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Cover image: Winter populations of bison grazing in the Greater Yellowstone ecosystem (see p. 476). Growing populations and harsh winters frequently force bison outside Yellowstone National Park to find forage where they may pose a risk of transmission of brucellosis to grazing cattle. Photo by Paul Cross.

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Editor's choice: Where the buffalo roam – bison and brucellosis in Yellowstone

Kilpatrick, A.M., Gillin, C.M. & Daszak, P. (2009) Wildlife–livestock conflict: the risk of pathogen transmission from bison to cattle outside Yellowstone National Park. *Journal of Applied Ecology,* **46**, 476–485.

An enduring symbol of the American West, great migratory herds of bison *Bison bison* once roamed the Great Plains in their millions (Berger & Cunningham 1994). Sadly, this wildlife spectacle is no more, as in parallel with population declines and extirpation in other migratory ungulates (Bolger *et al*. 2008; Harris *et al*. 2009), bison are now restricted to a number of small remnant populations. The causes of population decline in bison and other migrants are well known – hunting, habitat loss, fencing – and their need for space makes the conservation of these wide ranging species a major challenge (Berger 2004; Thirgood *et al*. 2004).

The only free-ranging herd of bison remaining in the United States is found in the Greater Yellowstone Ecosystem of Montana, Wyoming and Idaho. At the start of the 20th century, this population had been reduced to 23 individuals, but with protection it has increased to nearly 5000. Bison spend most of the year at higher altitudes in the Yellowstone National Park but during severe winters they graze at lower elevations outside the park. Here they come into conflict with cattle ranching because of the risk of transmission of brucellosis from bison to cattle. Brucellosis is a bacterial disease that causes weight loss, abortion and reduced milk yields in cattle. The maintenance of brucellosis-free status in cattle is economically important to the livestock industry, and as a result, culling bison is part of the Government interagency disease control strategy (Clarke *et al*. 2005). The conservation success of Yellowstone's bison indirectly led to the culling of 1600 bison during the 2007/08 winter.

For this issue's Editor's Choice selection, Kilpatrick *et al*. (2009) develop a quantitative risk assessment integrating both ecological and epidemiological data to assess the spatio-temporal risk of transmission of brucellosis from bison to cattle. The model demonstrates that the risk of transmission is highly variable in space, time and frequency and can be predicted by climatic conditions and the abundance of bison. Critically, the model suggests that the risk of brucellosis transmission is very low in most years and is periodically high only in certain localized areas around the park. The authors suggest alternative management strategies, such as financially compensating ranchers for grazing rights in localized areas, would be more cost-effective than the current policy of culling bison to control population size. Another management proposal is to the consider the section of the Greater Yellowstone Ecosystem which occurs in Montana as a separate zone from the rest of the state in terms of brucellosis infection status and provide yearly testing of cattle in that zone. This would cost a fraction of the $2.5 million that the current management strategies cost per year. Similarly, compensating ranchers for the financial value of all the cattle that graze in the affected areas around the park would cost about half the current yearly amount.

The results of Kilpatrick *et al*.'s study have generated considerable interest from scientists, managers and the general public – particularly in the United States. In the month since the paper was published online it has been picked up in the mainstream media more than 100 times. Perhaps this is a reflection of the iconic status of the bison in American popular culture – but it does highlight the critical role of good ecological research in influencing natural resource management decisions. The primary role of the Editor's Choice initiative is to showcase papers that we believe best fulfil the journal's mission of publishing ecological studies with management relevance. Kilpatrick *et al*.'s study is a particularly good example of the connection between good science and real-world problem solving and we expect that the paper will be both widely cited and highly influential.

SIMON THIRGOOD
E-mail: s.thirgood@macaulay.ac.uk

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

A. Marm Kilpatrick[1,2,*], Colin M. Gillin[3] and Peter Daszak[1]

[1]The Consortium for Conservation Medicine, New York, NY 10001, USA; [2]Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064, USA; and [3]Oregon 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; USDOI & 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; USDOI & 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 (USDOI & 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 calling ceased [the bison population has grown by ~72 individuals per year since 1984 including the effects of culling ($N = 72{\cdot}4 \times \text{year} + 2337$; year = 1 in 1984; $R^2 = 0{\cdot}36$), and ~287 individuals per year excluding culling effects ($N = 286{\cdot}8x + 1709$; $R^2 = 0{\cdot}96$; (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:

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

or in word form:

Relative Risk ∝ (no. of cattle)[Fraction of bison outside park × Bison population × *B. abortus* seroprevalence × infected birthing rate outside park if seropositive (abortions + births) × 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):

$$\text{F} = \sin(-4{\cdot}03 + 0{\cdot}042\,\text{SWE} + 1{\cdot}14\,\text{Log}_{10}\text{B})^2 \qquad \text{eqn 2}$$

($n = 22$; $R^2 = 80{\cdot}0\%$; $P_{\text{B}} = 0{\cdot}001$; $P_{\text{SWE}} = 0{\cdot}018$)

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 foetuses 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)

$$S = 0{\cdot}509(1 - e^{-0{\cdot}0015 \times \mathrm{B}})\ (n = 14;\ R^2 = 41{\cdot}0\%;\ P_{\mathrm{B}} = 0{\cdot}0062) \qquad \text{eqn 3}$$

We modelled the fraction of bison that would abort as a fraction of the seropositive bison (per cent aborting: 10·6% ± 4·2% × per cent seropositive) and that estimated that each aborted birth would result in 18·2 ± 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% × (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. arbortus* 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

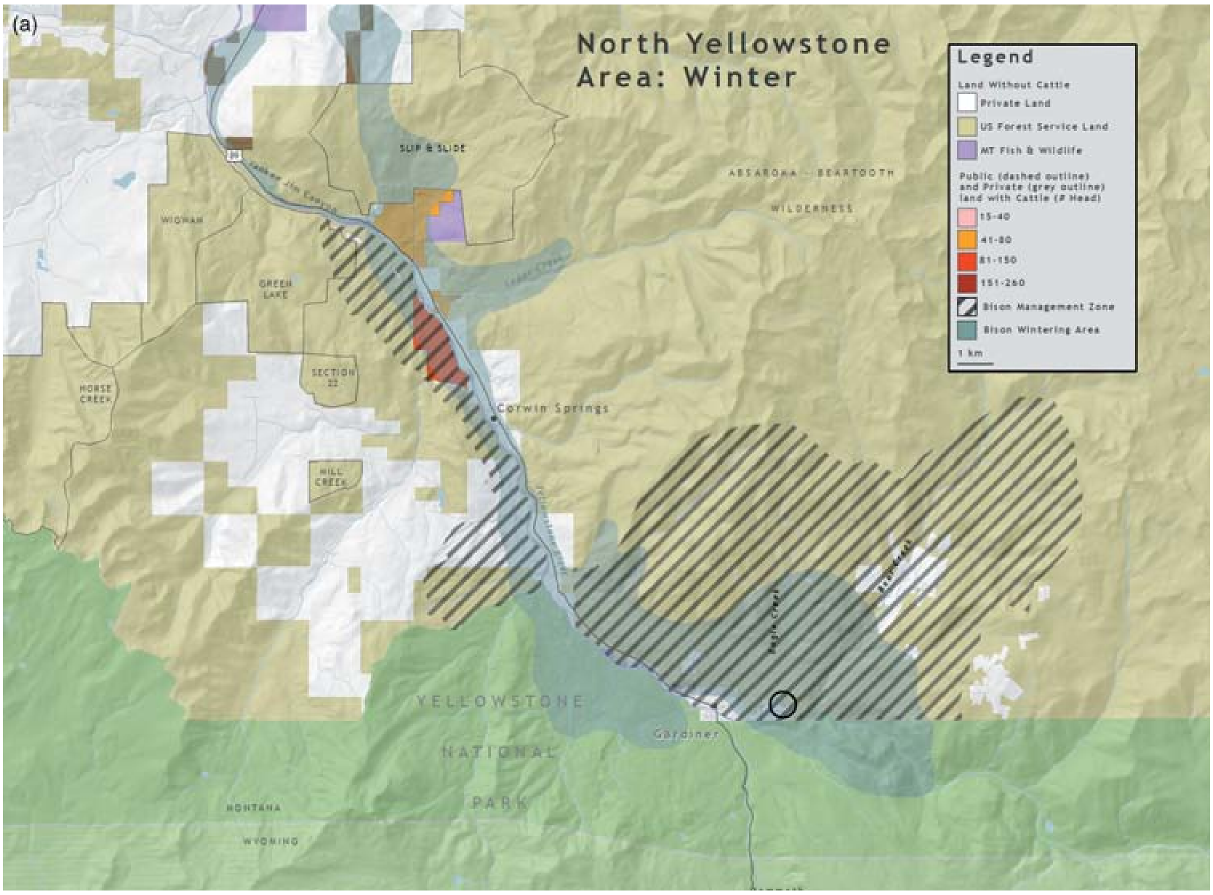

Fig. 1. The distribution and abundance of cattle on the northern edge of YNP near Gardiner during (a) winter and (b) spring and (c) the western area in spring in areas where bison are found outside the park. Cattle grazing allotments on public lands in the northern area start in mid-June. Cattle in the 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.

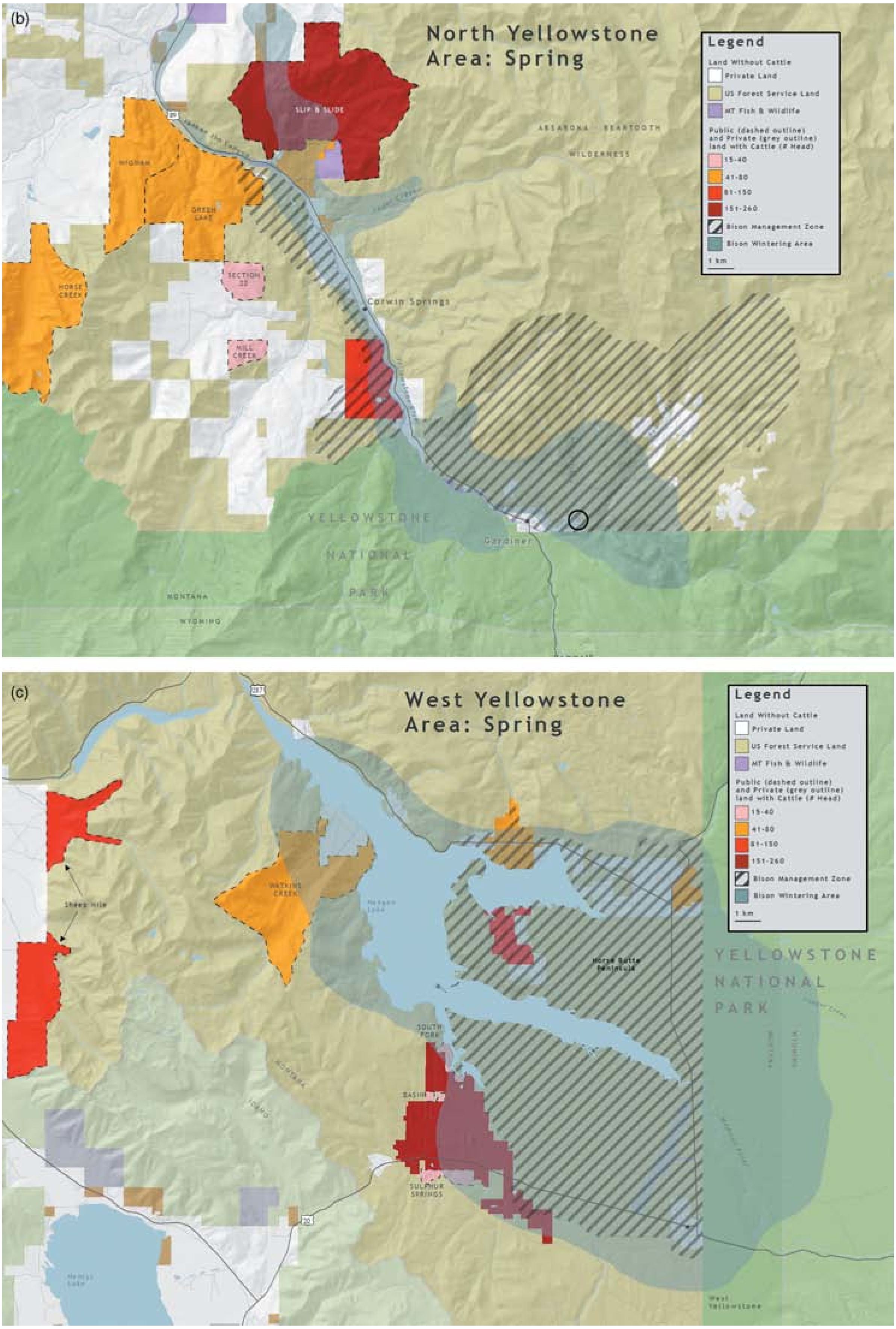

Fig. 1. *continued*

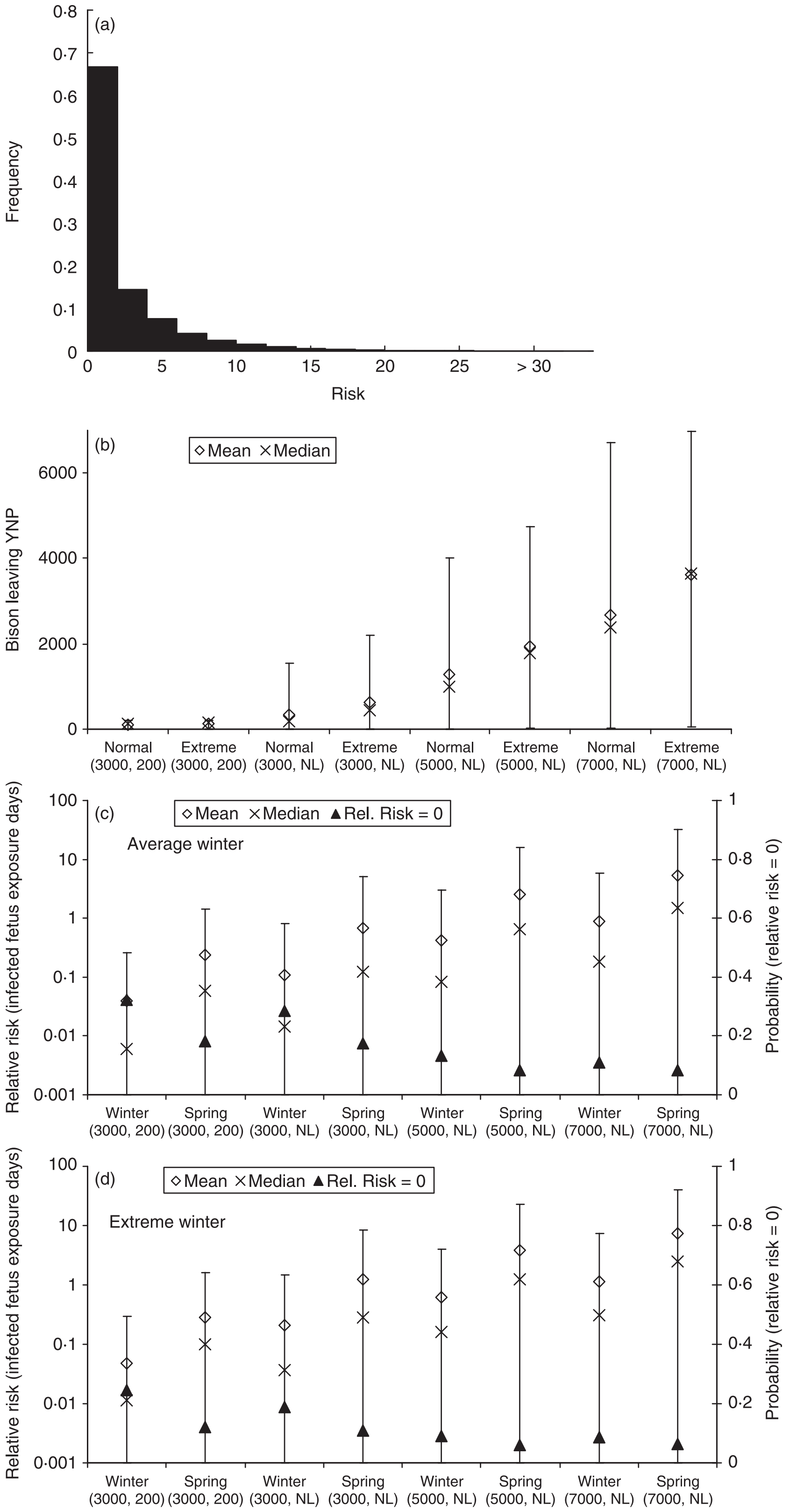

Fig. 2. Relative risk of transmission of *Brucella abortus* from bison to cattle under four scenarios (size of bison population and maximum number allowed outside YNP in parentheses; NL, no limit), two seasons (winter and spring), and average and extreme snow conditions. (a) Histogram of 50 000 draws 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 ± 95% CI). (c) Relative risk, on a log scale (mean ± 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 ± 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 foetuses, 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).

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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* $P = 0{\cdot}509(1 - e^{-0{\cdot}0015 \times \mathrm{B}})$; $n = 14$; $R^2 = 41{\cdot}0\%$; $P_{\mathrm{B}} = 0{\cdot}0062$.

Online Supporting Information

Transmission of *Brucella abortus* from bison to cattle can theoretically occur through one of three contact types: 1) contact between domestic cattle and Brucella infected tissue, soil or vegetation as a result of an infected female bison giving birth or aborting, 2) sexual transmission between an infected male bison and female cow, or 3) suckling of a domestic cow from an infected lactating female bison. Although sexual transmission is theoretically possible, it is highly unlikely for several reasons. First, while injection of infected sperm into the uterus of cows results in infection, injection into the vagina, or through natural copulation did not (Manthei, DeTray & Goode 1950). Second, the bison breeding season is primarily between August and October, when bison are rarely outside the park, and behavioural incompatibilities exist between bison and cattle in a free range setting (Gates *et al.* 2005; Meager 1973).

Similarly, cattle suckling from infected lactating female bison is also considered extremely unlikely under free ranging conditions, due to behaviour avoidance (Meyer & Meager 1997), and low shedding rates in milk (K. Aune, pers. comm.). Based on this evidence, we assumed that the risk from sexual transmission and suckling was extremely low ("vanishingly small"; (Cheville, McCullough & Paulson 1998)), especially compared to contact with infected birthing tissues, and do not consider these pathways further.

The number of bison that leave the park in a given year appears to be dependent both on the population size of bison and the severity of the winter (Cheville, McCullough & Paulson 1998; Gates *et al.* 2005). To predict the number of bison leaving the park, we fit the fraction, F, of the bison population removed from the population from 1984-1997 and the number of removals + bison hazed back into the park divided by the total population from 1998-2005 to a function of three variables: the total population size, log-transformed, B, (Clarke *et al.* 2005); the average (January – March) snow-water equivalent (SWE) in inches at Lupine Creek (P. Farnes pers. comm., YNP, unpublished data) and a categorical variable, X, that was 0 for 1984-97, and 1 for 1998-2005 to account for the fact that in this latter period many of the animals hazed back into the park could exit the park again and be double counted. Although snowfall (and SWE) varies significantly across YNP, the Lupine Creek data were strongly correlated with bison movements (see below). This link illustrates the influence of weather on bison movement, and while no causal association between Lupine Creek SWE and bison movements is claimed, our model using simulated variation in SWE is likely to capture the implications of severe winters on transmission risk. We arcsin square-root transformed of the fraction of the bison population leaving the park to normalize the residuals of the analysis, and back transformed the fit model. The fraction of the population that would leave the park, F, was estimated as (using X=0) (Fig. S1):

$$F = \sin(-4.03+0.042\ \mathrm{SWE}+ 0.50\ X + 1.14\ \mathrm{Log}_{10}B)^2 \qquad \text{eqn 2}$$

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

We simulated extreme winters using the upper 95% confidence bound of SWE, 10.91”, which averaged 6.54” (±SE (standard errors given, unless otherwise indicated) = 0.43) across 22 years (P. Farnes pers. comm., YNP, unpublished data). Incidentally, the number of bison culled each year (which underestimates the number attempting to leave YNP, since some were hazed back in) was also significantly related to bison population size and SWE (# culled = - 1152 + 0.236B + 96.6SWE; n = 22; $R^2 = 72.4\%$; $P_B < 0.001$; $P_{SWE} < 0.001$; normality test: $P = 0.79$). Nonetheless, we used eqn 3 because we were estimating the number of bison likely to leave the park under scenarios without hazing.

Groups of bison leaving the park in 2001-2005 consisted either entirely of bulls, or mixed bull-cow groups (Clarke *et al.* 2005). Most groups leaving the park near West Yellowstone before March of each year were entirely bulls, whereas from March-June both bull-only and mixed gender groups were equally likely (Clarke *et al.* 2005). Although some females also left the park into the western SMA during the harsh winter of 1996-7, the relative risk of transmission in the western SMA in winter is zero due to the absence of cattle in the winter. In spring, mixed gender groups made up ~80% of all animals hazed back into the park from 2000-2005 (Clarke *et al.* 2005). On average 23% ± 11% of the bison leaving YNP moved into the northern SMA (with the remainder exiting into the western SMA) and both bull only and mixed groups left the park throughout the winter and spring (Clarke *et al.* 2005). In considering the alternate management strategy of not hazing bison back into the park, we assumed that 50% of mixed group bison leaving the park were females (Meager 1973; Pac & Frey 1991).

The seroprevalence (see below for discussion of seroprevalence and infection prevalence) of *Brucella abortus* in bison appears to be an increasing function of bison population size in Yellowstone (Dobson & Meagher 1996) but not in other bison populations (Joly & Messier 2004) and only weakly in elk (Cross *et al.* 2007). We added additional abundance and seroprevalence data from 1996-7 (3600, 0.551), 2002-3 (4250, 0.468), 2003-4 (4070, 0.52) (Anderson *et al.* 2005; Aune *et al.* 2004; Cheville, McCullough & Paulson 1998) and 2005-6 (4879, 0.54) (P.R. Clark, pers. comm.) and fit linear and non-linear asymptotic relationships to the seroprevalence data vs. bison population size, B, for YNP bison only (data from herds outside YNP in Fig 2 of (Dobson & Meagher 1996) were excluded). A linear relationship was just barely significant ($\text{Prev} = 0.33 + 0.000047B$; $n=13$; $R^2 = 30.8\%$; $P = 0.04$) and the residuals were strongly indicative of a curvilinear trend. An asymptotic relationship was highly significant and the residuals were normal (P = 0.99) with no visual suggestion of heteroscedasticity, so this relationship was used for the model simulations (Fig. S2):

B. abortus Seroprevalence $P = 0.509(1-e^{-0.0015*B})$ (n = 14; R^2 = 41.0%; P_B = 0.0062) (3)

We calculated the fraction of births that would result in *Brucella*-infected abortions and infected birth sites separately, and we considered several lines of reasoning. First, the abortion rate of bison in a herd in Wyoming that had a seroprevalence of 77% was 4-6% (USDOI & USDA 2000a). This value is much lower than the fraction of Yellowstone bison that were culture positive (11.9% from a 1991-2 sample, and 19.8% from a 1997-9 sample) when the population was 47.7% and 74.0% seropositive, respectively (Dobson & Meagher 1996; USDOI & USDA 2000a). In addition, these culture rates may be artificially low due to sampling methods (Roffe *et al.* 1999; USDOI & USDA 2000a). This suggests that a significant fraction of culture-positive animals may not abort their pregnancies, perhaps due to some culture-positive animals being infected in non-reproductive tissues, or successfully giving birth (possibly with infected birthing materials) despite infection (Cheville, McCullough & Paulson 1998; Davis *et al.* 1990). Secondly, if bison abort only their first calf (and rarely their second), at 2-4 years of age, when they first become sexually mature (Meager 1973), and assuming that approximately 21.6% of the population at this age showed serological evidence of exposure (compared to a population average of 41.6% (Dobson & Meagher 1996)), then given that 13% of female bison pass through this age class at that time (Pac & Frey 1991), this would give an abortion rate due to *Brucella* of 0.13*0.216 = 0.028 or 2.8%. The ratio of this abortion rate to the population seroprevalence (0.028/0.477 = 0.0587), is very similar to the ratio for the Wyoming herd (0.05/0.77 = 0.0649). However, a recent study found an abortion rate of 6/96 = 6.25% in a sampled population that had a seroprevalence of 33% (Clarke *et al.* 2005); K. Aune, pers. comm.), which is a substantially higher fraction of seropositive individuals (0.0625/0.33 = 0.189) than the two other lines of reasoning just discussed. In addition, an additional 5.2% of 96 birth sites that were not abortions from the same population (seroprevalence = 33%) were also culture positive (K. Aune, pers. comm.).

We integrated these data and assumed that the fraction of bison that would abort was correlated with the fraction seropositive and used the average of the three estimates just described (percent aborting: 10.6%±4.2% * percent seropositive). We assumed that an additional 0.052/0.33 = 15.8% * (percent seropositive) of bison would have live birth sites infected with *B. abortus*. Live births take place in April and May, so 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). Abortions due to brucellosis have rarely been observed, so it is unknown whether they are temporally clumped (which lead to temporally concentrated risk) or evenly spread across the time period that bison are pregnant (as we have assumed).

We note that this approach avoids making assumptions about the fraction of seropositive animals that are culture positive, and instead focuses on the epidemiologically relevant relationship between seropositivity and abortions and infected births as measured with intrauterine radio transmitters. Finally, because of the method of measurement of this relationship, this estimate also captures abortions due to exposure during pregnancy, which some believe is the highest risk event due to the high levels of *Brucella* bacteria aborted under these circumstances (K. Aune, pers. comm.).

Recent research on the persistence of foetuses and suggests that they remain un-scavenged in the landscape (and thus could be contacted by a domestic cow) for an average of

18.2 ± SD 20.1 days (K. Aune, pers. comm.; (Clarke *et al.* 2005)). The survival of bacteria on the underside of foetuses varied between a maximum of 25 days in May and 85 days in February (Clarke *et al.* 2005) which is substantially longer than the average residence time for a foetus before being scavenged. Thus, using eqn 1, we assumed that each aborted birth would result in 18.2 ± SD 20.1 *Brucella*-infected carcass exposure days (but with a minimum of 1 day). If bacteria remained in the birthing area after scavenging of the foetus (K. Aune, pers. comm.), this would increase the number of potential exposure days. However, the probability of contact between domestic cattle and an 18 day-old birthing site without the presence of a fetal tissues is likely to be very small, especially after a snowfall (Cheville, McCullough & Paulson 1998), and we assumed it was small compared to the risk posed by the aborted foetus.

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.

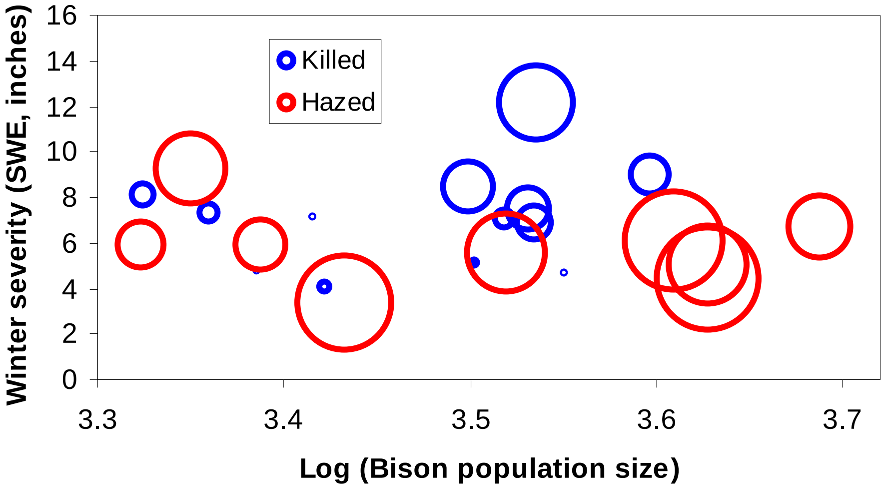

Fig. S2. Seroprevalence of bison for *B. abortus* plotted against number of bison in the population. The fitted equation 3 was *Brucella Seroprevalence P* = $0.509(1-e^{-0.0015*B})$; n = 14; R^2 = 41.0%; p_B = 0.0062.