

Spatio-temporal overlap between Yellowstone bison and elk – implications of wolf restoration and other factors for brucellosis transmission risk

Kelly M. Proffitt^{1*}, Patrick J. White² and Robert A. Garrott¹

¹Fish and Wildlife Management Program, Department of Ecology, Montana State University, 310 Lewis Hall, Bozeman, MT 59717, USA; and ²National Park Service, PO Box 168, Yellowstone National Park, Mammoth, WY 82190, USA

Summary

1. In the Greater Yellowstone Ecosystem, bison *Bison bison* and elk *Cervus canadensis nelsoni* act as hosts for *Brucella abortus*. The presence of *B. abortus* within wildlife populations is an important conservation issue because of the risk of brucellosis transmission from wildlife to cattle.

2. We investigated conditions facilitating contact between bison (40–60% seroprevalence) and elk on a shared winter range in the Madison headwaters area of Yellowstone National Park. We evaluated the effects of snow pack, season, elk and bison population sizes, and wolf *Canis lupus* predation risk on the degree of spatial overlap between bison and elk from 1991 to 2006.

3. Sixty-eight per cent of 10 093 independent elk observations occurred within the known bison wintering range, 29% occurred within the distribution of bison within the winter range at the time of sampling and 14% occurred within 100 m of bison. Spatial overlap between bison and elk measured across these three spatial scales increased with week of the season, snow pack, and on days when wolves were within the same drainage area as elk, but decreased with cumulative levels of wolf predation risk.

4. Wolves contributed to immediate, short-term responses by elk that increased spatial overlap with bison, but longer-term responses to wolves resulted in elk distributions that reduced spatial overlap with bison. Spatial overlap increased through the winter and peaked when late-term abortion events and parturition occurred for bison.

5. *Synthesis and applications.* Despite this high level of association, elk exposure to *B. abortus* in the Madison headwaters (2–4%) was similar to those in free-ranging elk populations that do not intermingle with bison (1–3%), suggesting that *B. abortus* transmission from bison-to-elk under natural conditions is rare. Our results suggest that risk-driven elk behavioural responses to wolves are unlikely to have important disease implications. Management of brucellosis in greater yellow stone ecosystem elk populations should focus on reducing elk-to-elk transmission risk and, wherever possible, curtailing practices that increase elk density and group sizes during the potential abortion period.

Key-words: bison, *Brucella abortus*, brucellosis, disease, elk, interspecific transmission, wolves, Yellowstone

Introduction

Wildlife, domestic animals and humans share a large and increasing number of infectious diseases. The continued globalization of society, human population growth, and associated

landscape changes, will multiply opportunities for contact between wildlife, domestic animals, and humans, facilitating emerging infectious diseases (Plumb *et al.* 2007). The potential for disease transmission between native wildlife to domestic livestock presents a challenge to wildlife managers worldwide, and attempts to eradicate disease may be particularly difficult when multiple wildlife populations act as reservoir hosts (Caron, Cross & Du Toit 2003; O'Brein *et al.* 2006). Similar to efforts to control bovine tuberculosis in African buffalo

*Correspondence author. Montana Department of Fish, Wildlife, and Parks, 1400 South 19th Avenue, Bozeman, MT 59718, USA. E-mail: kproffitt@mt.gov

Syncerus caffer (Caron *et al.* 2003), wildlife managers in the Greater Yellowstone Ecosystem (GYE) are faced with the challenge of controlling brucellosis in North American bison and elk populations, and mitigating the risk of transmission to livestock.

Bison *Bison bison* and elk *Cervus canadensis nelsoni* populations in the GYE are the primary wildlife reservoirs of brucellosis in North America and the potential for transmission of brucellosis from native ungulates to cattle has generated debate between environmentalists, ranchers and natural resource managers (Kilpatrick, Gillin & Daszak 2009). Management actions aimed at reducing the risk of brucellosis transmission to cattle have included culling thousands of bison leaving Yellowstone National Park (YNP), generating widespread controversy. Transmission within and between wildlife and livestock may occur when individuals ingest or feed near foetuses, placentas, or birthing fluids (Cheville, McCullough & Paulson 1998), and disease transmission and prevalence are a function of the number and density of infected animals, the number of susceptible hosts, and the conditions which facilitate contact between infectious and susceptible individuals.

Elk associated with feeding programmes in Wyoming and bison in Yellowstone National Park are the primary sources for brucellosis transmission to other elk and livestock in the GYE (Cheville *et al.* 1998). Elk are allowed to move throughout the GYE with few restrictions and often intermingle with cattle. In contrast, bison are subject to a relatively high level of disease control measures. Bison seldom intermingle with cattle because management agencies actively prevent bison dispersal and range expansion outside established conservation areas in and near Yellowstone National Park via hazing, hunting and/or sporadic brucellosis risk-management removals. However, the role of bison in sustaining brucellosis in Yellowstone elk is uncertain and this information is fundamental for policy makers charged with suppression of brucellosis in the GYE. If brucellosis transmission between bison and elk is rare and the disease is sustained independently in these species, species-specific strategies could mitigate risk and reduce prevalence. Otherwise, integrated multi-species brucellosis management will be required.

The purpose of this research was to evaluate ecological conditions that may facilitate contact and potential transmission of brucellosis between infectious bison and susceptible elk. In YNP, 40–60% of bison test positive for exposure to brucellosis (Treanor *et al.* 2007), although less than half of these bison are actively infectious females (Roffe *et al.* 1999). Seroprevalence of antibodies to *Brucella abortus* in YNP elk populations is a function of elk-to-elk transmission, bison-to-elk transmission, and immigration of seropositive elk from infected populations associated with feeding programmes in the southern GYE. Historically, 1–3% of elk in the northern portion of the GYE tested positive for brucellosis exposure (Etter & Drew 2006; Barber-Meyer, White & Mech 2007). These low seropositive rates may have been sustained by immigration of infected elk from the feed grounds in Wyoming, where brucellosis exposure was consistently higher (i.e. 7–26%; Cross *et al.* 2007). Interchange on the order of 3–17% regularly occurs among GYE

elk herd units (Craighead, Atwell & O'Gara 1972; Smith & Anderson 2001; Barber-Meyer, Mech & White 2008; Gower *et al.* 2009a). However, seroprevalence recently increased in some GYE elk populations not associated with feeding programmes to levels (7–18%) unlikely to be sustained by immigration of infected elk, suggesting that seroprevalence is now endemic and not immigration dependent (Cross *et al.* 2009). Potential explanations for increased seroprevalence in these elk populations include changes in elk density and grouping which may lead to increased elk-to-elk transmission, changes in dispersal patterns, changes in population size (Cross *et al.* 2009), or changes in elk and bison interactions which may lead to increased bison-to-elk transmission.

Interspecies transmission of brucellosis has occurred in domestic herds and under experimental conditions (Davis *et al.* 1990; Cheville *et al.* 1998). However, the high density of susceptible and infected animals in those locations may not reflect natural conditions. Within the Madison headwaters area of YNP, elk and bison share a winter range and frequently commingle, elk seroprevalence rates (3%) during 1996–1998 were similar to those in elk populations that did not share range with bison and lower than rates in elk populations associated with feeding programmes (Ferrari & Garrott 2002). These results suggested that the risk of bison-to-elk transmission under natural conditions may be low. However, since the study was conducted, wolves have recolonized the Madison headwaters area and risk-driven behavioural responses in elk resource selection and spatial dynamics may have changed the degree of spatial overlap with bison and altered the transmission risk.

Understanding biological and environmental factors affecting the degree and timing of spatial overlap between elk and bison populations is important for understanding the risk of interspecies *B. abortus* transmission and how levels of risk vary within seasons and years. Building on the previous study in the Madison headwaters area, we evaluated an additional 8 years of post-wolf reintroduction data and re-evaluated factors affecting the degree of elk and bison spatial overlap. We also assessed the elk population's exposure to *B. abortus* to identify potential effects of elk and bison spatial overlap on elk exposure.

Materials and methods

STUDY AREA

This study was conducted from 1991 to 2006 in the Madison, Gibbon and Firehole drainages of west-central YNP (Fig. 1, Garrott, White & Watson 2009a). Elevation ranges from 2000 to 2500 m. Winters are severe and snow pack is present 6–9 months per year.

The study area serves as a winter range for the migratory central Yellowstone bison population. Winter range is centred on lower elevation meadows associated with the geothermal basins and river bottoms. Over the course of this study, the central Yellowstone bison population ranged in size from approximately 2000 to 3500 (Fuller, Garrott & White 2007), with a maximum of 685–1728 bison wintering in the study area each year (NPS, unpublished data). A non-migratory herd of elk also occupies the study area, with population size declining from 680 animals in 1991 to 231 animals in 2006 (Garrott, White & Rotella 2009b). Elk winter range includes the lower elevation

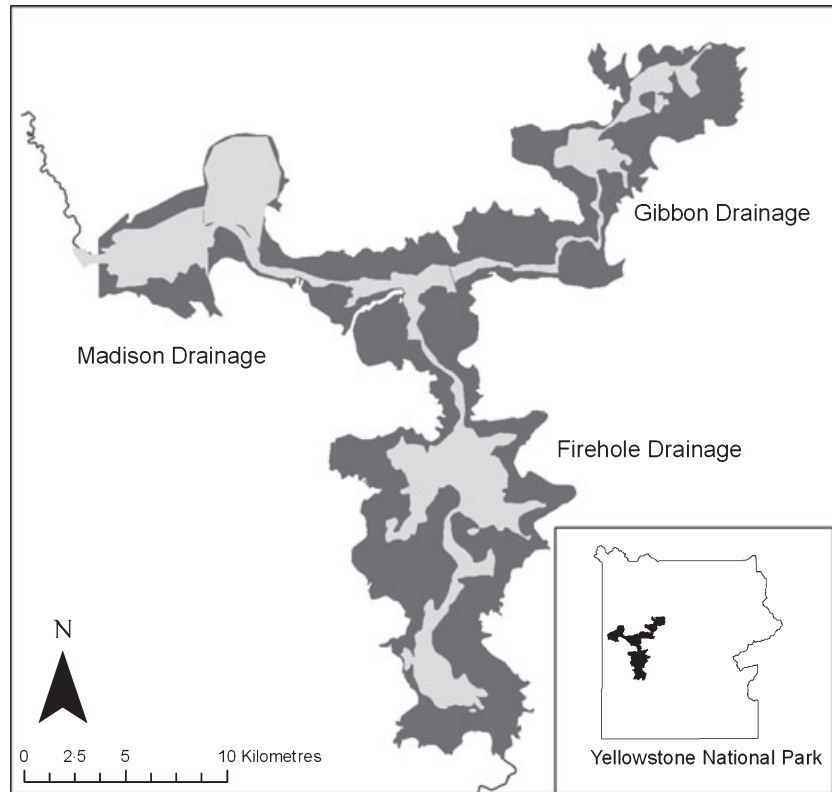


Fig. 1. The study area was located in the Madison, Gibbon, and Firehole drainages of west-central Yellowstone National Park. The bison wintering range (light grey) was centred on lower elevation, meadow areas associated with the geothermal basins and along the river bottoms. Elk wintering range (dark grey) included the lower elevation bison wintering range as well as higher elevation forested slopes throughout the Madison, Firehole, and Gibbon drainages.

bison winter range as well as higher elevation forested slopes throughout the Madison, Firehole and Gibbon drainages (Fig. 1). Deep snowpack constrains wintering bison and elk, and the physical attributes of the study area are likely to result in elk and bison being more closely associated than in other portions of the GYE.

INDICES OF ELK AND BISON SPATIAL OVERLAP

We captured and instrumented 115 adult female elk with VHF radio collars between 1991 and 2006 (Garrott *et al.* 2009b). Annually, we monitored 25–34 instrumented elk. We relocated instrumented elk using telemetry homing techniques according to a stratified sampling design. We stratified the study area into three strata corresponding to the three major drainages and randomly selected the drainage to be sampled. Instrumented elk within the drainage were located in a randomly determined order, and all remaining drainages were sampled before re-sampling. This resulted in locating individual elk at 3–7 day intervals. When we located elk, we recorded location and number of bison within 100 m of the instrumented animal. We collected elk locations from 1 December to 1 May each year from 1991 to 2006, except for the winter of 1995, and we used these relocation records to investigate elk spatial overlap with bison.

We investigated elk and bison spatial overlap at three scales: elk occupancy of the bison winter range, elk occupancy of the actual distribution of bison within the winter range at the time of sampling and observed elk and bison commingling (elk and bison within 100 m). At the broadest spatial scale, we investigated elk occupancy of the bison winter range. We defined the extent of the bison winter range based on bison observations collected from 1991 to 1996 during elk research activities (Ferrari & Garrott 2002) and confirmed that the winter range was similar during the entire period of this study through repeated aerial and ground surveys of the drainages (1991–2006). We determined if each elk location was either within or outside of the bison winter range.

Next, we investigated elk and bison spatial overlap at intermediate spatial and temporal scales. We conducted biweekly bison surveys to estimate bison distribution, and investigated elk occupancy of the biweekly bison distribution. From December to May, 1997–2006, we conducted ground-based bison surveys every 10–14 days to determine the number and distribution of bison within the winter range. We established 76 survey units along six survey routes that spanned the entire bison winter range and we surveyed bison along these six routes over a 2-day period. Bison survey units ranged in size from 0.6 to 7.2 km² with unit boundaries following topographic or physical features. For each bison group detected, we recorded location, survey unit and number of bison. To represent the biweekly bison distribution, we determined if bison occupied each of the 76 survey units. If at least one bison was located within a survey unit, we considered the survey unit occupied by bison. Next, we determined if each elk location was within an occupied or unoccupied bison survey unit during the survey nearest the date the elk location was collected. Elk locations collected more than 7 days before or after the nearest bison survey were censored. This resulted in elk locations being matched to bison distributions 1 week prior to and 1 week after elk location dates. In analyses of elk occupancy of the bison distribution, we censored elk locations from 1991 to 1996 because bison distribution data were not available.

At the finest spatial scale, we investigated variations in observed elk and bison commingling. We defined commingling as the presence of one or more bison ≤ 100 m from the randomly selected radio collared elk.

MODEL DEVELOPMENT AND EVALUATION

We evaluated competing hypotheses regarding the effects of elk population size, bison population size, snow pack, week of season and wolf predation risk on our three indices of elk and bison spatial overlap. Elk population size was estimated annually from mark–resighting

studies conducted as part of a long-term elk study (Garrott *et al.* 2009b). Bison population size was based on the maximum aerial survey counts of the central herd collected the previous summer. We predicted that higher elk and bison population sizes may lead to increased spatial overlap because both species tend to use similar winter ranges. The number of bison on winter range increases over the course of each winter (Bruggeman *et al.* 2009b), potentially increasing spatial overlap with elk. Thus, we developed a covariate representing the number of weeks since 1 December as a covariate representing seasonal effects on spatial overlap.

We defined snow pack based on centimetres of water in the snow pack (snow water equivalency, SWE) collected at the West Yellowstone snow telemetry site (SNOTEL, National Resources Conservation Services). The West Yellowstone SNOTEL site was located at 2042 m representing low to mid-elevations within the study area. A more refined snow pack metric was available from 1997 to 2006, and we used SWE values specific to the bison winter range predicted daily using the Langur snow pack model (Watson *et al.* 2009) as a covariate of elk occupancy of the bison distribution. The Langur snow pack model predicted an average daily SWE value within the bison winter range, but these data were not available over the time periods evaluated in the other analyses. We predicted elk–bison spatial overlap would increase with increasing snow pack because both elk and bison move into lower elevation winter range and geothermal areas as snow pack increases (Bruggeman *et al.* 2009a).

We evaluated two metrics of wolf predation risk: cumulative number of wolf pack-days documented during all winter field seasons and number of packs per drainage per day. The cumulative number of wolf pack-days provides an index of the variation in the magnitude of wolf activity within the study area throughout the study period and represented a coarse spatial and temporal scale metric of the effects of wolf predation risk over the course of this study (Gower *et al.* 2009a, b). This covariate captured the gradual changes in overall elk distribution as the elk population adjusted to the colonization and establishment of wolves throughout the study area. The number of wolf packs per drainage per day represented a fine spatial and temporal scale metric of the effects of wolf predation risk on individual elk locations. The fine-scale covariate captured the ephemeral behavioural responses of elk to immediate predation risk (Gower *et al.* 2009a, b). Wolves within the study area were collared as part of ongoing YNP wolf studies, and each day we intensively monitored wolf activity using radio-telemetry to identify wolf presence within the study area. Additionally, field personnel opportunistically observed tracks and uncollared wolves within the study area. A pack-day was defined as the presence of an individual pack within the study area, and cumulative number of pack-days was calculated as the sum of pack-days from the beginning of the annual field season until the day of the elk location. Because predation risk differed daily among the drainages in the study area, we calculated number of packs per day in each drainage and assigned the number of packs per day covariate to each elk location within the appropriate drainage. We predicted short term, ephemeral elk behavioural responses to wolf predation risk may increase spatial overlap with bison. Elk may move near rivers along valley bottoms or to lower elevation, open areas where escape from wolves is possible (White *et al.* 2009) and bison also tend to use these areas (Bruggeman *et al.* 2007). We predicted that longer-term changes in elk spatial dynamics and distributions associated with wolf restoration may reduce elk spatial overlap with bison. Following wolf reintroduction, elk distribution shifted from areas of high wolf activity (Gibbon and Firehole drainages) to

areas of lower wolf activity (the Madison drainage, Gower *et al.* 2009a). We predicted these longer-term responses to predation risk may reduce elk and bison spatial overlap.

We developed hypotheses representing relationships between the response variables (indices of elk and bison spatial overlap) and covariates, and expressed hypotheses as competing models. We used logistic models to estimate effects of covariates on elk occupancy of the winter range, elk occupancy of the bison distribution within the winter range at the time of sampling, and observed commingling. Variance inflation factors (VIF), which measure the degree of multi-collinearity among variables, were calculated for all combinations of predictors. We removed models that included predictor combinations with VIF > 5 or Pearson correlation > 0.9 from the list of competing models. We used Akaike's Information Criterion corrected for sample size, AIC_c, and Akaike model weights (w_i) to quantify the support from the data for each of our hypothesized models and to address model-selection uncertainty. A total of 35 *a priori* models explaining variations in elk occupancy of the bison winter range, occupancy of the bison distribution within the winter range, and commingling were evaluated.

We conducted a *post-hoc* exploratory analysis and evaluated models containing all possible combinations of the original covariates. We also replaced the covariate number of wolf packs per day per drainage with another fine-scale metric of wolf predation risk, number of kills per drainage per day. After detecting wolf packs within the study area, we backtracked packs daily to identify wolf kills. Therefore, this metric may represent a more refined quantification of predation risk than merely wolf presence in the drainage (Gower *et al.* 2009b). However, backtracking to identify kills was difficult during the later portion of the season (15 April–1 May) due to reduced snow pack, so we chose to use number of packs in *a priori* models.

PREVALENCE OF ANTIBODIES TO *B. ABORTUS* IN ELK

We collected blood from each elk during capture and screened serum for *B. abortus* antibodies. Serological tests indicate whether or not an individual has been exposed to *B. abortus*, but not whether they are currently infected. Thus, we used the prevalence of *B. abortus* antibodies as an index of elk exposure to brucellosis. We analysed serum samples using the standard plate agglutination (SPT), *B. abortus* antigen rapid card (card), rivanol precipitation (Riv), complement fixation (CFT) and buffered acidified plate antigen (BAPA) tests (Veterinary Diagnostic Laboratory, Bozeman, MT, USA). Serological profiles were categorized using the United States Department of Agriculture's brucellosis eradication uniform methods and rules (APHIS 91-45-8 013). Certain strains of bacteria including *E. coli*, *Salmonella* and *Yersinia enterocolitica* O:9 may cross-react in serologic tests designed for *B. abortus*, leading to false positive results. Therefore, all samples collected from 1999 to 2006 that tested seropositive or serosuspect in the standard tests were screened using the Western immunoblot test to determine if antibodies were due to a cross reaction with *Yersinia enterocolitica* O:9 (Edmonds *et al.* 1999).

Results

DATA SUMMARY

Snow water equivalency ranged from 0.0 to 48.3 cm, bison population size ranged from 685 to 1728, elk population size ranged from 231 to 680, cumulative number of wolves ranged

from 0 to 1377, and number of packs per day ranged from 0 to 4.

ELK OCCUPANCY OF THE BISON WINTER RANGE

Sixty-eight per cent of 10 093 independent elk observations were located within the bison winter range. Annually, elk occupancy of the bison winter range varied from a low of 50% in 2003 to a high of 81% in 2004 (Fig. 2a). The most supported model explaining variations in elk occupancy of the bison winter range contained the covariates week, SWE, elk population size, bison population size, wolf packs per day and cumulative wolf risk (see Appendix S1 in Supporting Information, $w_i = 0.80$). The estimated odds of elk occupying the bison winter range increased 5.1% (95% CI = 4.2%, 6.0%) each week of the season, 1.3% (95% CI = 0.9%, 1.8%) for 1 cm increase in SWE, and 16% (95% CI = 6%, 26%) for every one

additional wolf pack per drainage per day (Table 1). Estimated odds of occupancy decreased 0.07% (95% CI = 0.05%, 0.09%) for every one additional wolf pack day within the study area, 0.19% (95% CI = 0.15%, 0.24%) for every one additional elk in the population, and 0.02% (95% CI = 0.00%, 0.03%) for every one additional bison in the population. The predicted probability of elk occupying the bison winter range during the first week of the season increased from 0.48 during a low snowpack year to 0.54 during a high snowpack year. During the last week of the season, predicted probability of elk occupying the winter range increased from 0.72 during a low snowpack year to 0.78 during a high snowpack year (estimates created holding other values at the mean). A second ranked model also received support from the data ($w_i = 0.20$) and contained the covariates week, SWE, elk population size, wolf packs per day, and cumulative effect of wolves. Estimated coefficients were similar to the top ranked

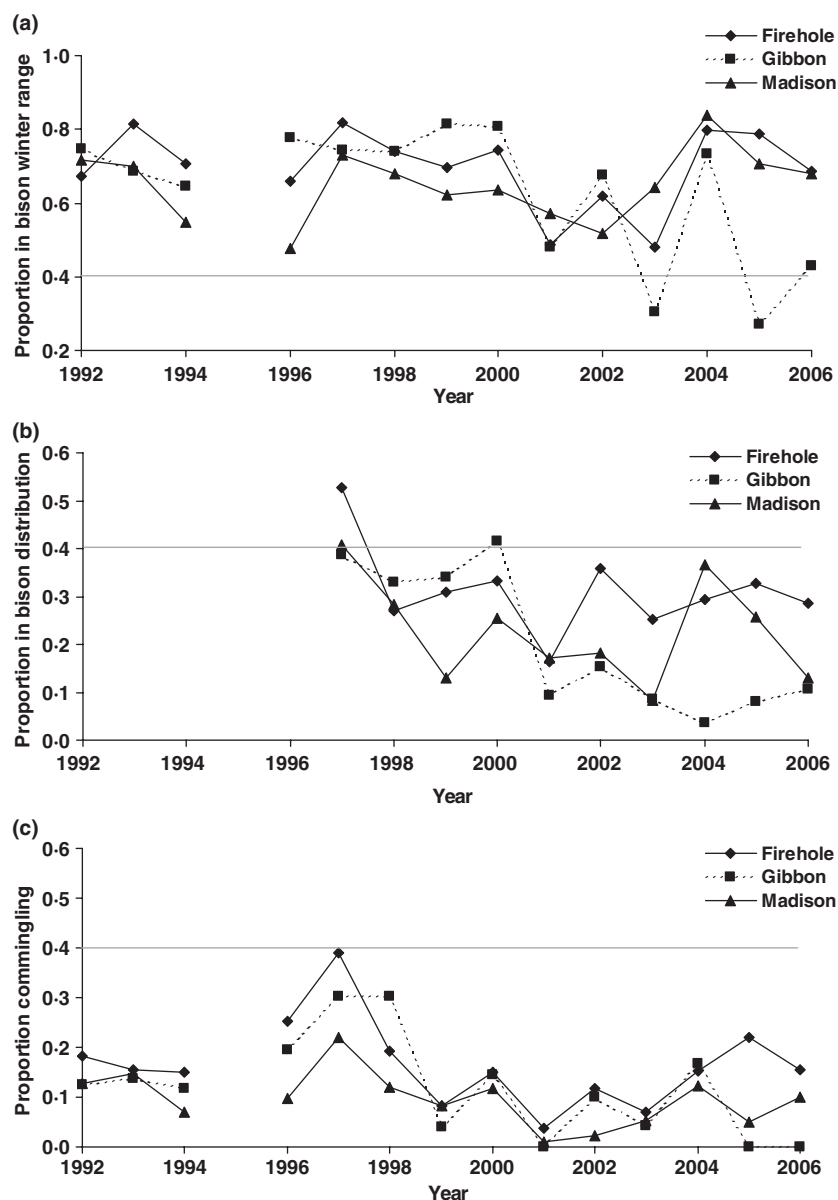


Fig. 2. The proportion of independent elk observations collected in the Madison, Firehole and Gibbon drainages of Yellowstone National Park that occurred within the bison winter range (panel a), within the bison distribution (panel b) and within 100 m of bison from 1991 to 2006 (panel c). A horizontal scale bar is provided for reference.

Table 1. Estimated coefficients and 95% confidence intervals for the effects of covariates on elk occupancy of the bison winter range, elk occupancy of the bison distribution, and elk and bison commingling in the Madison headwaters area of Yellowstone National Park from 1991 to 2006. Estimates from the top-ranked models are reported

Covariate	$\hat{\beta}_{\text{range}}$	LCI	UCI	$\hat{\beta}_{\text{distribution}}$	LCI	UCI	$\hat{\beta}_{\text{commingling}}$	LCI	UCI
Week of season	0.050	0.041	0.058	0.024	0.014	0.035	0.040	0.028	0.052
SWE	0.013	0.009	0.018	0.014	0.001	0.026	0.019	0.012	0.025
Elk population size	-0.0019	-0.0023	-0.0014	-0.004	-0.003	-0.005	-0.003	-0.004	-0.003
Bison population size	-0.0002	-0.0003	-0.0001	0.0002	0.0000	0.0004	0.0002	-0.0001	0.0004
Wolf packs per day	0.15	0.06	0.23	0.17	0.08	0.26	0.41	0.29	0.52
Cumulative wolf risk	-0.0007	-0.0009	-0.0005	-0.0012	-0.0014	-0.0009	-0.0016	-0.0018	-0.0013

model ($\hat{\beta}_{\text{Week}} = 0.051$, 95% CI = 0.043, 0.060; $\hat{\beta}_{\text{SWE}} = 0.012$, 95% CI = 0.007, 0.016; $\hat{\beta}_{\text{elk}} = -0.002$, 95% CI = -0.0016, -0.0024; $\hat{\beta}_{\text{Packs}} = 0.15$, 95% CI = 0.07, 0.24; $\hat{\beta}_{\text{risk}} = -0.0007$, 95% CI = -0.0009, -0.0005). No exploratory models were supported over the top ranked *a priori* models.

ELK OCCUPANCY OF THE BISON DISTRIBUTION

A total of 6165 independent elk observations were collected during 1997–2006 when bi-weekly bison surveys were conducted. Elk occupancy of the bison distribution differed by drainage and year (Fig. 2b), with 25% of all independent elk locations in the Madison drainage, 28% in the Gibbon drainage and 32% in the Firehole drainage. The most supported model explaining variations in elk occupancy of the bison distribution contained the covariates week, SWE, elk population size, bison population size, wolf packs per day, and cumulative wolf risk ($\Delta\text{AIC}_c = 0.0$, $w_i = 0.58$). Estimated odds of elk occupying the bison distribution increased 1.4% (95% CI = 0.1%, 2.6%) for every 1 cm increase in SWE and 19% (95% CI = 8%, 30%) for every additional wolf pack per drainage (Table 1). Estimated odds of elk occupying the bison distribution increased 2.4% (95% CI = 1.4%, 3.6%) per week from 1 December – 1 May. Estimated odds of elk occupying the bison distribution decreased 0.4% (95% CI = 0.3%, 0.5%) for every one additional elk in the population and 0.1% (95% CI = 0.1%, 0.1%) for every one additional wolf pack day within the study. The second ranked model contained the covariates week, SWE, elk population size, wolf packs per day, and cumulative wolf risk ($\Delta\text{AIC}_c = 0.59$, $w_i = 0.42$), and coefficient estimates were similar to the top ranked model ($\hat{\beta}_{\text{Week}} = 0.023$, 95% CI = 0.013, 0.034; $\hat{\beta}_{\text{SWE}} = 0.019$, 95% CI = 0.009, 0.029; $\hat{\beta}_{\text{elk}} = -0.004$, 95% CI = -0.003, -0.005; $\hat{\beta}_{\text{risk}} = -0.0011$, 95% CI = -0.0008, -0.0014; $\hat{\beta}_{\text{Packs}} = 0.16$, 95% CI = 0.07, 0.25). The third ranked model was 11.6 ΔAIC_c units from the top model. No exploratory models were supported over the top ranked *a priori* models.

ELK AND BISON COMMINGLING

Elk and bison commingling differed by drainage and year (Fig. 2c) during 1991–2006, with 9% of the 10 093 independent elk locations in the Madison drainage, 16% in the Gibbon drainage, and 17% in the Firehole drainage being ≤ 100 m from the nearest bison. The most supported model explaining

variations in elk and bison commingling contained the covariates week, SWE, elk population size, bison population size, wolf packs per day, and cumulative wolf risk ($\Delta\text{AIC}_c = 0.0$, $w_i = 0.86$). Estimated odds of commingling increased 1.9% (95% CI = 1.2%, 2.5%) for every 1 cm increase in SWE and 50% (95% CI = 33%, 69%) for every additional wolf pack per drainage (Table 1). Estimated odds of commingling increased 4.0% (95% CI = 2.8%, 5.3%) per week from 1 December to 1 May. Estimated odds of commingling decreased 0.3% (95% CI = 0.3%, 0.4%) for every one additional elk in the estimated elk population size and 0.2% (95% CI = 0.2%, 0.2%) for every one additional wolf-pack day throughout the study period. The second ranked model received some support from the data ($\Delta\text{AIC}_c = 3.58$, $w_i = 0.14$) and contained the covariates week, SWE, elk population size, cumulative wolf risk and wolf packs. Estimated coefficients were similar to the top ranked model ($\hat{\beta}_{\text{Week}} = 0.037$, 95% CI = 0.025, 0.048; $\hat{\beta}_{\text{SWE}} = 0.06$, 95% CI = 0.04, 0.07; $\hat{\beta}_{\text{elk}} = -0.001$, 95% CI = -0.004, -0.003; $\hat{\beta}_{\text{risk}} = -0.002$, 95% CI = -0.0018, -0.0013; $\hat{\beta}_{\text{Packs}} = 0.40$, 95% CI = 0.28, 0.52). The third ranked model was 45 ΔAIC_c units from the top ranked model. No exploratory models were supported over the top ranked *a priori* models.

ELK EXPOSURE TO *B. ABORTUS*

A total of 151 elk serum samples were collected from 135 individual elk and screened for the prevalence of *B. abortus* antibodies. Overall, 1.5% (2 of 135) of all individuals tested positive for antibodies to *B. abortus*, and an additional 2.2% (3 of 135) tested serosuspect. During the pre-wolf period (1996–1998), two of 73 individuals sampled tested positive (Ferrari & Garrott 2002). During the post-wolf period (1999–2006), six individuals initially tested positive for antibodies to *B. abortus*, but subsequent Western immunoblot tests revealed each of these individuals were *Yersinia* positive, and the initial results were produced by a *Yersinia* cross reaction. The Western immunoblot test revealed three of the six individuals had background banding patterns that may have been produced by a weak exposure to *B. abortus* due to previous vaccination, cross reactions with soil microbes having similar antigens to *B. abortus* or, most likely, a resolved infection that did not result in the animal becoming infectious (P. Elzer, personal communication). Therefore, we considered the three individuals with weak background exposures as serosuspect

for prevalence of *B. abortus* antibodies. Even if these samples were considered test-positive for brucellosis exposure, however, seroprevalence remained relatively low (3.7%; 5 of 135) and similar during the pre-wolf (2 of 73; 1996–1998) and post-wolf (3 of 71; 1999–2006) periods.

The two individuals testing positive for antibodies to *B. abortus* were both sampled in 1996. One individual was 9 years old and the other was 10 years old. Both tested positive on the BAPA, card, SPT, and CFT tests, and the 9-year-old also tested positive on the Riv test. Each of these animals had been in the study area for a minimum of 4 years prior to testing, and their previous histories are unknown. The three individuals with background exposures for *B. abortus* were sampled in 2000, 2003 and 2003 and were 4, 4 and 11 years old at the time of sampling, respectively.

Discussion

We found a high degree of spatial overlap between bison and elk using a shared winter range within YNP. Long-term declines in spatial overlap associated with cumulative wolf predation risk occurred from 1998 to 2006, and these patterns were detected at each of the three spatial scales evaluated. Previous studies at this site found elk increased home range size, were killed on their traditional ranges, or dispersed out of the study area in response to long term, cumulative effects of wolf predation risk (Gower *et al.* 2009a). Additionally, over time, variable risk and vulnerability to predation among the three drainages in the study area resulted in a larger proportion of elk being removed from certain parts of the elk winter range (White *et al.* 2009), such as the Gibbon and Firehole drainages, and consequently changed patterns of spatial overlap with bison. More dynamic movement patterns associated with increasing predation risk may result in reduced elk occupancy of the bison winter range and spatial overlap with bison.

In contrast to reductions in spatial overlap associated with cumulative wolf risk, on days when one or more wolf packs were within the same drainage as elk, the odds of elk occupying the bison winter range or distribution and commingling with bison increased. In response to immediate wolf predation risk, elk may move into lower elevation geothermal areas where reduced snow pack increases manoeuvrability and escape potential, or elk may move nearer the valley bottom and seek refuge in the rivers (White *et al.* 2009). Because bison select for valley bottoms and frequently travel along stream corridors (Bruggeman *et al.* 2007), increasing use of geothermal areas and valley bottoms in response to predation risk may indirectly increase spatial overlap with bison.

Transmission risk also depends on how bison and elk spatial overlap fluctuates over time relative to peak transmission periods. Consistent with a previous study, we found spatial overlap increased with increasing snow pack (Ferrari & Garrott 2002). Snow pack is spatially variable within the Madison headwaters area due to differences in aspect, elevation, and geothermal features (Watson *et al.* 2009), and as snow pack increases both elk and bison select for similar wet meadow communities and geothermal basins to reduce energetic constraints of foraging

in deep snow and improve access to available forage (Ferrari & Garrott 2002; Bruggeman *et al.* 2009b). Even after accounting for the effects of snow pack, elk and bison spatial overlap increased throughout the winter and reached a maximum in late April. This is probably due to increasing numbers of bison migrating into the study area from the central Yellowstone ranges (Hayden and Pelican valleys) in response to interactions between bison density, deep snow pack and freeze–thaw cycles during spring that crusted the snow and made foraging more difficult on central Yellowstone ranges. Thus, bison migrated from these higher elevation central ranges to the Madison headwaters area with its relatively lower snow pack due to geothermal influences and earlier vegetation green-up in the spring (Thein *et al.* 2009).

High levels of elk and bison interaction during mid- to late April, combined with late-term bison abortion and parturition events (Gogan *et al.* 2005), predict bison-to-elk transmission risk may be highest during this time period. The high snowfall in the study system casts uncertainty in applying seasonal variations in spatial overlap observed in this system elsewhere in lower elevation areas of the GYE. In lower elevation, lower snowfall areas, the peak of spatial overlap likely occurs earlier in the winter. Although risk from late term bison abortion events may occur, elk and bison in lower elevation areas are likely more dispersed during the bison parturition period. Exposure of elk to *B. abortus* during the bison parturition period, which occurs primarily during mid-April through May (Gogan *et al.* 2005), may also occur. Following parturition, female bison consume birthing materials and some of the vegetation contaminated with birthing materials, which probably reduces transmission risk. However, the degree to which bison clean a birthing area has not been documented. *B. abortus* has been cultured from bison birthing sites (Aune *et al.* 2004) and elk exposure to *B. abortus* exists during both the bison abortion and parturition periods.

The persistence of *B. abortus* and the amount of time bison foetuses or birthing materials remain potentially infectious varies seasonally and with environmental conditions and substrate. Persistence is highest during February and decreases seasonally to June (Aune *et al.* 2007). Field investigations conducted at bison birthing or abortion sites found that *B. abortus* persisted in birthing material, vegetation or soils for 10–43 days during April and 7–26 days during May. Elk in the Madison headwaters area of YNP show a high degree of spatial overlap with bison during the period when risk of exposure to *B. abortus* from aborted foetuses or birthing materials exists. However, despite high spatial overlap, rates of elk exposure to *B. abortus* in this population were similar to rates of exposure in other GYE free-ranging elk populations not in contact with bison, and lower than rates in elk populations associated with feeding programmes (Etter & Drew 2006; Barber-Meyer *et al.* 2007; Cross *et al.* 2009). Thus, it appears that the high degree of spatial overlap with bison during the period of transmission risk has little impact on elk exposure to *B. abortus*.

Predation risk associated with wolves may increase elk and bison spatial overlap, but our results suggested these risk-driven elk behavioural responses are unlikely to have

important disease implications. Elk-to-elk transmission or dispersal of elk from herds with relatively high levels of infection may be primarily responsible for the observed levels of *B. abortus* exposure within the northern GYE elk herds. Thus, management of brucellosis in GYE elk populations should focus on reducing elk-to-elk transmission risk and, to the extent feasible, curtailing practices that increase elk density and group sizes during the potential abortion period, including elk aggregation on feed grounds, elk use of cattle feed lines, and elk use of refuge areas where human harvests and/or natural predation are reduced.

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Supporting Information

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

Appendix S1. Model selection results for *a priori* models examining the effects of covariates on variation in elk occupancy of the bison winter range in the Madison headwaters area of Yellowstone National Park from 1991 to 2006.

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