An ecological perspective on *Brucella abortus* in the western United States

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Summary
After a hiatus during the 1990s, outbreaks of *Brucella abortus* in cattle are occurring more frequently in some of the western states of the United States, namely, Montana, Wyoming and Idaho. This increase is coincident with increasing brucellosis seroprevalence in elk (*Cervus elaphus*), which is correlated with elk density. Vaccines are a seductive solution, but their use in wildlife systems remains limited by logistical, financial, and scientific constraints. Cattle vaccination is ongoing in the region. Livestock regulations, however, tend to be based on serological tests that test for previous exposure and available vaccines do not protect against seroconversion. The authors review recent ecological studies of brucellosis, with particular emphasis on the Greater Yellowstone Area, and highlight the management options and implications of this work, including the potential utility of habitat modifications and targeted hunts, as well as scavengers and predators. Finally, the authors discuss future research directions that will help us to understand and manage brucellosis in wildlife.

Keywords
Bison – *Brucella abortus* – Ecology – Elk – Habitat modification – Scavenger – United States – Vaccination – Yellowstone.

Introduction

The seminal work of Anderson and May in the late 1970s and early 1980s integrated the fields of population biology, parasitology and epidemiology (1, 29). These studies were a launching pad for new fields of scientific work on the ecology and evolution of infectious diseases. Wildlife disease studies acquired additional importance following the emergence of several high-profile pathogens that originated from a wildlife reservoir (e.g. human immunodeficiency virus [HIV], severe acute respiratory syndrome [SARS] coronavirus, and Lyme disease [24]). Brucellosis research has seen a similar increase in the number of ecological studies, but ecological studies remain a minor component of the brucellosis research portfolio compared to vaccine development and basic immunology (Fig. 1).

In this paper, the authors review some of the insights gained from recent ecological work on brucellosis dynamics in wildlife, with an emphasis on *Brucella abortus* in the Greater Yellowstone Area (GYA), the last stronghold of brucellosis in the United States. Brucellosis in this region is maintained by infected bison and elk populations, with periodic spillover transmission to cattle herds (Fig. 2). Evidence for the importance of host ecology in brucellosis dynamics begins with the observation that ungulates within the *Bovini* tribe, e.g. African buffalo (*Syncerus caffer*), cattle and American bison (*Bison bison*), appear to maintain *B. abortus* at a higher seroprevalence than other ungulate species. This may be

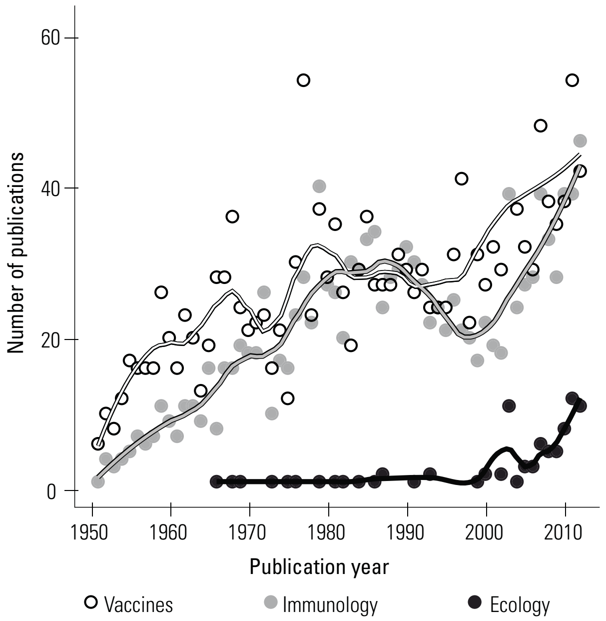

Fig. 1
Number of brucellosis-related publications per year on vaccines, immunology and ecology or wildlife
Lines are drawn using a locally weighted smoothing function. Data were derived from PubMed searches using the key phrases 'vaccine*', 'ecolog*' or 'wildlife', and 'immune* in the title or abstract, and all papers had 'brucell*' in the title

due to physiological and immunological characteristics common to *Bovini* species, but it also coincides with the behavioural pattern of larger social groups and with the fact that these animals give birth within groups rather than in seclusion; these are the characteristics that facilitate transmission of *B. abortus* via direct contact with abortion events (the main mechanism of transmission).

Blue wildebeest (*Connochaetes taurinus*) and Rocky Mountain elk (*Cervus elaphus*) are two non-*Bovini* species that can also form larger social groups. Blue wildebeest have been recorded with a seroprevalence of 18% and form some of the largest aggregations of any ungulate species (41). Until recently, elk were not thought to be a suitable reservoir for brucellosis (7, 27, 39). Elk populations in North America have been recovering from extensive harvesting by European settlers in the early 1900s, and elk populations in many western states are now at their highest levels in over a century (33). Coincident with increasing elk populations, and concurrent with the number of brucellosis outbreaks in cattle (Fig. 2), brucellosis seroprevalence appears to be increasing in several elk populations around the GYA (12).

Available epidemiological and genetic data suggest that these brucellosis infections in cattle were more likely due to spillover transmission from elk than bison (4, 23). Though bison remain a potential risk to cattle, the hazing or culling of bison that wander out of Yellowstone National Park minimises spatial and temporal overlap between the two species, reducing brucellosis transmission risk to cattle (26). Elk, on the other hand, are far more numerous and mobile than bison in the GYA and represent a less tractable management challenge.

Host density and brucellosis transmission

The relationship between host density and parasite transmission is fundamental to understanding infectious disease dynamics and implementing effective control strategies. Simulation models with density-dependent disease transmission have been used extensively in theoretical and applied epidemiology and predict that epidemics will not occur as long as host density is less than some threshold (21, 25). The abundance and spatial distribution of many wildlife species can be affected by hunting pressure, artificial food sources, habitat quality and manipulation (e.g. prescribed fire and weed removal), and abundance of predator or competitor species. Subsequently, if host density is a major driver of parasite transmission, then natural resource managers may have several ecological tools at their disposal. However, empirical support for the epidemiological importance of host density in disease transmission is mixed (5, 8, 14, 17, 35, 36).

The authors argue that brucellosis transmission is driven by host density at fine spatial scales (e.g. social groups of individuals within 100 m to 500 m of each other) during the months of January through June when brucellosis is mostly likely to cause abortion events. Transmission occurring within wintering social groups may be hard to detect when using broader measures of density, but it is nonetheless important as a management opportunity. For many social species, the group-size distribution does not vary widely over the range of population sizes (13) and this seems to be true of bison as well (Fig. 3a). Therefore, transmission may be more frequent in larger groups (local scale) but uncorrelated with total population size or density on a broad spatial scale because as the population size increases so does the number of groups.

In forested habitats, elk groups are relatively small and generally comprised of less than 30 individuals (11, 12, 22). However, in open habitats, elk group sizes can be over 1,000 individuals (12, 32). Elk group-size distributions tend to be highly right-skewed, whereby most groups are relatively small while a few are very large (Fig. 4). In addition, the largest groups appear to increase as the population increases, particularly in more open rangeland habitats (Fig. 3b). In bison and elk, individuals appear to interchange among groups relatively frequently (19, 20). With increasing movement among groups, the correlation between seroprevalence and group size is likely to decrease

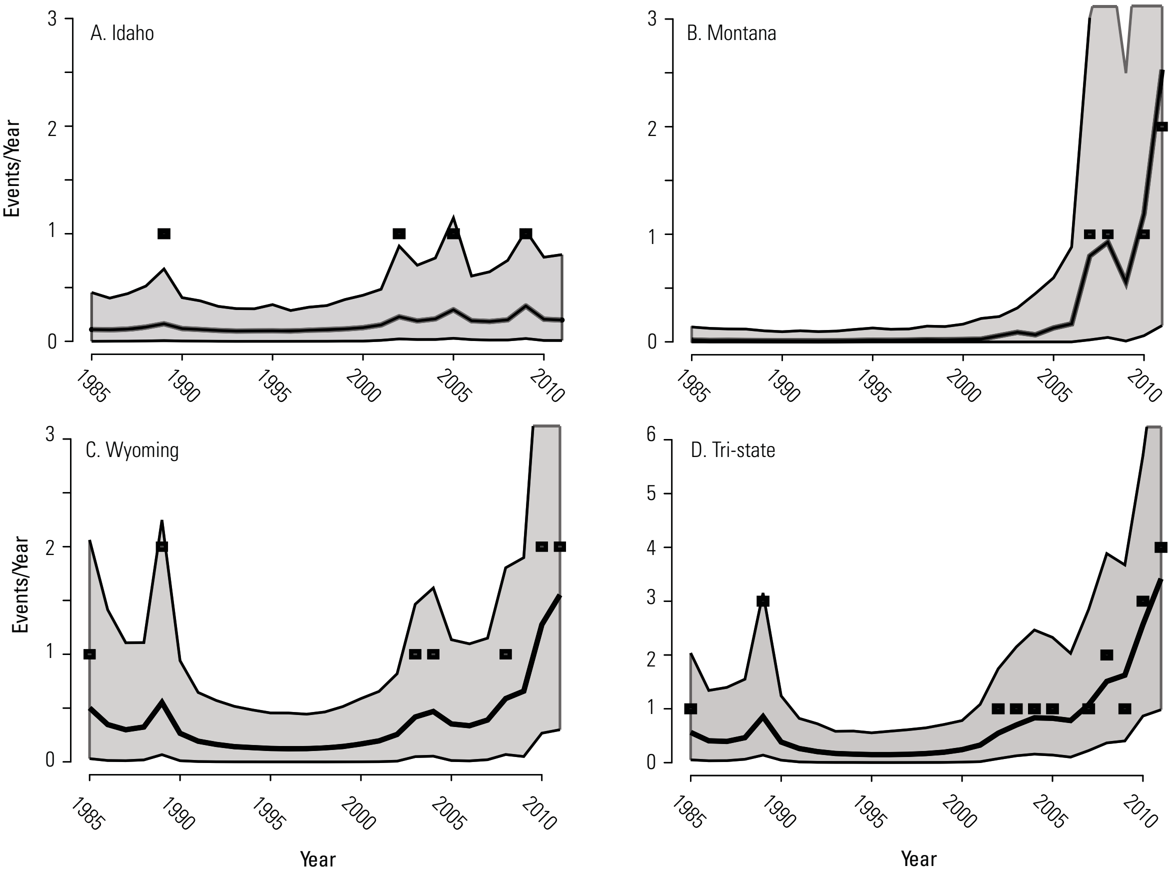

Fig. 2

Hazard of a cattle outbreak per calendar year in Idaho (A), Montana (B), Wyoming (C), or summed across all three states (D)

Estimates are based on a Bayesian intrinsic conditional autoregressive model. Grey areas indicate the 95% credible intervals. Actual numbers of outbreaks per year are indicated as squares. For clarity, years without outbreaks are not shown. Note the Y-axis for D is not the same as A–C

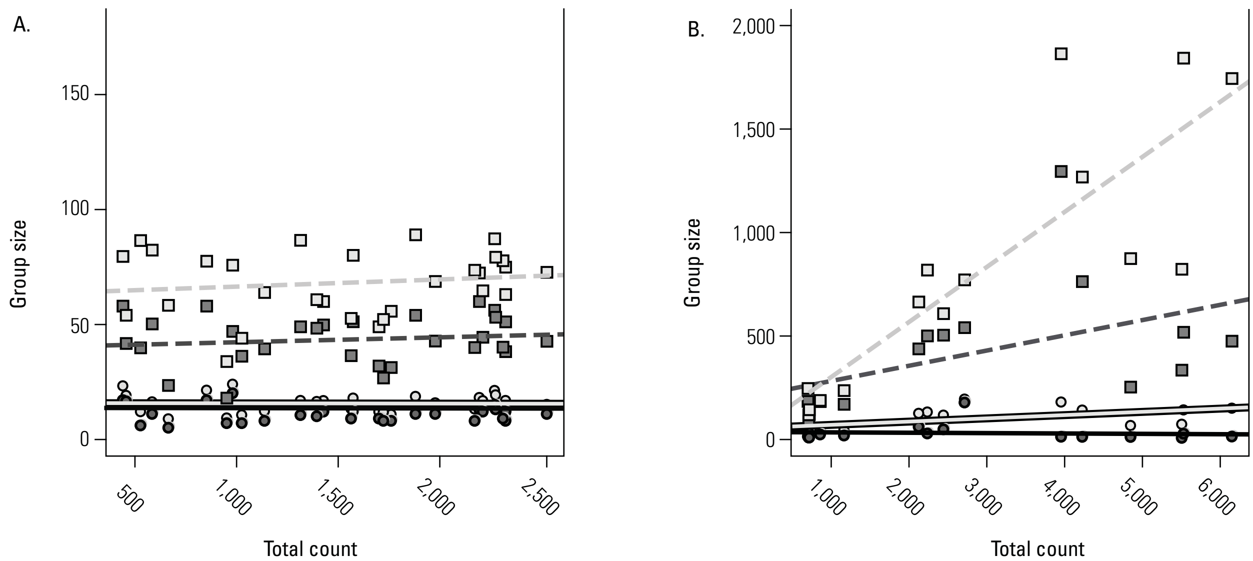

Fig. 3

The relationship between different measures of group size for bison (A) and elk (B) as a function of the total count of individuals

Median and mean group sizes are shown in dark and light grey circles, respectively. Upper 95th and 99th percentiles of group size are shown with dark and light grey squares, respectively. Lines are least-squares regressions. Bison data are derived from aerial flights from 1970 to 1997 of bison in Yellowstone National Park. Elk data are derived from aerial flight data from the Eastern Madison Valley of Montana (14). In each case, only one flight, some time between January and March each year, was used

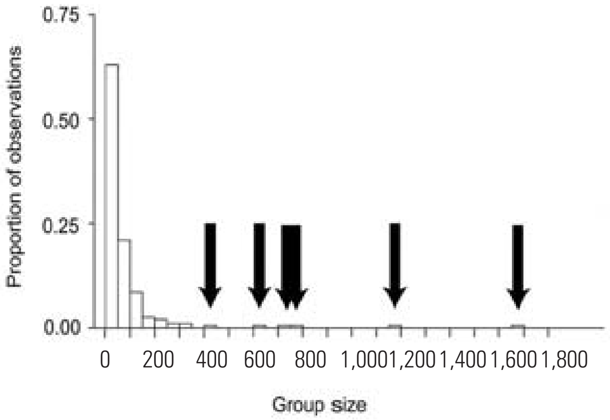

Fig. 4
Elk group-size distribution in February 2010 and 2011 from 204 groups seen on aerial transects of ten Wyoming hunt areas
Arrows indicate large groups

because individuals are infected in large groups, but then often move to a smaller group prior to being sampled. As a result, brucellosis seroprevalence may be only weakly correlated with either group size or population size even though disease transmission is driven by group size or density within a group. Despite these caveats, brucellosis seroprevalence does appear to increase with increasing elk density on coarse spatial scales (12, 15, 32).

At first glance, this host density effect appears to be contradicted by the authors' own work on feedgrounds in western Wyoming – 23 sites where state and federal wildlife managers provide supplemental hay to over 20,000 elk and 600 bison during winter, resulting in highly aggregated populations from December through April. At these feedgrounds, brucellosis seroprevalence appears uncorrelated with elk population size (14). For example, the National Elk Refuge (NER) has the largest elk population of all feedgrounds and, on average, one of the lowest levels of seroprevalence. The authors believe that this is due to an interaction between population size and length of the feeding season (Fig. 5a) (28). They found that brucellosis-induced abortions, detected by vaginal implant transmitters (ATS, Insanti, MI, USA), frequently occurred in late spring (Fig. 5b). Therefore, high elk densities earlier in winter at this site may be unrelated to transmission risk. Instead, the area under the curve of group, feedground, or population size during the transmission season is probably more important (Fig. 5a) (28). The authors found that feedgrounds with feeding periods extending later into spring had higher seroprevalence in elk (14). In that analysis, the end of the feeding season explained 59% of the variation in seroprevalence among sites and suggested that, if causal, a shortening of the feeding season by a month may result in a reduction in seroprevalence of around two-thirds.

The authors have also studied how elk–fetus contacts depend on elk density on feedgrounds. They used elk fetuses derived from a test and slaughter programme, observational sampling by humans and video cameras, and the novel technology of proximity logging devices. Elk–fetus contacts declined rapidly with distance from feedlines, where elk aggregations were at their highest levels (28). In addition, when the authors spread feed over larger areas, thereby reducing host density in a field experiment, they found that elk–fetus contacts decreased by 80% (Fig. 6) (10). These results prompted managers to initiate field experiments with truncated feeding seasons and low-density feeding regimes to test their effects on reducing brucellosis seroprevalence over time.

Scavengers and environmental persistence of *Brucella abortus*

On the Wyoming feedgrounds, managers attempt to reduce transmission by dispersing hay on clean snow and recovering aborted fetuses. Despite these and other management actions, seroprevalence among feedground elk populations has averaged 22% (37). Vertebrate scavengers exploit spatially and temporally predictable increases of domestic and free-ranging carrion (18), particularly during periods of cold temperatures (38) when animals are susceptible to nutritional stress and/or predation (42). In addition to brucellosis-induced abortions, several dozen elk may die annually on each feedground. This provides dependable sources of carrion for scavengers. Scavengers quickly removed almost all fetuses placed on feedground and non-feedground sites in the GYA (3, 9, 28).

The rate that fetuses disappear was fastest on feedgrounds (< 2 days on average compared to 6 days in Grand Teton National Park). The rates were slowest in and around Yellowstone National Park, where the average was 18 days (3, 9, 28). Scavengers have not been implicated in transmission of brucellosis from wildlife to livestock, except during close confinement under experimental conditions (16). Thus, the authors suspect that scavengers reduce brucellosis transmission by limiting the time an infectious fetus remains in the environment. Furthermore, different scavenging rates may explain how elk attending feedgrounds exhibit similar, or even lower, seroprevalence than some non-fed elk populations despite the dense aggregations observed on feedgrounds. As part of their management of elk feedgrounds, the Wyoming Game and Fish Department (WGFD) has recently began to protect scavengers (particularly coyotes and red fox) on feedgrounds, because they act as sustainable, no-cost, biological control agents. Expanding this seasonal protection to include areas adjacent to feedgrounds, or locations with high seroprevalence in non-fed elk, could reduce transmission and resulting seroprevalence.

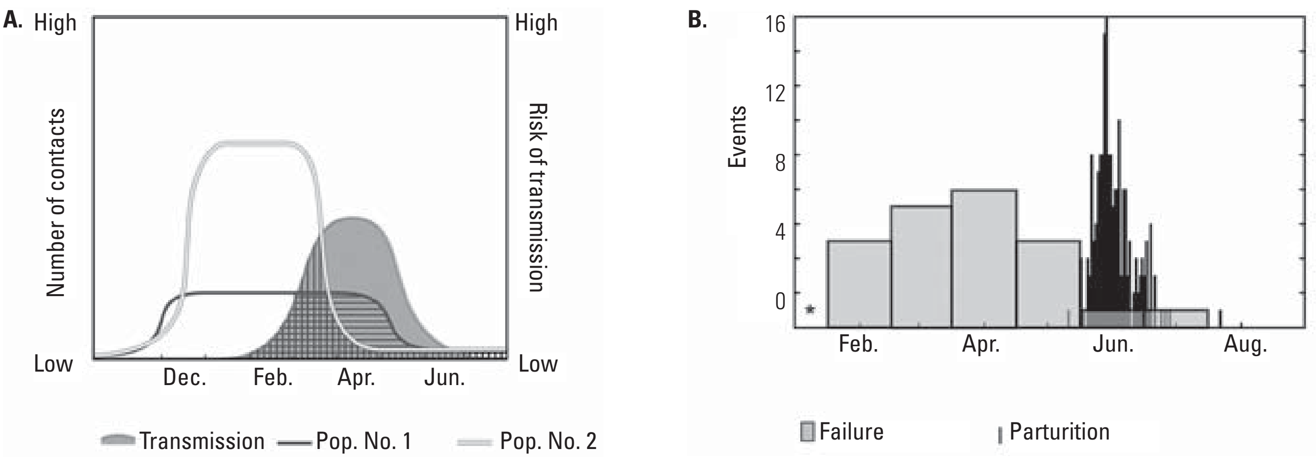

Fig. 5

Interaction between the timing of abortion events and elk density may drive brucellosis transmission

Elk densities vary annually, but may not coincide with transmission periods (A). As a result, the interaction of density and transmission timing (i.e. the cross-hatched areas) is likely to drive brucellosis transmission, such that high densities early in the winter may be irrelevant. Data from 244 seropositive elk fitted with vaginal implant transmitters suggest that abortions occur from February through July, with a peak in April, while normal births occur primarily from 15 May to 20 June (B)

Wildlife brucellosis vaccination

Vaccines are seductive solutions to many wildlife disease problems (31). The authors believe, however, that the cost of brucellosis vaccination in wildlife is likely to be prohibitively high for the next 20 years, although they hope to be proven wrong. This pessimistic view is based upon several ecological, political and immunological factors:

– large and well-connected wildlife populations, such as elk in the GYA, are a success story of 20th Century wildlife management, but that success makes the delivery of vaccines to many individuals logistically challenging on a broad spatial scale

– *B. abortus* reservoir hosts are herbivores, which will complicate oral vaccine delivery in areas without feedgrounds. Past successes with oral vaccines for rabies have targeted carnivorous or omnivorous hosts (6), which may be more likely to be attracted to baits

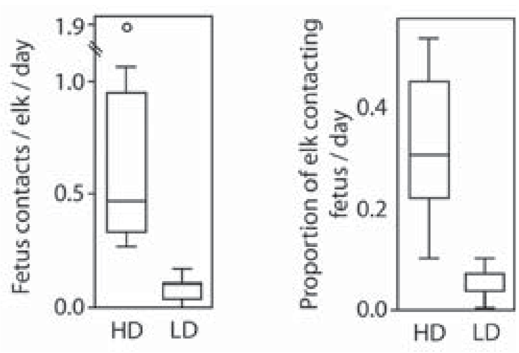

Fig. 6

Effects of feedground manipulations on elk–fetus contact rates

Feedground manipulations showed that spreading feed over larger areas (low density: LD) reduces the average number of elk–fetus contacts (within 2 m) by around 80% compared to traditional feeding (high density: HD) (10). During traditional feeding, most elk on the feedground are likely to come within 2 m of a fetus if it persists on a feedline for 2–3 days

– in some systems there may be more than one host species that is capable of independently maintaining brucellosis. As a result, if eradication is the goal, then it would have to be coordinated across all reservoir hosts. If brucellosis reduction is the goal then it would need to be maintained over time to control against spillover from alternative hosts

– multiple jurisdictions and managing agencies with differing mandates will confound coordination of a vaccination campaign. Local vaccination efforts may be possible for targeted populations but, as in the case of brucellosis reduction, they would need to be maintained in perpetuity or are likely to be eroded by immigrating infectious individuals

– the status of *B. abortus* in the United States as a potential bioterrorism threat results in a limited availability of approved sites to conduct captive trials

– vaccination of elk with *Brucella* strain 19 has been conducted on feedgrounds in Wyoming since 1985 with no effect on seroprevalence and limited effect on abortion.

A safe and effective vaccine for brucellosis in wildlife remains elusive (30), but an oral vaccine may be on the horizon (2). In their own epidemiological studies, the authors have observed little impact of *Brucella* strain 19 vaccination on brucellosis in elk. With the exception of the Dell Creek feedground (operated by WGFD), juvenile elk at the remaining supplemental feedgrounds in Wyoming are vaccinated annually via biobullets. The annual coverage at other feedgrounds tends to include over 98% of juveniles (WGFD, unpublished data), but seroprevalence at Dell

Creek appears to be no higher than would be expected given its feeding season length (14).

Improved vaccines for use in cattle are more logistically feasible. However, vaccines are typically not as good at directly preventing infection and seroconversion as they are at reducing transmission. In elk, vaccinated individuals were 25% more likely to have viable calves, but there was no difference in the infection rate of vaccinated and control individuals (34). For vaccination to benefit individual livestock owners, control regulations must be based on the potential for disease transmission rather than whether individual animals are seropositive, because seropositive findings are only an indication of exposure to *Brucella*. Although differentiating between infectious and recovered individuals is not currently possible for a given individual, probabilistic statements can be made (40).

Conclusions and future research

Adaptive management is a process by which managers can synergise learning and management decision-making while learning about the system and reducing future uncertainty. Without an easily delivered, highly effective, and safe vaccine, difficult decisions and compromises are necessary to protect the open spaces that livestock operations require, and that wildlife conservationists and ranchers both value. Ecological interventions (e.g. altering hunting regulations, habitat manipulation, or predator and scavenger conservation) to manage brucellosis around the GYA are likely to be controversial and involve uncertain outcomes, but they are logistically plausible interventions in a system where there are no easy solutions.

Whole genome sequencing of *Brucella* isolates may allow for better estimates of the amount of transmission that occurs among host species. As far as the authors are aware, however, no one has quantitatively estimated cross-species transmission for a bacterial pathogen and this is likely to be a challenging endeavour. In the past, the authors have connected the trend of increasing elk seroprevalence with changing aggregation patterns. This increase might be explained, in part, by the evolution of a more transmissible strain of *B. abortus* in elk. A study of genetic variation in *Brucella* isolates across space, time, and host species would be informative. Additionally, combining serological (or culture) data with elk genetics would allow researchers to assign seropositive (or culture positive) individuals to their most likely population of origin, allowing researchers to estimate how much of the epidemic is being driven by other populations and regions. These estimates of connectivity could then be used in modelling analyses to determine how management in one area may affect brucellosis seroprevalence in neighbouring regions (12).

Despite the use of feedgrounds in western Wyoming to prevent elk and livestock co-mingling, several elk–livestock transmission events have occurred there, and in Idaho and Montana, during the last ten years (Fig. 2). The correlation between elk seroprevalence and elk density suggests that actions to alter elk aggregation patterns may be effective. Most of these management interventions, however, involve complicated trade-offs. Feasible alternatives in some Wyoming feedgrounds include shortening the length of the supplemental feeding season and distributing feed across a larger area. While a shortened feeding season may reduce brucellosis transmission among elk, increased contact of elk and cattle could be an undesired consequence. Managers at the WGFD are conducting these experiments on several feedgrounds, embracing an adaptive management philosophy.

Other options may be possible for reducing brucellosis among elk populations that do not receive supplemental feed during the winter. Targeted hunts later in winter in areas with the largest elk groups may redistribute elk, reducing the largest groups and total population size. Several areas around western Wyoming began the use of targeted hunts in 2011, but it is too early to determine their effects on brucellosis transmission. At present, the extent to which the largest groups drive the dynamics of brucellosis in elk remains unclear. However, much like efforts to control individual superspreaders, targeted efforts on these largest groups may be more effective than uniformly allocating efforts across all groups. Increased scavenger protection may also play a role in limiting the increase and spread of brucellosis in elk (3, 9, 28). By removing contaminated birthing materials from the environment, scavengers likely reduce both the infectiousness of that birthing event and the duration that it is infectious. Additionally, to reduce the risk of brucellosis infections in cattle, managers could identify areas of high risk for brucellosis transmission based on location data of elk and bison, and develop cattle herd plans to minimise temporal and spatial overlap of cattle in the high-risk areas. Finally, investigating alternative resources that drive host concentration (e.g. mineral licks) may further prevent disease transmission.

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Une perspective écologique sur *Brucella abortus* dans l'Ouest des États-Unis

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Résumé

Après une période d'accalmie dans les années 1990, on assiste actuellement à une recrudescence des foyers dus à *Brucella abortus* dans certains États de l'Ouest des États-Unis, à savoir le Montana, le Wyoming et l'Idaho. Cette évolution s'accompagne d'une hausse de la prévalence sérologique chez le cerf élaphe (*Cervus elaphus*), proportionnelle à la densité des populations de cette espèce. La vaccination est une solution attirante mais sa mise en œuvre dans la faune sauvage est limitée par des difficultés logistiques, financières et scientifiques. La vaccination des bovins domestiques de la région est en cours. Les prescriptions applicables au bétail sont toutefois basées sur les résultats des épreuves sérologiques, qui révèlent une exposition passée, tandis que les vaccins disponibles n'empêchent pas la réapparition d'anticorps. Les auteurs font le point sur les études écologiques récentes dédiées à la brucellose, notamment celles conduites dans l'écosystème du Grand Yellowstone et mettent l'accent sur les solutions de gestion et les conclusions de ces travaux, en particulier concernant l'utilité potentielle d'une modification des habitats et des chasses ciblées, et le rôle que jouent les charognards et les prédateurs. Enfin, les auteurs évoquent les pistes futures de la recherche qui pourraient contribuer à améliorer la connaissance de la brucellose et sa gestion chez les animaux sauvages.

Mots-clés

Bison – *Brucella abortus* – Cerf élaphe – Charognard – Écologie – États-Unis – Modification de l'habitat – Vaccination – Yellowstone.

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Brucella abortus en el oeste de los Estados Unidos desde el punto de vista ecológico

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Resumen

Tras una interrupción en la década de 1990, algunos de los estados occidentales de los Estados Unidos, a saber, Montana, Wyoming e Idaho, vienen padeciendo cada vez con más frecuencia brotes de *Brucella abortus* en el ganado vacuno. Este incremento coincide con una creciente seroprevalencia de la brucelosis en el ciervo (*Cervus elaphus*), que a su vez guarda relación directa con un aumento de la densidad de esta especie. Las vacunas son una solución atractiva, pero su utilización en sistemas de fauna salvaje aún está sujeta a limitaciones logísticas, económicas y científicas. En la región se está procediendo actualmente a vacunar al ganado. La reglamentación de la ganadería, sin embargo, suele basarse en pruebas serológicas concebidas para detectar una exposición previa, y las vacunas disponibles no protegen de la seroconversión. Los autores pasan revista a una serie de estudios ecológicos recientes sobre la brucelosis, centrándose especialmente en el perímetro del Gran Yellowstone, y destacan posibles opciones de gestión y las consecuencias de esa labor, en particular la eventual utilidad de las modificaciones de hábitat y las cacerías dirigidas, y el papel de los carroñeros y predadores. Por último, los autores se refieren a las futuras líneas de investigación que nos ayudarán a entender y combatir la brucelosis en los animales salvajes.

Palabras clave
Bisonte – *Brucella abortus* – Ciervo – Carroñero – Ecología – Estados Unidos – Modificación de hábitat – Vacunación – Yellowstone.

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