Bovine brucellosis in wildlife: using adaptive management to improve understanding, technology and suppression

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Summary
Eradication of brucellosis from bison *(Bison bison)* and elk *(Cervus elaphus)* populations in the Greater Yellowstone Area is not possible with current technology. There are considerable uncertainties regarding the effectiveness of management techniques and unintended effects on wildlife behaviour and demography. However, adaptive management provides a framework for learning about the disease, improving suppression techniques, and lowering brucellosis transmission among wildlife and to cattle. Since it takes approximately three years after birth for female bison to become reproductively active and contribute to brucellosis transmission, there is an opportunity to implement actions such as vaccination and the selective removal of infectious bison based on age and assay results to reduce the potential for transmission. Older adult bison that have been exposed to the bacteria, but recovered from acute infection, could be retained in the population to provide some immunity (resistance) against future transmission. Through careful predictions, research, and monitoring, our understanding and technology will be improved and management actions can be adjusted to better achieve desired outcomes.

Keywords
Adaptive management – Bison – Brucellosis – Disease – Vaccination – Yellowstone.

Introduction

In the Greater Yellowstone Area (GYA) of the western United States, which encompasses Yellowstone National Park and portions of Idaho, Montana, and Wyoming, management of the disease brucellosis in wildlife has been a contentious issue for decades. Bovine brucellosis is a bacterial disease caused by *Brucella abortus* that can induce abortions or the birth of non-viable calves in livestock and wildlife (2). Transmission occurs within and among wildlife (bison [*Bison bison*], elk [*Cervus elaphus*]) and cattle populations when individuals come into contact with infected fetuses, placentas, or birthing fluids (2). Only pregnant females become infectious, with a high probability of shedding *B. abortus* during late gestation. Several studies have failed to document sexual transmission from males to females in either cattle or bison (e.g. 18). The disease can be transmitted through milk as actively infected females nurse their calves (2, 17), although this mode appears less important than transmission between unrelated bison (8).

Though brucellosis was likely introduced from cattle to elk and bison early in the 20th Century (12), these wildlife species in the GYA are now the only reservoir remaining for bovine brucellosis in the United States. The transmission of brucellosis from wildlife to cattle results in economic loss to producers from slaughtering infected animals, increased disease testing requirements and, possibly, decreased marketability of their cattle (2). Approximately 40% to 60% of Yellowstone bison test positive for exposure to *B. abortus* based on the presence of antibodies in blood (i.e. seroprevalence [27]). Antibodies may be detected in blood for several years, even in individuals that appear to have recovered from acute infection (21).

The Yellowstone bison population is one of the most important populations in the world because the animals are managed as wildlife rather than livestock and they have learned to survive in habitats in which they are subject to natural selection factors, such as predation, competition for food and mates, and harsh environmental conditions. Consequently, they have retained the adaptive capabilities of plains bison (7, 15). Some of these bison migrate from summer ranges in Yellowstone to lower elevation winter ranges in Montana, where snow pack is lower and forage is more available, but there is also a risk of brucellosis transmission to cattle that graze on public and private lands (9). In the 1990s, these migrations led to a series of conflicts among federal and state agencies, environmental groups, and livestock producers regarding bison conservation and disease containment (15). Thus, the federal government and the state of Montana negotiated a plan to cooperatively manage the risk of brucellosis transmission from bison to cattle, while conserving the bison population and allowing some bison to occupy winter ranges in Montana (24).

Under this plan, intensive management near the park boundary has maintained separation between bison and cattle, with no transmission of brucellosis (27). However, it is difficult to balance the competing objectives of the different stakeholders. Their objectives are assessed at different spatial and temporal scales and some of them are based on limited understanding of bison ecology and disease dynamics. Managers from federal and state agencies act to prevent brucellosis transmission annually in localised areas, but the demographic and genetic effects on bison may not be detectable for decades and, as a result, unintended consequences may occur (27). For example, more than 3,600 bison were removed from the population for risk management purposes between 2001 and 2012, with more than 1,000 bison and 1,700 bison being culled from the population during the winters of 2006 and 2008, respectively. These culls differentially affected breeding herds, altered gender structure, created reduced female cohorts, and dampened productivity of bison (27). Furthermore, 200 to 800 bison were held in confinement pastures and fed hay for months during some winters to prevent their mass migration north of the park. These animals were released during spring, but confinement and feeding obviously conflicts with the management of bison as wildlife subject to natural selection factors and could have unintended consequences (e.g. food conditioning, disease transmission during confinement). Consequently, there is a need to adjust management to better protect migratory bison and avoid artificial concentration during calving. Herein, the authors recommend adaptive management adjustments designed to improve understanding of how to reduce the prevalence of brucellosis in bison, while avoiding effects on the population that undermine long-term conservation efforts.

Context for resolution

The vaccination of Yellowstone bison has been proposed to reduce the risk of brucellosis transmission from bison to cattle (24). In 2006, in a report on brucellosis in the GYA, the United States Animal Health Association (23) noted many deficiencies in the effectiveness and duration of vaccines and the effectiveness of vaccine delivery methods and diagnostics. However, progress at resolving issues has been slow owing to a lack of market incentives and restrictions on research due to the classification of *B. abortus* as a select agent (www.selectagents.gov), i.e. an agent that could be misused to pose a severe threat to public health or national security. Thus, managers must be content with trying to suppress the transmission of *B. abortus* among wildlife and livestock by maintaining separation between them. Further suppression may be accomplished by combining vaccination, which reduces *B. abortus* transmission in vaccinated animals, with the removal of actively infected individuals, which reduces the number of new infections (21). However, a successful vaccination programme will require consistent delivery of known doses of an effective vaccine to most female bison annually, which will be difficult to accomplish with free-ranging bison.

Vaccination could reduce the prevalence of infection in Yellowstone bison by diminishing the clinical effects of brucellosis (i.e. induced abortions, infectious live births) that transmit the disease (22). The available vaccine for bison (strain RB51) has reduced brucellosis transmission in experimentally infected bison, but is less effective at preventing infection, and will not prevent vaccinated bison (or cattle) from reacting positively in serological tests if they become infected with field strains of *B. abortus* (13). Results under real-life field conditions will almost certainly vary from the results of these experimental trials. Regardless, it is unlikely that another vaccine with higher efficacy (i.e. ability to reduce risk factors such as abortions and bacterial shedding) will be available soon. Other vaccines (e.g. strain 82, DNA) are undergoing testing, but it will likely be more than a decade before these evaluations are completed and their use is possible on bison or cattle in the United States (4, 11).

In addition to an efficacious vaccine, the success of a vaccination programme for bison will require an effective vaccine delivery method that can reliably deliver the vaccine to a large proportion of the target population in most years. The most effective way to vaccinate bison is by subcutaneous delivery using a syringe. Under these conditions, bison receive the intended dose and vaccinated animals can be marked to facilitate monitoring. Optimally, vaccine delivery should occur a minimum of 12 to 16 weeks prior to potential exposure in late February or March to allow the development of protective immune responses (14). However, existing capture facilities are located near the park boundary and only a portion of the bison population typically migrates to low-elevation ranges near the boundary and, when they do, it is generally during late winter (March to April). Syringe vaccination in late winter may be less effective given chronic under-nutrition and pregnancy or lactation in bison. With remote delivery (e.g. biobullet, dart [3]) of vaccine, it cannot be known for certain that the animal has received the intended dose and, because animals are not identified, the vaccination status of individual animals is unknown. Therefore, it is difficult to accurately and precisely estimate the portion of the population that has received the intended dose of vaccine and would be protected following *B. abortus* exposure. Also, capture and handling or remote delivery vaccination are likely unpleasant experiences for bison. Therefore, they may avoid humans and become more difficult to vaccinate over time. As a result, it will probably become more and more difficult to vaccinate a large portion of the bison population.

In summary, there are many uncertainties associated with a vaccination programme for bison that make it extremely difficult to predict whether substantial brucellosis reduction is achievable and sustainable.

– Will the vaccine be effective following delivery (i.e. reduction in bacterial shedding)?

– How many bison should be vaccinated each year and for how long will it be possible to continue vaccinating that number?

– Is hand delivery a feasible option or will remote vaccine delivery be needed?

– Will bison behaviour change in response to vaccine delivery either following capture or remote delivery (e.g. food conditioning, avoidance)?

Vaccination of bison is further complicated by the fact that elk may serve as a reservoir host and a source of re-infection for bison. In the past decade, elk abundance has increased in some portions of the GYA, with coincident increases in brucellosis prevalence of up to 20% in some areas (5). This increase in elk brucellosis in the GYA is independent of bison, which suggests that bison from Yellowstone are not sustaining the disease in elk. The peak calving period for bison occurs one month earlier than for elk and, overall, there is little overlap in the distributions of bison and elk during the times when the majority of *B. abortus* shedding is expected for both species. In areas where elk mingle with Yellowstone bison during winter and spring, elk have lower seroprevalence rates for brucellosis (3%) than bison or than elk that mingle with other elk at feedgrounds in Wyoming (5, 16). Brucellosis transmission risk from bison to elk was quite low in the Madison headwaters area of Yellowstone, despite high spatial overlap during times when *B. abortus* is typically shed (16). However, recent DNA genotyping suggests that brucellosis transmission has occurred between bison and elk in Yellowstone in the past, before eventually being transmitted among elk and by elk to cattle in Montana (G. Luikart, University of Montana, unpublished data). Clearly, brucellosis in the GYA is a disease sustained by multiple hosts and control measures aimed at managing the risk of transmission to cattle must take into account both wildlife reservoirs and factors involved in maintaining infection. Management of brucellosis in elk might best be achieved by curtailing practices that unnaturally increase densities and group sizes during times when abortions occur (1, 5).

Proposed resolution: an adaptive management approach

Adaptive management provides a framework for improving vaccine and delivery technology and learning how to reduce bovine brucellosis transmission among wildlife in the face of substantial uncertainties regarding vaccine efficacy, delivery, duration of immune response, and wildlife behaviour. Adaptive management is an iterative decision-making process whereby:

– the problem and uncertainties are described

– factors contributing to the problem are assessed

– understanding of the system is modelled

– measurable desired outcomes (objectives) are described and responses to management actions are predicted

– management actions to reach these desired outcomes are designed and implemented

– the effects and effectiveness of actions are monitored to evaluate if progress is being made towards the desired outcomes

– actions and models are adjusted to enhance progress towards the desired outcomes (28).

Adaptive management is based on the premise that uncertainties exist in resolving natural resource management issues and, as a result, learning is valuable (10, 25). Through careful predictions and monitoring of management actions our understanding of system dynamics is improved and actions can be adjusted to better achieve desired outcomes. In other words, adaptive management offers a reasonable method for action in the absence of complete information (10, 25). In fact, adaptive management is necessary to conserve ecosystems because they are constantly changing and, as a result, there is substantial uncertainty regarding how they will respond to management actions and other human interventions (19, 20).

Pursuant to the bison management plan developed by the federal government and state of Montana, with subsequent adjustments, the desired outcomes managers are attempting to reach include:

– a total population of at least 3,000 bison (which should maintain 90% to 95% of existing genetic diversity over the next 200 years)

– an equal number of males and females

– an age structure of about 80% adults and 20% juveniles

– equal abundance in the central and northern breeding herds

– continued migration and dispersal within the conservation area, but separation between bison and cattle to prevent brucellosis transmission (27).

Furthermore, managers desire to minimise the risk of brucellosis transmission to cattle and suppress transmission among bison. If brucellosis prevalence is used as a surrogate for measuring transmission, then a desired outcome would be a 90% decrease in the portion of bison testing positive for brucellosis exposure (currently 40% to 60% of bison test positive). This outcome would decrease seroprevalence to approximately 5% – the same level as brucellosis exposure in Yellowstone elk. However, this outcome is not attainable given current technology (vaccines are not sufficiently effective and delivery options are inadequate). A more realistic outcome may be a 50% decrease in seroprevalence, which would decrease seroprevalence in bison to approximately 20% to 30%.

The high seroprevalence of brucellosis infection in Yellowstone bison (e.g. approximately 50%) underscores how challenging it will be to substantially reduce disease prevalence and the associated risk of transmission. However, most Yellowstone bison are unlikely to transmit brucellosis for most of their lifespan (21). The dominant route of brucellosis transmission appears to be between unrelated bison rather than from mother to offspring (8), with young females serving as the primary source of transmission (21). The course of brucellosis infection in bison is likely affected by the timing of exposure. Many bison are exposed early in life, with more than 40% of reproductively immature females testing seropositive for brucellosis exposure (21). The disease can remain dormant in these animals for some time, with a transition to the infectious stage during the first pregnancy (21). However, exposure early in life may reduce the severity of brucellosis infection and reduce the probability of abortion (8). In contrast, bison exposed during gestation appear to rapidly progress into the infective stage because conditions are favourable to bacteria proliferation and spread (8, 17). Some animals can remain infectious for multiple pregnancies, perhaps owing to their condition and genetic variations in the pathogen (17). Therefore, management strategies that target females less than six years of age will be most successful at influencing brucellosis transmission (6).

Because female bison do not become reproductively active and contribute to brucellosis transmission until at least three years of age (17), there is an opportunity to implement management actions such as vaccination and selective removal of animals that are likely maintaining brucellosis within the population. For example, individual bison could be vaccinated several times before they become reproductively active in an attempt to maximise protective immune responses (22). Also, the selective culling of young females (three to five years of age) that are pregnant and infected may further suppress transmission, especially after brucellosis prevalence has been reduced through vaccination. Finally, older adult females that have a high probability of active infection can be identified through serological tests and removed from the population, while other animals that have recovered from acute infection can be retained to increase population immunity (resistance) against brucellosis (21). It is hypothesised that these recovered animals have acquired some level of immune protection, which reduces the risk factors that contribute to brucellosis transmission (8).

The authors anticipate that, as vaccination coverage of the population increases, seroprevalence will eventually decrease as *B. abortus* transmission is reduced in vaccine-protected bison. Over time, vaccination is expected to lead to a reduction in bacterial shedding and subsequent transmission. However, if vaccination does not result in a substantial decrease in bacterial shedding and transmission, the authors do not expect decreases in seroprevalence. Since the risk factors (e.g. abortions and bacterial shedding) that influence transmission cannot be effectively monitored, measuring seroprevalence will be the primary method for assessing the effectiveness of a vaccination programme. However, seroprevalence is not a precise indicator of changes in the prevalence of infection. Therefore, monitoring more sensitive epidemiological indicators (e.g. incidence rates) in addition to population seroprevalence will be necessary for adaptively managing the risk of brucellosis transmission from wildlife to cattle, as well as for suppressing infection prevalence within wildlife populations.

Future directions: monitoring and research

The National Park Service has implemented a rigorous surveillance plan to monitor the effects and effectiveness of management actions and implement research to answer existing uncertainties (26). Examples of monitoring and research actions that could be conducted to improve our understanding of likely effects and inform the decision process for future adaptive management adjustments include:

– evaluating if multiple vaccinations within a given year or across years increase protective responses (i.e. cell-mediated immune responses are strong and consistent)

– evaluating if late-winter vaccinations elicit protective immune responses by the following year

– identifying the portion of each age class of bison that can be consistently vaccinated each year, and evaluating if this level is adequate to drive the reproductive capability of brucellosis below the level of sustainability

– confirming that potentially infectious bison (i.e. high probability of shedding *B. abortus*) can be identified based on age and immune response by validating active infection in culled bison

– determining how to evaluate the effectiveness of raising overall population resistance to brucellosis

– evaluating the safety and effectiveness of alternative vaccines and delivery methods

– evaluating behavioural responses of animals subject to syringe or remote vaccine delivery methods to avoid deleterious effects.

In addition, an effective brucellosis control programme would require that all possible routes of re-infection be mitigated. Thus, the potential for elk to maintain the disease and re-infect susceptible bison that have not been previously exposed to *B. abortus* cannot be disregarded, particularly if brucellosis prevalence in bison is significantly reduced from current levels.

Conclusion

Given current technology and existing conditions, it is unrealistic to expect substantial decreases in brucellosis prevalence in wild bison and elk in the near future without implementing actions that could adversely affect their behaviour and demography. Delivery of vaccine to most females annually during autumn is difficult, and wildlife behaviour will change in response to capture or pursuit, thereby making the delivery of vaccine more difficult. However, adaptive management can be used to learn more about brucellosis and develop or improve suppression techniques. The successful implementation of adaptive management for complex issues that involve migratory wildlife and zoonotic diseases requires agencies with differing jurisdictions and missions to work collaboratively to achieve conservation and disease management objectives. Unfortunately, many times, agencies (and other stakeholders) have differing goals and differ on management objectives and courses of action (28). Consequently, before adaptive management can be used effectively, it is often necessary to overcome historic biases, misguided perceptions, and political wrangling (28). The National Park Service will continue to use an adaptive management approach with other agencies, American Indian tribes, academic institutions and stakeholders to develop comprehensive, holistic management approaches, better vaccines and delivery methods, and diagnostics for reducing the prevalence of brucellosis in bison and elk and the risk of transmission to cattle.

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La brucellose bovine chez les animaux sauvages : intérêt de la gestion adaptative pour mieux comprendre la maladie, améliorer les techniques employées et avancer sur la voie de l'élimination

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Résumé

L'état actuel des technologies ne permet pas d'éradiquer la brucellose au sein des populations de bisons *(Bison bison)* et de cerfs élaphes *(Cervus elaphus)* de la région du grand Yellowstone. D'importantes incertitudes subsistent quant à l'efficacité des techniques de gestion et à leurs effets imprévus sur le comportement et sur la démographie de la faune sauvage. Néanmoins, la gestion adaptative fournit un cadre pour mieux comprendre la maladie, améliorer les solutions techniques et limiter les probabilités de transmission, entre animaux sauvages, d'une part, et de ceux-ci aux bovins, d'autre part. Sachant qu'une bisonne ne devient active au plan de la reproduction (et donc capable de transmettre la brucellose) qu'à l'âge de trois ans, certaines mesures peuvent être prises telles que la vaccination et le retrait sélectif des bisons infectés (en fonction de leur âge et des résultats du dépistage), afin de réduire les possibilités de transmission. Les bisons adultes précédemment exposés et guéris suite à une infection aiguë peuvent être maintenus dans le cheptel afin d'apporter une immunité à l'échelle du troupeau. Des études prédictives pointues, des travaux de recherche approfondis et un suivi attentif permettront d'améliorer les connaissances et les techniques mises en œuvre afin d'adapter les activités de gestion pour de meilleurs résultats.

Mots-clés
Bison – Brucellose – Gestion adaptative – Grand Yellowstone – Maladie – Vaccination.

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Brucelosis bovina en la fauna salvaje: uso de la gestión adaptable para entender mejor la enfermedad, mejorar la tecnología y lograr mayores niveles de supresión

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Resumen
Con las técnicas actuales no es posible erradicar la brucelosis de las poblaciones de ciervo común *(Cervus elaphus)* y bisonte *(Bison bison)* de la zona del Gran Yellowstone. Existen importantes incertidumbres respecto a la eficacia de las técnicas de gestión y a eventuales efectos imprevistos sobre el comportamiento y la demografía de los animales salvajes. Sin embargo, la gestión adaptable ofrece un marco para ir aprendiendo sobre la enfermedad, mejorando la tecnología y frenando la transmisión de la brucelosis entre los animales salvajes y de estos al ganado vacuno. Los tres años que discurren entre el nacimiento de una hembra de bisonte y el momento en que empieza a ser reproductivamente activa (y por ende a contribuir a la transmisión de la brucelosis) ofrecen la posibilidad de aplicar medidas como la vacunación o la eliminación selectiva de bisontes infecciosos atendiendo a la edad y a los resultados de pruebas de diagnóstico con objeto de reducir las probabilidades de transmisión. A fin de instaurar la inmunidad de rebaño cabría la posibilidad de retener a bisontes adultos de más edad que, habiendo estado expuestos a la bacteria, se hayan recobrado de la infección aguda. Gracias a una cuidadosa labor de predicción, investigación y seguimiento nos será posible entender mejor la enfermedad, perfeccionar nuestra tecnología y afinar las medidas de gestión para tener más probabilidades de conseguir los resultados buscados.

Palabras clave
Bisonte – Brucelosis – Enfermedad – Gestión adaptable – Vacunación – Yellowstone.

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