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# Effects of Low-Density Feeding on Elk–Fetus Contact Rates on Wyoming Feedgrounds

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**ABSTRACT** High seroprevalance for *Brucella abortus* among elk on Wyoming feedgrounds suggests that supplemental feeding may influence parasite transmission and disease dynamics by altering the rate at which elk contact infectious materials in their environment. We used proximity loggers and video cameras to estimate rates of elk-to-fetus contact (the primary source of brucellosis transmission) during winter supplemental feeding. We compared contact rates during high-density and low-density (LD) feeding treatments that provided the same total amount of food distributed over different areas. Low-density feeding led to >70% reductions in total number of contacts and number of individuals contacting a fetus. Proximity loggers and video cameras provided similar estimates of elk–fetus contact rates. Elk contacted fetuses and random control points equally, suggesting that elk were not attracted to fetuses but encountered them incidentally while feeding. The modeled relationship between contact rate and disease prevalence is nonlinear and LD feeding may result in large reductions in brucellosis prevalence, but this depends on the amount of transmission that occurs on and off feedgrounds. 

**KEY WORDS** brucellosis, *Cervus elaphus*, contacts, density, disease transmission, elk, feedgrounds, individual heterogeneity, proximity logger, Wyoming.

The rate at which individuals contact other individuals or infectious materials in their environment has a strong effect on the transmission and persistence of diseases. Contact rate is directly related to disease transmission rate (whereby transmission rate is equal to contact rate × probability of transmission given contact) and may often be correlated with population density (McCallum et al. 2001). There are strong theoretical underpinnings for an effect of animal density on disease transmission (Anderson and May 1979, McCallum et al. 2001) and empirical studies of mammals have positively linked population density to disease prevalence (Cross et al. 2010) and parasite abundance (Arneberg et al. 1998), although results from meta-analyses have been mixed (Côté and Poulin 1995, Ezenwa 2004).

One way that humans influence wildlife population density and contact rates is through supplemental feeding, which may increase disease transmission by aggregating animals at high densities around concentrated food sources. Supplemental feeding has been associated with increased disease prevalence in elk (Thorne and Herriges 1992, Scurlock and Edwards 2010) and white-tailed deer (Schmitt et al. 1997, Miller et al. 2003, Rudolph et al. 2006). Wyoming's elk feedgrounds comprise the largest and best-known supplemental feeding program in the United States. Since 1910, elk in western Wyoming have been supplementally fed during winters to compensate for loss of native winter range and to minimize conflicts on agricultural lands (Smith 2001). Today, approximately 22,000 elk are fed each year on 21 state-maintained feedgrounds and the National Elk Refuge (Wyoming Game and Fish Department [WGFD] 2010).

Currently, the most problematic disease on these feedgrounds is brucellosis, a chronic bacterial disease caused by *Brucella abortus*. Within the United States, *B. abortus* in wildlife is limited to the Greater Yellowstone Ecosystem (GYE), where it was likely introduced to bison from imported European cattle prior to 1917 (Meagher and Meyer 1994) and subsequently spread to elk by 1930 (Murie 1951). The primary symptom of brucellosis in elk is abortion during the first pregnancy following infection and occasionally during subsequent pregnancies (Thorne et al. 1978). The disease is not considered a major mortality factor in elk herds (Cheville et al. 1998) but may reduce herd reproductive potential by as much as 12% (Thorne et al. 1991).

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Brucellosis is typically transmitted among elk via direct contact with infectious abortion materials including fetuses, placentas, and fetal fluids (Thorne et al. 1978). Vertical transmission from mother to calf through milk has been reported in cattle (Cheville et al. 1998) and aerosol transmission may also be possible (Nicoletti 1980), but both are believed to be uncommon routes of transmission among elk. Contacts between elk and naturally aborted fetuses on feedgrounds are rarely observed, but elk have been seen investigating fetuses placed on feedgrounds by researchers (Cook et al. 2004, Maichak et al. 2009), and supplemental feeding is believed to play a key role in *B. abortus* transmission. Historically, seroprevalence has averaged approximately 22% for feedground elk and 2–4% for unfed elk in the GYE (Aune et al. 2002, Etter and Drew 2006, Scurlock and Edwards 2010), although recently seroprevalence has been increasing in some areas distant from feedgrounds (Cross et al. 2010).

Because *B. abortus* can infect humans through contaminated dairy products, a United States Department of Agriculture (USDA) program to eradicate the disease from cattle herds was instituted in 1934, and by 1998 an estimated $3.5 billion dollars had been spent on eradication efforts (Cheville et al. 1998). The USDA declared all cattle herds in the United States brucellosis-free in 2008, but infections have since been reported in Montana, Wyoming, and Idaho. Cattle infections have economic consequences for state cattle industries because of increased testing requirements, stricter regulations on in-state cattle movement, and refusal by some states to allow importation of cattle from infected states (Healey et al. 1997). Genetic analysis of *B. abortus* strains from elk, bison, and cattle indicates that elk are the most probable source of some of the recent cattle infections (Beja-Pereira et al. 2009), increasing the pressure on state and federal wildlife management agencies to control brucellosis in elk.

The WGFD has sought to reduce intraspecific *B. abortus* transmission on feedgrounds through management actions, such as increasing forage production in surrounding habitat, shortening feeding seasons, feeding on fresh snow, protecting scavengers, and most recently by reducing feeding density (Cross et al. 2007, WGFD 2008). Feed has historically been distributed on elk feedgrounds along continuous, high-density (HD) feedlines (Fig. 1A), but in 2008 WGFD began a low-density (LD) feeding technique at 5 feedgrounds (WGFD 2008). Low-density feeding involves distributing feed in small, discrete units over a larger area, encouraging elk to disperse evenly across the feedground (Fig. 1B), and reducing animal densities along feedlines (Forristal et al. 2012). If fetuses are a strong attractant to elk, then reducing feeding density may not prevent elk–fetus

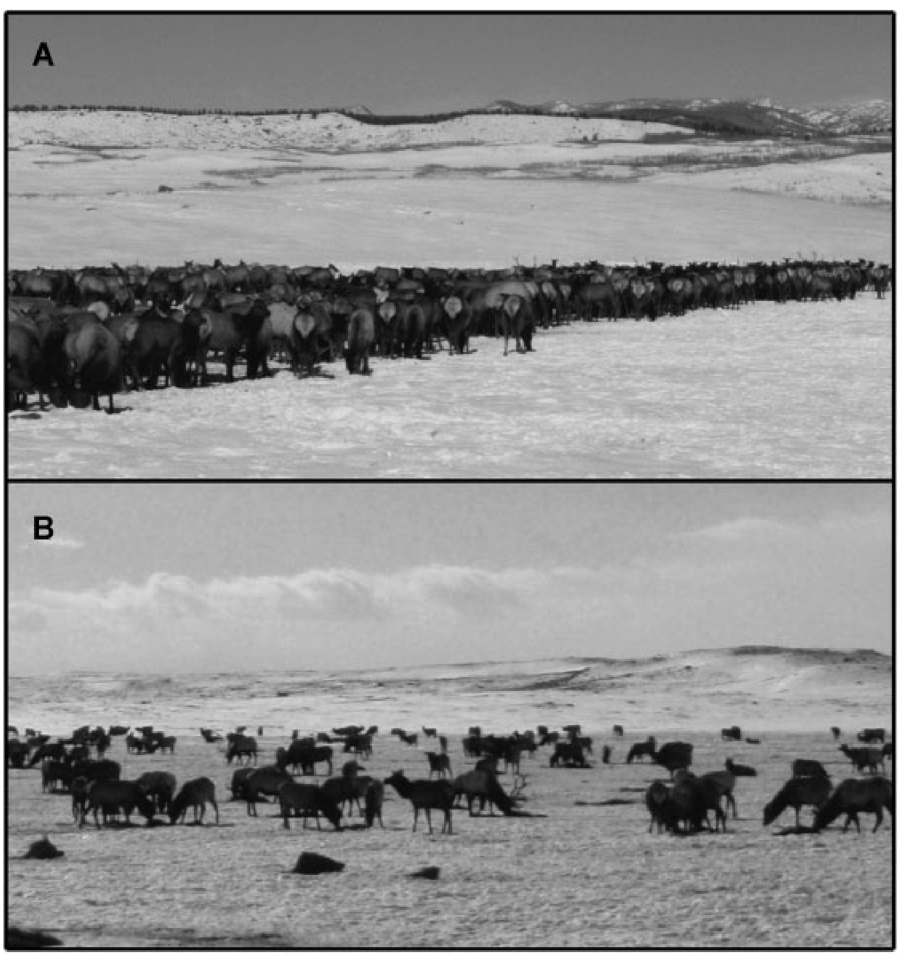


**Figure 1.** Typical elk distribution patterns on Wyoming feedgrounds during (A) high-density feeding and (B) low-density feeding. Photo credits: Jared Rogerson.

contacts, but if elk are not attracted to fetuses, then reducing density may reduce contacts both with other elk and with fetuses.

We used 2 technologies to measure contact rates between elk and fetuses in this study: proximity loggers and video cameras. Proximity loggers transmit and receive unique ultrahigh frequency (UHF) signals and record the date, time, duration, and individual logger identities when they are within a user-defined contact distance of each other (Prange et al. 2006). This technology has tremendous potential in wildlife disease ecology studies because it provides continuous, individual-level contact data without requiring direct observation by researchers (e.g., Hamede et al. 2009, Marsh et al. 2010). Individual heterogeneity in contact rate is an influential determinant of disease dynamics (Dwyer et al. 1997, Lloyd-Smith et al. 2005, Bolzoni et al. 2007), but is commonly ignored in wildlife disease management, potentially leading to poor disease models and ineffective control strategies. Brucellosis management stands to benefit from any information on individual heterogeneity in infection risk, one component of which is elk–fetus contact rate, and we use individual-level proximity logger data to investigate this heterogeneity. Video cameras do not provide individual-level contact data unless animals are uniquely marked in a way that makes them identifiable in video footage, but they have the advantage of allowing the researcher to assess the quality of contacts (i.e., what type of interaction has occurred). For instance, proximity logger data can only reveal that an elk was within a specified distance of a fetus, but camera data can reveal the behavioral response of an elk to a fetus.

The objectives of our study were: 1) to evaluate the effectiveness of LD feeding in reducing elk–fetus contact rates relative to traditional HD feeding practices, 2) to determine the extent to which elk–fetus contact rates vary among individuals on feedgrounds, 3) to model potential changes in *Brucella* seroprevalence if LD feeding were implemented throughout the feedground system, and 4) to compare 2 alternative technologies used to measure elk–fetus contact rates.

## STUDY AREA

We conducted our study at the WGFD-administered Soda Lake feedground (SLF) near Pinedale, Wyoming in the Wind River Range foothills (42°95′N, 109°81′W, elevation 2,314 m). The regional climate was characterized by long, cold winters and brief, warm summers with most precipitation falling as winter snow. Regional vegetation was composed of sagebrush (*Artemesia* spp.) communities at lower elevations and mixed conifer (*Pinus* spp., *Abies lasiocarpa*, *Picea engelmannii*) forests at higher elevations. The feedground area was dominated by herbaceous species with limited shrubs. Depending on winter severity, 500–900 elk are fed at SLF between December and April. The elk population at SLF varied between 553 and 653 elk during our study period in late February and early March 2009.

## METHODS

We used proximity loggers (Sirtrack Ltd., Havelock North, New Zealand) and digital video cameras (Model X100, Sandpiper Technologies Inc., Manteca, CA) to record cow elk contacts with fetuses placed along feedlines; we defined a contact as an elk approaching within 2 m of a fetus. In a disease context, contact rate is often multiplied by the probability of transmission given contact, which in our case was an unknown function of distance. Smaller contact distances may result in relatively few contacts to analyze, whereas larger distances may be less relevant for disease transmission. We chose a 2-m contact distance to reflect that brucellosis transmission requires relatively close contact with infectious materials, while still recording a sufficient number of contacts for analysis.

We calibrated proximity loggers to recorded contacts within 2 m in the field using a modified version of the laboratory calibration procedure described by Prange et al. (2006); the receiving range of each logger was tested using 5 other loggers to transmit UHF signals, and we adjusted power settings on the receiving logger until its mean receiving range in the laboratory setting was as close to 3.5 m as possible. Previous research has shown that the receiving range of loggers is reduced by approximately half when attached to animals compared to laboratory conditions (Böhm et al. 2009). We did not have captive elk to test this directly, but field tests conducted with horses revealed that a 3.5-m laboratory receiving range was approximately equivalent to a 2-m receiving range in the field.

In January and February 2009, we captured 30 cow elk ($\geq$1.5 yr old) at SLF and fitted them with proximity loggers in the form of collars. We excluded bulls from the study because they likely do not contribute to brucellosis transmission (Thorne et al. 1978). We captured elk via chemical immobilization using 1.5-ml darts loaded with carfentanil (0.01 mg/kg) and xylazine (0.1 mg/kg; Kreeger et al. 2002). We performed captures in accordance with approved Montana State University Animal Care and Use Protocol (no. 2010-02). We obtained 14 *Brucella* culture-negative fetuses, placentas, and fetal fluids (hereafter collectively termed fetuses) from elk killed at Muddy Creek and Fall Creek feedgrounds in late January and early March 2008 during a concurrent WGFD project (Scurlock et al. 2010). We processed and cultured fetuses as described by Maichak et al. (2009) and Alton et al. (1988).

We conducted experimental feeding trials during 14 days at SLF in late February and early March 2009. We fed elk once per day from a horse-drawn sled using either the HD or LD feeding technique, with a Global Positioning System (GPS) unit attached to the sled to record its path during the distribution of feed. We structured the feeding schedule as 7 pairs of back-to-back HD and LD feeding days, and we randomly assigned the order of feeding techniques within each pair of days. This design allowed us to minimize any temporal effects on contact rate (because we made comparisons between HD and LD feeding over short time intervals of 2 days) and to control for changes in the amount of feed distributed daily during the study (because amount of feed was constant within each pair). We used daily ground counts to estimate the number of elk present during feeding each day, and we calculated the feeding area for each day by applying a 2-m buffer to the GPS track from the feeding sled (since elk generally remained within 2 m of the feedline during feeding). We then calculated daily feeding density as number of elk per hectare of feeding area.

Each day, we placed a single fetus at a random point along the feedline with a proximity logger (hereafter termed the fetus logger) buried in snow 15 cm below the fetus. We buried another proximity logger without an accompanying fetus (hereafter termed the control logger) at a second random point along the feedline to determine a baseline rate of contact against which to measure the attractiveness of the fetus to elk. We placed loggers directly along the path of the sled because contacts with fetuses >2 m from a feedline occur very rarely (Maichak et al. 2009). We set up digital video cameras with infrared lights approximately 10 m from fetus and control loggers to visually record contact events. Cameras allowed us to count elk–fetus contacts for feedground cow elk without proximity loggers and to distinguish between incidental contacts (e.g., elk feeding next to a fetus) and investigations (sniffing, licking, or other physical contact with the fetus). We conditioned elk to the presence of cameras for 2 weeks prior to the experiment.

We downloaded proximity data from the fetus and control loggers at the end of the study period. Prior to analysis, we removed all 1-s duration contacts from the dataset as recommended by Prange et al. (2006) to avoid counting interactions outside the 2-m continuous receiving range of the proximity loggers. We assigned contacts to feeding days commencing at the time of logger placement during feed distribution and ending 18 hours later; this was necessary because the time period between consecutive feedings varied from day to day, and the shortest of these periods was 18 hours. Censoring all contacts recorded >18 hours after logger placement allowed us to standardize by the shortest period between consecutive feedings and had negligible influence on our analysis because approximately 90% of contacts occurred within 18 hours of logger placement.

We reviewed video camera footage and recorded for each feeding day the number of times a cow elk approached within 2 m of the fetus or control logger, and how many times a cow elk investigated the fetus. Unlike proximity loggers, which captured only those contacts made by a sample of 30 individuals outfitted with loggers, video cameras captured contacts made by all elk on the feedground, with or without loggers. We did not record contacts made by bulls or calves. Because elk were not individually identifiable in camera footage, we could determine the total number of contact events but not the number of unique individuals making contacts. We also did not record durations of contacts for elk in camera footage because of time limitations. Thus, only data on total numbers of contacts were available from camera footage for analysis.

We analyzed proximity logger and camera data independently, but used the same statistical methods for the 2 datasets. For each feeding day, we calculated contact rates (i.e., the frequency or duration of contacts) for fetus contacts and control contacts using 3 metrics: 1) total contacts—the number of contact events recorded; 2) unique contacts—the number of individuals that contacted the logger at least once; and 3) mean duration—the mean duration per contact (i.e., the sum of the durations of all contacts made by all individuals on a feeding day divided by the number of such contacts). Note that we did not calculate unique contacts and mean duration for camera data because we did not collect these data. To analyze the effect of LD feeding on elk–fetus contact rates, we treated density as a categorical variable (i.e., HD or LD) and determined the percent reduction in contact rate during LD feeding relative to HD feeding, calculated as

$$[(\text{HD contact rate} - \text{LD contact rate})/\text{HD contact rate}] \times 100$$

for each feeding day pair using each metric. Similarly, we compared the rate of contact with the fetus logger and control logger within each feeding day for each contact metric to determine relative attractiveness of fetuses. We collapsed contact data among all individuals for each feeding day, leading to conservative estimates of the significance of the treatment effect. We used nonparametric, 1-tailed Wilcoxon signed-rank tests (Zar 1999) to determine if mean percent reductions from HD to LD feeding were greater than 0, and 2-tailed Wilcoxon tests to determine if the ratios of fetus contacts to control contacts were different than 1. To explore individual heterogeneity in elk–fetus contact rate amongst cow elk on SLF, we examined the distribution of total contacts for our 30 proximity logger-equipped elk, and we compared the variation in daily fetus contact rates, both within individuals and between individuals. We conducted all analyses in R version 2.7.2 (R Development Core Team 2008).

## RESULTS

The mean daily feeding density was 2,055 $\pm$ 325 (mean $\pm$ SD) elk/ha on HD feeding days and 343 $\pm$ 90 elk/ha on LD feeding days, a reduction of 83%. Proximity loggers recorded 168 fetus contacts and 142 control contacts (after removing 96 <1-sec contacts and 30 contacts occurring outside the feeding day). Camera footage was less complete than proximity logger data because of battery failures, elk tampering with cables and lighting, and heavy snowfall obscuring the camera lens. Complete camera footage was available for 8 of 14 feeding days for fetus contacts and 6 of 14 feeding days for control contacts. We limited our analysis of camera data to portions of feeding days for which footage was available for both days in a pair (when comparing contact rates on HD and LD days) or for both loggers simultaneously (when comparing fetus and control contact rates), totaling 273 hours and 200 hours of fetus and control footage, respectively.

Proximity logger data showed mixed evidence of individual heterogeneity in elk–fetus contact rate. Twenty-nine of 30 elk made at least 1 fetus contact during the 14-day study. Individuals made between 0 and 17 contacts with fetuses during 7 days of HD feeding (mean contact rate: 0.74

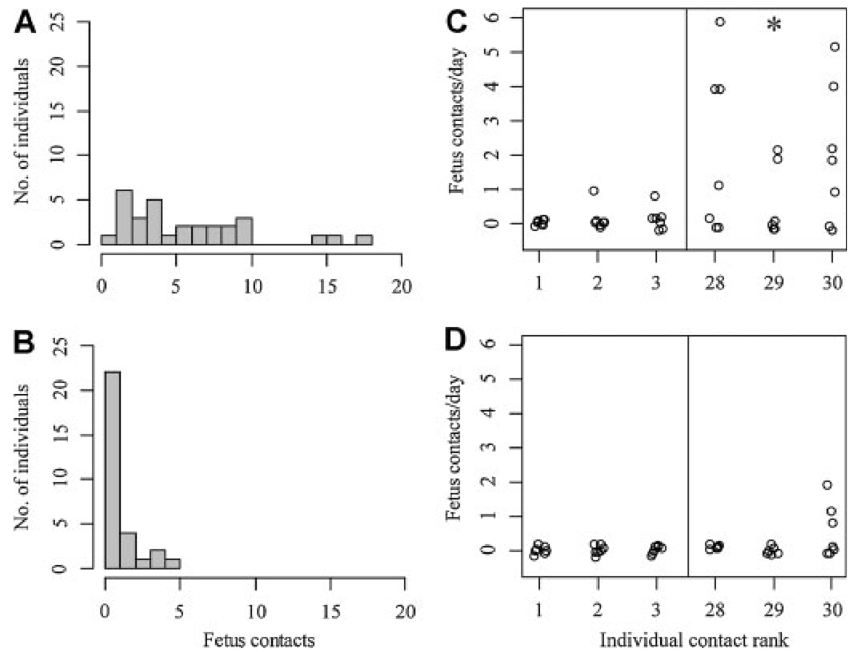


**Figure 2.** Individual heterogeneity in elk–fetus contact rates on Soda Lake feedground, Wyoming, in 2009 during high-density (HD) and low-density (LD) feeding. Left panels show distribution of total number of fetus contacts made by 30 proximity logger-outfitted elk during 7 HD feeding days (A) and 7 LD feeding days (B). Right panels show daily elk–fetus contact rates for individuals with the 3 lowest (ranks 1–3) and 3 highest (ranks 28–30) numbers of contacts during the entire study for HD feeding days (C) and LD feeding days (D). Points are jittered to show overlapping values. The asterisk represents a value not shown because of *y*-axis scaling; individual 29 had 12 fetus contacts during 1 HD feeding day.

contacts/individual/day; Fig. 2A), and between 0 and 4 contacts during 7 days of LD feeding (mean contact rate: 0.08 contacts/individual/day; Fig. 2B). We found considerable variation in elk–fetus contact rate among individuals on HD feeding days; although most individuals had consistently low or zero daily fetus contact rates, a few individuals made several fetus contacts during most HD feeding days (Fig. 2C). On LD feeding days, however, we found almost no variation in daily contact rate among individuals; all 30 individuals had a median daily total contact rate of 0, and even those individuals with the highest overall contact rates during the study very rarely contacted a fetus (Fig. 2D).

From our analysis of proximity logger data, we found large reductions in total contact rate and unique contact rate on LD feeding days relative to HD feeding days (Fig. 3); the median reduction was 91% for total contact rate ($P = 0.011$, $T = 28$, $n = 7$) and 82% for unique contact rate ($P = 0.011$, $T = 28$, $n = 7$). The median reduction in the mean duration of a contact was 96%, but this reduction was not statistically significant ($P = 0.14$, $T = 21$, $n = 7$) because the percent reduction for 1 feeding day pair was highly negative due to several extremely long contacts during a LD feeding day. Excluding this outlier, the median reduction in mean duration was 97% ($P = 0.017$, $T = 21$, $n = 6$). We found no difference between rate of contact with the fetus logger and the control logger for total contacts ($P = 0.780$, $T = 41$, $n = 12$; Fig. 4), unique contacts ($P = 0.794$, $T = 92$, $n = 12$), or mean duration ($P = 0.305$, $T = 69$, $n = 12$).

We found similar results from our analysis of video camera data. The median reduction in total contact rate on LD feeding days relative to HD feeding days was 74% for <2-m contacts ($P = 0.016$, $T = 21$, $n = 6$) and 72% for investigations ($P = 0.016$, $T = 21$, $n = 6$; Fig. 3). Fetuses and control points did not differ in total contact rate ($P = 0.652$, $T = 69$, $n = 9$; Fig. 4). Of those elk approaching within 2 m of the fetus, 24% investigated the fetus. The percentage of elk investigating the fetus at <2 m did not differ between HD and LD feeding days ($P = 0.393$, $T = 24$, $n = 6$).

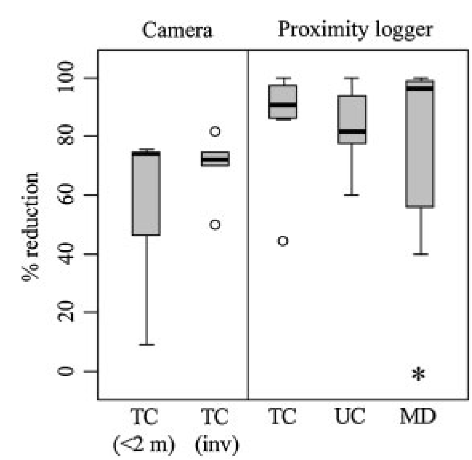


**Figure 3.** Reduction in elk–fetus contact rates for low-density feeding relative to high-density feeding on Soda Lake feedground, Wyoming in 2009. Left: percent reduction in total contacts (TC) for <2-m contacts and investigations (inv) based on camera data ($n = 6$). Right: percent reduction in total contacts (TC), unique contacts (UC), and mean duration (MD; all <2 m) based on proximity logger data ($n = 7$). Boxes show interquartile ranges and black bars show medians. Whiskers extend to the most extreme values that are no more than 1.5 times the interquartile range above or below the box. Outliers are shown as points. The asterisk represents an extreme outlier of −183% reduction in mean duration; it is not shown in the figure because of *y*-axis scaling.

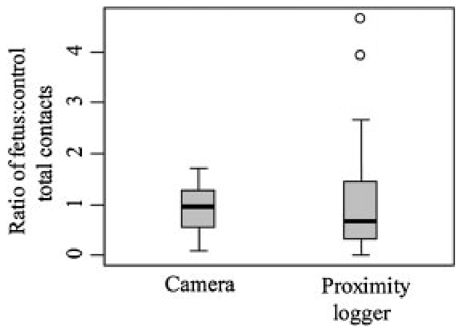


**Figure 4.** Ratio of fetus:control total contact rate by cow elk on Soda Lake feedground, Wyoming, in 2009 based on camera data ($n = 9$) and proximity logger data ($n = 14$). Boxes show interquartile ranges and black bars show medians. Whiskers extend to the most extreme values that are no more than 1.5 times the interquartile range above or below the box. Outliers are shown as points.

# DISCUSSION

Low-density feeding dramatically decreased elk–fetus contact rates and may reduce brucellosis transmission among cow elk on Wyoming feedgrounds. We found large and significant reductions in total contact rate and unique contact rate despite the small sample size ($n = 7$ pairs) and conservative statistical methods used in our analysis. Proximity loggers allowed us to collect information on unique individuals that was unavailable from camera data, but the associated need to capture many individuals at a given site limited our ability to replicate the study across many sites. However, camera data from HD and LD feeding in 2008 at 5 additional Wyoming feedgrounds (Bench Corral, South Park, Greys River, Franz, and Muddy Creek) corroborate our finding of reduced numbers of elk–fetus contacts by cow elk with LD feeding (E. Maichak, WGFD, unpublished data). Assuming that LD feeding is causally responsible for the observed reductions in contact rates, we expect our results from Soda Lake would apply to other feedgrounds, depending on the extent to which each site allows for dispersed feeding.

We used multiple measures of contact rate because the probability of disease transmission depends on several characteristics of contact events. The total number of contact events with a fetus is a logical indicator of transmission risk, but how those contacts are distributed among the population is also influential. For instance, 5 elk–fetus contacts could be distributed as 5 contacts by a single individual or 1 contact by each of 5 different individuals, with differing disease dynamics expected for these scenarios, particularly if the probability of transmission from a single contact is large. The unique contact rate thus provides additional information critical to assessing transmission. Duration of contact events is also informative, as lengthy contact events may be more likely to result in transmission. The observed reductions in total contact rate and unique contact rate, with no significant change in mean duration of a contact, provide convincing evidence that LD feeding could reduce transmission rate.

The impacts of LD feeding on transmission risk may be larger than estimated by our study. We examined changes only in contact rate, but recent research suggests that probability of transmission given contact may also vary as a function of feeding density. Forristal et al. (2012) found higher stress levels among feedground elk than among unfed elk, and stress has been linked to immune system suppression and increased disease susceptibility in some species (Barnard et al. 1994, Oppliger et al. 1998). Thus, in addition to reducing contact rate, LD feeding may decrease probability of transmission given contact by reducing stress levels, although probably not to levels observed in unfed elk.

We calibrated proximity loggers to record contacts at a distance of <2 m in order to ensure enough contacts for a sufficiently powerful analysis. Although one could argue that *B. abortus* transmission is unlikely from 2 m away, we still found contact rates at this distance to be informative regarding the effect of LD feeding on contact rate. Analysis of camera data suggests that although only a quarter of <2-m contacts were investigations, the percent reductions in <2-m contacts and investigations due to LD feeding were similar. We acknowledge, however, that our study did not directly assess reductions in actual transmission. If the probability of transmission given close contact with a fetus is high, then contact rate should be a strong predictor of transmission, but the relationship may be weak if transmission probability is very low.

In our study, $32 \pm 6\%$ (mean $\pm$ SE) of cow elk approached within 2 m of a fetus during a typical HD feeding day. If we assume that all cow elk are equally likely to contact a fetus, which seems reasonable given the limited heterogeneity we observed, then almost 80% of cows would be exposed after only 4 abortion events along feedlines. Yet, the average seroprevalence on feedgrounds in 2010 was only 19% (B. Scurlock, WGFD, unpublished data). This suggests that the probability of infection given contact at <2 m is small, reinforcing that transmission typically requires direct contacts with abortion materials, not all of which may provide the infectious dose of *B. abortus* required for transmission. Alternatively, this discrepancy could be explained if antibody titer loss is common (and seroprevalence estimates at a given point in time therefore underestimate the proportion of individuals having been infected during their life), if fetuses are aborted very rarely along feedlines, or if some individuals are unlikely to seroconvert even after repeated exposures. We discuss these possibilities in more detail below.

Although previous studies have documented elk investigating fetuses, we are unaware of any that have rigorously assessed the attractiveness of fetuses to elk. Cow elk are widely believed to be behaviorally predisposed to investigate fetuses (Geist 1982), but similar contact rates with fetus and control loggers in our study suggest that fetuses are encountered incidentally during feeding and are not actively sought out by cow elk. Camera footage of contact events showed that less than a quarter of cow elk passing within 2 m of a fetus actively investigated it, further suggesting that elk are minimally inclined to investigate fetuses. However, we have examined fetus attractiveness only in the feedground environment using previously frozen fetuses; elk possibly respond differently to fetuses on native winter ranges or to fetuses that have not been frozen. Additionally, we obtained the fetuses for our study from pregnant cows killed during late January and early February. Wyoming Game and Fish Department has recovered *B. abortus* from abortion events documented on feedgrounds from February through April (B. Scurlock, unpublished data). Fetuses aborted in April would likely be further developed than those used in our study, and this difference in development could influence the attractiveness of the fetus, but we suspect this effect would be very minor.

We observed inconclusive evidence of individual heterogeneity in elk–fetus contact rate. If individuals differ in their tendency to contact fetuses, then we would expect some individuals to have consistently greater daily contact rates than others. This expectation was met to some extent during HD feeding, with a subset of individuals making contacts with fetuses more frequently than the rest of the individuals we observed. However, this variation among individuals did not hold up during LD feeding days, when all individuals made zero contacts on most or all days. Strong conclusions about individual heterogeneity are difficult to draw with a sample size of only 14 days per individual, and a longer experimental study may be necessary to clarify the extent to which individuals vary in their tendency to contact fetuses on feedgrounds. Individual heterogeneity in animal contact rates remains an understudied aspect of wildlife ecology, but proximity logger technology should facilitate additional investigations.

In light of the strong evidence that LD feeding reduces elk–fetus contact rates of cow elk attending feedgrounds, we explore how seroprevalence might change with the implementation of LD feeding throughout the feedground system. The reduction we observed in contact rate cannot be assumed to cause an equivalent reduction in seroprevalence, as theoretical models of disease transmission suggest that contact rate and seroprevalence may not be linearly related (Anderson and May 1991). We related seroprevalence to contact rate using a simple SIR disease model that partitions individuals into susceptible (S), infected (I), and recovered (R) disease classes based on their exposure to *B. abortus* (Anderson and May 1991). For this model, the equilibrium seroprevalence ($P^*$) is a function of 3 parameters: 1) $\beta$, a transmission coefficient incorporating both contact rate and probability of transmission given contact; 2) $\gamma$, the annual recovery rate for infected individuals (and the inverse of the mean time to recovery in years); and 3) $\delta$, the demographic turnover, which reflects the rate at which individuals in the population are replaced at equilibrium through offsetting births and deaths. For simplicity, we used a non-age structured model, and as a result $\delta$ was not equivalent to a traditional fecundity or mortality rate. It can be better conceptualized as a birth or death rate averaged across all age classes and weighted by the proportion of the population in each age class. We assume density-dependent transmission, but because population size remained constant in our equilibrium model, ours was a case where density-dependent transmission was equivalent to frequency-dependent transmission with $\beta$ rescaled by population size (Anderson and May 1991). Our equation for equilibrium seroprevalence is thus:

$$P^* = 1 - \frac{\delta + \gamma}{\beta}$$

This model formulation is typically applied to pathogens transmitted directly from animal to animal, rather than indirectly (e.g., from infectious fetus to elk). However, we believe the model is adaptable to our case if we assume the number of infected individuals is an index of the number of infectious fetuses in the environment, with the coefficient $\beta$ appropriately rescaled to reflect this distinction (and because fetuses are typically scavenged within 48 hours on feedgrounds, modeling the buildup of infectious materials in the environmental is not necessary).

We considered a range of $P^*$ in our model because seroprevalence varies by feedground and year. We let $P^* = 0.10$ or 0.30, roughly corresponding to the lowest and highest long-term seroprevalence estimates among Wyoming feedgrounds (B. Scurlock, unpublished data). We let $\delta = 0.13$, based on estimates of female elk mortality from 12 western United States elk populations (Raithel et al. 2007). This value is greater than a typical cow elk mortality rate and less than a typical cow elk fecundity rate because it incorporates calves and senescent individuals with relatively high mortality and low fecundity. We let $\gamma = 0.5$ based on limited evidence from artificial infections (Thorne et al. 1978). Although the recovery rate of elk has never been well estimated in the literature, in our model the predicted reduction in seroprevalence due to LD feeding is unaffected by the specific value of $\gamma$ chosen; only $\beta$ is affected because it is scaled by $\gamma$ and $P^*$.

Substituting in these parameter values and solving for $\beta$ yielded a transmission coefficient of 0.7 or 0.9 (for $P^* = 0.10$ or 0.30, respectively) for our system. Because $\beta$ is the product of contact rate and probability of transmission given contact, a proportional reduction in contact rate causes an equivalent proportional reduction in $\beta$. Using the more conservative of our 2 point estimates of reduction in total contact rate (74% from the camera data), $\beta$ would be reduced to 0.182 (for $P^* = 0.10$) or 0.234 (for $P^* = 0.30$) if LD feeding were implemented on feedgrounds; both $\beta$ values correspond to a seroprevalence of 0, suggesting that LD feeding would eventually eliminate the disease. However, this assumes that all transmission occurs along feedlines. The fraction of transmission events occurring along feedlines, $\theta$, is the subject of ongoing research but is certainly less than 1, so the observed reduction in $\beta$ should be rescaled by $\theta$ to account for off-feedline transmission events that contribute to regional seroprevalence.

Seroprevalence declines nonlinearly with transmission, and predicted reductions are dependent on the initial seroprevalence (Fig. 5). When initial seroprevalence is low, even small values of $\theta$ correspond to major reductions in seroprevalence. Our model predicts seroprevalence would drop to 0 if $\theta > 0.14$, given initial seroprevalence of 10%. If initial seroprevalence is greater, reductions in seroprevalence expected

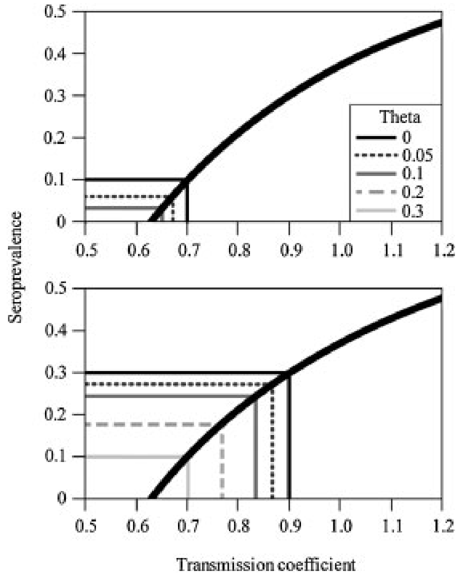


**Figure 5.** Potential reductions in *Brucella abortus* seroprevalence of Wyoming elk from low-density (LD) feeding given initial seroprevalence of 0.10 (top) or 0.30 (bottom). The thick line shows the relationship between the transmission coefficient ($\beta$) and equilibrium seroprevalence ($P^*$) when $\delta = 0.13$ and $\gamma = 0.5$. Thin lines show predicted values of $\beta$ and corresponding $P^*$ if LD feeding is implemented and the proportion of transmission events occurring along feedlines ($\theta$) is 0, 0.05, 0.1, 0.2, and 0.3. $\theta = 0$ represents initial $P^*$ and $\beta$. Lines for $\theta = 0.2$ and $\theta = 0.3$ do not appear in the top figure because $P^* = 0$ for these $\theta$ values.

from LD feeding are more modest for a given value of $\theta$. With initial seroprevalence of 30%, our model predicts seroprevalence would drop to 0 if $\theta > 0.41$. Thus, we expect that LD feeding could potentially lead to dramatic declines in seroprevalence, with the greatest reductions in areas where initial seroprevalence is low.

These results are unexpected in the context of recent research on brucellosis seroprevalence among Wyoming elk populations. Cross et al. (2010) found that seroprevalence of some unfed elk populations in the GYE is now comparable to seroprevalence of some feedground populations, yet animal densities in unfed groups are generally thought to be less than densities during LD feeding. How can we reconcile the high seroprevalence of these unfed elk with our model results suggesting that large reductions in seroprevalence of feedground elk could be achieved with a relatively modest decrease in feeding density? We propose several possible explanations for this apparent contradiction.

First, $\theta$ may be very small and only minor reductions in seroprevalence may occur with LD feeding because most transmission occurs away from feedlines. This could occur if elk are behaviorally predisposed to move away from feedlines when aborting, which has never been examined. Alternatively, LD feeding may reduce the seroprevalence of brucellosis below that of unfed populations despite greater elk densities because of differences in the persistence of fetuses on feedgrounds versus native winter range. Scavengers may key in on feedgrounds as a reliable source of food during winters, and recent research suggests that this is probably occurring. In a study by Maichak et al. (2009), 95% of elk fetuses placed by researchers on feedgrounds were scavenged within 24 hours, whereas only 38% of fetuses placed on native winter range were scavenged within this period. Similarly, Cook et al. (2004) found that it took 2.9 days and 5.9 days, respectively, for 90% of bovine fetuses placed on Wyoming elk feedgrounds and in Grand Teton National Park to be scavenged. We believe this difference in scavenging rate is the most likely explanation for the discrepancy between our modeling results and the high seroprevalence observed in some unfed elk populations.

Another possible explanation is that the form or parameterization of our SIR model does not accurately represent *B. abortus* transmission dynamics in elk. Three notable assumptions of our model are: 1) the rate of recovery is constant, resulting in an exponentially distributed infectious period; 2) no variation in transmission rate exists among individuals in the population; and 3) the population has no age structure. Each of these assumptions has been shown to affect transmission dynamics in disease models (Lloyd-Smith et al. 2005, Wearing et al. 2005, Brooks-Pollock et al. 2010) and a more sophisticated model that does not rely on these assumptions could produce quantitatively different results from our model (though we suspect they would be qualitatively similar). Regardless of its effect on overall seroprevalence in the region, LD feeding will likely decrease transmission on feedgrounds and should be considered as an alternative to HD feeding.

Proximity loggers and cameras were both useful tools for assessing contact rates, but proximity loggers collected data more reliably than cameras, did not require daily attention as cameras did, and provided data in a convenient format upon download. Logger calibration was time consuming, but even more time was spent viewing and counting elk contacts in camera footage. However, the ability to distinguish between investigations and incidental <2-m contacts provided by cameras was particularly useful for understanding how elk interact with fetuses. Managers and researchers should compare the cost and effort associated with cameras (purchasing, assembling, monitoring, reviewing footage) and proximity loggers (purchasing, calibrating, capturing animals) when designing future studies.

Most proximity logger studies will require sampling of individuals from the population of interest, a problem that camera studies will not face. We outfitted approximately 7% of cow elk on our study feedgrounds with proximity loggers but found reasonable correspondence between contact rate estimates from proximity logger data and camera data, suggesting that our low sampling intensity was sufficient to reveal population-level effects. However, whether this sampling intensity would be sufficiently powerful for studies in different environments or of different species is unclear. In situations where contact events are rare or vary strongly by individual, a much greater proportion of the population of interest may need to be sampled.

## MANAGEMENT IMPLICATIONS

Managers should consider implementing LD feeding throughout Wyoming's feedground system and in other western states where regular or emergency feeding of elk still occurs and may exacerbate the transmission of diseases. Low-density feeding is likely to reduce *B. abortus* transmission with negligible effect on the total cost of feedground operation (B. Scurlock, unpublished data). Other management actions designed to reduce transmission have had mixed results (e.g., vaccination of feedground elk; Herriges et al. 1989, Roffe et al. 2004), were of limited use or applicability (e.g., habitat enhancements in areas or years with deep snow), or have been scrutinized for potentially redistributing elk from feedgrounds to private lands (e.g., habitat enhancements, shortened feeding seasons), but we expect that LD feeding would avoid these shortcomings. We recommend proximity loggers for future studies of animal contacts with infectious materials in the environment, but note that their greatest potential lies in documenting direct contacts among animals that occur unpredictably in time or space and thus cannot be easily captured with cameras.

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