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EFFECTS OF MANAGEMENT, BEHAVIOR, AND SCAVENGING ON RISK OF BRUCELLOSIS TRANSMISSION IN ELK OF WESTERN WYOMING

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ABSTRACT: Brucellosis is endemic in elk (*Cervus elaphus nelsoni*) using winter feedgrounds of western Wyoming, USA presumably because of increased animal density, duration of attendance, and subsequent contact with aborted fetuses. However, previous research addressed antibody prevalence rather than more direct measures of transmission and did not account for elk behavior or scavenging in transmission risk. Throughout March and early April 2005–07, we monitored 48 sets of culture-negative, pseudoaborted elk fetuses, placentas, and fluids (fetal units, FUs) on one winter free-ranging (WFR) location and four sites (Feedline, High Traffic, Low Traffic, Adjacent) associated with four feedgrounds. "At-risk" elk (total elk within 5 m of FU) and proportions of elk sniffing and contacting FUs were highest on Feedlines and decreased toward Low Traffic sites. We did not observe elk investigating FUs Adjacent to feedgrounds or on the WFR location. At-risk elk on Feedline and High Traffic sites decreased throughout the sampling period, whereas proportions of elk investigating FUs were correlated positively to at-risk elk among all sites within feedgrounds. At-risk elk and proportions of elk investigating FUs were correlated with total feedground elk density and population only on High Traffic and Low Traffic sites. Proportions of sex/age groups (female, juvenile, male) investigating FUs did not differ from background populations. Females, however, spent more time (mean [SE], 21.07 [3.47] sec) investigating FUs than juveniles (14.73 [3.53] sec) and males (10.12 [1.45] sec), with positive correlation between total investigations and time spent investigating per female. Eight species of scavengers consumed FUs, removing FUs faster on feedgrounds than WFR locations and reducing proportions of elk that investigated FUs. Our results suggest that 1) reduction of elk density and time attending feedgrounds, particularly on Feedlines; and 2) protection of scavengers on and adjacent to feedgrounds would likely reduce intraspecific transmission risk of brucellosis.

Key words: Brucellosis, *Cervus elaphus*, density-dependent, disease transmission, elk, feedgrounds, scavengers, Wyoming.

INTRODUCTION

Bovine brucellosis, caused by infection with the bacterium *Brucella abortus*, has sparked controversy because of its persistence in Rocky Mountain elk (*Cervus elaphus nelsoni*) using winter feedgrounds (Thorne et al., 1978) and its potential threat to domestic livestock (Kistner et al., 1982) of the Greater Yellowstone Ecosystem (GYE) of Wyoming, USA. This threat was realized when Wyoming, USA, lost its "brucellosis class–free" status in 2004, following identification of two separate livestock herds infected with brucellosis in 2003 and 2004 (Galey et al., 2005). Although aerosol transmission has been reported in humans and may occur in cattle (Nicoletti, 1980), intraspecific transmission of brucellosis on feedgrounds likely occurs following oral ingestion of bacteria that occur in high numbers in aborted fetuses, fetal membranes and fluids, and/or uterine discharges (Cook, 1999). Infection usually results in reproductive failure (abortion of the first pregnancy following infection) and synovitis, carpal bursitis, and lameness in chronically infected animals (Thorne et al., 1978).

Currently, 23 winter elk feedgrounds exist in western Wyoming, USA. The

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National Elk Refuge (NER) is maintained by the US Fish and Wildlife Service near Jackson, Wyoming, USA; the other 22 feedgrounds are scattered throughout three counties in western Wyoming, USA, and are maintained by the Wyoming Game and Fish Department (WGFD). All feedgrounds in western Wyoming, USA, are used as substitutes for native winter range and to minimize depredation of private hay stores, winter mortality of elk, and elk-cattle commingling (Thorne et al., 1991). Feeding of about 15,000 and 7,000 elk on WGFD feedgrounds and the NER, respectively (WGFD, 2006a), occurs typically from December to April and overlaps temporally with the period (February to June) of brucellosis-induced abortions (Thorne et al., 1991; Roffe et al., 2004). Theoretic models (Anderson and May, 1991; McCallum et al., 2001) and general observations (Thorne et al., 1979) suggest that animal-fetus contact levels should increase with density. However, few observations exist regarding brucellosis transmission events on feedgrounds, where up to 150 elk may investigate a pseudoaborted bovine fetus (Cook et al., 2004). Because actual *Brucella*-induced abortions and subsequent investigation by susceptible animals are extremely difficult to predict and observe, WGFD has monitored annual trends in brucellosis prevalence, using serologic tests of feedground and winter free-ranging (WFR) elk since the mid-1970s. However, antibody prevalence has been higher in elk on feedgrounds compared to neighboring winter ranges, suggesting that there is a relationship between elk population size and/or density and brucellosis (see Cross et al., In review; Scurlock and Edwards, In review). Cross et al. (2007), however, found no relationship between brucellosis antibody prevalence and feedground density or population size. Joly and Messier (2004) also showed no significant association between brucellosis antibody prevalence and population density in wood bison (*Bison bison athabascae*), whereas Dobson and Meagher (1996) concluded that antibody prevalence did increase with plains bison (*Bison bison bison*) population size. The effect of elk population or density on specific brucellosis transmission events (i.e., investigation of aborted fetuses by susceptible animals) has not been quantified in laboratory or field studies and is poorly understood.

Management strategies to control brucellosis in feedground elk have included the strain 19 vaccination program (instituted in 1984; Herriges et al. 1991), habitat enhancement projects (e.g., prescribed fire, mechanical, chemical) to reduce elk dependency and subsequent densities and time spent on feedgrounds (Clause et al., 2002), and several Best Management Practices that include feeding hay on clean snow, recovering aborted fetuses, and preventing elk-cattle commingling (WGFD, 2007b). No difference in brucellosis antibody prevalence was detected when 22 yr of prevalence data from vaccinated and nonvaccinated feedground elk were examined; antibody prevalence also did not decrease over time for either group (WGFD, 2007a). These data are complemented by controlled studies where vaccination with strain 19 prevented abortion in 29% (Roffe et al., 2004) to 62% (Herriges et al., 1989) of captive pregnant elk challenged with *B. abortus* strain 2308. Habitat enhancements can reduce the length of feeding season on some feedgrounds (WGFD, unpubl. data). However, limited accessibility of forage because of deep or crusted snow conditions on and adjacent to many feedgrounds preclude use of habitat enhancement to disperse elk (WGFD, 2006b) or reduce feeding season length and antibody prevalence levels (Cross et al., 2007). Furthermore, because antibody prevalence estimates continue to average 25% (WGFD, unpubl. data) and range as high as 67% (Thorne et al., 1997), current management practices do not appear to be reducing the prevalence of brucellosis antibodies in elk. Additional control mea-

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sures should be investigated and potentially employed (Bienen and Tabor, 2006).

Numerous studies have documented that vertebrate scavengers will exploit spatially and temporally predictable pulses of carrion of domestic and free-ranging animals (DeVault et al., 2003). Annually, up to several dozen elk (<1% of individual feedground population) may die on a feedground because of predation, disease, or unknown factors (WGFD, 2006a). Cook et al. (2004) found at least 16 vertebrate species readily consumed 100% (n=89) of bovine fetuses placed on feedground and nonfeedground sites in the GYE. Scavenging rates for bovine fetuses placed on the NER (mean±SD, 26.8±25.3 hr) and WGFD feedgrounds (40.7±31.1 hr) were faster than a nonfeedground site (Grand Teton National Park, 57.5±48.0 hr; Cook et al., 2004). Feedgrounds likely provide dependable sources of carrion; therefore, vertebrate scavengers within the GYE probably rely on feedgrounds to some degree for diet supplementation. Investigation of scavengers as potential biological control agents (Louda et al., 2003) of brucellosis in the GYE has not occurred.

To investigate potential effects of management, elk behavior, and scavenging on risk of brucellosis transmission, we observed elk, scavengers, and their behavior in relation to pseudoaborted elk fetuses, placentas, and fluids (hereafter termed *fetal unit* [FU]) placed on feedground and winter free-range (WFR) locations in western Wyoming, USA. Regarding elk, we wished to determine 1) density, 2) overall total and the total within specific sex/age groups investigating FUs, 3) total investigations as well as time spent per animal investigating FUs, and 4) whether these measures differed among, or were associated with, various sites on and off the feedgrounds. For scavengers, we wished to determine 1) individual species scavenging FUs, 2) whether scavenging rates differed among feedground and WFR locations, and 3) whether scavenging reduced total animals investigating FUs. These data will be used to quantify how management practices and elk density, demography, and behavior, as well as generalist scavengers, influence risk of intraspecific brucellosis transmission for assessment and potential alteration of current feedground management regimes in the GYE.

MATERIALS AND METHODS

Study sites

Our study occurred on four WGFD-operated feedground locations (Grey's River, 43°15′N, 11°03′W, 1,716 m elevation; Franz, 43°08′N, 110°18′W, 2,438 m; Soda Lake, 42°95′N, 109°81′W, 2,314 m; and Muddy Creek, 42°63′N, 109°36′W, 2,331 m) and one WFR location (Buffalo Valley, 43°84′N, 110°45′W, 2,184 m) in the brucellosis endemic area of the GYE in western Wyoming, USA. Climate conditions within the region consist of long, cold winters and short, warm summers, with most precipitation resulting from early and late winter snowstorms. Vegetation composition on the feedgrounds was dominated by herbaceous species with a few shrubs (*Artemisia* spp.), whereas general habitat conditions in the WFR location range from irrigated hay meadows and willow (*Salix* spp.) stands in riparian areas to areas comprising shrubs (*Artemisia* spp., *Amelanchier alnifolia*), aspen (*Populus tremuloides*), conifer (*Pinus* spp., *Abies lasiocarpa*, *Picea* spp.), and aspen/shrub or aspen/conifer communities on upland sites.

Observations of elk and scavengers

We obtained 48 sets of *Brucella* culture-negative FUs from elk killed at Grey's River and Muddy Creek feedgrounds in association with the Test and Slaughter pilot project (Scurlock, 2006). All fetal tissues and fluids were collected immediately following killing of the animals and were later cultured as described by Alton et al. (1988). All remaining tissues and fluids were frozen and stored until required for this study. Each FU was thawed for approximately 48 to 72 hr before placement. Mass (Chatillon NS-15 scale, Ametek, Largo, Florida, USA; mean±SD, 1.79±0.66 kg) and internal temperature (Ekco meat thermometer, Ekco Housewares Inc., Franklin Park, Illinois, USA; mean±SD, 4.41±2.78 C) of FUs were measured and recorded immediately before placement.

Throughout March and early April 2005–07,

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we placed FUs on a feedground or WFR location for observations of scavenging, elk density, and elk-FU investigation. Only the Franz feedground was observed in 2005. All four feedgrounds and the WFR location were observed in 2006, and only the Franz feedground and the WFR location were observed in 2007. Only one FU was placed on a location per sampling period. No other FUs were placed on a feedground or WFR location until the previous FU was removed. On feedgrounds, we placed one FU on a randomly selected site immediately following daily feeding of the elk (typically 10:00 AM to 2:00 PM). We categorized sites on feedgrounds as Feedline (within 5 m of the feedline), High Traffic (areas 5 m to 15 m adjacent to feedlines or where elk trailed regularly between feedlines), Low Traffic (areas >15 m adjacent to feedlines or where elk did not trail regularly, often relatively deep, undisturbed patches of snow), and Adjacent (areas of relatively deep, undisturbed snow, 10 m to 50 m off of the feedground proper). Following placement on feedgrounds, we monitored each FU with binoculars or spotting scope from the feedground haystack at distances of 20 m to 200 m during a sampling period of up to 4 hr. Observation of FUs within these distances did not appear to affect elk or scavenger behavior because observers were hidden and typically downwind of the FU. If the fetus and placenta of an FU were removed from the feedground or consumed entirely by a scavenger before 4 hr, we ended all sampling. Because elk can spend up to 6 hr on feedlines (Thorne and Butler, 1976), we defined our sampling period on feedgrounds as up to 4 hr because this timeframe allowed most elk to pass by a particular FU only once and minimized pseudoreplication of individual elk investigations. At the WFR location, FUs were placed on randomly selected sites within areas currently or potentially occupied by elk at approximately midday (10:00 AM to 2:00 PM) and monitored with infrared, motion-sensitive cameras (Trailmaster, Lenexa, Kansas, USA) until the FU was removed.

To estimate elk density among sites within and adjacent to feedgrounds, we counted all elk within approximately 5 m of each FU (hereafter, categorized as *at-risk* elk) during a 1–5 sec scan-sample (Altmann, 1974) every 10 min throughout the sampling period in 2006 and 2007. To investigate potential behavioral predisposition to risk of transmission, we first categorized specific sex/age classes of elk as female (yearling and adult females), juvenile (young of the year), and male (yearling and adult males). The WGFD personnel conducted annual demographic classifications in late January to early February on each feedground, which we used to define the sex/age structure of the background population. For individual elk investigations of FUs, we recorded total sniffs (one sniff defined as an elk approaching within approximately 1 m of the FU, dropping head to sniff the FU, then picking head back up), contacts (one contact defined as any bite, lick, or nasal touch; contact via hoof or leg was not recorded), and time (total time spent within approximately 3 m of FU while actively investigating the FU) per elk.

We also recorded presence or absence of individual species consuming FUs and scavenging rates. On feedgrounds, FUs that were removed before the 4-hr sampling period were recorded as total time elapsed since placement. If any portion of an FU placed on a feedground was present at the end of the sampling period, we contacted feedground personnel within the following days to determine whether the FU was consumed within that 24-hr period. Fetal units that were removed after the 4-hr sampling period were recorded as 24-hr if they were scavenged within 1 day, as 48 hr if scavenged within 2 days, etc. On the WFR location, scavenging rates were recorded continuously.

Data analyses

For all statistical analyses, we considered each FU as the experimental unit, set $\alpha=0.05$, and used the SYSTAT (SSI Services, San Jose, California, USA) statistical analysis program. Although up to two FUs may have been placed on different locations (feedground or WFR) within the same day, we believe that sampling units were independent because of the relatively long distances (>25 km) between adjacent locations (Cook et al., 2004). We pooled density, behavior, and investigation data among feedground locations and years within feedground sites and among years within the WFR location because of low sample sizes. Before determination of significance through post hoc multiple pairwise comparisons, we incorporated a Bonferroni correction (i.e., $\alpha=0.05/k$; Zar, 1999).

For all estimates of at-risk elk within feedground sites (treatment) and the WFR location (control site), we averaged total elk counted within 5 m of each FU per FU per site within feedground and WFR locations and incorporated a logarithmic transformation [i.e., $X'=\log(X+1)$] to normalize data (Zar, 1999). To analyze potential differences of at-risk elk among feedground sites, we compared

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data among and between sites adjacent to one another (i.e., Feedline vs. High Traffic, High Traffic vs. Low Traffic, and Low Traffic vs. Adjacent) with analysis of variance (ANOVA) and 2-tailed Fisher's least significant difference (LSD) pairwise comparisons, respectively. To compare estimates of at-risk elk between individual feedground sites (treatment) and the WFR location (control), we used 1-tailed Dunnett's pairwise comparisons. To assess the potential influence of time since placement of the FU on at-risk elk within Feedline, High Traffic, and Low Traffic sites, we used univariate least-squares linear regression.

We transformed the total elk within each sex/age category that were observed sniffing and contacting FUs to the relative percentage of elk within each category that were classified on the feedground, averaged those to obtain a mean relative percentage of total elk observed sniffing and contacting FUs, and further transformed these data with an arcsine square-root transformation (i.e., $p' = \arcsin \sqrt{p}$) to normalize data (Zar, 1999). We then compared the percentage of elk sniffing and contacting FUs by use of ANOVA and compared estimates between sites adjacent to one another (i.e., Feedline vs. High Traffic, High Traffic vs. Low Traffic, and Low Traffic vs. Adjacent) with 2-tailed Fisher's LSD pairwise comparisons. To compare the percentage of elk sniffing and contacting FUs between individual feedground sites (treatment) with the WFR location (control), we used 1-tailed Dunnett's pairwise comparisons.

To assess the influence of overall feedground population size (total elk classified) and density (*total elk classified/total feeding area*) on at-risk elk and the percentages of elk investigating FUs, we used univariate least-squares linear regression. For analysis of within-feedground density effects, we pooled and compared at-risk elk to percentages of elk sniffing and contacting FUs within Feedline, High Traffic, Low Traffic, and Adjacent sites. For analyses of overall feedground density effects among feedgrounds, we first compared at-risk elk within individual Feedline, High Traffic, and Low Traffic sites to elk density from respective feedgrounds. We then compared the percentages of elk sniffing and contacting FUs within individual Feedline, High Traffic, and Low Traffic sites with elk density and population on respective feedgrounds.

For behavioral analyses among cohorts, we used 2×3 Chi-square contingency tables to compare the proportion of total elk observed sniffing or contacting FUs to total elk classified that did not sniff or contact FUs. For additional behavioral analysis among cohorts, we compared log-transformed mean investigations (total sniffs, contacts, and time spent with the FU) per elk among and between cohort classes with ANOVA and 2-tailed Fisher's LSD pairwise comparisons, respectively. We assessed the influence of time on risk of transmission to females by comparing log-transformed mean sniffs and contacts per elk to paired samples of log-transformed estimates of time spent investigating FUs. All mean investigations were derived from greater than two observations per individual elk.

Because of limited sample sizes, we pooled scavenging data among species, sites, and years within feedground and WFR locations. Because of differences in sampling methods between feedground and WFR locations, we assessed differences in scavenging rates between feedground and WFR locations with a 3×2 Chi-square contingency table, comparing proportions of FUs scavenged in less than 4 hr, 4 hr to 24 hr, and greater than 24 hr. To determine whether scavenging significantly reduced total elk investigating FUs, we used 2×2 Chi-square contingency tables to compare the proportion of total elk observed sniffing and contacting FUs when FUs were removed before the end of the 4-hr sampling period to the proportion of total elk observed sniffing and contacting FUs when FUs remained on a feedground location for the entire 4-hr sampling period. Although scavengers removed FUs from all sites associated with feedgrounds, we used only those data from Feedline, High Traffic, and Low Traffic sites because no elk were observed sniffing or contacting FUs on Adjacent sites.

RESULTS

Elk density and investigations

We found that the number of at-risk elk increased from Adjacent to Feedline sites (Fig. 1A) and differed among feedgrounds sites ($F_{3,33}=12.85$, $P<0.001$). Post hoc comparisons revealed that Feedlines had more at-risk elk than High Traffic sites ($\alpha=0.016$, $P=0.002$). Dunnett's test ($\alpha=0.013$) showed that Feedline ($P<0.001$) and High Traffic ($P=0.013$) sites had more at-risk elk than the WFR location. The percentage of elk sniffing FUs differed among feedground sites ($F_{3,40}=29.52$, $P<0.001$), generally increasing from Adjacent to Feedline sites (Fig. 1B). Addition-

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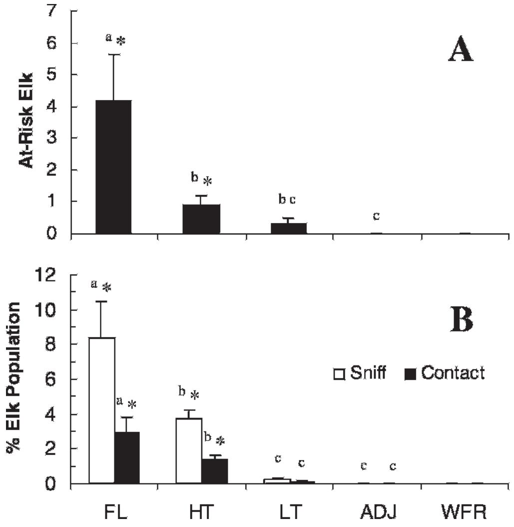

FIGURE 1. (A) At-risk elk (i.e., mean±SE, elk within 5 m of fetal unit) and (B) mean relative percentage (±SE) of total population observed sniffing and contacting fetal units on Feedline (FL), High Traffic (HT), Low Traffic (LT), and Adjacent (ADJ) sites within feedgrounds and winter free-range (WFR) locations in western Wyoming. Bars within the same letter grouping are not different (post hoc multiple comparisons, $P<0.016$) for sites adjacent to one another within feedgrounds (i.e., FL vs. HT, HT vs. LT, and LT vs. ADJ). Asterisk (*) indicates greater ($P<0.013$) at-risk elk or percentage of population observed sniffing or contacting fetal units on individual feedground site than on WFR location.

ally, the percentage of elk sniffing FUs was higher ($\alpha=0.016$, $P=0.012$) on Feedlines than on High Traffic sites and higher ($P<0.001$) on High Traffic than on Low Traffic sites. Dunnett's tests revealed that only Feedline ($\alpha=0.013$, $P<0.001$) and High Traffic ($P<0.001$) sites had higher percentages of elk sniffing FUs than the WFR location (Fig. 1B). The percentage of elk contacting FUs differed among feedground sites ($F_{3,40}=14.25$, $P<0.001$), again increasing from Adjacent to Feedline sites (Fig. 1B). The percentage of elk contacting FUs was marginally higher ($\alpha=0.016$, $P=0.05$) on Feedlines than on High Traffic sites and higher ($P=0.001$) on High Traffic than on Low Traffic sites. Dunnett's tests revealed that only Feedline ($\alpha=0.013$, $P<0.001$) and High Traffic ($P<0.001$) sites had higher percentages of elk contacting FUs than the WFR location (Fig. 1B). We found that at-risk elk were inversely correlated to time elapsed following placement of the FUs on Feedline ($t_{1,24}=-2.42$, $r^2=0.21$, $P=0.024$) and High Traffic ($t_{1,24}=-4.06$, $r^2=0.43$, $P=0.001$) sites (Fig. 2), but were uncorrelated on Low Traffic sites ($t_{1,24}=0.60$, $r^2=0.02$, $P=0.56$).

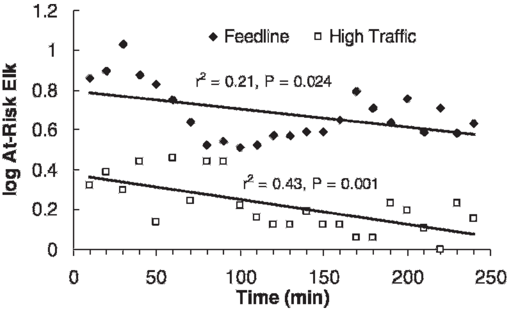

FIGURE 2. Log-transformed mean at-risk elk (total elk within 5 m of fetal unit) numbers linearly regressed over 10-min intervals throughout the sampling period on Feedline and High Traffic sites within feedgrounds in western Wyoming, USA.

Among feedground sites, we found that the percentage of elk sniffing ($t_{1,33}=6.48$, $r^2=0.58$, $P<0.001$) and contacting ($t_{1,33}=4.61$, $r^2=0.41$, $P<0.001$) FUs were correlated positively with at-risk elk (Fig. 3A, B). Among feedgrounds, we found that elk density was not correlated with at-risk elk or with percentages of elk sniffing and contacting FUs on Feedlines (Fig. 4A, B). However, elk density was positively correlated with at-risk elk on High and Low Traffic sites, and positively correlated with percentages of elk sniffing and contacting FUs on Low Traffic sites (Fig. 4 C–F).

Although it appeared that a larger proportion of females than juveniles, and more juveniles than males, investigated FUs, relative to the total animals investigating FUs, Chi-square analyses revealed no differences among sex/age groups for proportions of animals sniffing ($\chi^2_{2,810}=3.56$, $P=0.17$) or contacting ($\chi^2_{2,284}=2.71$, $P=0.26$) FUs relative to proportions classified on feedgrounds that did not sniff

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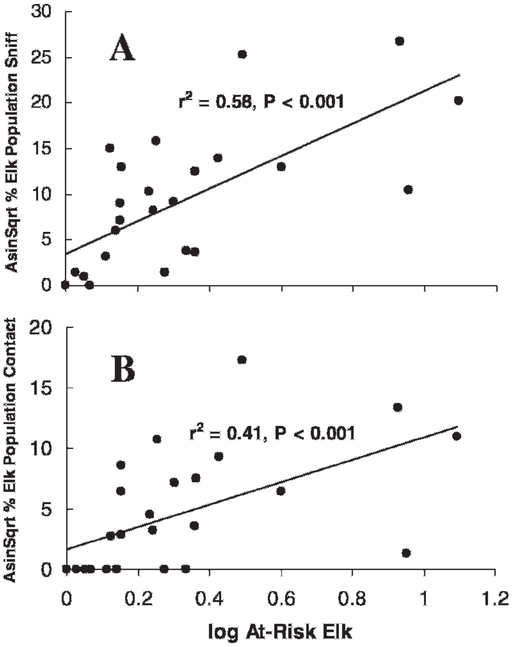

FIGURE 3. Arcsine-square root–transformed mean relative percentage of total feedground elk (A) sniffing or (B) contacting fetal units linearly regressed over log-transformed mean at-risk elk (total elk within 5 m of fetal unit) among individual sites on feedgrounds in western Wyoming, USA.

or contact FUs. We found that total average time spent investigating FUs per animal generally increased from males (mean±SE, 10.12±1.45 sec) to juveniles (14.73±3.53 sec) to females (21.07±3.47 sec). Time investigating FUs differed among sex/age groups ($F_{2,43}$=4.06, P=0.025), with females investigating FUs significantly longer than males (α=0.016, P=0.01) but only marginally longer than juveniles (P=0.05). Average sniffs (1.66±0.12, $F_{2,63}$ = 0.99, P=0.38) and contacts (1.41±0.09, $F_{2,40}$=0.22, P=0.80) per elk did not differ among groups. Out of 460 females and 206 juveniles investigating FUs, we observed one female (0.2%) and two juveniles (0.9%) attempt to consume a portion of the FU. For females, we found positive correlations between average time spent investigating and average sniffs ($t_{20,22}$=11.34, r^2=0.87, P<0.001) and contacts ($t_{21,23}$=3.48, r^2=0.37, P=0.002) per animal (Fig. 5A, B).

Scavenging

We observed eight species (six on feedground, six on WFR locations) of scavengers consuming FUs (Table 1). Primary scavengers (i.e., those species that we observed consuming or removing ≥50% of each FU) included coyotes (*Canis latrans*), Golden Eagles (*Aquila chrysaetos*) and Bald Eagles (*Haliaetus leucocephalus*), and red fox (*Vulpes vulpes*), whereas Magpies (*Pica pica*) and Ravens (*Corvus corax*) were common but removed only minor portions of FUs. Scavengers removed FUs faster from feedgrounds than WFR locations ($\chi^2_{2,48}$=18.205, P<0.001; Table 1). Twenty-five percent (10 of 40) and 0% (0 of eight) of all FUs placed on feedground and WFR locations, respectively, were scavenged within 4 hr. In contrast, 70% (28 of 40) and 38% (three of eight) of FUs placed on feedground and WFR locations, respectively, were scavenged between 4 hr and 24 hr following placement. Although the effect was modest, scavengers reduced ($\chi^2_{1,810}$=48.512, P<0.001) the proportion of elk on feedgrounds that sniffed FUs when scavengers removed (mean±SE, 2.38%±1.03%) rather than did not remove (4.30%±1.02%) FUs before the end of sampling. Results were similar for proportions of elk contacting ($\chi^2_{1,290}$=21.96, P<0.001) FUs when scavengers removed (0.72%±0.37%) rather than did not remove (1.55%±0.39%) FUs before end of sampling.

DISCUSSION

Theoretic models of infectious disease often assume that transmission increases with host density (Anderson and May, 1991; McCallum et al., 2001). Early observations of elk using feedgrounds suggested that transmission of *B. abortus* could be density dependent (Thorne et al., 1979). Recent studies on bison and elk, however, have resulted in mixed conclusions (Dobson and Meagher, 1996; Joly and Messier, 2004; Cross et al., 2007). Our

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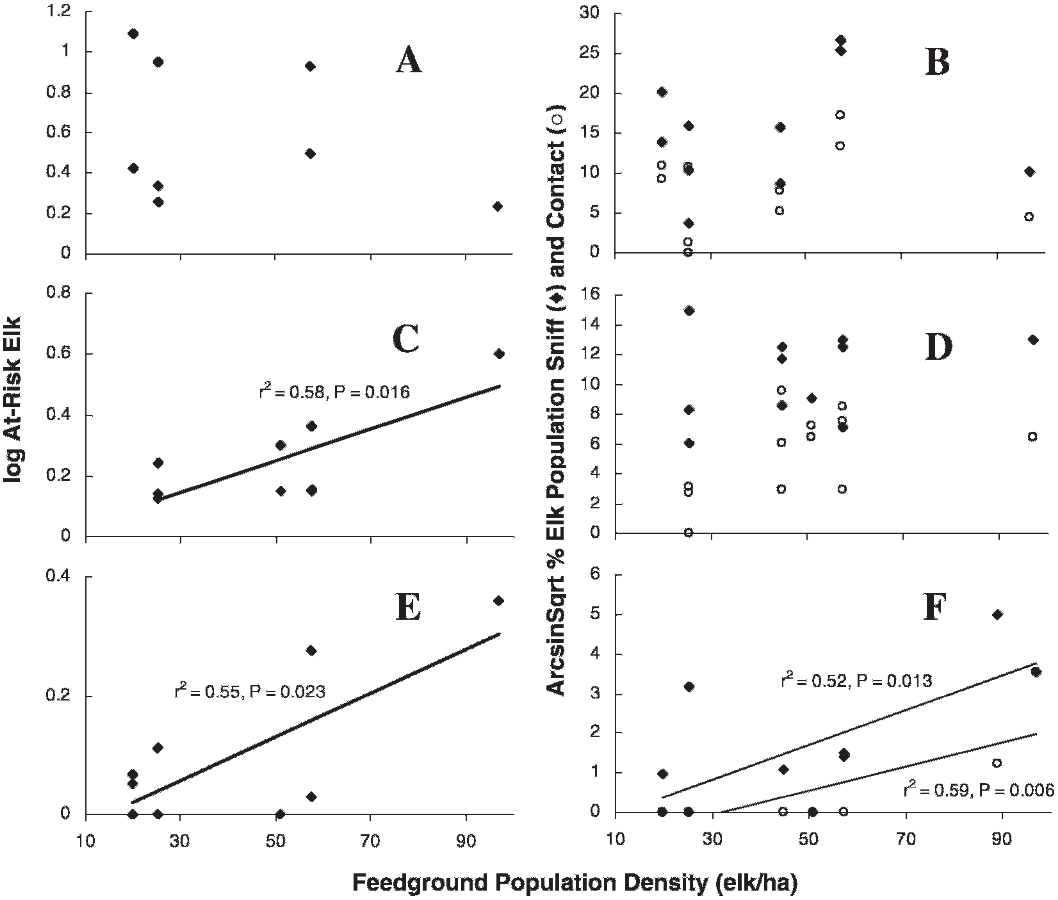

FIGURE 4. Log-transformed mean at-risk elk (total elk within 5 m of fetal unit) numbers and arcsine-square root–transformed mean relative percentage of total feedground elk sniffing and contacting fetal units linearly regressed with overall feedground density (elk/ha) on (A, B) Feedline, (C, D) High Traffic, and (E, F) Low Traffic sites within feedgrounds.

results suggest that within feedgrounds, investigation rates with aborted fetuses are facilitated by increased animal populations and densities, particularly on Feedlines (Fig. 1). Each day throughout the feeding season on most feedgrounds, feed is typically dispersed rapidly (e.g., about 2–30 kg/linear m of feedline) in one to three lines (e.g., oval, hooked, straight), depending on the method of feeding (i.e., horse-drawn or vehicle-drawn sleigh or wagon), feed type (i.e., large or small bales on WGFD-operated feedgrounds; pelleted alfalfa on NER feedgrounds), total amount of feed dispersed per load, and size (i.e., length, width) of the feedground. Although at-risk elk decrease over time on Feedline and High Traffic sites as elk consume the daily ration of feed (Fig. 2), the current Feedline-style method of dispersing hay appears to facilitate density-dependent transmission within feedgrounds (Fig. 3). Because at-risk elk and investigation rates with FUs are correlated with overall feedground elk density only on High Traffic and Low Traffic sites (Fig. 4), it is presumable that elk density cannot be higher than on Feedlines. Activity budgets and abortion locations from telemetered feedground elk are unknown. However, dispersing feed evenly throughout the entire feedground rather than on Feedlines would likely reduce elk densities, investigation rates with

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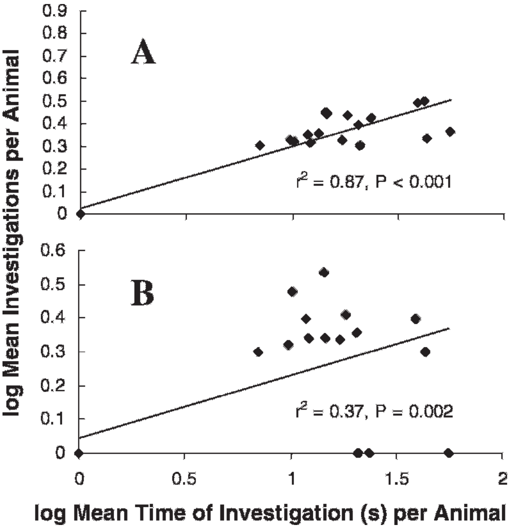

FIGURE 5. Log-transformed mean (A) sniffs and (B) contacts per female elk, with numbers linearly regressed over log-transformed mean time of investigation per female elk on feedgrounds in western Wyoming, USA.

aborted fetuses, and brucellosis seroprevalence, particularly if implemented during the presumed brucellosis-induced abortion period (February to June; Thorne et al., 1991; Roffe et al., 2004).

Our results conflict with those of Cross et al. (2007), who found that brucellosis antibody prevalence was associated with longer feeding seasons but not with population density. We believe that these differences are due largely to the temporal scale of the analyses. In this study, we have shown that at a given point in time, investigation levels with FUs appear to be density dependent (Figs. 1, 3, 4), and elk density within feedgrounds (based on at-risk elk; Fig. 2), as well as investigation rates of individual animals (Fig. 5), can fluctuate over time. Antibody prevalence, however, depends upon the cumulative number of exposures, which, in the case of elk feedgrounds, is associated with length of the feeding season (Cross et al., 2007). For example, at a given point in time during the feeding season, one may expect investigation levels with an aborted fetus to be higher on the NER (range of population sizes, 5,000–10,500 elk) than on the Dell Creek feedground (range of population sizes, 159–365 elk). Because of the shorter feeding season at the NER (range of total days fed, 0–122) than at Dell Creek (range of total days fed, 84–184; WGFD, 2007b, c), however, cumulative exposures and transmission rates are probably much less (Fig. 6). Thus, transmission levels can be density dependent at a given point in time, and antibody

TABLE 1. Total fetal units scavenged by individual species and within time periods following placement on feedground (FG) and winter free-range (WFR) locations in western Wyoming, USA.[a]

Scavenger species	Fetal units scavenged	
	FG	WFR
Magpie (*Pica pica*)	34	5
Raven (*Corvus corax*)	17	2
American Crow (*Corvus brachyrhynchos*)	2	0
Golden Eagle (*Aquila chrysaetos*)	4	0
Bald Eagle (*Haliaetus leucocephalus*)	4	1
Coyote (*Canis latrans*)	6	2
Red fox (*Vulpes vulpes*)	0	6
Gray Jay (*Perisoreus canadensis*)	0	1
Time period (hr)		
0–4	10	0
4–24	28	3
>24	2	5
Total	40	8

[a] Scavengers removed greater proportions of fetal units in shorter time periods from the FG than from the WFR locations ($\chi^2_{2,48}=18.205$, $P<0.001$).

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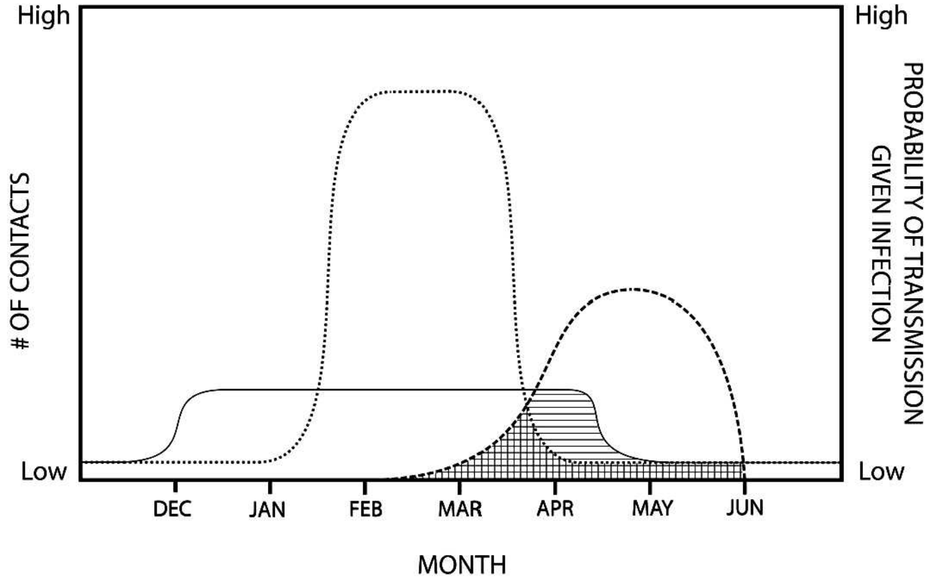

FIGURE 6. Conceptual illustration of how elk-fetus contact levels on feedgrounds with differing populations and lengths of feeding season (solid and dotted lines) may interact with the time period when individuals are infectious (dashed line) to affect the cumulative amount of brucellosis transmission (hashed areas). Supplemental feeding aggregates elk during the winter months, increasing the potential number of contacts. If abortions and infectious births occur late in the season, however, larger aggregations may not increase probability of brucellosis transmission if the timing of aggregation occurs outside of the peak period of transmission.

prevalence can be unassociated with the maximum density on feedgrounds because of the overpowering effect of total days spent on feedgrounds.

On feedgrounds, elk are gregarious (Murie, 1951) and may spend up to 6 hr attending feedlines (Thorne and Butler, 1976). Although up to 150 elk may investigate a fetus on a feedline (Cook et al., 2004), we found no behavioral predisposition among sex/age groups toward investigating FUs. On Feedlines, most elk appeared to investigate only those FUs placed within approximately 2 m of the Feedline, and typically, those were animals that were walking around animals actively consuming feed. On High Traffic and Low Traffic sites, individual elk appeared to investigate a FU only when it intersected their route of travel. When individual elk did investigate an FU, they generally would sniff or contact the FU one to two times after deliberate acknowledgement (i.e., alert posture; head forward, neck outstretched, ears raised) and approach to the FU. Similar to Thorne et al. (1979), we observed a few elk attempt to consume portions of FUs (n=3/810; 4%), yet of all elk sniffing FUs (n=810), about 36% made contact. If aerosol transmission of brucellosis is possible (Nicoletti, 1980), a lower dose of *Brucella* may be ingested from sniffing rather than contacting an FU (Cook, 1999), but the effects on antibody prevalence and/or culture prevalence have not been investigated. We found that the amount of time spent investigating FUs was higher for females than for juveniles or males, and occasionally, we observed females defend FUs from scavengers, including coyotes. This suggests that maternal instincts (Geist, 1982) may predispose females to exposure and infection.

Previous research documented that 100% (n=89) of pseudoaborted bovine fetuses placed on feedground and nonfeedground locations were consumed by 16 different species of scavengers (includ-

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ing unknowns; Cook et al., 2004). We observed eight individual species consuming 100% ($n=48$) of FUs placed on and off of feedgrounds, with scavenging rates faster both on and off feedgrounds (Table 1) than those documented by Cook et al. (2004). Explanation for observed differences in total scavenger species is likely due to differences in sampling methodologies (Cook et al., 2004: direct observation, track and scat identification; our study: direct observation). However, differences in scavenger species and scavenging rates is also likely due to time of year when each study was conducted (Cook et al., 2004: February to March and May; our study: March to early April). Many scavengers in the GYE are migratory, and it is likely that because our study did not occur into May, Turkey Vultures (*Cathartes aura*), Red-tailed Hawk (*Buteo jamaicensis*), or other avian species may not yet have arrived within the study area. Also, scavengers are known to exploit carrion more during periods of cold temperatures (e.g., winter; Selva et al., 2005) when availability of carrion is greater because of nutritional stress and/or predation (Crabtree and Sheldon, 1999; Wilmers et al. 2003a). Coyotes (Crabtree and Sheldon, 1999), Ravens (Stahler et al., 2002), Bald and Golden Eagles, Magpies, and red fox typically capitalize on spatially or temporally predictable sources of food, including those of predators (Wilmers et al., 2003b). Annually, up to several dozen elk may die on a feedground because of predation, disease, or unknown factors (WGFD, 2006a), providing a predictable food source for scavengers. Although risk of human harassment or harvest of some scavenger species (particularly coyotes and fox) can be relatively high on and adjacent to many feedgrounds, the nutritional supplementation provided by feedgrounds appears to concentrate foraging activity. Coyotes (Davis et al., 1979), wolves (*Canis lupus*; Tessaro and Forbes, 2004) and, presumably, red fox (Hoff et al., 1974) can be infected with brucellosis, likely from ingestion of contaminated tissues or fluids. Transmission of brucellosis from coyotes to cattle has been observed under experimental conditions of close confinement (Davis et al., 1988), yet no confirmed case of natural interspecific transmission from coyotes (Forbes, 1990), wolves, or any scavenger (including raptors) has been documented. Similar to Cook et al. (2004), we found that scavenging rates were faster on feedgrounds than on WFR locations and, unlike any study to our knowledge, that scavengers reduced the proportion of elk exposed to FUs. Essentially, scavengers native to the GYE likely function as a biologic control agent (Louda et al., 2003) of brucellosis. Expansion of a Best Management Practice by WGFD that eliminated targeted and recreational harvest of scavengers on or adjacent to feedgrounds by WGFD personnel (WGFD, 2007b) to include the general public may further increase scavenging rates and subsequently decrease investigation rates and antibody prevalence levels in feedground elk.

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