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Brucellosis in the Greater Yellowstone area: disease management at the wildlife–livestock interface

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***Abstract*:** Elk (*Cervus elaphus*) and bison (*Bison bison*) of the Greater Yellowstone area are the last known reservoir of bovine brucellosis (*Brucella abortus*) in the United States. Domestic cattle occasionally contract the disease while grazing in areas where infected wild ungulates have aborted their fetuses or have given birth. Cases of brucellosis in cattle trigger costly quarantine, testing, and culling procedures. Government agencies and stakeholders, therefore, allocate valuable resources to prevent wildlife-to-cattle transmission. Scientific uncertainty about the biology, epidemiology, and economics of brucellosis makes it difficult to determine the length to which society should go to control it or the combination of management activities they should use to achieve the desired level of control. Research over the last decade has generated new information about brucellosis and alternative approaches for management. Stakeholders and decision makers must synthesize this growing body of information and re-assess current brucellosis goals and management strategies. Economic principles provide an objective framework in which to do this.

***Key words*:** bison, bovine brucellosis, *Brucella abortus*, cattle, cost-effectiveness, economics, elk, epidemiology, feedgrounds, human–wildlife conflicts, test-and-slaughter

BOVINE BRUCELLOSIS (*BRUCELLA ABORTUS*) is a bacterial disease that affects free-ranging and domestic ungulates, including elk (*Cervus elaphus*), bison (*Bison bison)* and cattle (Creech 1930, Thorne et al. 1978, Enright 1990). *Brucella abortus*, a gram-negative, facultative, and intracellular bacterium, causes the disease. It infects the reproductive tract, causing placentitis, with abortions in females (typically during the third trimester); orchitis and epididymitis in males; and swollen joints due to bursitis and synovitis. Infiltrated reproductive tissues and fluids from an abortion or live parturition event are directly infectious and may also contaminate the environment. Given cool and dark conditions, the bacteria can persist in the environment for up to 70 to 180 days (Corbel 1989, Crawford et al. 1990, Aune et al. 2007). A susceptible animal can become infected by licking, sniffing, or ingesting contaminated material (Cook 1999, Maichak et al. 2009).

Humans can also contract brucellosis (also known commonly as undulant fever or Bang's disease) by consuming unpasteurized dairy products from an infected animal or handling infectious materials. Health complications can include meningitis, spondylitis, endocarditis, and arthritis. Treatment involves long-term administration of multiple antibiotics (Young 1995). The few cases of undulant fever observed in the United States (80 cases in 2008 compared to a peak of 6,321 cases in 1947) are attributed primarily to consumption of unpasteurized milk products from other countries; hunters who handle infected wildlife carcasses; and ranchers, veterinarians, and lab technicians who handle infectious materials or inhale aerosolized bacteria (Wise 1980, Centers for Disease Control and Prevention 2010, Seleem et al. 2010). Although brucellosis in humans is relatively rare in the United States, it is one of the most common zoonotic diseases worldwide (Pappas et al. 2006; Seleem et al. 2010). Most human cases are caused by *B. melitensis* from unpasteurized dairy products from goats and sheep. *B. abortus* infections also are common in countries where its prevalence in cattle is high and pasteurization rare, especially in the former Soviet Union (Seleem et al. 2010).

In the United States, the state-federal cooperative brucellosis eradication program has been effective in decreasing the number of cattle herds in the United States that have bovine brucellosis (Ragan 2002). Today, *B. abortus* in the United States is found almost exclusively at the wildlife–livestock interface in the Greater

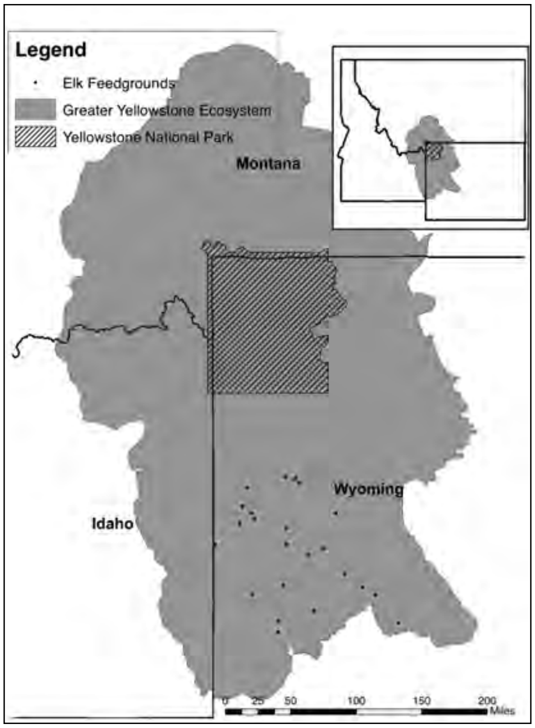

Figure 1. Elk feedgrounds in Greater Yellowstone National Park area.

Yellowstone area (GYA) of Yellowstone National Park, Wyoming, where it occurs in free-ranging elk and bison (Figure 1). Bovine brucellosis in elk and bison is a less substantial source of human brucellosis than consumption of unpasteurized milk products from countries where brucellosis is common (Chomel et al. 1994). However, elk and bison pose a risk to cattle herds that may come in contact with infected wildlife tissues (aborted fetuses or birth fluids). When cattle contract brucellosis, federal policies require infected herds to be destroyed or quarantined and tested multiple times (USDA Animal and Plant Health Inspection Service [USDA-APHIS] 2009). Additionally, any herd that has come in contact with the infected herd through animal commingling or exchange must be quarantined and tested. These and other brucellosis-related regulations impose direct costs on individual cattle producers, the livestock industry, and state and federal animal health agencies.

Risk of transmission from elk and bison to cattle also imposes costs on state wildlife agencies, which face political pressure to invest in risk management activities, such as wildlife hazing, vaccination, and test-and-slaughter. Activities that reduce elk and bison populations are controversial because they may negatively impact outdoor recreationists and businesses that derive revenue from wildlife. Thus, brucellosis management is highly complex and controversial, affecting a diverse set of stakeholders who assign a wide array of economic and cultural values to both livestock and wildlife. Successful management hinges on understanding not only the epidemiology of the disease, but also the economic ramifications of alternative management goals and approaches (Peck 2010). The purpose of this paper is to review the current status of bovine brucellosis in the GYA, describe the suite of management activities currently being implemented, and discuss a few economic principles that can help society identify the optimal level of brucellosis control and achieve it at least cost.

Methods

The remainder of this paper is based on information gathered through a literature review following a framework similar to that in Ford and Pearce (2010). We limited the review to articles available in English related to bovine brucellosis within the GYA and published primarily between 1995 and 2011. Publications with a strictly molecular focus were excluded. Initial searches using the terms "bovine brucellosis," "wildlife disease management," "brucellosis transmission," and "brucellosis management" yielded >1,682 results. Findings from these broad searches helped define a final library of search terms that was then used in searches of the Web of Science, PubMed, and Google Scholar, generating 515 publications, of which 124 were directly relevant to this research.

Epidemiology of brucellosis in the GYA

Bovine brucellosis in GYA wildlife is thought to have originated from cattle kept within the boundaries of Yellowstone National Park (YNP) for park employees (Meagher and Meyer 1994). The disease was first observed in YNP bison in 1917 (Mohler 1917), and it was thought that bison subsequently transmitted it to YNP elk. Elk outside the park are thought to have contracted the disease directly from cattle (Meagher and Meyer 1994). Despite efforts over the last 75 years to eradicate the disease, it persists today

Figure 2. Elk on the National Elk Refuge, Jackson, Wyoming.

in free-ranging elk and bison, and, occasionally, it spills over into cattle (Wyoming Game and Fish Department 2004, Maichak et al. 2009).

High concentrations of elk on winter feedgrounds in the southern GYA contribute to the persistence of brucellosis in the region (Figure 2). State and federal wildlife agencies feed hay to elk during the winter at 23 locations in Wyoming to deter them from moving onto private lands where they depredate private haystacks and commingle with cattle. Roughly 73 to 84% of the 23,000 elk that inhabit the southern GYA overwinter on Wyoming feedgrounds (Wyoming Game and Fish Department 2004). Elk infected with brucellosis often abort their fetuses during the third trimester of gestation, which typically occurs while they are on feedgrounds. In the event of an abortion caused by *B. abortus* infection, elk are sufficiently concentrated at feedgrounds that contact with aborted fetuses and other infectious material is almost inevitable (Cook 1999, Maichak et al. 2009). Exposure to brucellosis and subsequent infection are, therefore, maintained at relatively high levels among elk that overwinter on Wyoming feedgrounds. Such elk also are known as feedground elk.

Elk that have been infected with brucellosis for >1 calving season can give birth to viable calves, but *B. abortus* may still be found in their placental tissues (Thorne et al. 1997). Parturition dates for elk in the GYA typically range from mid-May to mid-July (National Agricultural Statistics Service 2010). Environmental contamination at parturition sites of infected elk that give birth to a viable calf could therefore persist through July, and, theoretically, into August if conditions were dark and cool. This window might be even longer if supplemental feeding causes elk reproduction to become less synchronized, as Smith (1994) suggests. If sufficiently well-fed, an elk could conceive in mid- to late winter and, therefore, calve much later in the summer, potentially when cattle are grazing in the area. Elk typically isolate themselves during normal parturition and clean up much of their tissues and fluids. These behaviors reduce the risk of brucellosis infection from exposure to contaminated birthing sites (Thorne et al. 1997), but they do not eliminate the risk entirely.

The proportion of feedground elk with antibodies to brucellosis (i.e., the proportion that are seropositive, which indicates previous exposure but not necessarily active infection) averaged 22% in 2009, compared to just 3.7% among winter free-ranging elk in the brucellosis endemic area in 2008 (Scurlock and Edwards 2010). The proportion of elk actually infected with brucellosis is more difficult to estimate. In past sampling efforts, 35 to 63% of seropositive elk were actually infected (i.e., culture positive; Scurlock 2010).

Although recent samples suggest that a higher proportion of feedground elk are exposed to brucellosis than are non-feedground elk, seroprevalance in the latter population appears to be increasing for reasons not fully understood (Scurlock and Edwards 2010). Non-feedground elk herds that show increasing seroprevalance are not known to interact with bison, so interspecies transmission is an unlikely explanation. A small number of feedground elk are known to disperse to non-feedground areas, carrying brucellosis with them, but this number is not sufficient to provide a reasonable explanation (Cross et al. 2010). Increasing herd sizes and densities in non-feedground regions currently are the suspected cause (Cross et al. 2010). As land ownership patterns have changed, access to private land for hunting has declined. Elk can now more easily evade hunting pressure by seeking refuge on private land where hunters are not allowed (Haggerty and Travis 2006, Cross et al. 2010). In some areas of the GYA, elk are moving to these lands earlier in the fall and staying later in the spring (Van Campen and Rhyan 2010). Burcham et al. (1999) found that once elk begin using a private land refuge, additional elk are attracted to the area and tend to stay longer. As increasingly large groups of elk congregate on inaccessible private lands, transmission of brucellosis becomes more likely, and a new reservoir for the disease appears to have emerged.

Brucellosis is also prevalent among bison in the GYA. Roughly 50% of YNP bison and 64% of the Jackson, Wyoming, bison herd are seropositive (Rhyan et al. 2009, Fenichel et al. 2010). The proportion of seropositive bison actively infected is uncertain, but estimates range from 7 to 46% (Cheville et al. 1998, Roffe et al. 1999). Seroprevalence in YNP bison is nearly as high as it is in the Jackson bison herd, even though YNP bison do not rely on feedgrounds, although Jackson bison do (Wyoming Game and Fish Department 2008).

Reasons for the relatively high seroprevalence proportion among bison, including YNP bison, are unclear. Meyer and Meagher (1995) hypothesized that it might be due to fundamental differences in antibody response in bison versus elk or to vertical transmission of brucellosis from female bison to their calves while nursing. Others hypothesize that because bison tend to give birth in close proximity to other group members (Lott and Galland 1985, Treanor et al. 2010), the likelihood of intraspecific transmission is higher than in elk, which tend to be more secretive and isolated during parturition (Geist 1982, Vore and Schmidt 2001, 2006). Interaction of YNP bison with elk from Wyoming feedgrounds could also increase seroprevalence. However, only a small portion of elk on the National Elk Refuge feedground migrate to YNP, and they typically arrive in June or July (Smith and Robbins 1994). Elk infected with brucellosis, in contrast, typically abort their fetuses between February and June (Thorne et al. 1997; Roffe et al. 2004). Most of the feedground elk that migrate north to YNP would, therefore, have aborted before reaching the park and interacting with YNP bison.

Transmission risk from bison to elk within YNP also appears to be low. Elk that winter in the headwaters of the Madison River basin, for example, showed 53% winter range overlap with Yellowstone bison in December and 76% overlap in May (Ferrari and Garrott 2002). Commingling between elk and bison was positively correlated with snowpack, and 18% of elk locations were within 100 m of bison. Despite these interactions, elk in the Madison River basin showed no evidence of higher *B. abortus* exposure than elk populations that are separated spatio-temporally from bison (Ferrari and Garrott 2002, Proffitt et al. 2010*b*).

Interspecific transmission may be less common than intraspecific transmission, but they do occur occasionally. Transmission from elk or bison to cattle is of particular concern for the cattle industry because it triggers economic consequences. Between 2004 and 2008, infection was detected in 9 cattle herds in the GYA. Five of these cases occurred in Wyoming herds, 2 cases in Montana, and 2 cases in Idaho (Donch and Gertonson 2008). Between 2009 and early 2011, 6 additional infected herds were detected, including 3 cattle herds and 1 domestic bison herd in Wyoming, 1 domestic bison herd in Montana, and 1 cattle herd in Idaho (International Society for Infectious Diseases [ISID] 2009, ISID 2010*a*, ISID 2010*b*, ISID 2010*c*, ISID 2011). In most cases detected in the southern GYA, domestic herds are thought to have contracted brucellosis while grazing elk feedgrounds or on private land where infected elk aborted or gave birth (Elzer et al. 1998, Thorne 2001, Beja-Pereira et al. 2009). Cases in northern GYA cattle have been qualitatively attributed to elk (Galey et al. 2005). Recent quantitative risk assessments also indicate that bison impose less risk to cattle than was previously thought and that management and research should focus more on elk (Kilpatrick et al. 2009, Proffitt et al. 2010*b*).

Brucellosis management: past and present

The USDA-APHIS began a campaign to eradicate bovine brucellosis in 1934. At that time, 11.5% of adult cattle tested positive for the disease (USDA-APHIS Veterinary Services [VS] 2009). After investing >$3.5 billion in the eradication campaign (Cheville et al. 1998), prevalence in U.S. cattle is now <0.0001% (USDA-APHIS-VS 2009). Infected elk and bison in the GYA are the only remaining obstacle to eradication of the disease in the United States, but significant technical and sociopolitical challenges must be overcome to clear it. Significant financial and physical resources will be needed to do so, but such resources are increasingly limited and difficult to secure.

The expected high cost of eliminating bovine brucellosis from the last known reservoir in the United States has prompted USDA-APHIS to revise its traditional approaches to eradication. Its policies, both traditional (USDA-APHIS 2003) and revised interim policies (USDA-APHIS 2009), require a detailed epidemiological investigation any time a reproductively intact bovine tests positive for brucellosis; most cases are detected through mandatory testing at sale barns and slaughter facilities. Investigation identifies an infected animal's herd of origin and all cattle herds that may have contacted it. The USDA-APHIS quarantines the infected cattle herd, which is then either destroyed or subjected to a testing protocol that takes roughly 1 year to complete; USDA-APHIS also quarantines contact herds, which are then subjected to a testing protocol that takes roughly 1 month to complete.

Producers whose herds are destroyed historically have received compensation for the difference between their cattle's fair-market and slaughter values. Producers whose herds are quarantined but not destroyed are not compensated for extra costs they incur (Jim Logan, Wyoming Livestock Board, personal communication). With or without compensation, herd quarantine or destruction can be costly and emotionally devastating for a producer. Based on preliminary estimates, a producer whose 400-head herd is quarantined for 1 to 6 months during the winter feeding season because it interacted with an infected herd could incur $2,000 to $8,000 in uncompensated costs. A producer whose herd actually contracts brucellosis could incur $35,000 to $200,000 in uncompensated costs, depending on whether the herd is destroyed and whether the producer receives compensation for the herd's market value. Destruction of a herd is also costly for USDA-APHIS and the taxpayers who help fund them, particularly when destroyed herds are large.

Under traditional USDA-APHIS policy, states are considered brucellosis Class-Free if the cattle or bison herds in the state have remained free from infections of field strains of brucellosis for ≥1 year and all affected herds must be legally released from quarantine. (USDA-APHIS 2003). If ≥2 infected herds were detected in the same state within a 2-year period or if the owner of an infected herd chose to test-out rather than destroy the herd, the entire state is downgraded from Class-Free to Class-A status, provided that the infection rate in cattle and bison herds were <0.1% during the previous 12 months and the successful closure rate for cases was ≥95%. Loss of Class-Free status triggered mandatory statewide brucellosis testing of any reproductively intact cattle being sold or moved across state lines. A state could petition for reinstatement of their Class-Free status only if no additional brucellosis cases were detected within 12 months of the date on which the last infected herd was destroyed or successfully tested out.

State-federal cooperative brucellosis eradication program

In 2010, USDA-APHIS decided to revise its policy by replacing the state-level brucellosis classification system (i.e., Class-Free versus Class-A) with an interim approach that focuses on designated surveillance areas (DSAs; USDA-APHIS 2009); USDA-APHIS has collaborated with Wyoming, Montana, and Idaho to define a DSA for brucellosis in the GYA. The DSA boundaries are evaluated using a quantitative risk-based model developed by USDA-APHIS (Katie Portacci, personal communication). The USDA-APHIS's interim policy enforces the same epidemiologic investigations, quarantines, and testing protocols in response to individual infected herds, but statewide testing and movement restrictions are not enforced when ≥2 infected herds in the same state are detected. Instead, cattle within the DSA must now be tested for brucellosis, regardless of whether infected herds have been detected there, recently or not, before they can be sold or moved across the DSA boundary. Additionally, the states of Nebraska and Colorado recently tightened their animal identification requirements for all imported, sexually intact cattle and bison that came from or spent time in the DSA (Hughes 2011).

This new policy aims to reduce the total cost of a brucellosis outbreak by eliminating mandatory testing of cattle in brucellosis-free areas of a state in which multiple infected herds have been detected. The USDA-APHIS has proposed to redirect any cost-savings toward the eradication of brucellosis in the GYA, but it is unclear whether this will occur. Recent federal budget shortfalls have made it difficult for USDA-APHIS to fund current activities, including compensation to producers for whole-herd destruction, let alone new initiatives (USDA Animal and Plant Health Inspection Service 2009). In recent outbreaks, producers were paid indemnity for individual reactor and suspect animals removed for diagnostic purposes but would not have received federal funding for whole herd destruction. Instead the herds were quarantined without compensation (Jim Logan, Wyoming Livestock Board, personal communication).

Cattle brucellosis risk management

Cattle producers, in an effort to reduce the risk of their herds contracting brucellosis and being destroyed or quarantined, are implementing a variety of brucellosis management activities, such as fencing haystacks, modifying winter feeding practices, and allowing state wildlife agencies to haze elk off private property, all of which discourage elk from commingling with cattle during high-risk months. Producers also are administering calfhood and adult-booster vaccinations and spaying heifers because only reproductively intact animals are subject to brucellosis testing. A small number of producers are delaying grazing on high-risk grazing allotments, particularly those that overlap with elk feedgrounds. No producers, to our knowledge, have converted their cow-calf operations to stocker operations for disease management purposes. Stocker operations run steers and spayed heifers only and, therefore, face no consequence if these animals contract brucellosis. Stocker enterprises tend to have larger variability in income than cow-calf operations, and, therefore, tend to be less appealing to risk-averse producers (Eikenberry 1966; McKissick and Ikerd 1996). The cost of ranch-level brucellosis management practices ranges from $200 to $18,000 per unit or year (Roberts 2011) . The extent to which they reduce risk is unknown in most cases. They contribute to USDA-APHIS's goal of eradication, but it is not clear which practices generate the biggest reduction in risk per dollar invested.

Obvious solutions to the brucellosis issue seem to be delayed grazing in areas in which elk overwinter or exclusion of elk from areas where cattle graze in spring and early summer. These approaches are challenging, however, for 2 reasons. Forage is limited in spring and early summer, so excluding cattle from (or delaying grazing on) areas in which elk may have aborted is expensive. It would cost roughly $15,000 to move a 400-head cattle herd to a privately leased, brucellosis-free pasture to delay grazing on public land for 1 month (Roberts 2011). Further, elk are highly abundant and mobile, so abortions can occur over a large spatial area and a wide temporal window. Even though elk tend to abort weeks or months before cattle are turned out to pasture in the spring, *B. abortus* can persist in the environment sufficiently long for cattle to ingest live bacteria while grazing. Laboratory strains of *B. abortus* have been successfully cultured from the exposed surface of experimental fetuses up to 17 days after they were placed outdoors, and up to 60 days from underneath the fetuses (Rushton 2009). Similarly, soil, vegetation, and tissue at birth or abortion sites in the GYA that were naturally infected with field strain *B. abortus* remained viable for up to 43 days in April and 26 days in May (Aune et al. 2007). Cattle grazing would, therefore, have to be delayed for several weeks after the elk calving season ended.

The GYA supported roughly 450,000 cattle and calves (comprising those in Bonneville, Caribou, Franklin, Fremont, and Teton counties in Idaho; Gallatin, Madison and Park counties in Montana; and Lincoln, Park, Sublette, and Teton counties in Wyoming; USDA National Agricultural Statistics Service 2011). These cattle have the potential to interact with roughly 30,000 to 40,000 elk (Toman et al. 1997, Wyoming Game and Fish Department 2004, Vucetich et al. 2005, Etter and Drew 2006), and 3,000 to 6,000 bison that inhabit the GYA (Fuller et al. 2007;

Wyoming Game and Fish Department 2008). Given the large number of cattle, elk, and bison sharing vast areas of both private and public lands, complete spatio-temporal separation is not feasible. Even the delay of grazing in strictly the highest-risk areas is costly.

Vaccination of cattle is a more affordable and popular management activity, and its effectiveness is relatively well-understood (Elzer et al. 1998). The RB51 vaccine, currently the only vaccine approved for use in U.S. cattle, provides protection against abortion in approximately 60% of animals (Poester et al. 2006). Research to develop a more effective vaccine continues. A desirable characteristic of RB51 is that, unlike its predecessor (S19 vaccine), RB51 does not elicit positive diagnostic test results. Infected animals, therefore, can easily be distinguished from vaccinated animals (Olsen 2000). Vaccination has also been suggested as a control strategy for brucellosis in elk and bison. Development of an effective vaccine for these species remains problematic, however, due in part to limited scientific understanding of their immune systems (Davis and Elzer 2002). Wildlife managers also lack a practical means for delivering such a vaccine to a sufficiently large proportion of the elk and bison populations to have a meaningful impact on disease dynamics.

Wildlife brucellosis risk management

In lieu of effective vaccines for wild ungulates, WGFD has undertaken several other brucellosis management activities, including an experimental test-and-slaughter program. The pilot program, which was initiated in 2006 and concluded in 2010, involved trapping elk on selected feedgrounds, testing for antibodies against *B. abortus*, and culling females that tested seropositive. Tissue samples from culled elk were then sampled to determine whether seropositive individuals were actively infected with *B. abortus*. The program's goals were to improve methods of detecting and preventing infections in elk, reduce seroprevalence by removing affected animals, and offer insights for vaccine development. The preliminary results of this pilot program indicate a decrease in brucellosis seroprevalence in captured elk on select feedgrounds (Fenichel et al. 2010). However, its social and economic costs limit its suitability for use at a regional level or over a sustained period.

Figure 3. Brucellosis was first observed in Greater Yellowstone area bison in 1917.

The WGFD also vaccinates elk calves on most feedgrounds with the S19 vaccine, delivered via biobullets (Doll and Orazem 1984). Additionally, they have changed the spatial pattern of hay distribution on feedgrounds from continuous lines to discrete and dispersed piles (to reduce elk-to-elk contact), and tried to shorten feeding seasons (to reduce the probability of elk contacting an infectious fetus; Scurlock 2010). Lastly, WGFD is improving native winter habitat via controlled burns and other management techniques to improve elk winter range and reduce the need for feedgrounds (Thorne 2001).

Until recently, bison, rather than elk, were thought to be the main source of transmission risk for cattle (Figure 3). Bison migrating north out of YNP and into Montana, therefore, traditionally have been perceived as a serious threat to the cattle industry and have either been hazed back into YNP or culled (Government Accountability Office 2008). There is some concern that systematically culling migratory bison could reduce the overall health and resilience of the YNP bison herd by favoring less migratory bison, which may also select for a genetic defect that decreases their fitness for escaping predators, tolerating the cold, and mating (Pringle 2011). To mitigate public relations issues surrounding bison culling, state and federal agencies are now experimenting with alternative management approaches.

Bison data suggest that large-scale migration out of YNP is influenced by both population size and winter snowpack (Plumb et al. 2009;

Schumaker 2010). Simulation of bison migrations indicates that the only way to avoid having to cull large numbers of bison in the future may be to allow increased numbers of bison to migrate outside of park boundaries. Continuing to kill all bison that leave the park may not be a feasible long-term plan (Geremia et al. 2011). In January 2011, 25 seronegative bison were experimentally relocated to a 6-km segment of national forest north of YNP (Associated Press 2011*b*). By mid-February, all 25 of the bison had moved off the federal land and onto private land. After several unsuccessful attempts to haze them back to the national forest, all 25 bison were culled (Associated Press 2011*a*). The governor of Montana has since blocked the shipment of YNP bison to slaughter, drawing attention to the urgent need for a more effective bison management plan (Brown 2011).

Sources of controversy in brucellosis management

Brucellosis management in the GYA is controversial because cattle, elk, and bison each play important roles in the epidemiology of the disease, as well as the region's economy, culture, and politics. Brucellosis and brucellosis management, therefore, affect a diverse set of stakeholders and can affect an individual stakeholder in multiple ways. Cattle producers, for example, incur production losses and disease management costs because of infected elk, but they also benefit from elk-watching on their property or leasing access to outfitters for hunting. In 2009, 62,620 elk-hunting licenses were sold in Wyoming. This resulted in $8,649,005 in license sales alone, and $40,543,406 in hunter expenditures. The cost to the department per animal was $638, and the economic return per animal was $1,765 (Wyoming Game and Fish Department 2010).

According to the National Survey of Fishing, Hunting, and Wildlife Associated Recreation (2006), 762,000 people took part in wildlife-associated recreation in Wyoming in 2006, and these people spent $1.1 billion. Of these, 84% of the people reported participating in wildlife watching, and 13% participated in hunting. Of the money spent, 44% was trip-related (e.g., fuel, hotels). In 2010, there were 1.32 million cattle in Wyoming worth $1.24 billion (National Agricultural Statistics Service [NASS] 2010).

Hunters and outfitters benefit from the robust elk populations made possible by winter feedgrounds, but they also know that feedgrounds leave elk more vulnerable to highly contagious diseases that could arrive in the near future, such as chronic wasting disease and bovine tuberculosis. These conflicting values make it difficult for individual stakeholders to decide whether to support or oppose certain management activities. Debate over the most controversial management activities often boils down to (1) scientific uncertainty about a management activity's potential benefits and costs, and (2) the potential for benefits and costs to be distributed unequally across stakeholders.

Proposals to close elk feedgrounds, for example, are controversial because the potential benefits and costs are scientifically uncertain and because some stakeholders believe it might generate more costs than benefits for them in particular. Feedground closures could potentially reduce the proportion of elk exposed to or infected with brucellosis, slow the spread of other highly contagious diseases that could reach the region in the near future, and reduce wildlife agencies' operating costs. However, closure would also inevitably decrease elk populations (Cook 1999) and, consequently, the quantity and quality of elk hunting in the region (Kauffman 2010). Closure might also cause elk to disperse to private agricultural land in search of winter forage, which could actually increase the probability of cattle contracting brucellosis from elk (Cook 1999, Cross et al. 2007). It is not clear whether feedground closures would generate positive net benefits for other stakeholders, such as cattle producers. Biological, epidemiologic, and economic research would be necessary to answer this question. In light of new pockets of increasing elk seroprevalence distant from the elk feedgrounds (Scurlock and Edwards 2010), attempts to manage brucellosis only within the feedground area may no longer be sufficient. Cross et al. (2010) describe elk populations that have increased in group size as a risk factor for maintenance of brucellosis in elk outside the winter feedground area. Private ownership and lack of hunter access may make managing these elk populations particularly difficult.

Controversy surrounding the WGFD's pilot test-and-slaughter project in the southern GYA also stems from scientific uncertainty about the relative magnitude of benefits and costs, and dissatisfaction with the potential distribution of gains and losses among stakeholders. During the 5-year pilot project, WGFD allocated labor and materials worth $1.3 million to capturing 2,226 elk, testing 1,286 cow elk, and culling 197 seropositive animals. They reduced seroprevalence on ≥1 feedground from 37 to 5% (Scurlock, unpublished data). Despite its apparent success at reducing seroprevalence, it was an expensive undertaking, and the extent to which it has reduced the probability of cattle contracting brucellosis is not known. It is, therefore, difficult to assess the cost-effectiveness of test-and-slaughter. Controversy also arises because wildlife agencies bear much of the cost of test-and-slaughter, while cattle producers reap most of the benefits.

More complete information about the benefits and costs of alternative brucellosis management activities, including feedground closures and test-and-slaughter, would reduce controversy arising from scientific uncertainty and would inform stakeholder discussions about the distribution of gains and losses. Benefit and cost estimates would also help stakeholders decide how much brucellosis control is optimal and which management activities are most cost-effective. After the socially optimal management strategy is identified, conflicts between winners and losers can potentially be resolved by redistributing gains and losses.

Identifying the optimal level of brucellosis control

Government agencies and stakeholders continue to allocate valuable resources to the management of bovine brucellosis in GYA cattle and wildlife in the hopes of eventually eradicating it. Regardless of whether an individual believes brucellosis eradication is technically feasible, recent experiences with test-and-slaughter of elk, retirement of cattle-grazing permits, a proposed remote vaccination program for bison, and other controversial management activities suggest that eradication might be politically and economically difficult to achieve. This does not necessarily imply that society should do nothing to control brucellosis. Disease management is not an all-or-nothing decision; a continuum of management options exists, ranging from no control through intermediate levels of control to complete control (i.e., regional, national, or even global eradication; Dijkhuizen et al. 1995, Forster and Gilligan 2007). Intermediate levels of control might not lead to eradication, but they might perform better, from an economic perspective, than eradication (Horan et al. 2010).

Controlling brucellosis in the GYA into perpetuity might seem more costly by its very definition than eradicating it from the GYA. This might not be true in all cases, though, for 2 reasons. First, even if brucellosis were successfully eradicated from the United States, society would still incur perpetual costs to prevent its reintroduction. Alternatively, society would have to incur large up-front costs to eradicate it globally (Miller et al. 2006). Second, because people do not currently view costs and benefits the same as those who may in the future, eradication should not be compared to perpetual control unless benefits and costs are discounted to account for time preferences (Dijkhuizen et al. 1995, Klein et al. 2007, Rushton 2009). Eradication might generate more total benefit (e.g., increased cattle production) than perpetual control; however, it might also require larger up-front investments, whereas, perpetual control might push costs farther into the future. Because people tend to value the present more than the future, some might prefer perpetual control over elimination (or eradication) even if it generates less benefit and more cost (see Peck 2010). Forster and Gilligan (2007) demonstrate that inclusion of a discount rate (even a relatively small one, such as 1%) can change the optimal disease management strategy from eradication to control.

The debate over brucellosis eradication versus perpetual control is controversial and may distract stakeholders from other meaningful discussions about brucellosis management. Such distraction can be reduced by discussing a simpler, less controversial question: will the next dollar spent on brucellosis control generate at least $1 of benefit? If so, the dollar should be invested; otherwise, it should not (McInerney et al. 1992, Peck 2010). By answering this question for each dollar that society considers investing in brucellosis control, the economically optimal level (i.e., the level of control at which the benefit of investing an additional dollar no longer outweighs the cost, assuming total cost does not exceed total benefit at that point) will eventually be found (Dijkhuizen et al. 1995, Tisdell 2009). This level may or may not achieve eradication but will maximize society's net benefit (Miller et al. 2006, Horan et al. 2010).

Although the process described above guarantees the socially optimal level of brucellosis control, it does not guarantee that all stakeholders will be satisfied with the outcome. Dissatisfaction typically occurs when stakeholders consider only their private benefits and costs from brucellosis control and ignore the benefits and costs to other members of society (i.e., when the potential for externalities exists; Jaeger 2005, Rushton and Leonard 2009). Such behavior may cause the privately optimal level of control to differ from the socially optimal level (Klein et al. 2007, Peck 2010). As a result, stakeholders might be disappointed when the socially optimal level of control is implemented because an alternative level of control exists that would make them better off, albeit at the expense of other stakeholders.

Achieving the optimal level of brucellosis control at least cost

A wide variety of brucellosis management activities are available, ranging from adult-booster vaccination of cattle to improved winter habitat for elk and bison. Once the benefits and costs of individual activities are known, the socially optimal level of control and the least-cost means of achieving it can be determined simultaneously (McInerney et al. 1992, Rushton 2009, Horan et al. 2010). Activities, however, often differ in both cost and effectiveness, complicating efforts to compare their cost-effectiveness. Some activities may be very effective, but also very costly. Other activities might reduce the risk of cattle contracting brucellosis by only modest amounts, but might also be very inexpensive. Ideally, an activity would be highly effective and very inexpensive.

Comparison of activities to determine which method should be used to achieve the socially optimal level of brucellosis is made easier by calculating each activity's "bang-per-buck," that is, by dividing an activity's marginal benefit by its marginal cost (or its marginal physical product by its marginal factor cost; Rushton 2009). An activity's cost-benefit ratio is interpreted as the benefit (measured in either physical or monetary units) generated by an additional dollar invested in the activity. Because cost-benefit ratio has the same denominator for every activity ($1), it can easily be compared to determine in which activity (if any) society should invest its next dollar.

According to the least-cost criterion, or the equimarginal principle (Doll and Orazem 1984), society should invest its first dollar in whichever management activity generates the greatest advantage, or the greatest reduction in the risk of cattle contracting brucellosis per dollar spent. To decide how to invest its second dollar, society should again evaluate which activity would generate the greatest advantage. Keep in mind, the second unit of the same activity may be less effective than the first unit; that is, the activity may exhibit decreasing marginal productivity or diminishing marginal returns (McInerney et al. 1992). This process of comparing the activity's cost-benefit ratio should be repeated for each dollar spent until society reaches the point at which the next dollar would generate insufficient benefits to justify its investment (Rushton 2009). At this point, no additional resources should be invested in control. If activities exhibit constant or decreasing marginal productivity, the decision process will identify both the optimal level of brucellosis control and the combination of activities that achieve it at least cost. By achieving the optimal level of control as cheaply as possible, any remaining resources can be put toward the control of other animal diseases or towards other social goals (Fenichel et al. 2010).

The application of economic principles to brucellosis management requires information about the costs incurred when cattle contract brucellosis (or equivalently, the benefit of preventing outbreaks in cattle), as well as the cost and effectiveness of alternative brucellosis management activities. Agricultural economists are working to estimate the aforementioned costs (Kauffman 2010, Roberts 2011), but little is known about the effectiveness of brucellosis management activities. It is not clear, for example, the extent to which fencing a haystack, closing an elk feedground, or hazing elk from private property would reduce the risk of cattle contracting brucellosis. The extent to which spaying heifers, vaccinating cattle, and delaying grazing reduce risk is better understood, but still not known with certainty. More biological and epidemiologic research is needed to improve society's understanding of management activities' effectiveness. Such information would help economists, in collaboration with epidemiologists and biologists, to identify the socially optimal level of brucellosis control and the least-cost means of achieving it.

Conclusions

It is difficult to objectively identify the socially optimal level of brucellosis management or the least-cost means of achieving it, because elk and bison in the GYA play such pivotal and complex roles in the epidemiology of brucellosis and generate such a wide variety of benefits and costs. In the absence of complete information about the cost-effectiveness of alternative brucellosis management activities, stakeholders and policymakers tend to focus on technical details of the brucellosis issue rather than bigger-picture questions, such as whether additional investment to reduce the number of outbreaks among cattle is economically justified. In the absence of complete information, discussions and management decisions are driven by personal opinion rather than objective consideration of the available epidemiologic and economic information. Trade-offs associated with alternative brucellosis management goals and activities are far too complex and consequential to allow personal opinion to drive discussions and subsequent decisions.

Scientific discoveries over the last decade have enhanced society's understanding of the brucellosis issue. DNA genotyping studies have revealed that elk, rather than bison, are the likely source of brucellosis outbreaks in cattle (Beja-Pereira et al. 2009). Advances in epidemiological modeling and risk assessment have also shifted the focus from bison to elk (Ferrari and Garrott 2002, Kilpatrick et al. 2009, Proffitt et al. 2010*a*, Schumaker 2010) and highlighted the role of land-use, hunter access, and predator–prey dynamics in disease dynamics (Cross et al. 2010, Proffitt et al. 2010*b*). A pilot test-and-slaughter project in Wyoming has provided more reliable data on the seroprevalence of feedground elk, and the cost of identifying and culling seropositive animals (Scurlock 2010). Biological research has improved our understanding of elk behavior on feedgrounds and the location of elk parturition sites (Maichak et al. 2009, NASS 2010). Economic research has provided preliminary estimates of the cost of outbreaks in cattle, and the cost of implementing a subset of brucellosis management activities (Kauffman 2010, Roberts 2011). Lastly, government policies and regulations have evolved to reduce the economic impact of brucellosis outbreaks (USDA-APHIS 2009).

Although our understanding of brucellosis has improved over the last decade, stakeholders and policymakers face the same daunting task: to synthesize this information and use it to reassess current management goals and strategies. The economic principles described above provide an objective framework by which to tackle this difficult process. Although all information required for a complete economic analysis is not available, the process of thinking through the framework's components and concepts is a useful exercise. It helps distill information on the biology, epidemiology, politics, and economics of brucellosis into 2 straightforward measures: benefits and costs. With just 2 measures to consider, individuals can focus more easily on the most important overarching management questions, such as, "What is the socially optimal level of brucellosis?" and "Which combination of management activities will achieve this level at least cost?" In the process of applying these economic principles, remaining knowledge gaps will emerge. Society can then prioritize those gaps, just as they did for brucellosis management activities, by comparing their greatest advantage.

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