Modeling the Epidemiology of Brucellosis in the Greater Yellowstone Area

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Management of brucellosis in the Greater Yellowstone Area (GYA) is difficult because the disease exists in a complex ecological and political system and there is a high degree of uncertainty in our understanding of important processes. Decisions on control of brucellosis are further complicated by the need to consider economic, social, political, and biological consequences of management activities. Because there are so may factors to be considered, quantitative models are likely to be an essential part of any process for evaluating alternative management options. In particular, quantitative models of brucellosis dynamics are required to generate credible estimates for costs and benefits of vaccination, test and slaughter, or other alternative actions. Quantitative models are necessary to realistically estimate both the magnitude and duration of management efforts that target specific outcomes. Most importantly, quantitative models also offer the possibility of devising management strategies that are robust to the multitude of uncertainties in any wildlife population or epidemiological forecast. Using these models, adaptive management strategies can be devised that include recommended responses to future situations that cannot be fully predicted.

Disease management in free-ranging wildlife populations is inherently more complex and difficult than control of disease in domestic or captive animals. With free-ranging wildlife, it is usually difficult and expensive to estimate the size or geographical extent of the target population accurately. It may be impossible to precisely estimate disease prevalence or transmission rate, and the efficacy of vaccines may be unknown or variable. Even when these factors are known, our ability to capture or treat animals will almost always vary between years and locations. Under these conditions - where variability and uncertainty are high - models may be particularly useful because they can help focus resources where they will have the greatest impact. Active adaptive management programs use management actions to probe the system in systematic ways that will simultaneously achieve management goals and improve knowledge of system dynamics. Competing models that acknowledge uncertainly are core components of most adaptive management programs. During the initial phase of model development, we may have little confidence in model predictions, and the most important role of the modeling process is to synthesize knowledge and focus research. As more knowledge becomes available, confidence in model predictions increases and results become more valuable for supporting management decisions.

In this paper, we review past and current efforts to model dynamics of brucellosis in free-ranging bison and elk populations and summarize findings from these efforts. We identify high-priority needs for work to be done and our ongoing efforts to address some of these issues.

Design of Models for Brucellosis

All brucellosis models are simplified abstractions of a highly complex system and they are constructed from assumptions that are more-or-less supported by data. These assumptions can be considered to be testable hypotheses. As Box (1979:201) so astutely observed, "All models are wrong, but some are

useful." In a management context, models are most appropriately evaluated by considering whether decisions made with their use are better than decisions made in their absence.

Disease models range from simple to complex, and from statistical to highly mechanistic. Key decisions in model development are to determine the appropriate level detail required and the mathematical forms of the important relationships. As the number of model parameters increases, there is generally a statistical tradeoff between bias and variance in model results that should be considered (Figure 1). The ability of any model to reproduce observations will be improved by adding additional parameters, but each parameter has an associated error term that contributes to model variance. Models with too few parameters will be biased and they will fail to identify observed effects. Models with too many parameters are unlikely to be biased, but they may identify spurious effects and may suffer from excessive variance. Statistical procedures have been developed to estimate the number of parameters in the most parsimonious model, where parsimony is a tradeoff between bias and variance (Burnham and Anderson, 1998; Hilborn and Mangel, 1997). Parsimony can easily be evaluated in relatively simple population models, but it is extremely difficult to apply similar criteria to complex simulation models. Development of models for simulating the dynamics of brucellosis in elk and bison are constrained by availability of suitable data for estimating model parameters and evaluating model results, particularly for elk.

The best model, in terms of detail, is determined by the intended use of the model, and the level of detail may not be at the intersection of the lines in Figure 1. Simulation models for research may include processes or mechanisms that are poorly understood in order to generate testable hypotheses; an important role of these models is to identify critical experiments or measurements that can distinguish

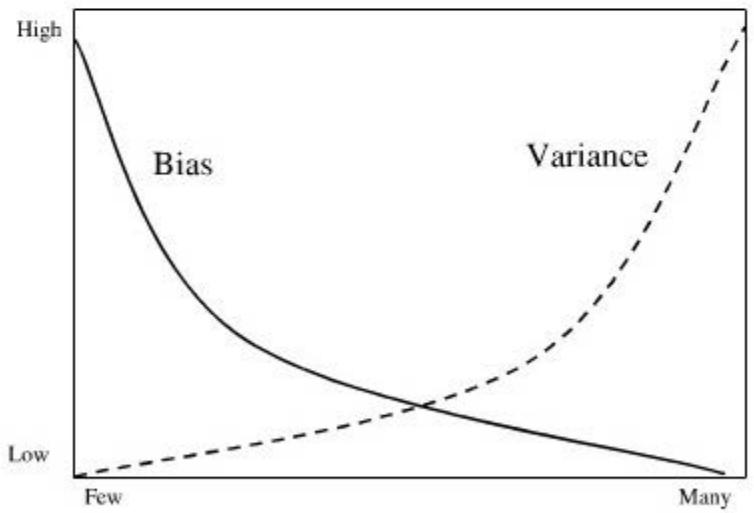

Figure 1. There is a tradeoff between model bias and variance with increasing model detail (i.e., number of parameters). The "ideal" level of detail may not be where the lines cross, and the consequences of over-fitting a model are likely to be less serious than under-fitting (Burnham and Anderson, 1998).

between competing hypotheses. For example, Dobson and Meagher (1996) compared models with contrasting assumptions on disease transmission. Based on observed patterns of seroprevalence, they concluded that a threshold population size existed, below which the disease would not persist. Models that incorporate the most important processes and mechanisms can sometimes predict behaviors that have not previously been observed, including "threshold" conditions where the system responds in a highly non-linear fashion. In wildlife biology, models used to guide management decisions generally require a high degree of confidence. These models may consist of one or a few statistical relationships specific to a narrow set of circumstances, and their ability to forecast population dynamics at a specific location and time is more important than their ability to lend insight to system dynamics, generate understanding, or evaluate novel situations.

Brucellosis Models for Elk and Bison

The first published models for brucellosis in the Greater Yellowstone Area (GYA) were used to evaluate vaccination as a control of brucellosis in Grand Teton bison (Peterson et al., 1991a; 1991b). Peterson et al. (1991a; 1991b) estimated population characteristics from data collected on a private ranch and at the National Bison Range, Montana, and used these data to estimate parameters in their model of the Grand Teton bison herd. The model was age-structured, operated on a yearly time step, and it accurately simulated population dynamics of the Jackson bison herd up to 1989. It successfully reproduced the observed rate of seroprevalence and the increase in seroprevalence over the period since the herd was infected. Peterson et al. (1991b) evaluated vaccination of calves or all females, with vaccine efficacies of 24% to 90%, and with or without a simultaneous test and slaughter program that lasted for 3 years. Simulation results suggested that no existing vaccine could reduce seroprevalence of brucellosis to meet the target rate of <10% by 2010. To achieve the targeted outcome, a vaccine administered to 95% of calves would need an efficacy of about 90%. Because bison (in the model) were continually exposed to infection, Peterson et al. (1991b) did not identify conditions that would eventually lead to eradication of brucellosis.

The model by Peterson et al. (1991a; 1991b) was highly insightful at the time and it emphasized the long-term commitment needed to control brucellosis by vaccination. In addition, it clearly identified some of the key processes that need to be measured to accurately estimate both vertical and horizontal transmission. Peterson et al. (1991a; 1991b) provided an initial indication of the likely effectiveness of vaccination to control brucellosis, but their model used a simplified representation for dynamics of brucellosis transmission. In the model, transmission resulted from a constant contact rate of cows with an infectious source, and through the birth of infected calves from infectious cows. These transmission dynamics were appropriate because there was a constant source of contamination and relatively constant contact with the contamination. However, when transmission of disease results primarily from contact with other individuals, or the probability of contact with infectious material varies over time, these assumptions on transmission will generate misleading results. Infected elk on the National Elk Refuge provide a significant source of contamination to the Grand Teton bison herd, but this situation appears to be unusual and results from Peterson et al. (1991a) have limited application to other bison or elk populations.

In most populations the rate of infection depends on the ratio of infectious to susceptible individuals (reviewed by Anderson and May, 1991). Infection rates are typically highest when the population is first infected, because contacts by an infectious individual are almost certain to be with a susceptible animal. In freely mixing populations, vaccination reduces the rate of infection by two processes. First, vaccinated individuals do not contract the disease. Second, by increasing the proportion of immune

individuals, the probability of contact between an infectious and susceptible individual is reduced. This is the concept of "herd immunity" (Fox et al., 1971), and is the reason that vaccination can confer benefits that extend beyond those individuals that receive vaccination. Increasing the proportion of recovered (and immune) individuals in the population has the same consequence as vaccination – recovered individuals act to reduce the rate of transmission because they cannot be infected, and they increase the probability that contacts by infectious individuals do not result in a new infection.

In contrast to the age-structured model developed by Peterson et al. (1991a), Dobson and Meagher (1996) developed brucellosis models that pooled animals across all age classes into categories of susceptible, infected, and recovered. This highly aggregated SIR (susceptible-infected-recovered) framework for modeling disease has been widely applied to both human and wildlife populations for more than 200 years (McCallum and Scott, 1994). A major advantage of the highly aggregated approach employed by Dobson and Meagher (1996) is that model dynamics can be evaluated analytically and, in theory, critical thresholds can be precisely identified. Critical thresholds include the rate of vaccination necessary to eradicate the disease, or a threshold population size required for disease persistence.

The SIR framework facilitates construction of relatively simple models with clearly defined assumptions on rates of birth, death, and transmission. A key task in developing disease models is to determine the appropriate functional form of disease transmission (McCallum et al., 2001). Dobson and Meagher (1996) examined both density and frequency dependent transmission. With density-dependent transmission, the probability that an animal becomes infected is determined solely by the density of infected animals; this results in the proportion infected increasing with population size. With frequency-dependent transmission, the proportion of infected individuals in the population determines the probability that an animal becomes infected; the result is a constant proportion of the population infected regardless of population size. Although outcomes of assumptions on the mode of transmission are easily stated, estimating transmission rates or the functional form of transmission in disease models is almost always a challenging task.
Dobson and Meagher (1996) evaluated control of brucellosis in Yellowstone's bison by vaccination or by reducing the size of the population. Their analysis suggested that Yellowstone's Northern Range bison herd would have to be maintained at fewer than 200 animals to eradicate brucellosis. They felt this was neither ethically nor practically possible. Dobson and Meagher also concluded that vaccination could, in theory, be used to eradicate brucellosis from the Northern Range bison herd if slightly more than 50% of bison were effectively inoculated. The major differences in predictions between Dobson and Meagher (1996) and Peterson et al. (1991a) can be attributed to assumptions on transmission rates, and these differences emphasize the importance of representing transmission dynamics in an appropriate manner (McCarty, 1999; McCallum et al., 2001).

The Yellowstone National Park Environmental Statement (NPS, 2000) presented results from two models simulating brucellosis in bison. The first model was developed early in the process of preparing the EIS, and was a relatively simple model based primarily on population dynamics. In this model, only susceptible calves could become infected and the seroprevalence of calves was set annually to that of adult cows. While this model helped evaluate the relative consequences of different management options, the lack of realistic dynamics in transmission of brucellosis limited its applicability. Recognizing this, the NPS commissioned the development of a more refined model.

The second, more refined, model in the EIS was referred to as the "enhanced stochastic model" and it followed the general SIR approach used by Dobson and Meagher (1996). However, the stochastic

model incorporated three age classes (calves, sub-adults, and adults) and considered a much wider range of management alternatives (NPS, 2000; Robyn Angliss, personal communication). A brief description of the refined model was published in the YNP Bison EIS (NPS, 2000), as were predictions of the relative consequences of proposed bison management plans. The model explicitly represented females, and overall consequences for both sexes were calculated by doubling the number of females affected (e.g., slaughtered, vaccinated, infected, etc.). Management options examined in the EIS included vaccination, test and slaughter, and various combinations of these actions. Test and slaughter was restricted to bison that were predicted to leave YNP for most modeled scenarios, and migration of bison out of YNP was a function of snow. Snow was represented by snow water equivalent (inches), and yearly snow water equivalent in the model was determined by drawing a random variable from a normal distribution (Robyn Angliss, personal communication).

Results presented in the Yellowstone bison EIS used a standard set of conditions to permit comparison of alternative management plans. These conditions included a constant infection rate of 1 case each 15 years, a calfhood vaccination rate of 75%, and a vaccine efficacy of 70%. Vaccination thus resulted in an effective protection rate of about 50%; all plans included vaccination of calves and one plan included vaccination of all females. Demographic parameters in the model were estimated from observations of Yellowstone's bison herd, and the model was initialized with a population structure representative of YNP. It modeled the northern range and Madison herds as separate populations. Interestingly, most proposed actions that were simulated led to rates of decline in seroprevalence from about 40% to 10-15% in 18 years. There were, however, large differences in the number of bison slaughtered or quarantined between different management plans.

A comparison of results from the NPS refined (stochastic) model and the deterministic model shows the need to represent host-disease interactions as a dynamic (rather than static) system. In contrast to the deterministic model, the stochastic model incorporated equations that accounted for effects of changes in the ratio of susceptible to infectious individuals (i.e., herd immunity). As a result, the stochastic model predicted that vaccination would be about 50% more effective over a 10-year period than did the deterministic model (NPS, 2000:393).

The models described above focused on vaccination, test and slaughter, or population reductions, but they contained insufficient detail for evaluating the full range of proposed and existing management alternatives, which include reducing the time on winter feedgrounds or using selective contraceptives. We felt there was a need to build a model that incorporated our increasing understanding of the dynamics of *Brucella abortus* infections, and that could be used to evaluate alternative hypotheses about controversial model functions and parameters.

We therefore constructed an individual-based model with a highly detailed representation of brucellosis dynamics (Gross et al., 1998; Figure 2). Individual-based models are increasingly used to simulate disease because traditional approaches break down when individuals with stochastic behavior are considered (Durrett and Levin, 1994; Dobson and Grenfell, 1995; Keeling and Grenfell, 2000). In addition, complex behaviors are more easily represented by individual-based models, and they can easily be adapted to represent genetic processes (Gross, 2000) such as resistance to disease. Our model (Gross et al., 1998) followed the sex, age, and disease status of each individual in the population, and it operated on a variable time step. Most population processes occurred once per year, but disease dynamics and reproduction were simulated with a weekly time step. By using an individual-based approach, model parameters have a clear biological interpretation, the model is able to use much of the existing

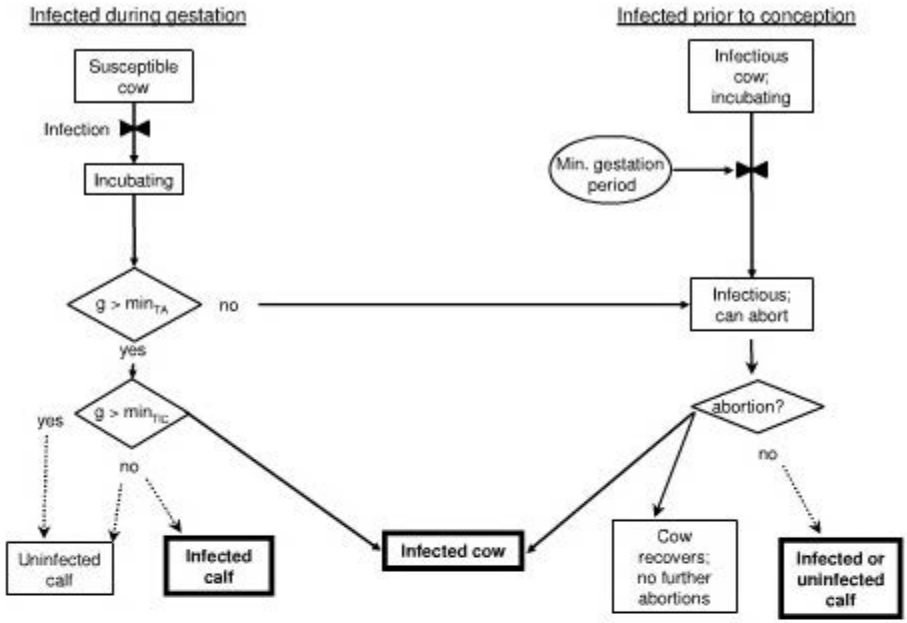

Figure 2. Simplified diagram of the brucellosis submodel for pregnant cows in a detailed model of brucellosis (Gross et al., 1998). The submodel accounted different incubation periods for animals infected during pregnancy (left side) or infected prior to conception (right column). The submodel operated on a weekly time step; solid lines represent cows, dotted lines calves. g = week of gestation, min_{TA} = minimum time to abortion, min_{TIC} = minimum period of incubation to infect a fetus.

data on brucellosis in elk and bison, and it can simulate a broader range of current and proposed management efforts. The short time step during the period of active disease transmission (late gestation and birth) provided a better representation of processes that occur on winter feedgrounds and it allows examination of hypotheses about the timing of infections. Models with a similar structure have been used to simulate other wildlife diseases (Gross et al., 2000; Gross and Miller, 2001).

This brucellosis model (Gross et al., 1998) synthesized information from research on brucellosis in cattle, elk, and bison. The disease submodel included parameters that explicitly accounted for proliferation of *Brucella* during gestation, and it was thus able to address the temporal dynamics of incubation and infection within a single season. The model accounted for changes in disease dynamics on and off feedgrounds by using two transmission rates – a high rate for periods when animals attended a feedground, and a low rate the rest of the time. A short (weekly) time step was necessary to represent this level of detail. Disease transmission was frequency-dependent (McCarty and Miller, 1998) and parameters were adjusted to reflect the social structures typical of elk and bison. Unlike other models, the individual-based model included parameters that permitted age and sex-specific harvest scenarios. Harvest is important because the age and sex structure of the population affects transmission rates, population growth rate, and the number (and therefore cost) of animals handled or treated. Like other

disease models, Gross et al. (1998) estimated most parameters from previous studies, while transmission rates were calibrated to observed rates of seroprevalence.

The dynamic representation of disease transmissions and a detailed model structure permitted Gross et al. (1998) to project age-specific rates of seroprevalence and to project the timing, on a weekly basis, of new infections. Significant refinements to the 1998 model included changes to account for age-specific changes in the probability of infection (Grenfell and Anderson, 1985), capabilities for simulating spatial structure, and increasing the range and complexity of management options that can be simulated. By including a decline in the probability of infection with age, results from the model closely matched observed patterns of age-specific seroprevalence in bison (Figure 3). The close fit of the model to observations provided confidence that the model included the most important processes that determined brucellosis dynamics, but it did not prove the model was correct. Some processes, such as disease transmission on elk feedgrounds, are still poorly defined and forecasts from the model should be treated with caution. This model will be refined as new data become available.

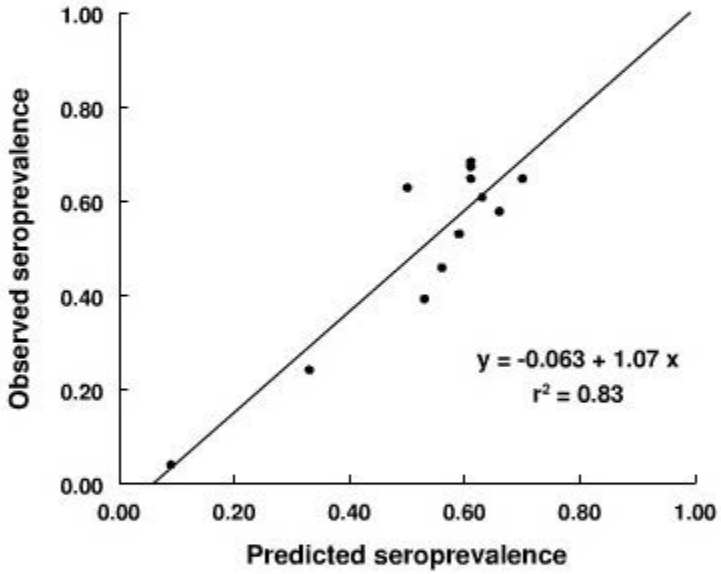

Figure 3. Relationship between age-specific seroprevalence of bison from Yellowstone National Park and seroprevalence predicted by a detailed model of brucellosis dynamics (Gross et al. 1998). Observations from bison that left Yellowstone National Park during winter (Pac and Frey, 1991; James, personal communication). Observations of bison with an estimated age of 8 or older were pooled.

What Do the Models Tell Us about Control of Brucellosis?

Although some aspects of brucellosis ecology remain controversial, we can identify general results from simulations that are robust to changes in model assumptions and to variation in model parameters. To evaluate control of brucellosis in Yellowstone's bison, we used parameter values representative of YNP bison with a refined model based on Gross et al. (1998). These simulations showed:

- Vaccination and/or test and slaughter limited to bison outside YNP boundaries are ineffective or detrimental (see below).
- Population control reduces exposure risk, but does little for disease reduction or eradication.
- Vaccination alone could reduce exposure risk and avoid killing bison, but eradication of brucellosis is slow and difficult. To eradicate brucellosis, 40-50% of bison will need to be effectively vaccinated for a period of several decades; lesser levels of vaccination can reduce risk (Gross et al., 1998; Dobson and Meagher, 1996).
- Test and slaughter are effective only if a large proportion of the population can be consistently captured and tested. If too few animals are tested, the result can be a sustained reduction in population size.
- Combining test and slaughter with vaccination is synergistic.

Model results provided several counterintuitive insights that are broadly applicable to management of brucellosis. First, test and slaughter of a relatively small proportion of the population (say, 10–25%) is ineffective. This strategy will not, by itself, lead to eradication of brucellosis, but it will result in the slaughter of a large number of animals and lead to major reductions population size (Figure 4). An unforseen outcome is that, over time, most seropositive animals in the population will be individuals infected within the previous year or two, and they therefore belong to the class of highly infectious animals most likely to shed *B. abortus* at birth or abortion. While the proportion of seropositive animals

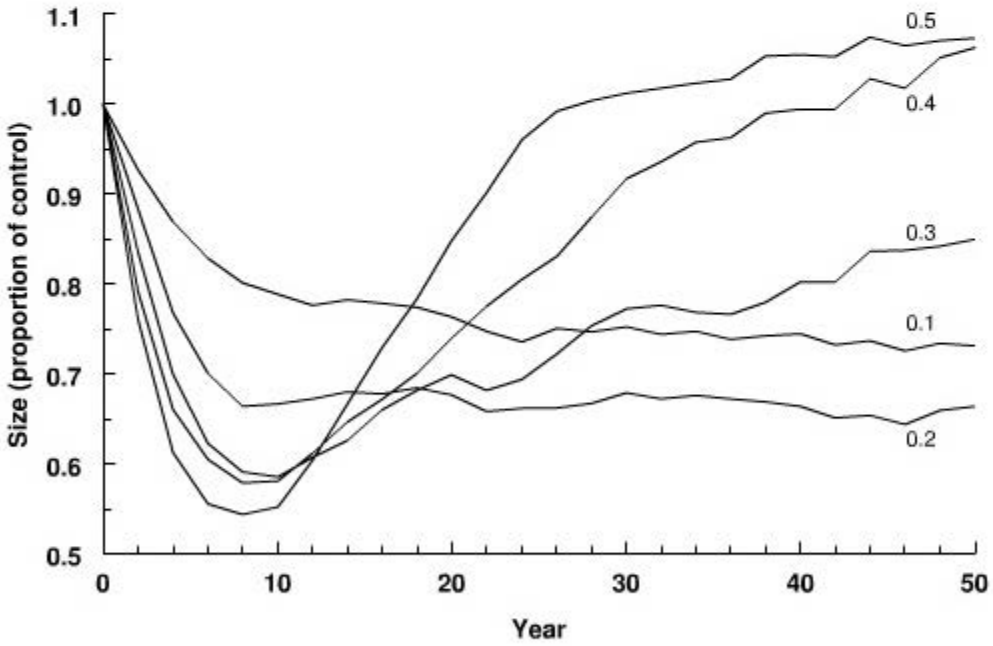

Figure 4. Effect of simulated test and slaughter on a bison herd similar to the Yellowstone bison. Numbers near lines are the proportion of the population subjected to test and slaughter each year. Test rates of 10-25% result in long-term depression of population size compared to a population not subjected to test and slaughter. Model parameters were adjusted so the population stabilized at about 4500 animals.

in the population will decline, the proportion of highly infectious animals in the population can actually rise. Furthermore, an infectious contact is more likely to be with a susceptible animal because test and slaughter programs remove *all* seropositive animals – infectious *and* recovered animals. Transmission efficiency is therefore high relative to a population not subject to test and slaughter and the rate of increase in the number of infected animals is very high.

A second unforseen result was the synergistic effect of a strategy than combines test and slaughter and vaccination. When combined, a much smaller proportion of the population must be "treated" than when either treatment is used alone. Simulations suggest that, in theory, eradication is possible by treating (testing and then either slaughtering or vaccinating, depending on serology results) as few as 15% of the population (Figure 5). To achieve a similar result using either treatment alone, the proportion of animals handled would need to be more than doubled. This result affirms the utility of simulation models – it would be virtually impossible to identify such a synergistic result without a quantitative model.

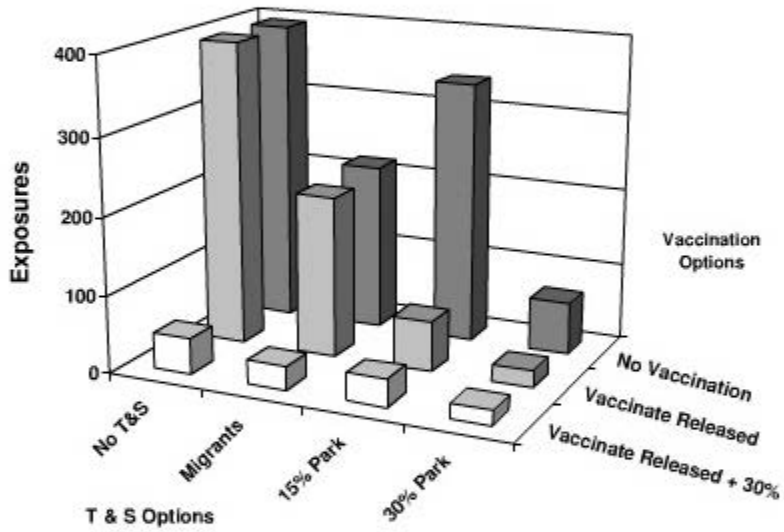

Figure 5. Projected effect of different vaccination and test and slaughter options on exposures to infectious bison leaving Yellowstone National Park. At intermediate levels of treatment, a combination of the two treatments is much more effective than either one by itself.

Uncertain Parameters and Processes

An area of uncertainty in our understanding of brucellosis epizootiology is the duration over which infected animals actively shed *Brucella abortus*. Some believe that most elk and bison become non-infective within several years after their first abortion, while others believe that most infectious animals remain actively infectious for life. Virtually all data pertaining to this issue are from cattle, and even for cattle relatively few data are suitable for quantitative analysis (Fitch et al., 1930; Manthei and Carter, 1950; Lambert et al., 1960; Philippon et al., 1970; Plommet et al., 1973). Evaluation of these data is complicated because experimental protocols differed between studies, sample sizes were small, few studies followed animals for sufficiently long periods, and, perhaps most importantly, it is unclear

whether responses of elk and bison are similar to those of cattle. Despite the methodological difficulties, studies consistently show that in cattle rates of abortion and shedding rapidly decline in the years following an abortion, and few animals shed *Brucella* by the third year after their first abortion (Schroeder, 1922; Fitch et al., 1930; Manthei and Carter, 1950; Washko et al, 1952; Nelson et al., 1966; Pleuderleith, 1970; Plommet et al., 1971, 1973). These results are consistent with the pattern of age-specific results of culture tests for the presence of *Brucella abortus* in bison. In YNP bison, the proportion of seropositive bison that are culture-positive declines sharply in animals less than 5–6 years old (Pac and Frey, 1991; Owen James, personal communication; Rhyan and Philo, personal communication).

To estimate the number of infectious bison, we assumed that culture-negative animals do not shed *Brucella abortus*. We used age-specific rates of seroprevalence and culture results to mathematically estimate the annual rate of change in the proportion of seropositive bison that were culture positive. Our estimate accounted for mortality, but it did not include new infections and it thus underestimates the transition rate of animals from the infectious to recovered pool. Using data for 3–8-year-old bison (those ages with a sample size of >15 animals), this procedure led to an estimate that about 60% of bison that are both seropositive and culture positive would be culture-negative the following year. Our analysis does not indicate that animals "recover" for life; it simply accounts for observed patterns of sero- and culture-positive results. In the model, we assume that once animals are culture-negative, they remain in the resistant and non-infectious pool. Simulation results are relatively insensitive to this assumption except when there are few seropositive animals in the population. By the time this situation exists in wild populations, we should have better data for evaluating this assumption.

There is widespread agreement that *Brucella abortus* is shed almost exclusively during the process of reproduction – either with an aborted fetus, at the birth of a calf, or via vaginal exudates (Cheville et al., 1998). The role of lactation in brucellosis transmission is unknown. Similarly, most agree that the likelihood of abortion is much greater during the first pregnancy after infection, and the likelihood of abortion rapidly declines in subsequent years. However, we know little about the time of abortion, or about rates of vertical transmission in wildlife. The study of the Grand Teton bison herd (Cain et al., 2001) should generate important information on these aspects of disease dynamics.

An important outcome of constructing and using simulation models is to identify functions and parameters that have a large influence on model results and those that have little effect (i.e., parameters to which the model is "sensitive" or "insensitive"). Simulations showed that brucellosis dynamics are relatively insensitive to parameters that determine population size or growth rates. The growth rate or size of a population has little effect on disease dynamics, but these variables will influence the potential cost of treatment. In rapidly growing populations, the number of animals that will need to be treated (vaccinated, tested, slaughtered, or otherwise treated) will be greater than in populations with low growth rates. Population processes can thus affect decisions on the most cost-effective approach for controlling a disease.

Evaluating Management Actions

For elk, most management of brucellosis will focus on management of feedgrounds because the disease appears to persist only in herds that are seasonally concentrated at high densities. To simulate fed populations, we therefore need to understand how winter feeding influences disease dynamics. Characteristics of artificially fed populations that may influence brucellosis dynamics are the:

- proportion of the herd that attends a winter feedground
- total number of animals in the fed group

- duration of time spent on a feedground
- average date that the population leaves the feedground

Initial simulations of elk on winter feedgrounds (Gross et al., 1998) suggested that it might be possible to reduce brucellosis infection by encouraging elk to leave feedgrounds earlier. However, confidence in these early predictions is limited because of the lack of data for estimating age-specific infection rates in elk, and estimates of infection rates on winter feedgrounds are highly variable. We are attempting to refine our understanding of brucellosis dynamics in herds of winter-fed elk by evaluating data from feedgrounds, herd population estimates, and harvest records. Validation of serology tests that consistently distinguish vaccinated elk from other seropositive animals will greatly contribute to the value of data from vaccinated herds.

Addressing Uncertainty through Adaptive Management

Although consequences of numerous management alternatives have been simulated, these analyses fall short of offering a coherent adaptive management program for brucellosis in the GYA. Adaptive management has become an abused term that means many things to many people. Here, we follow the formal definition is most typically used in the technical literature (Walters, 1986). In this context, adaptive management is the recognition of uncertainty and the application of techniques for accommodating that uncertainty into robust management strategies. These management strategies include monitoring changes in the managed system, flexible management that responds to observed changes, and intelligently incorporating the knowledge of system behavior gained through these observations into future decisions. Using management actions to explicitly seek additional knowledge about the managed system, rather than incorporating knowledge gain as an unintended byproduct, is known as active adaptive management (Walters and Holling, 1990). Adaptive management addresses uncertainty arising from diverse sources. These uncertainties can be classified as:

- environmental stochasticity – fluctuations in natural processes over time;
- control error – the inability for management goals to be implemented precisely;
- observation error – the imprecision of measuring the critical variables that inform the management decision;
- parameter uncertainty – the imperfect estimates of parameters critical to predicting the consequences of management actions; and,
- model structural uncertainty – the imperfect understanding of the factors and functional relationships that are required to predict the effects of alternative management actions.

The process of adaptive management is sometimes construed to include the process of seeking compromise among diverse stakeholder groups with disparate goals, or changing management in response to changing goals. We do not share this interpretation of the term adaptive management. The more narrowly focused approach to adaptive management *begins* with a well-defined goal that incorporates the tradeoffs needed to satisfy different social, economic, environmental, and political objectives. Once the goals can be explicitly stated (typically as a quantitative metric of some sort, supplemented by quantitative constraints on certain variables) then the process of identifying adaptive management strategies that achieve these goals despite the many uncertainties can begin.

It can be important to develop quantitative models early in the process of seeking solutions to a complex problem. Even when a quantitative goal for a wildlife management program is explicitly stated, the management actions proposed to attain that goal are frequently developed by management agencies in close consultation with their stakeholders. Providing evaluations of proposed management actions at

many points in this process will help ensure that a consensus-based management program has some chance of also meeting the short- and long-term quantitative goals of the program.

Models, such as those we described here, are often considered central to the adaptive management approach. Models can be used to facilitate adaptive management by integrating existing information on the managed system and by evaluating the consequences of each of the various types of uncertainty listed above. Alternative management policies can be simulated, not only to obtain prediction of effects, but also to examine the robustness of these predictions to each type of uncertainty. More significantly, however, mathematical techniques exist to derive management strategies that optimize the manager's objective given the uncertainty and changing conditions (Lubow, 1997). Consequently, we can identify new combinations of management actions, or varying levels of these actions over time, that improve the result relative to informally generated management alternatives. These management strategies are dynamic and can respond to observed conditions, which are certain to change over time.

Models of host-brucellosis dynamics in the GYA are now reaching a level of sophistication that permits us to apply adaptive management analysis techniques. This should lead to recommendations for refining existing management programs and initiating others. In the case of brucellosis, the optimal strategy to reduce seroprevalence will probably differ from the strategy to eradicate the disease once its prevalence has been greatly reduced. Adaptive management solutions seek to make the best possible use of existing knowledge, accommodate the feedback offered by ongoing monitoring of responses to management actions, and even recommend actions that intentionally probe the system to produce informative responses. Adaptive management provides a formal strategy founded on the principle of "learning by doing" and it provides for the optimal tradeoff between actions that improve future decisions versus the need for short-term results.

Conclusions

A wide variety of models now exist for simulating brucellosis dynamics in the Greater Yellowstone Area. Model structure ranges from highly aggregated SIR-type models to a highly detailed individual-based model. These models can be used to evaluate a range of management options including vaccination, test and slaughter, feedground management, or combinations of these actions. Model predictions for the effects of test and slaughter and vaccination of bison are generally consistent, but only the more detailed, individual-based model is suitably designed for evaluating specific management plans for elk, particularly those that involve a combination of actions that can include the simultaneous use of selective harvest, vaccination, and test and slaughter. Models for elk are more limited by the availability of data than are those for bison, and we are less confident of our ability to forecast brucellosis dynamics in elk herds that attend winter feedgrounds. In particular, age-specific data from elk on seroprevalence and tissue culture for *Brucella* would vastly improve our ability to evaluate both dynamics and control of brucellosis in that species. Our ability to manage brucellosis is compromised by uncertainty in our understanding of host-disease dynamics, variable environmental conditions, and our inability to accurately monitor and implement management actions. Active adaptive management provides a coherent strategy for addressing uncertainty by identifying the optimal tradeoff between actions that increase knowledge to improve long-term management and the need to achieve short-term goals. Adaptive management techniques are usually based on quantitative models, and model development and refinement is now at a stage that permits us to apply adaptive management techniques.

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