snowpack, and we measured it at the nearest snowpack telemetry (SNOTEL) site (Beaver Creek, MT) located 30 km southeast and *c.* 300 m higher in elevation than the study area. Although we expected SWE measurements at the SNOTEL site to be greater than actual SWE within the study areas, we expected the patterns of snow accumulation and retreat to be similar between the study areas and SNOTEL stations. We also evaluated the interactive effects of SWE with vegetation to represent the hypothesis that the strength of selection for different vegetation types may vary as SWE varied. For each used and available location, we extracted the Advanced Very High Resolution Radiometer NDVI value from a 1-km resolution weekly averaged NDVI data layer that was corrected for cloud cover (Bartlette, Timerstein & Eidenshink 2006; http://www.wfas.net/). Although our snowpack metric was applied uniformly over the landscape, NDVI varied spatially and detected variations in the landscape when some areas were snow covered and others had begun to green-up.

We evaluated two metrics of human activity and development potentially affecting resource selection: road density (Grover & Thompson 1986; Unsworth *et al.* 1998; Rowland *et al.* 2000; McCorquodale 2003) and land ownership. We calculated road density within a 400-m radius of each point using a detailed road coverage map that included public and private highways, roads and driveways, as well as U.S. Forest Service motorized roads (Cassirer, Freddy & Ables 1992). We developed a categorical covariate contrasting all publicly owned land open for hunting during the previous year's hunting season with privately owned lands and publicly owned lands closed to hunting during the previous hunting season.

We evaluated one metric of wolf predation risk potentially affecting resource selection: the relative probability of wolf occupancy. We used an existing map depicting the estimated probability of wolf occupancy at a 3-km resolution, developed using forest cover, human population density, elk density and sheep density as predictors (Oakleaf *et al.* 2006).

STATISTICAL ANALYSES

We screened covariates for correlations and excluded pairs with Pearson's correlation coefficients correlations $|r| \geq 0 \cdot 7$ or variance inflation factors > 5 from entering the same model. Vegetation openness and vegetation type were strongly correlated, and we removed openness from models. We developed a total of 28 exploratory models representing potential effects of landscape attributes, seasonal variations, wolf risk and human activity on elk resource selection during the brucellosis risk period in the Madison Valley.

We used a discrete choice model with two choices (used or available) to estimate RSF coefficients (Proc LOGISTIC, SAS Institute 2000; Manly *et al.* 2002). Each used location and the 20 corresponding available locations defined unique strata. Used locations were matched temporally to their corresponding available locations and available locations assumed the time-varying attribute of the used location. Therefore, we could not estimate the main effects of SWE, the time-varying attribute, however, we did estimate interactive effects of SWE and non-time-varying attributes. Although NDVI was also a time-varying attribute, NDVI also varied spatially and therefore we were able to estimate main effects of NDVI on resource selection.

Using pooled data from all animals, we fit all candidate models and used AIC for model selection (Burnham & Anderson 2002). The data set contained an approximately equal number of observations from each individual and therefore we expected our model selection results to be unbiased towards individual animals. Next, we fit the top-ranked model for each individual animal and averaged coefficients of all the individual animal models to account for individual animal differences (Sawyer *et al*. 2006; Fieberg *et al*. 2010). We used the coefficients averaged across individual animals for all model predictions and validations.

MODEL PREDICTIONS AND VALIDATION

For prediction and validation (but not for model development), we divided the risk period into two time periods [abortion risk period (15 February–14 May) and calving period (15 May–15 June) Barber-Meyer, Mech & White 2008] and extrapolated RSF maps for each period. The predicted relative probability of elk occupancy across the landscape was based on covariate attributes (i.e. landscape attributes) within a 30-m pixel. Predicted relative probability of occupancy was calculated using covariate values within a pixel and coefficient estimates from the top-ranked model. For predictions, we used NDVI and SWE values averaged over the abortion risk or calving periods. All other covariate values used for predictions corresponded to values in the GIS layers used in model development.

We validated extrapolated RSF maps to determine model generalizability (reproducibility and transportability) across the GYE (Justice, Covinsky & Berlin 1999). Reproducibility evaluates the degree to which the model represents real patterns in the data rather than random noise. We validated predictions using a new sample of Madison Valley GPS location data to estimate reproducibility. Transportability evaluates the degree to which the model extrapolation produces accurate predictions in a sample drawn from a different but plausibly related population (Justice, Covinsky & Berlin 1999). We validated the extrapolated resource selection predictions using GPS location data collected from individuals in the Gallatin Canyon and Northern Yellowstone herds to estimate transportability. We randomly selected one location per animal per day for inclusion into the validation data sets.

To assess how well predictive maps fit the test data, we classified pixels of the predictive map into 20 equal-interval RSF intervals that corresponded to the relative probability of use (i.e. 0–5%, 5–10%, 10–15%, etc.; Durner *et al*. 2009). We plotted data corresponding to the appropriate time period on the predictive map and calculated the frequency distributions of observed elk locations within RSF intervals.

PREDICTING ELK AND LIVESTOCK COMMINGLING

To define the relative probability of elk and livestock commingling, we integrated the predicted relative probability of elk occurrence estimated from the RSF maps, elk population sizes and livestock presence/absence information. Adequate epidemiological information does not exist to define herd-specific levels of infection. Therefore, we assumed levels of brucellosis seroprevalence and infection were similar among elk herd units (Anderson 2007; Montana Fish, Wildlife, and Parks, unpublished data). The number of elk per herd was estimated from 2006 aerial survey counts (Montana Fish, Wildlife, and Parks, unpublished data). We defined areas of potential livestock grazing during the abortion risk period as all private ranchlands with 0·4 or more hectares of grazing area and we defined areas of potential grazing during the calving period as all private ranchlands with 0·4 or more hectares of grazing area and all public grazing allotments (livestock are not grazed on allotments during the abortion risk period; http://www.fs.fed.us/r1/gis). We defined the distribution of potentially infectious elk according to the State of Montana hunting district boundaries. If at least one elk per hunting district tested positive for exposure to brucellosis or if telemetry data indicated movement of elk from a hunting district containing potentially infectious elk to an adjacent hunting district, we classified the district as containing potentially infectious elk. To calculate relative probability of commingling across the study area, we multiplied the potential for livestock grazing (defined as 1 for potential grazing areas and 0 for areas without grazing), the presence of potentially infectious elk (defined as 1 for seropositive elk within the hunting district and 0 for districts with no seropositive elk), the relative probability of elk occupying a given pixel (derived from the extrapolated RSF maps) and the estimated number of elk in the corresponding herd.

Results

GPS COLLAR PERFORMANCE AND DATA SUMMARY

Madison Valley GPS collars had a fix success rate of 96%. We censored 1% of all locations with PDOP >10 prior to randomly selecting our used locations. We included a total of 5020 used locations collected from 44 individuals and 100 400 available locations in our analyses. Of the used locations, 48% were located in shrublands, 39% in grassland, 11% in coniferous forest and 2% in deciduous forest. Eighteen per cent were located on public lands that permitted hunter access and 82% were located on privately owned lands and public lands where hunting was prohibited. Average road distance of 11 m was estimated within a 400-m radius of used locations. Slope averaged 8·06° and elevation averaged 1957 m. Seventeen per cent of used locations were south facing. Compared to the seven-year SWE averages, 2005 was a relatively low snowpack year and 2006 was a relatively high snowpack year. SWE averaged 35·1 cm (26·5 cm in 2005 and 41·0 cm in 2006). The seven-year average (2002–2008) SWE for this time period (February 15–June 15) was 33·6 cm and annual average SWE values ranged from 22·2 to 43·9 cm. NDVI averaged 137·0 (136·7 in 2005 and 137·2 in 2006).

MADISON VALLEY RESOURCE SELECTION MODELS

The top model representing variations in elk occupancy received an AIC model weight of $>0{\cdot}99$ and contained the covariates Vegetation, NDVI, roads, ownership, wolf risk, slope, aspect, elevation, SWE, SWE × Vegetation and SWE × Elevation (Fig. 2). Coefficient estimates indicate areas selected by elk had a lower probability of wolf occupancy, were privately owned and south facing, and had steeper slopes, lower road densities and higher NDVI (Table 1). Elk selected for forests and shrublands over grasslands, however, the strength of selection for forests and shrublands over grassland

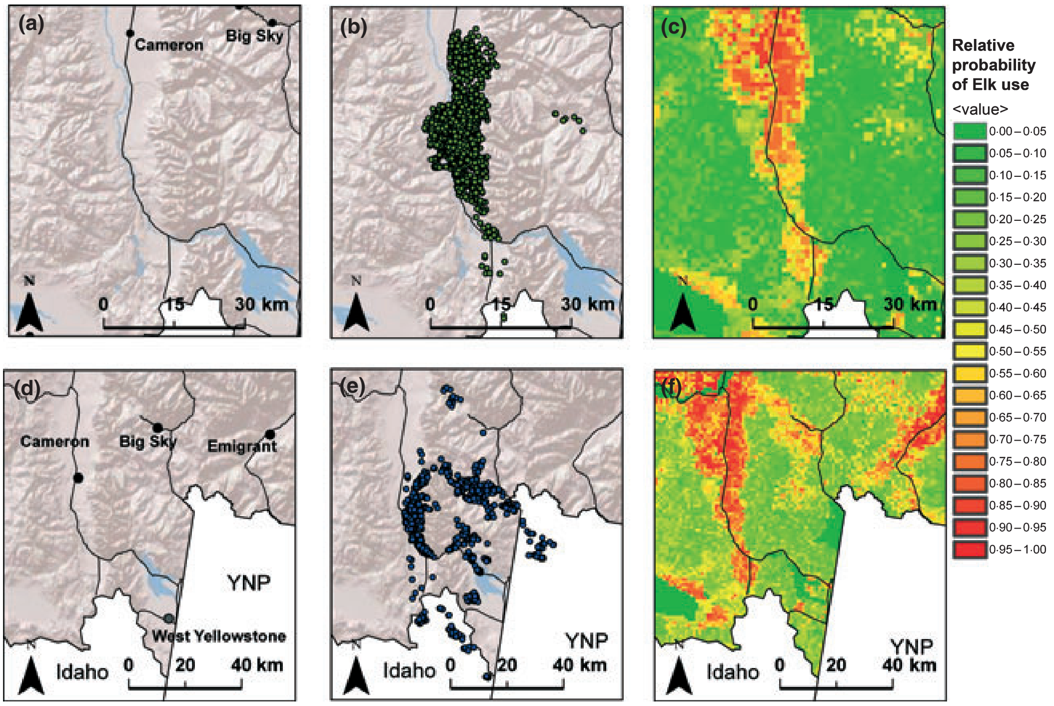

Fig. 2. The model development area, animal locations and predicted relative probability of elk use during the abortion risk period (February 15–May 14, a–c) and calving risk period (May 15–June 15, d–f). Areas of highest relative probability of use are shown in red and areas of lowest relative probability of use are shown in green.

Table 1. Coefficient estimates averaged across all individual models and standard errors representing variation in individual coefficient estimates from the top-ranked elk resource selection model in the Madison Valley study areas during the brucellosis risk period, 2005–2006

	Madison Valley	
Covariate	Estimate	SE
Conifer forest	0·159	0·276
Deciduous forest	0·865	0·308
Shrubland	0·381	0·221
Slope	0·016	0·004
Aspect	0·135	0·059
Elevation	−0·0005	0·0003
NDVI	0·0019	0·0007
Road density	−11·733	1·051
Ownership	−1·644	0·408
Wolves	−1·084	0·217
SWE × Conifer	−0·067	0·031
SWE × Deciduous	−0·041	0·009
SWE × Shrubland	−0·010	0·007
SWE × Elevation	−0·00003	0·000009

NDVI, Normalized Difference Vegetation Index; SWE, snow water equivalence.

Values for vegetation covariates represent the strength of selection relative to the base category, grasslands.

areas decreased as snowpack increased. Coefficient estimates averaged across the individual models were similar to estimates from the full model (Table S1, Supporting Information). The second ranked model was more than 100 ΔAIC units from the top-ranked model and received little support from the data (Burnham & Anderson 2002).

The predictive accuracy of the Madison Valley resource selection model was higher during the abortion risk period than during the calving period and was higher in the Madison Valley than in the Gallatin Canyon or Northern Yellowstone study areas (Tables S2 and S3). For the Madison Valley data, 67% of abortion risk period locations occurred in >75% RSF interval and 91% of locations occurred in the >50% RSF interval. Forty per cent of calving period locations occurred in >75% RSF interval and 59% of locations occurred in the >50% RSF interval (Tables S2 and S3).

Predictive accuracy was lower for the Northern Yellowstone area during the abortion risk period and similar during the calving period. For the Northern Yellowstone data, 47% of abortion risk period locations occurred in >75% RSF interval and 63% of locations occurred in the >50% RSF interval. Forty-eight per cent of calving period locations occurred in >75% RSF interval and 80% of locations occurred in the >50% RSF interval. Predictive accuracy was lowest for the Gallatin Canyon area and model predictive ability was not transportable to the Gallatin Canyon study area. For the Gallatin Canyon data, 7% of abortion risk period locations occurred in >75% RSF interval and 48% of locations occurred in the >50% RSF interval. Only 15% of calving period locations occurred in >75% RSF interval and 48% of locations occurred in the >50% RSF interval (Tables S2 and S3).

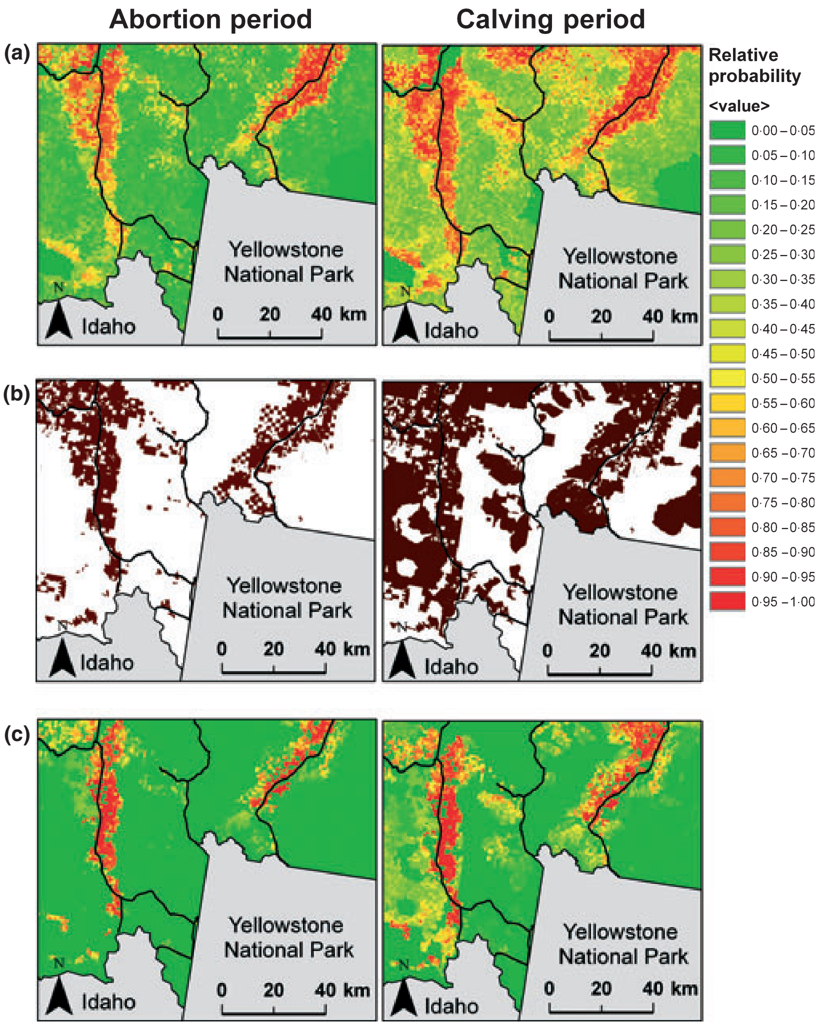

Fig. 3. The predicted relative probability of elk use (a), potential cattle grazing areas (b) and probability of elk and livestock commingling (c) in the Montana portion of the Greater Yellowstone Ecosystem. Areas of highest relative probability of use are shown in red and areas of lowest relative probability of use are shown in green.

PREDICTING ELK AND LIVESTOCK COMMINGLING

The relative probability of commingling showed a highly skewed distribution with much of the landscape containing either no elk or no livestock having zero risk of commingling (Fig. 3). As the potential area of livestock distribution increased during the calving risk period, the spatial extent of commingling increased during the calving period.

Discussion

Our work provides a modelling framework for quantifying potential spatial and temporal variation in elk and livestock commingling and the potential risk of disease transmission between elk and livestock. Management actions to eradicate disease in wildlife populations such as test and slaughter, whole-herd culling and vaccination may not currently be logistically or politically possible for brucellosis eradication in GYE wildlife populations (Beinen & Tabor 2006; Government Accountability Office 2008). Therefore, wildlife and livestock managers may need to rely on management actions aimed at minimizing wildlife and livestock commingling during the brucellosis risk period (Donnelly *et al.* 2003; Kilpatrick, Gillin & Daszak 2009). Our extrapolated RSF and commingling maps provide a foundation for identifying the highest risk areas of elk and livestock spatial overlap and targeting management actions in these locations.

During the abortion period, commingling was concentrated on lower elevation private ranchlands and during the calving period, commingling was more broadly distributed across private ranchlands and public grazing allotments. Our predictions regarding commingling are based on the assumption that any elk within the brucellosis risk area has an equal probability of infection. More specific information regarding the distribution of potentially infectious elk and level of infection in individual elk herds is needed to better define the relationship between commingling and actual risk of brucellosis transmission. Efforts are underway to increase testing and estimate interchange between infected and potentially infection-free elk herds. Our models of elk resource selection and spatial overlap with livestock should be tested and validated in other GYE areas and integrated with new data regarding spatial variation in infection rates to better understand risk of brucellosis transmission across the GYE. Additionally, actual transmission risk is dependent upon many factors other than those considered here (spatio-temporal elk and livestock overlap and elk population sizes; Kilpatrick, Gillin & Daszak 2009). The persistence of bacteria in the environment (Aune *et al.* in press), the number of susceptible and infectious elk and livestock and the probability that contact leads to infection may each affect actual transmission risk. However, unless these factors vary among areas with the highest potential for commingling, as we have defined here based on elk resource selection and distribution, cattle grazing distribution and elk population sizes, our results should prove adequate to identify areas on the northern GYE landscape that have the highest probability of elk and livestock commingling and potential transmission risk.

Estimating the predictive ability of extrapolated RSF and commingling maps is integral in model application (Pearce & Ferrier 2000). Furthermore, commingling maps should be validated with spatially explicit disease infection information in cattle, if and when cattle become infected with brucellosis from elk. This will help to relate our maps of commingling to actual transmission risk. We found predicted elk distributions to be accurate in the Madison Valley model development area, providing strength in forecasting commingling and applying predictions to on-the-ground management within the Madison Valley. However, model development and validation was conducted under low to average snowpack years, and model predictive ability under severe winter conditions is unknown. Predictive accuracy of elk distributions differed as predictions were extrapolated across the larger landscape and across other years, probably due to differences in the available habitat or winter conditions (Mysterud & Ims 1998). In the Northern Yellowstone area, a low-elevation open landscape similar to the model development area, predictive accuracy was slightly lower during the abortion period and higher during the calving period. In the Gallatin Canyon area, a higher elevation more forested landscape, predictive accuracy was very low and forecasted commingling in this area was unreliable. These results indicate that predictive accuracy of model extrapolations may be low and extrapolating RSF maps beyond model development areas to areas of obvious habitat differences should be done with caution. In this case, additional elk telemetry and distribution studies may be necessary to develop independent predictive models in portions of the GYE with different landscape characteristics.

The extrapolated RSF and commingling maps may be used as a tool for focusing future disease monitoring and research efforts. Identifying the herds predicted to have the highest probability of commingling with livestock may allow focused disease monitoring efforts in these areas to confirm the disease is actually present and quantify the level of infection. Additionally, commingling maps may be used as a tool for focusing management actions aimed at minimizing elk and livestock spatial overlap during the transmission risk period. At a broad spatial scale, wildlife managers can prioritize funding management actions such as hiring herders to disperse (Cross *et al.* 2010) or redistribute elk and fencing haystacks in portions of the GYE where commingling is predicted to be highest. At a finer scale, wildlife mangers can work with livestock producers to develop grazing systems and winter feeding locations that place livestock in pastures predicted to have the lowest relative probability of elk occupancy during the abortion and calving periods. To develop the most accurate predictions regarding elk distributions, commingling with livestock and potential brucellosis transmission risk, data specific to each herd should be collected across a range of environmental conditions and used to forecast commingling. Furthermore, our results suggest caution should be taken in generalizing resource selection models across populations and beyond landscapes where model development data were collected, as the predictive accuracy of models may be reduced in different populations or landscapes. Managers should consider model accuracy and extrapolation issues when basing management actions on extrapolated RSF predictions.

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Supporting Information

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

Table S1. Coefficient estimates and standard errors of covariates in the top-ranked elk resource selection model in the Madison Valley study areas during the brucellosis risk period, 2005–2006.

Table S2. Frequency distributions and percentage of Madison Valley, Gallatin Canyon and Northern Yellowstone elk locations within equal-area RSF intervals during the abortion risk period.

Table S3. Frequency distributions and percentage of Madison Valley, Gallatin Canyon and Northern Yellowstone elk locations within equal-area RSF intervals during the calving period.