

Wildlife–livestock conflict: the risk of pathogen transmission from bison to cattle outside Yellowstone National Park

A. Marm Kilpatrick^{1,2,*}, Colin M. Gillin³ and Peter Daszak¹

¹The Consortium for Conservation Medicine, New York, NY 10001, USA; ²Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064, USA; and ³Oregon Department of Fish & Wildlife, Corvallis, OR 97330, USA

Summary

1. Interactions between wildlife and domestic livestock have created conflict for centuries because of pathogen transmission, competition for space and food, and predation. However, the transmission of pathogens from wildlife to domestic animals has recently gained prominence, including H5N1 avian influenza from wild ducks to poultry, bovine tuberculosis from badgers to cattle, and brucellosis from elk and bison to cattle. The risk of transmission of *Brucella abortus* (the causative agent of brucellosis) from bison (*Bison bison*) to cattle around Yellowstone National Park (YNP) is a hotly debated topic and an important conservation issue.

2. Here we use a model to integrate epidemiological and ecological data to assess the spatio-temporal relative risk of transmission of *Brucella* from bison to cattle outside YNP under different scenarios.

3. Our risk assessment shows that relative risk is spatially and temporally heterogeneous with local hotspots, shows a highly skewed distribution with predominantly low risk, and is strongly dependent on climate and the abundance of bison. We outline two strategies for managing this risk, and highlight the consequences of the current adaptive management plan.

4. *Synthesis and applications.* Our results provide a detailed quantitative assessment of risk that offers several advantages over projections of numbers of bison leaving Yellowstone National Park. They suggest that risk could be effectively managed with lower costs, but that land use issues and the larger question of bison population management and movement outside the park might hinder the prospect of solutions that will please all stakeholders. More broadly, our work provides a model framework for quantifying the risk of wildlife–livestock pathogen transmission to guide management actions.

Key-words: disease control, climate change, wildlife disease, GIS, buffalo, emerging infectious disease, zoonotic, population regulation, animal disease

Introduction

Interactions between wildlife and domestic livestock have been a potential source of conflict for centuries (Prins 1992; Treves *et al.* 2004). However, the spillover of disease-causing pathogens from wildlife to domestic animals has more recently gained prominence, including H5N1 avian influenza from wild ducks to poultry (Gilbert *et al.* 2006; Kilpatrick *et al.* 2006a), bovine tuberculosis from badgers *Meles meles*

L. to cattle *Bos taurus* L. (Donnelly *et al.* 2003), and brucellosis from elk *Cervus canadensis Nelsoni* and bison *Bison bison* L. to cattle (Cheville, McCullough & Paulson 1998). The traditional methods of disease control, including test and slaughter, whole-herd or whole-flock culling, and vaccination, are often difficult or impossible (logistically or politically) to fully implement in free-ranging wildlife (Peterson, Grant & Davis 1991a; Thorne *et al.* 1997; Clarke *et al.* 2005). As a result, wildlife and livestock managers are often confronted with the challenge of minimizing contact between infectious animals and livestock (and possible pathogen transmission)

*Correspondence author. E-mail: marm@biology.ucsc.edu

by altering spatio-temporal patterns of livestock land use, and movement patterns of wildlife (e.g. Donnelly *et al.* 2003; Cross *et al.* 2007). This is the case in the greater Yellowstone area where the risk of transmission of brucellosis from bison to cattle is a hotly debated topic and an important conservation issue (Peterson 1991; Meyer & Meagher 1995; Keiter 1997; Baskin 1998; USDOJ & USDA 2000a,b; Clarke *et al.* 2005; Bienen & Tabor 2006). A study commissioned by the National Academy of Sciences following an exodus and culling of a third of the bison population in 1996–1997 performed a qualitative (not quantitative) risk assessment and found that the risk of transmission from bison to cattle around Yellowstone National Park (YNP) was low but not zero (Cheville, McCullough & Paulson 1998).

Brucellosis is a disease caused by bacteria in the genus *Brucella* which causes weight loss, abortion, and reduced milk production in domestic cattle and other ruminants, undulant fever in humans, and a range of outcomes in wildlife (Moore 1947; Thorne *et al.* 1978; Rhyan *et al.* 1994, 2001; Meyer & Meagher 1995; Tessaro & Forbes 2004). Brucellosis is thought to have been introduced to the USA in the 19th century and was previously widespread in cattle and swine in the USA (Cheville, McCullough & Paulson 1998), but following an intense \$3.5-billion targeted plan by the USDA (Frye & Hillman 1997), cattle in all but a few states are currently considered brucellosis-free, meaning all cattle have tested seronegative and/or culture negative for the bacteria for 2 years (USDA-APHIS 2007). Brucellosis-free status provides significant economic benefits to a state's cattle industry, including reduced testing, easier shipment and within-state movement of cattle, and access to stringent markets (Healey *et al.* 1997). As a result, there is significant effort to keep a state's cattle free from infection.

Bison in Yellowstone National Park (YNP) are the last remaining herd in the USA of continuously free-ranging animals, from a species that once roamed the plains in the millions (Hornaday 1889). Yellowstone bison were reduced by hunting to near-extinction (~25 animals) in 1902, but have since recovered, and over the past decade, the population has grown from 2105 to 4879 individuals with fluctuations depending on the season, winter severity, and management actions (Meager 1973; Clarke *et al.* 2005). Clearly, without management actions, the population will continue to grow and expand beyond YNP as it exceeds the carrying capacity of the park (Boyce 1990; Boyce & Gaillard 1992). As a result, a controlled hunt has been instituted to attempt to stabilize the population.

Yellowstone bison have been infected with *Brucella abortus* since at least 1917 (Mohler 1917) and are thought to have become infected from cattle that were grazed in YNP a century ago (Meagher & Meyer 1994). The prevalence of infection in bison is difficult to measure in live animals, but the fraction that have antibodies to *Brucella* (seroprevalence) has fluctuated between 40% and 60% over the last decade (Dobson & Meagher 1996; Clarke *et al.* 2005). Simultaneous testing by serology and bacterial culture conducted on killed animals suggests that the seroprevalence can overestimate the

prevalence of infection (by culture) from two- (Roffe *et al.* 1999) to fourfold (Dobson & Meagher 1996; USDOJ & USDA 2000a). However, due to difficulties with culturing techniques, the relationship between serological and culture findings and infectiousness in bison is not fully known (Cheville, McCullough & Paulson 1998).

For bison to transmit *B. abortus* to cattle, infected bison must leave YNP (where there are no cattle), enter areas where cattle graze and, most probably, abort or give birth with infected birthing materials that cattle then contact. For much of the early summer and fall, the current bison population prefers to forage on the new growth of vegetation within YNP, which is at higher elevations than much of the surrounding area (Meager 1973; Gates *et al.* 2005). In past years of low bison abundance, most bison also remained inside the park during the winter. However, in severe winters with heavy snow or when ice prevents bison from accessing grass underneath the snow, many bison move to lower elevations and leave the boundaries of YNP (Fig. 1), primarily in the north-west, near Gardiner during the months of January to May, and near West Yellowstone, Montana from September to June (Cheville, McCullough & Paulson 1998; Clarke *et al.* 2005; Gates *et al.* 2005). Cattle are grazed on public and private lands in these areas where bison leave YNP and this raises the concern that bison infected with *B. abortus* may come in contact with cattle. Horizontal (within generation) transmission of *B. abortus* is thought to occur primarily by contact with a foetus or birth area of an infected female (Davis *et al.* 1990; Cheville, McCullough & Paulson 1998). Transmission through other forms of contact (e.g. sexual) are thought to be much less likely. It should be noted that no transmission between YNP bison and cattle outside a captive setting has ever been documented.

There have been several calls for a quantitative risk assessment of transmission, but, until recently, sufficient data were unavailable to quantify several key aspects of transmission (Keiter 1997; Cheville, McCullough & Paulson 1998; Clarke *et al.* 2005). Here we integrate epidemiological, population dynamical, and ecological data to assess the spatio-temporal risk of transmission of brucellosis from bison to cattle at the boundary of YNP (Fig. 1). Although the current management plan (USDOJ & USDA 2000a) prevents bison from coming near grazing cattle in space and time (essentially reducing the risk of transmission to zero), it requires intensive efforts, is costly, and results in significant culling of bison (more than 3400 bison have been killed since the year 2000). Thus, we sought to quantify the risk of transmission to determine if alternative management strategies might keep risk low while reducing the cost of management and culling and hazing of bison.

Methods

Our goal was to assess the risk of *B. abortus* transmission from bison to cattle that is mitigated by the present management plan of culling and hazing (attempts to use riders on horseback and helicopters to induce the cattle to move to other areas) bison, and to determine

how this risk might differ if more bison were allowed on low elevation winter ranges outside the National Park. Management of the Yellowstone bison herd is governed by the Interagency Bison Management Plan (IBMP) using the strategies outlined in the 'Modified Preferred Alternative' (USDOI & USDA 2000b). This plan allows for up to 100 untested bison outside YNP in both the northern Special Management Area (SMA), near Gardiner, Montana and western SMA, near West Yellowstone, Montana, areas (and an unspecified number in the Eagle Creek/Bear Creek area) as long as the bison are inside the boundaries of the management zone, away from cattle, and do not threaten property or human safety. In addition, the plan requires that the bison outside YNP return to the park (of their own accord or by hazing) by set dates (15 April in the north; 15 May in the west, pending research on the persistence of bacteria and foetuses; (Clarke *et al.* 2005)), or be removed by lethal means. Under all three steps of this plan, bison are kept away from cattle or areas where cattle will be in the next 45 days by hazing or shooting, and thus, the risk of transmission is essentially zero (USDOI & USDA 2000a). It should also be noted that although the original management plan set strict numbers for bison outside the park in the two SMAs (100 in each), managers have been somewhat flexible in both the number allowed outside the park and in allowing some movement beyond the management zones, as long as no cattle were present (K. Aune, personal communication.).

We estimated the risk of transmission under four scenarios, with an aim to estimate the risk being mitigated by hazing and culling bison outside the park, keeping cattle off allotments until June or July, and to determine the influence of weather and changes in bison population size. Except for the first scenario which requires management action (hazing and culling), we were essentially estimating risk under a 'no-plan' strategy (USDOI & USDA 2000a) in which there was no management of bison inside or outside YNP, in order to estimate the risk posed by bison. The four scenarios included: (1) a population abundance of 3000 bison, with a maximum of 200 outside YNP. This is similar to that of the latest phase of the IBMP. However, currently more than 200 are sometimes tolerated, and more are allowed into the Eagle Creek/Bear Creek area (K. Aune and R. Wallen, personal communication), and 3 scenarios providing unlimited numbers of bison outside the park, with the following bison population sizes: (2) 3000; (3) 5000, near a recent estimate of population size of 4879, estimated in 2005–2006 (Yellowstone National Park unpublished data); and (4) 7000, which the projected size, based on past growth rate, that the population would reach in 7.5 years if culling ceased [the bison population has grown by ~72 individuals per year since 1984 including the effects of culling ($N = 72.4 \times \text{year} + 2337$; year = 1 in 1984; $R^2 = 0.36$), and ~287 individuals per year excluding culling effects ($N = 286.8x + 1709$; $R^2 = 0.96$; (Cheville, McCullough & Paulson 1998)].

We assumed that the primary risk of transmission was through contact between cattle and an infected foetus from an abortion or from infected birthing materials from a live birth (see Supporting Information). Thus, we determined the risk of transmission by estimating the number and duration of persistence of *Brucella*-infected foetuses or birth sites on the landscape. We assumed that transmission was density dependent (i.e. increased with the number of cattle that might contact infected foetuses or birth areas). We estimated the risk of transmission from contact with infected birthing materials as:

$$\text{Relative Risk} \propto (C) [F \times B \times S \times b \times \min(t_{cp}, t_{bp})] \quad \text{eqn 1}$$

or in word form:

Relative Risk \propto (no. of cattle)[Fraction of bison outside park \times Bison population \times *B. abortus* seroprevalence \times infected birthing rate outside park if seropositive (abortions + births) \times minimum (carcass persistence time, bacterial persistence time) for abortions and births]

This equation estimates the density of infected births (abortions + infected live births) in the wintering areas multiplied by the duration of their persistence (calculated separately for abortions and live infected births), and the number of cattle in these wintering areas [Fig. 1; 9360 ha in size for the northern SMA, 31 025 ha for the western SMA; (USDOI & USDA 2000a); see below for discussion of movement outside these areas]. We focus on these areas because they are immediately adjacent to YNP, they are where bison have historically left the park, and where management actions have been focused.

If the cattle (266 head in four herds in winter, 1441 head in 18 herds in spring; Fig. 1) grazed the entire wintering area (40 385 ha) during each carcass persistence period (~18.3 days; see below), the risk equation would give the number of infected foetuses that could be contacted by all cattle over the winter–spring. However, the risk values from equation 1 do not equal the true number of infected birth sites likely to be encountered (necessitating the use of the proportional symbol in equation 1), because cattle graze less than 56–300 ha month⁻¹ and the spatial distributions of bison and cattle are likely to be patchy. Nonetheless, this equation provides an estimate of the relative risk, and could be translated into actual yearly probabilities of contact with infected birth sites if data could be obtained on cattle grazing rates (area encountered), attraction or repulsion between cattle and bison, and attraction or repulsion of cattle to a bison foetus or birthing area.

We obtained estimates for each quantity in equation 1 from previously published and unpublished data sources (see Supporting Information). Because several key factors in the risk of transmission differ depending on the weather and between early winter (January–February) and late spring (May–July), we estimated risk separately for each of these two periods and for average and extreme winters (see below).

The number of cattle being grazed in the western and northern Special Management Areas was obtained from the US Forest Service in March 2006 with the help of Amy McNamara from the Greater Yellowstone Coalition. For the northern and western SMAs, the number of head of cattle were 266 (four herds) and 0 in winter, respectively, and 677 (nine herds) and 686 (nine herds) in spring, respectively. We note that if bison move outside the management areas, as they increasingly do (R. Wallen and K. Aune, personal communication), risk will change with the number (and critically, density) of bison and cattle in these areas.

The grazing period in the western SMA begins in July on public lands and June–July on private lands. Thus there is essentially no risk of transmission in the western SMA before these months, and most bison usually move back into Yellowstone by June. However, if an infected foetus was left on land where cattle subsequently graze, the potential for transmission exists, and this is the thrust of the calculations done for the western SMA.

The fraction of the bison population that leave the park (F) was modelled as a function of population size (B) and the severity of the winter as measured by the snow water equivalent (SWE) in inches and was estimated from empirical data as (see Supporting Information):

$$F = \sin(-4.03 + 0.042 \text{ SWE} + 1.14 \text{ Log}_{10} B)^2 \quad \text{eqn 2}$$

($n = 22$; $R^2 = 80.0\%$; $P_B = 0.001$; $P_{\text{SWE}} = 0.018$)

Table 1. Relative risk of transmission of *B. abortus* from bison to cattle under the current management plan, and three 'no plan' (no management of bison outside YNP) scenarios (Sc) under average [(snow water equivalent) SWE = 6.54] and extreme (SWE = 10.91) snow conditions. Relative risk is the product of the number of cattle, the estimated density (no. of cattle per hectare) of *Brucella*-infected fetuses birthed outside YNP multiplied by the estimated number of days that each foetus will persist (equation 1; Methods)

		Bison outside park (mean, median, 95% CI)		Relative risk (mean, median, 95% CI; % of simulations where risk = 0)		
Sc*	Bison	Season	Average winter	Extreme winter	Average winter	Extreme winter
1	3000	Winter	116, 128 (0.4–200)	143, 169 (1.2–200)	0.04, 0.01 (0–0.27; 32%)	0.05, 0.01 (0–0.30; 24%)
1	3000	Spring	†	†	0.23, 0.06 (0–1.43; 18%)	0.29, 0.10 (0–1.62; 12%)
2	3000	Winter	354, 188 (0.4–1550)	634, 440 (1.2–2207)	0.11, 0.01 (0–0.83; 29%)	0.21, 0.04 (0–1.47; 19%)
2	3000	Spring	†	†	0.69, 0.12 (0–5.08; 18%)	1.25, 0.29 (0–8.30; 11%)
3	5000	Winter	1277, 987 (3.3–4003)	1950, 1785 (15.2–4746)	0.42, 0.08 (0–2.95; 13%)	0.63, 0.16 (0–4.06; 9%)
3	5000	Spring	†	†	2.56, 0.66 (0–16.24; 8%)	3.89, 1.26 (0–22.96; 6%)
4	7000	Winter	2671, 2385 (13.4–6708)	3614, 3655 (57.1–6965)	0.88, 0.19 (0–5.93; 11%)	1.16, 0.31 (0–7.23; 9%)
4	7000	Spring	†	†	5.42, 1.48 (0–32.21; 8%)	7.22, 2.46 (0–40.91; 7%)

*Scenarios: 1 (modified preferred alternative); target bison population size 3000, up to 100 bison allowed outside park in each SMA.

2 (no plan): 3000 bison, no limit on number outside park.

3 (no plan): 5000 bison, no limit on number outside park.

4 (no plan): 7000 bison, no limit on number outside park.

†The number of bison outside YNP is assumed to be the same for winter and spring. Numbers given are totals for the year (winter + spring).

The relationship the fraction of bison seropositive for *B. abortus* (S) and bison population size (B), and was estimated as (see Supporting Information)

$$S = 0.509(1 - e^{-0.0015 \times B}) \quad (n = 14; R^2 = 41.0\%; P_B = 0.0062) \quad \text{eqn 3}$$

We modelled the fraction of bison that would abort as a fraction of the seropositive bison (per cent aborting: $10.6\% \pm 4.2\% \times$ per cent seropositive) and that estimated that each aborted birth would result in $18.2 \pm \text{SD } 20.1$ *Brucella*-infected carcass exposure days (but with a minimum of 1 day; Clarke *et al.* 2005; K. Aune, personal communication; see Supporting Information). We assumed that an additional $0.052/0.33 = 15.8\% \times$ (per cent seropositive) of bison would have live birth sites infected with *B. abortus*. Live births take place in April and May, and hence, we used data from a study that suggested that bacteria at these birth sites would remain infectious for 0.45 ± 0.21 days (USDOI & USDA 2000a).

We used equations 1–3 and the parameter values and error estimates described above to determine the mean, median, and 95% confidence intervals (assuming no covariance of parameters) for the '*B. abortus* exposure days' or number of *B. abortus*-infected births multiplied by the duration they would persist on the landscape. We then estimated relative risk by multiplying this by the density of cattle in areas where these births were likely to take place (equation 1). We note that this is an estimate of relative risk, due to uncertainty between seroprevalence and infection prevalence, and contact rates between cattle and infected birth sites. To estimate the 95% confidence intervals we drew one value for each parameter from normal distributions with mean and variance as described above or from the predicted value distributions using equations 2 and 3 (Kilpatrick *et al.* 2006b). We estimated the number of female bison that would have an infected birth site (given a number giving birth outside the park) by repeatedly sampling from a binomial distribution, with the fraction described above. We then inserted these parameter values into equation 1 to calculate one value of risk. We repeated this 50 000 times and took the upper and lower 2.5% of observations as the 95% confidence intervals. We also estimated the probability or fraction of these 50 000 simulations that risk was zero (no infected birth sites outside the park).

Results

Our model analyses indicated that the number of bison outside the park and the relative risk of transmission of *B. abortus* from bison to cattle is extremely heterogeneous, both temporally (Table 1; Fig. 2) and at several spatial scales (Fig. 1), and varies significantly with the number of bison and the climate (Table 1; Fig. 2). For example, at a population size of 7000, with average snowfall, less than 100 bison will leave the park with 10% probability, but over 1000 bison are expected to leave the park 74% of the time. Years when over 1000 bison leave the park and are culled (as was the case in 1996–1997 and 2005–2006; (Cheville, McCullough & Paulson 1998; Bienen & Tabor 2006)) will be much more frequent at higher populations, but are also likely to occur 9% of the time with a population of 3000 bison, with average snow, and 25% of the time, under severe snow conditions.

The relative risk of transmission of *Brucella* from bison to cattle had a highly skewed distribution with zero or relatively low risk much of the time, but occasional years of substantially higher risk (Table 1; Fig. 2A). This skewed distribution is a result of risk being a product of several variables that were approximately normally distributed, resulting in an approximately log-normal distribution. An important consequence of the skewed distribution of relative risk is that in most years, the risk is very low (Table 1), and in a substantial fraction of the simulations, the relative risk was equal to zero (Table 1 – last entry in each risk cell). In addition, the stochastic processes of birthing outside the park, carcass removal by scavengers (Wilmers *et al.* 2003; Wilmers & Getz 2005), and stochastic variation in individual infection status make the mean relative risk of transmission low most of the time, even when moderate numbers of bison leave the park (Table 1).

The differences between the four scenarios, the two seasons, and differing snow conditions all had strong impacts on the number of bison leaving the park and on the relative risk of

transmission (Table 1; Figs 1,2). The current management plan scenario, when the bison population was assumed to be 3000 and no more than 200 bison were allowed outside YNP, produced the lowest risk of the four scenarios. The effect of restricting the number of bison outside YNP to no more than 200 (Table 1; compare scenario 1 to scenario 2) was especially evident in extreme snow conditions, when many more than 200 bison are likely to leave YNP (Table 1, scenario 2; mean 634; median 440) unless they are hazed back into YNP or removed by management actions.

Increases in the size of the bison population significantly increased the number of bison leaving YNP and the relative risk of transmission (compare scenarios 2, 3, and 4; Table 1; Figs 1, 2), primarily through increases in the number of bison leaving the park (equation 2). For example, with a bison population size of 5000 individuals under average snow conditions (close to the population size of bison in the fall of 2005), the mean relative risk is three- to fourfold higher, and the probability of zero risk decreases from 29 to 13% compared to a population of 3000 individuals (Table 1). Additional growth of the population to 7000 individuals is predicted to substantially increase the number of bison leaving the park, and the risk of transmission by 20-fold compared to scenario 1 (Table 1; Fig. 2C,D).

The distribution of relative risk differs significantly between the north and west and is patchily distributed in both. During the winter, there are no cattle in the western SMA and 266 head of cattle are present in the northern SMA (Fig. 1A) and these occur on a few private ranches in the area where bison exit the park. In contrast, in July, a total of 1441 head of cattle are present on several private ranches and public land grazing allotments in both the northern SMA (Fig. 1B) and the western SMA (Fig. 1C). This presence results in a substantially higher risk of transmission in spring compared to winter (Table 1). The northern SMA accounted for 100% of the relative risk in winter and, on average, 48% in spring. This is despite the fact that only 23% of bison exit the park into the northern SMA in spring, and results from the smaller area that bison usually occupy outside the park in the northern SMA, resulting in a higher density of bison.

Discussion

A previous risk assessment (which was qualitative, not quantitative) of transmission of *Brucella abortus* from bison to cattle found the risk to be small, but not zero (Cheville, McCullough & Paulson 1998). As a result, the National Park

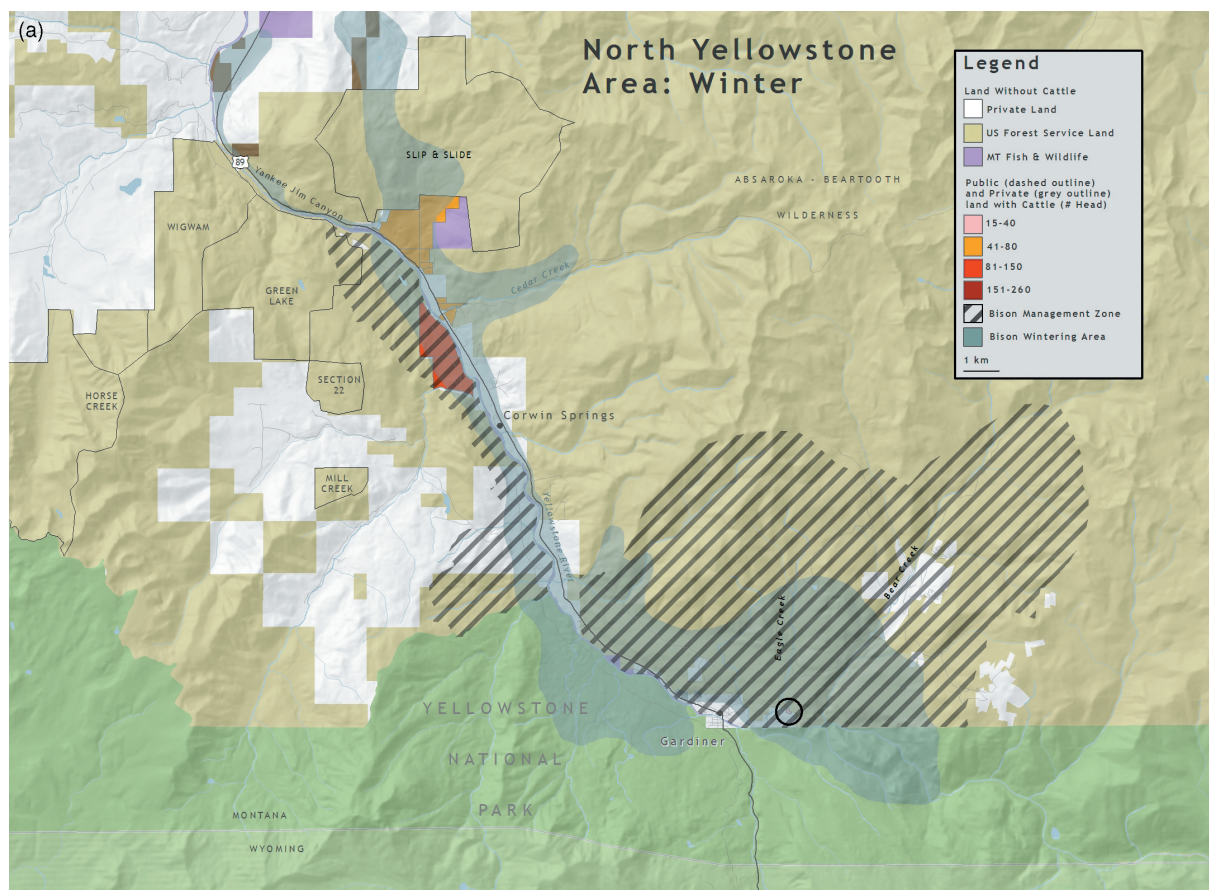


Fig. 1. The distribution and abundance of cattle on the northern edge of YNP near Gardiner during (a) winter and (b) spring and (c) the western area in spring in areas where bison are found outside the park. Cattle grazing allotments on public lands in the northern area start in mid-June. Cattle in the western area are brought onto private lands and public lands in June and July, respectively. There are no cattle in the western area in winter, due to excessive snowfall.

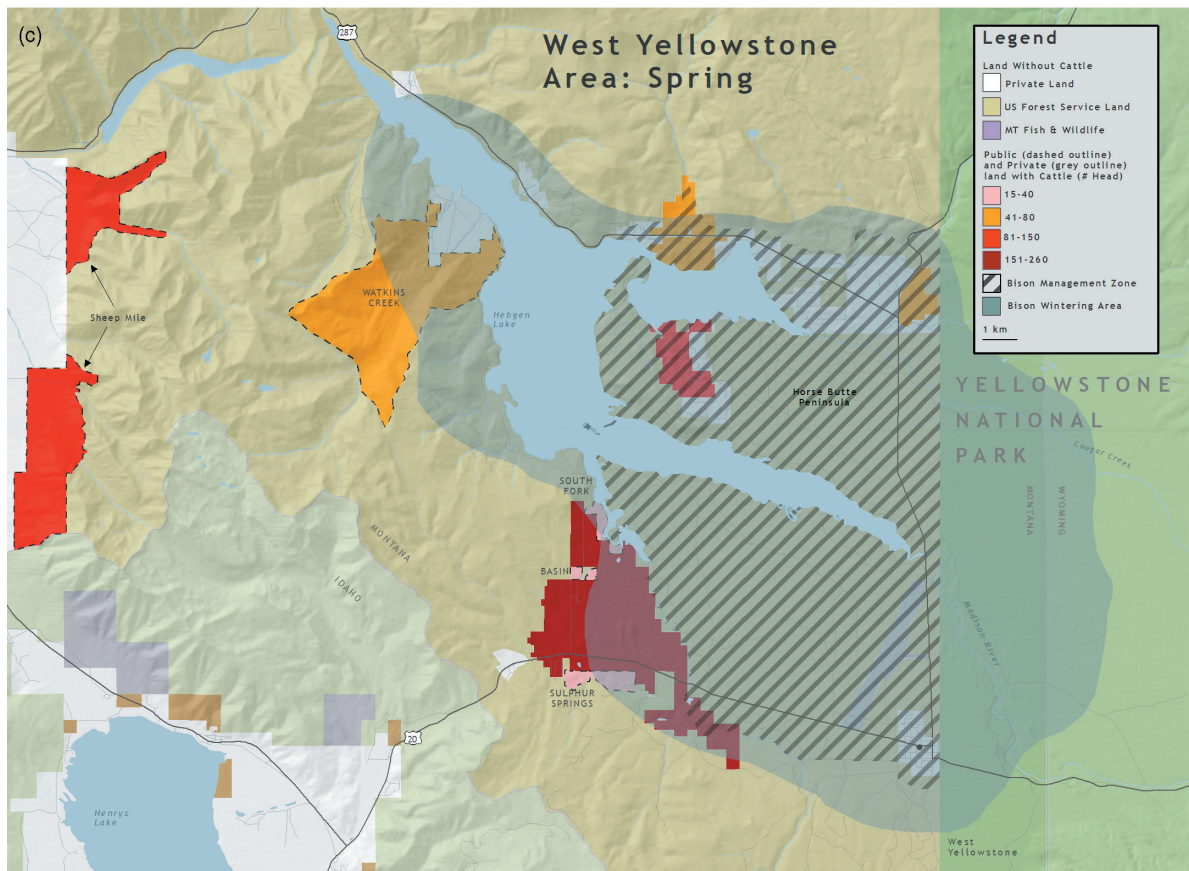
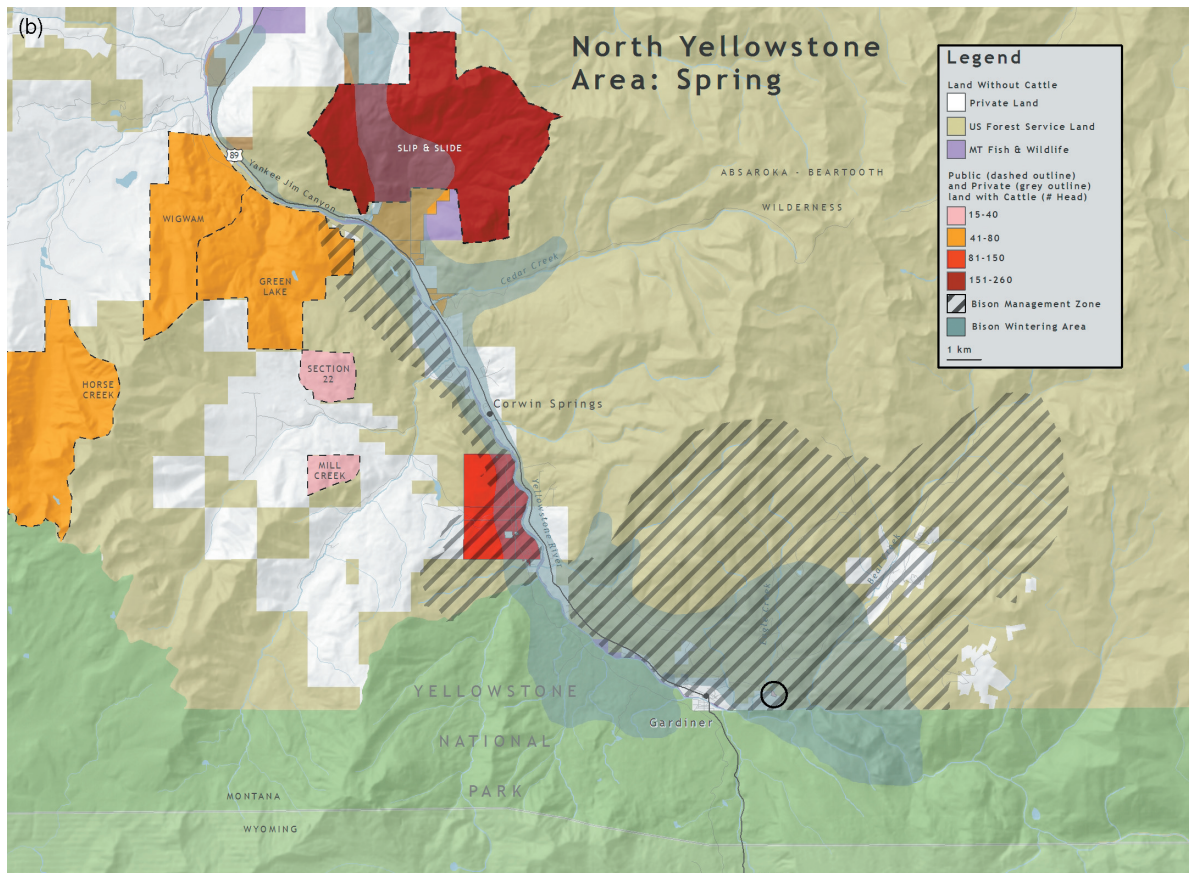


Fig. 1. continued

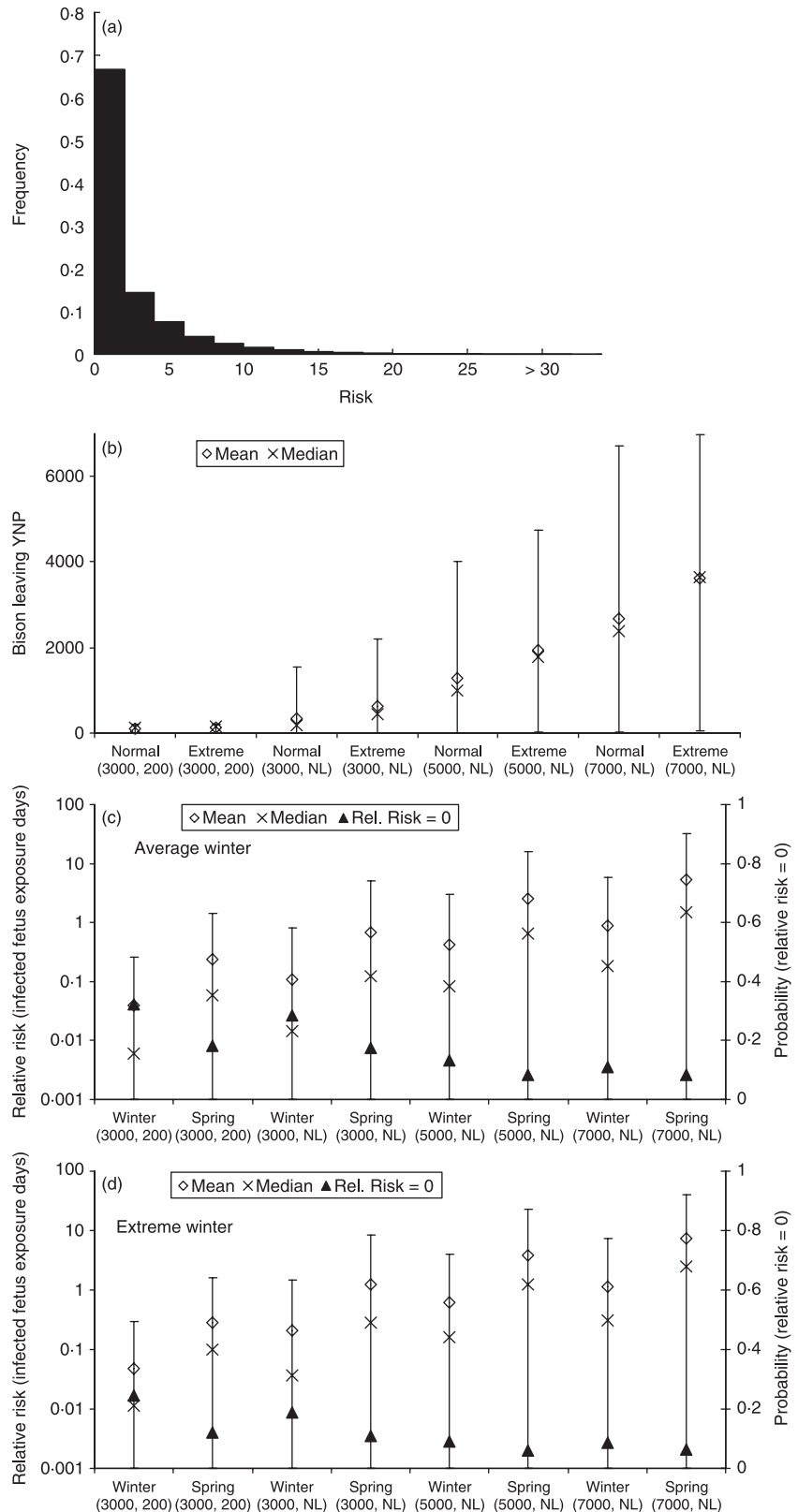


Fig. 2. Relative risk of transmission of *Brucella abortus* from bison to cattle under four scenarios (size of bison population and maximum number allowed outside YNP in parentheses; NL, no limit), two seasons (winter and spring), and average and extreme snow conditions. (a) Histogram of 50 000 draws for relative risk for scenario 3 (5000 bison) spring under extreme weather conditions, illustrating the highly skewed distribution of relative risk with most years resulting in zero or relatively low risk, but a small fraction of years with much higher risk of transmission (max = 62.4; <5% were >10). Other scenarios had a similar distribution, but a different mean relative risk. (b) Number of bison leaving YNP for each of the four scenarios under average and extreme snow conditions (mean \pm 95% CI). (c) Relative risk, on a log scale (mean \pm 95% CI), of transmission for average snow conditions. The lower bound of the 95% CI is 0 for all scenarios so it does not appear on the graph. (d) Relative risk, on a log scale (mean \pm 95% CI), of transmission for extreme snow conditions. The lower bound of the 95% CI is 0 for all scenarios so it does not appear on the graph. Relative risk is the product of the number of cattle, the estimated density (no. of cattle per hectare) of *Brucella*-infected foetuses birthed outside the park, and the estimated number of days that each foetus will persist (see Methods).

Service, the US Forest Service, Animal and Plant Health Inspection Service, and the state of Montana have put into place a plan, the IBMP, that costs ~\$2.5 million per year in 2000 to reduce this risk (Table 10 in (USDOI & USDA 2000a)). Unless brucellosis can be eradicated from bison, there is no

apparent endpoint for this management plan. At present, efforts are underway to vaccinate bison remotely and when animals are captured outside the park. However, given the efficacy of the current vaccine (Clarke *et al.* 2005), eradication in the near future will be difficult (Peterson, Grant & Davis

1991b; Bienen & Tabor 2006). As a result, the risk of transmission of brucellosis from bison to cattle will remain, and quantification of this risk is necessary to assure cost-effective management.

Our analyses highlight the spatial and temporal heterogeneity in, and skewed distribution of, the risk of transmission. Risk in winter is highly focal, with just a few private ranches supporting cattle in the northern SMA, and no risk in the western SMA, where bison are nonetheless hazed and removed when they leave YNP. A greater risk occurs in the late spring and early summer months of June–July when many additional cattle are brought to public and private lands in both the northern and western SMAs. At this time, the high-elevation snows in YNP are melting, and bison are starting to follow the first spring grasses, but some may remain in the lower-elevation areas outside the park where cattle graze (Clarke *et al.* 2005; Gates *et al.* 2005). Our analyses show a substantial probability that the relative risk of transmission will be zero under all scenarios, and years of high risk are comparatively rare. However, they increase with increasing bison populations and severe snowfall or thawing and freezing events (Gates *et al.* 2005). In addition, as bison alter their behaviour and move outside the current management area to explore new territory (R. Wallen, personal communication), additional cattle grazing areas may be encountered. Clearly adaptive management will be most effective.

Given this skewed distribution of relative risk, two options for management merit additional consideration. The first, establishing a local brucellosis infection status zone for cattle in the greater Yellowstone area of Montana and testing all cattle within this area for brucellosis (with a 'split status' for the rest of Montana), has been discussed earlier (USDOI & USDA 2000a). Our results highlight the benefits of this strategy and suggest that transmission of brucellosis from bison to cattle even under a 'no plan' (no management of bison) strategy is likely to be a relatively rare event, and the costs of yearly testing of cattle (\$2500 to \$5000 a year per test for the cattle in areas shown in Fig. 1) are a thousand-fold lower than the current management plan. The second management option would be to cease grazing cattle in the areas where bison leave the park in winter and compensate the ranchers for lost earnings and wages. Assuming a value of \$875 per head of cattle (based on a \$691 per head in 2000 (USDOI & USDA 2000a) and 3% inflation over the past 8 years), the yearly cost for the 1441 cattle grazing on public and private property in the northern and western SMAs would be \$1 261 362 which is half of the current management costs, and much less than the potential impacts to Montana's livestock industry, valued at \$1.1 billion in 1997, if it loses its brucellosis-free status. (USDOI & USDA 2000a). If local ranchers were willing to sell their grazing rights through a conservation easement, to delay grazing to provide greater temporal separation between cattle and bison, or sell their land, the recurring management costs could be eliminated in exchange for a one-time cost that would be higher. This last strategy is being pursued by local conservation organizations and government agencies and has been used in the past successfully (USDOI & USDA 2000a).

However, the cost of doing so is often much higher than the value of the cattle (K. Aune, personal communication), which greatly increases the cost of easements and buy-outs of land or grazing rights.

Regardless of which strategy is taken, bison will continue to attempt to leave YNP in the winter, and will venture beyond the current wintering areas (indicated in Fig. 1) as populations grow (Fuller, Garrott & White 2007). Recent analyses indicate that brucellosis has significant effects on bison fecundity, and a reduction in the prevalence of brucellosis that is the goal of current vaccination efforts would lead to faster growing populations (Fuller *et al.* 2007). The strong relationship between bison population size and the number of bison that leave the park (equation 2), and the stochasticity inherent in snowfall and weather processes, suggest that the risk of transmission will grow as bison populations grow, but in a haphazard fashion, and with great year-to-year variability.

Although the population size triggering management action under the original IBMP is 3000 bison, management has allowed the population to grow substantially higher since 2001, and it will likely continue to grow in the future, unless hunting and culling are significantly increased. Extension of past growth rates suggests that, in the absence of culling and density-dependent decreases in population growth, the population would reach 7000 in 2012. A recent analysis found some evidence of density dependence and movement between the northern and central herds (Fuller, Garrott & White 2007), but the population in 2005–2006 (4879) was well beyond the estimate for the population growth rate, r , to level off at 0 (~3300–3700). This discrepancy may result from some of the changes that have occurred in YNP (decreasing elk populations) or from variability, error in parameter estimates, and model selection in using the density dependent functions to estimate carrying capacity [J. Cunningham (formerly J. Fuller), personal communication]. In any case, to meet the population size of 3000 outlined in the original IBMP, substantial additional culling would be required, and even this population target is higher than a previous estimate of 2700 for the carrying capacity of bison in YNP based on forage (Boyce 1990; Boyce & Gaillard 1992). It should be noted that some have suggested that the carrying capacity may be significantly higher. Our results show that the current strategy of culling bison outside YNP, if they cannot be hazed back in (above the 200 bison limit), will result in several years of little or no culling followed by years with exceptionally high management removals.

It should also be noted that the results of our analyses are only as good as the data and assumptions they are based on. For example, as the area bison occupy outside YNP in the winter encompasses new area and additional cattle grazing areas (as is presently occurring; K. Aune and R. Wallen, personal communication), the risk of transmission will change. Similarly, since we have calculated risk as a simple product of several quantities (equation 1), the sensitivity of risk to biases or measurement error in each of the estimated parameters is the same for all parameters and scales directly with the error or bias in parameter estimates. Thus, while our estimates

explicitly incorporate observed variability in parameters, a bias of 20% in a single parameter would result in a 20% bias in our risk estimate. Two aspects that deserve additional research effort are (i) the attraction of cattle to bison birthing areas and aborted fetuses, and (ii) the impacts of climate change on transmission which may decrease snowpack, winter mortality, and/or the propensity of bison to leave the park.

In summary, we have shown that the quantitative risk of transmission of *Brucella abortus*, the causative agent of brucellosis, from bison to cattle outside Yellowstone National Park is highly variable in space, time, and frequency. We believe that this variability offers great potential for focused adaptive management effort that will reduce the costs of brucellosis management, reduce the need for hazing of bison, and maintain very low risk for the cattle industry of Montana.

More broadly, our work provides a model framework for quantifying the risk of wildlife–livestock pathogen transmission to guide management actions. Where data are available to fully (or nearly fully) parameterize a risk model, doing so is likely to highlight the consequences of different actions, and may offer solutions that lead to resolution of the conflict without continuous management actions (Kilpatrick 2006).

Acknowledgements

We are extremely grateful to Amy McNamara and Michael Scott of Greater Yellowstone Coalition, Tim Schaub at Commenspace, Tris Hoffman of the Gallatin Forest Service, Phil Farnes at Snowcap Hydrology, K. Aune of WCS, and Karen Cooper from the MT department of livestock, for assistance with maps and data, and A. Dobson, P. Hudson, G. Tabor, G. Smith, J. Miller, and other attendees of the Chico brucellosis meeting for helpful discussion. K. Aune, R. Wallen, A. McNamara, P. Cross, and C. Wilmers provided helpful comments on the manuscript. Funding was provided by the Wilburforce Foundation, the National Fish and Wildlife Foundation, NSF grant EF-0622391, and through core funding to the Consortium for Conservation Medicine from the V. Kann Rasmussen Foundation.

References

Anderson, N., Atkinson, M., Aune, K., Clarke, R., Edwards, H., Flowers, P., Galey, F., Gertonson, A., Gocke, M., Hamlin, K., Linfield, T., Mamer, P., Moon, B., Oldham, D., Rhyhan, J., Scurlock, B., Shannon, L., Wallen, R. & Willer, R. (2005). *2004 GYBC Annual Report*. Greater Yellowstone Interagency Brucellosis Committee.

Aune, K., Corso, B., DeLong, D., Flowers, P., Gertonson, A., Gocke, M., Kreeger, T., Logan, J., Mamer, P., Rhyhan, J., Roffe, T., Thorne, T. & Wallen, R. (2004). *2003 GYBC Annual Report*. Greater Yellowstone Interagency Brucellosis Committee.

Baskin, Y. (1998) Home on the range—Scientists are scrambling to understand the complexities of brucellosis in Yellowstone's bison. *Bioscience*, **48**, 245–251.

Bienen, L. & Tabor, G. (2006) Applying an ecosystem approach to brucellosis control: can an old conflict between wildlife and agriculture be successfully managed? *Frontiers in Ecology and the Environment*, **4**, 319–327.

Boyce, M.S. (1990). Wolf recovery in Yellowstone National Park: a simulation model. *Wolves for Yellowstone?: A Report to the United States Congress* (eds J.D. Varlye & W.G. Brewster), Vol. 2, Research and Analysis, pp. 3–3 to 3–59. National Park Service, Yellowstone National Park, WY, USA.

Boyce, M.S. & Gaillard, J.M. (1992). Wolves in Yellowstone, Jackson Hole, and the North Fork of the Shoshone River: simulating ungulate consequences of wolf recovery. *Wolves for Yellowstone?: A Report to the United States Congress* (eds J.D. Varlye & W.G. Brewster), Vol. 4, Research and Analysis, pp. 4–71 to 4–116. National Park Service, Yellowstone National Park, WY, USA.

Cheville, N.F., McCullough, D.R. & Paulson, L.R. (1998) *Brucellosis in the Greater Yellowstone Area*. National Academy of Sciences, Washington D.C.

Clarke, R., Jourdonnais, C., Munding, J., Stoeffler, L. & Wallen, R. (2005). *Interagency Bison Management Plan: A Status Review of Adaptive Management*

Elements, 2000 to 2005. National Park Service, US Department of Agriculture Animal and Plant Health Inspection System, Montana Department of Livestock, Montana Fish, Wildlife and Parks.

Cross, P.C., Edwards, W.H., Scurlock, B.M., Maichak, E.J. & Rogerson, J.D. (2007) Effects of management and climate on elk brucellosis in the Greater Yellowstone Ecosystem. *Ecological Applications*, **17**, 957–964.

Davis, D.S., Templeton, J.W., Ficht, T.A., Williams, J.D., Kopec, J.D. & Adams, L.G. (1990) *Brucella abortus* in captive bison. I. Serology, bacteriology, pathogenesis, and transmission to cattle. *Journal of Wildlife Diseases*, **26**, 360–371.

Dobson, A. & Meagher, M. (1996) The population dynamics of brucellosis in the Yellowstone National Park. *Ecology*, **77**, 1026–1036.

Donnelly, C.A., Woodroffe, R., Cox, D.R., Bourne, J., Gettinby, G., Le Fevre, A.M., McInerney, J.P. & Morrison, W.I. (2003) Impact of localized badger culling on tuberculosis incidence in British cattle. *Nature*, **426**, 834–837.

Frye, G.H. & Hillman, B.R. (1997). National cooperative brucellosis eradication program. *Brucellosis, Bison, Elk and Cattle in the Greater Yellowstone Area: Defining the Problem, Exploring Solutions* (eds E.T. Thorne, M.S. Boyce, P. Nicoletti & T.J. Kreeger), pp. 79–85. Pioneer Printing, Cheyenne, WY, USA.

Fuller, J.A., Garrott, R.A. & White, P.J. (2007) Emigration and density dependence in Yellowstone bison. *Journal of Wildlife Management*, **71**, 1924–1933.

Fuller, J.A., Garrott, R.A., White, P.J., Aune, K.E., Roffe, T.J. & Rhyhan, J.C. (2007) Reproduction and survival of Yellowstone bison. *Journal of Wildlife Management*, **71**, 2365–2372.

Gates, C.C., Stelfox, B., Muhly, T., Chowns, C. & Hudson, R.J. (2005) The ecology of bison movements and distribution in and beyond Yellowstone National Park. *A Critical Review with Implications for Winter Use and Transboundary Management*. Faculty of Environmental Design, University of Calgary, Calgary, Alberta, Canada.

Gilbert, M., Chaitaweesub, P., Parakamawongsa, T., Premashthira, S., Tiensin, T., Kalpravidh, W., Wagner, H. & Slingerbergh, J. (2006) Free-grazing ducks and highly pathogenic avian influenza, Thailand. *Emerging Infectious Diseases*, **12**, 227–234.

Healey, B., Weber, G., Keating, A., Alley, J.L., Adams, L.G. & Slack, G. (1997). The importance of brucellosis eradication to the national cattle industry. *Brucellosis, Bison, Elk and Cattle in the Greater Yellowstone Area: Defining the Problem, Exploring Solutions* (eds E.T. Thorne, M.S. Boyce, P. Nicoletti & T.J. Kreeger), pp. 195–197. Pioneer Printing, Cheyenne, WY, USA.

Hornaday, W.T. (1889) *The Extinction of the American Bison, with a Sketch of its Discovery and Life History*. US National Museum, Washington DC.

Joly, D.O. & Messier, F. (2004) Factors affecting apparent prevalence of tuberculosis and brucellosis in wood bison. *Journal of Animal Ecology*, **73**, 623–631.

Keiter, R.B. (1997) Greater Yellowstone's bison: unraveling of an early American wildlife conservation achievement. *Journal of Wildlife Management*, **61**, 1–11.

Kilpatrick, A.M. (2006) Facilitating the evolution of resistance to avian malaria in Hawaiian birds. *Biological Conservation*, **128**, 475–485.

Kilpatrick, A.M., Chmura, A.A., Gibbons, D.W., Fleischer, R.C., Marra, P.P. & Daszak, P. (2006a) Predicting the global spread of H5N1 avian influenza. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 19368–19373.

Kilpatrick, A.M., Daszak, P., Goodman, S.J., Rogg, H., Kramer, L.D., Cedeno, V. & Cunningham, A.A. (2006b) Predicting pathogen introduction: West Nile virus spread to Galapagos. *Conservation Biology*, **20**, 1224–1231.

Manthei, C.A., DeTray, D.E. & Goode, E.R. (1950) *Brucella* infection in bulls and the spread of brucellosis in cattle by artificial insemination. I. Intrauterine infection. *American Veterinary Medical Association, Proceedings of the 87th Annual Meeting*, 177–184.

Meager, M.M. (1973) *The Bison of Yellowstone National Park*. National Park Service Scientific Monographs, Washington, D.C.

Meagher, M. & Meyer, M.E. (1994) On the origin of brucellosis in bison of Yellowstone-National-Park – a review. *Conservation Biology*, **8**(3), 645–653.

Meyer, M.E. & Meager, M.M. (1997). *Brucella abortus* infection in the free-ranging bison of Yellowstone National Park. *Brucellosis, Bison, Elk and Cattle in the Greater Yellowstone Area: Defining the Problem, Exploring Solutions* (eds E.T. Thorne, M.S. Boyce, P. Nicoletti & T.J. Kreeger), pp. 20–32. Pioneer Printing, Cheyenne, WY, USA.

Meyer, M.E. & Meagher, M. (1995) Brucellosis in free-ranging bison (*Bison bison*) in Yellowstone National Park, Grand Teton National Park, and Wood Buffalo National Park – a review. *Journal of Wildlife Diseases*, **31**, 579–598.

Mohler, J.R. (1917). Abortion disease. *Annual Reports*, pp. 105–106. US Department of Agriculture, Washington D.C.

Moore, T. (1947) A survey of buffalo and elk herds to determine the extent of *Brucella* infection. *Canadian Journal of Comparative Medicine*, **11**: 131.

- Pac, H. & Frey, K. (1991). *Some Population Characteristics of the Northern Yellowstone Bison Herd during the Winter of 1988–1989*. Montana Department of Fish, Wildlife and Parks, Bozeman, MT, USA.
- Peterson, M.J. (1991) Wildlife parasitism, science, and management policy. *Journal of Wildlife Management*, **55**, 782–789.
- Peterson, M.J., Grant, W.E. & Davis, D.S. (1991a) Bison-brucellosis management – simulation of alternative strategies. *Journal of Wildlife Management*, **55**, 205–213.
- Peterson, M.J., Grant, W.E. & Davis, D.S. (1991b) Simulation of host–parasite interactions within a resource-management framework – impact of brucellosis on bison population dynamics. *Ecological Modelling*, **54**, 299–320.
- Prins, H.H.T. (1992) The pastoral road to extinction – competition between wildlife and traditional pastoralism in East Africa. *Environmental Conservation*, **19**, 117–123.
- Rhyan, J.C., Gidlewski, T., Roffe, T.J., Aune, K., Philo, L.M. & Ewalt, D.R. (2001) Pathology of brucellosis in bison from Yellowstone National Park. *Journal of Wildlife Diseases*, **37**, 101–109.
- Rhyan, J.C., Quinn, W.J., Stackhouse, L.S., Henderson, J.J., Ewalt, D.R., Payeur, J.B., Johnson, M. & Meagher, M. (1994) Abortion caused by *Brucella abortus* biovar-1 in a free-ranging bison (*Bison bison*) from Yellowstone National Park. *Journal of Wildlife Diseases*, **30**, 445–446.
- Roffe, T.J., Rhyan, J.C., Aune, K., Philo, L.M., Ewalt, D.R., Gidlewski, T. & Hennager, S.G. (1999) Brucellosis in Yellowstone National Park bison: quantitative serology and infection. *Journal of Wildlife Management*, **63**, 1132–1137.
- Tessaro, S.V. & Forbes, L.B. (2004) Experimental *Brucella abortus* infection in wolves. *Journal of Wildlife Diseases*, **40**, 60–65.
- Thorne, E.T., Morton, J.K., Blunt, F.M. & Dawson, H.A. (1978) Brucellosis in elk. 2. Clinical effects and means of transmission as determined through artificial infections. *Journal of Wildlife Diseases*, **14**, 280–291.
- Thorne, E.T., Price, D., Kopec, J., Hunter, D., Smith, S.G., Roffe, T.J. & Aune, K. (1997). Efforts to control and eradicate brucellosis in wildlife of the Greater Yellowstone Area. *Brucellosis, Bison, Elk and Cattle in the Greater Yellowstone Area: Defining the Problem, Exploring Solutions* (eds E.T. Thorne, M.S. Boyce, P. Nicoletti & T.J. Kreeger), pp. 101–119. Pioneer Printing, Cheyenne, WY, USA.
- Treves, A., Naughton-Treves, L., Harper, E.K., Mladenoff, D.J., Rose, R.A., Sickley, T.A. & Wydeven, A.P. (2004) Predicting human-carnivore conflict: a spatial model derived from 25 years of data on wolf predation on livestock. *Conservation Biology*, **18**, 114–125.
- USDA-APHIS. (2007) *Brucellosis*. In: Vol. 2007. US Department of Agriculture–Animal and Plant Health Inspection Service, Washington D.C. <http://www.aphis.usda.gov/vs/hahps/brucellosis/>.
- USDOI & USDA. (2000a) *Final Environmental Impact Statement for the Interagency Bison Management Plan for the State of Montana and Yellowstone National Park*. US Department of Interior, US Department of Agriculture. www.planning.nps.gov/document/yellwinterusevol1.pdf
- USDOI & USDA. (2000b) *Record of Decision for Final Environmental Impact Statement and Bison Management Plan for the State of Montana and Yellowstone National Park*. US Department of Interior, US Department of Agriculture, <http://planning.nps.gov/document/yellbisonrod.pdf>.
- Wilmers, C.C. & Getz, W.M. (2005) Gray wolves as climate change buffers in Yellowstone. *Public Library of Science, Biology*, **3**, 571–576.
- Wilmers, C.C., Stahler, D.R., Crabtree, R.L., Smith, D.W. & Getz, W.M. (2003) Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. *Ecology Letters*, **6**, 996–1003.

Received 31 May 2008; accepted 24 November 2008
Handling Editor: Simon Thirgood

Supporting Information

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

Fig. S1. The fraction of the bison population leaving the park and either hazed back into the park or killed as a function of winter severity (y -axis) and total population size (x -axis on a log scale). The size of the circle shows the fraction of bison leaving the park. The fitted function (equation 2) indicates that the fraction of the population (size of the circle) outside the park increases with population size, winter severity, and is larger for years where bison outside YNP were primarily hazed rather than killed.

Fig. S2. Seroprevalence of bison for *B. abortus* plotted against number of bison in the population. The fitted equation 3 was *Brucella Seroprevalence* $P = 0.509(1 - e^{-0.0015 \times B})$; $n = 14$; $R^2 = 41.0\%$; $P_B = 0.0062$.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.