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Scavengers reduce potential brucellosis transmission risk in the Greater Yellowstone Ecosystem

Kimberly E. Szcodronski and Paul C. Cross†

Northern Rocky Mountain Science Center, U.S. Geological Survey, Bozeman, Montana 59715 USA

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Abstract. Scavengers likely play an important role in ecosystem energy flow as well as disease transmission, but whether they facilitate or reduce disease transmission is often unknown. In the Greater Yellowstone Ecosystem, scavengers are likely to reduce the transmission and subsequent spread of brucellosis within and between livestock and elk by consuming infectious abortion materials, thereby removing the infectious agent from the landscape. We used remote cameras to monitor the time to removal of simulated abortion materials by scavengers at 264 sites from February to June in 2017 and 2018 and assessed the effects of habitat and land management on time to removal in southwest Montana. Time to removal of fetal materials decreased in grassland habitats ($\bar{x}$ = 2.9 d, credible interval = [1.8–5.0]) in comparison to sagebrush habitats ($\bar{x}$ = 5.4 d [3.4–9.3]) and forest habitats ($\bar{x}$ = 5.2 d [3.3–9.0]). In addition, there was an 88% probability that time to removal of fetal materials was slower at sites where mammalian scavengers were actively reduced ($\bar{x}$ = 6.5 d [3.4–12.8]) compared to sites with no scavenger reduction ($\bar{x}$ = 4.1 d [2.3–7.8]). Our research indicates that if elk and livestock are commingling during the brucellosis risk period, there is a 90% probability that abortion materials will be removed by scavengers within 16 d across all sites. Coyotes, red foxes, golden and bald eagles, *Corvus* spp., and turkey vultures were the dominant scavengers, removing 90% of the fetal materials. Actions to maintain the breadth and diversity of scavengers on the landscape are potential management options that could reduce disease transmission risk to livestock in a system where the wildlife reservoir is difficult to address.

Key words: *Brucella abortus;* brucellosis; disease transmission; fetal disappearance; Greater Yellowstone Ecosystem; lead poisoning; scavenger; scavenger removal; wildlife disease.

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† **E-mail:** pcross@usgs.gov

Introduction

Terrestrial and avian scavengers provide an important yet understudied ecosystem function by removing carcasses from the landscape (DeVault et al. 2003, Dupont et al. 2012, Ćirović et al. 2016, Morales-Reyes et al. 2017). Dominant scavengers are declining worldwide (IUCN 2020), and in areas where scavengers are rare, carcasses remain on the landscape longer (Morales-Reyes et al. 2017, Peisley et al. 2017, Cunningham et al. 2018). Scavengers are likely to play a role in disease dynamics, although whether they facilitate or reduce transmission and spread is case-dependent (Beasley et al. 2015, Vicente and VerCauteren 2019). Scavengers can be exposed to pathogens via the consumption of infected carcasses and thus may be an additional host species that serves to transmit the infection (VerCauteren et al. 2012, Fischer et al.

2013). However, in cases where scavengers are unlikely to transmit the infection, they may serve to reduce the potential transmission among host species by quickly removing carcasses from the landscape (Bellan et al. 2013, Le Sage et al. 2019).

The abundance of scavengers and the diversity of scavenger species in an ecosystem may influence the removal rate of carcasses, which in turn impacts the role scavengers may play in disease transmission. Mammalian scavengers are impacted by predator–livestock conflicts, predator–game conflicts, and human resistance to the reintroduction of extirpated predators (Graham et al. 2005, Treves et al. 2006), which are all factors that lead to less scavengers on the landscape. Meanwhile, avian scavengers such as eagles, condors, and ravens are negatively affected by lead poisoning, land-use changes, collisions with vehicles and fences, and mortalities related to energy development including collisions with wind turbines and power lines (Kochert and Steenhof 2002, Smallwood and Thelander 2008, Bedrosian et al. 2012, Finkelstein et al. 2012, Loss et al. 2014).

Even in areas without empirical evidence of an overall decline in the abundance of scavengers, changes in scavenger communities can also have significant impacts on the time to removal of carcasses. Studies suggest that even in areas where overall species richness of scavengers increased due to the decline of dominant scavengers, mesoscavengers were unable to compensate for the decrease of dominant scavengers, and as a result, carcasses persisted on the landscape longer (Ogada et al. 2012, Olson et al. 2012, Morales-Reyes et al. 2017, Cunningham et al. 2018). The benefits of a full suite of scavengers being present on the landscape have been quantified in these studies, as observed in the decline of the Tasmanian devil (*Sarcophilus harrisii*) in Tasmania (Cunningham et al. 2018), the extirpation and decline of vultures (*Accipitridae* spp. and *Cathartidae* spp.) in Kenya and Spain (Ogada et al. 2012, Morales-Reyes et al. 2017), and the removal of racoons (*Rocyon lotor*) in agroecosystems in the United States (Olson et al. 2012).

Scavengers likely play an important role in the Greater Yellowstone Ecosystem (GYE), USA, by reducing the transmission risk of brucellosis, a chronic bacterial disease caused by *Brucella abortus*. Brucellosis is a major concern for livestock producers due to potential transmission of *B. abortus* from elk (*Cervus canadensis*) to livestock. Infection by *B. abortus* leads to reproductive failure and abortion in 50% of infected female elk within the first year post-infection (Thorne et al. 1978). The disease is primarily transmitted within elk and between elk and livestock when individuals contact infected reproductive tissues left behind after abortion events including fetuses, placentas, and birthing fluids (Thorne et al. 1978, Cheville et al. 1998, Thorne 2001, NASEM 2017). Documented brucellosis-induced abortion events have occurred in the GYE from February through July, with the highest transmission risk period from March through May (Cross et al. 2015).

Brucella abortus can persist in abortion materials for several weeks to several months depending on the abiotic conditions at the time of the abortion event (Aune et al. 2012). The risk of transmission to elk or livestock is therefore likely a function of how long infected abortion materials remain on the landscape and are available to be contacted. As would be expected, *B. abortus* seroprevalence is high on supplemental feedgrounds for wintering elk in Wyoming due to unnaturally high elk densities. However, seroprevalence has also increased in some free-ranging elk populations in Montana in association with larger group sizes and now these populations have comparable *B. abortus* seroprevalence to elk on feedgrounds (Cross et al. 2010, Scurlock and Edwards 2010, Proffitt et al. 2015, Brennan et al. 2017). High densities of elk subsequently attract scavengers to feedgrounds where they can quickly remove fetuses, and therefore potentially transmission risk, from the landscape (Cook et al. 2004, Maichak et al. 2009). Faster removal time of abortion materials on feedgrounds in combination with larger elk populations and group sizes in Montana may help explain why the seroprevalence in fed populations is similar to some unfed elk populations.

Three previous studies have investigated the time to removal of fetal materials by scavengers (hereafter, time to removal) in Wyoming. Maichak et al. (2009) found that 70% of elk fetuses were removed by scavengers within 24 h from Wyoming state feedgrounds, while 38% were removed within 24 h from neighboring winter range locations where elk were not fed. Similarly, Cook et al. (2004) found the mean removal rate of bovine fetuses was 27 h at the National Elk Refuge in Wyoming, 40 h at Wyoming state feedgrounds, and 58 h at native winter range locations within Grand Teton National Park. In contrast, Aune et al. (2012) conducted a similar study near Yellowstone National Park and estimated the mean removal rate of bovine fetuses was 18 d (range: 1–78 d). We expand on this work by investigating the role of habitat and management on time to removal in areas of likely transmission between elk and livestock in Montana.

During 2017–2018, we investigated time to removal of bovine fetal materials, meant to stimulate an elk abortion event, in the southwest Montana portion of the GYE. The purpose of this study was to quantify the length of time fetal materials remained on the landscape across habitat types (grassland, sagebrush, forest) and management types (no mammalian scavenger reduction, recreation-based mammalian scavenger reduction, active mammalian scavenger reduction) on rangelands that are used for livestock grazing. We sought to estimate how habitat and predator management influenced scavenger communities and their potential impact on brucellosis transmission in elk. We hypothesized that time to removal would be fastest in more open habitats (grassland > sagebrush > forest) due to increased detectability of carcasses by avian and terrestrial scavengers. We further hypothesized that sites with active mammalian scavenger reduction would have slower time to removal in comparison to sites with recreation-based mammalian scavenger reduction and no mammalian scavenger reduction due to decreased abundance and diversity of scavengers in those areas.

Methods

Study area

We established 13 study locations in southwest Montana on private property and U.S. Forest Service (USFS) lands where elk and livestock are likely to commingle from February to June (Table 1). Eighty percent of sites were on private ranches in the Madison Valley, Paradise Valley, Gallatin Valley, and Ruby Valley ranging in size from 1896 to 45,977 hectares ($\bar{x}$ = 9908 ha). The remaining sites were on public land in the Gravelly Range and Tobacco Root Mountains in the Beaverhead-Deerlodge National Forest and in the Custer Gallatin National Forest surrounding Yellowstone National Park. Study locations near Yellowstone National Park were added in 2018 to compare our findings with those of Aune et al. (2012) who conducted a similar study in that area.

We targeted our sampling effort to assess three different management regimes with varying degrees of scavenger reduction practices including the following: (1) private ranches with no mammalian scavenger reduction, (2) private ranches with active mammalian scavenger reduction, and (3) USFS lands with recreational hunting that includes unregulated coyote and fox hunting and hunting seasons on mountain lions and wolves administrated by Montana Department of Fish, Wildlife and Parks. Ranches with no scavenger reduction did not shoot or trap any scavengers on their property, while ranches with active scavenger reduction removed common mammalian scavengers (e.g., coyotes and foxes) from their property as part of their management practices. There were three dominant habitat types in the study area including intermountain grasslands, sagebrush steppe (*Artemisia* spp.), and mixed-conifer forest including subalpine fir (*Abies lasiocarpa*), Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), and whitebark pine (*Pinus albicaulis*). We evenly distributed sites across the dominant habitat types (33% in grassland, 32% in sagebrush, 35% in forest) and across the time span of the brucellosis transmission risk period. Elevations ranged from 1349 to 3101 m, with habitat types distributed across the elevation gradient.

Sampling procedures

We acquired bovine fetuses and placentas from a livestock processing plant, where they were confirmed disease-free based on antemortem and postmortem inspection of the cows from which they came by an USDA veterinary inspector. Fetus collection was restricted to the early stages of pregnancy to maintain a consistent size and development stage across sites. Fetuses ranged in size from 1.3 to 5.4 kg. Upon collection, we weighed the fetuses and placentas, placed them in plastic bags, and froze them until deployment in the field. We thawed the fetal

Table 1. Distribution of camera stations across 13 study locations in southwest Montana from 2017 to 2018 and the raw time to removal (mean ± SE) of fetal units by scavengers for each study location.

Study location	General area	Management type	2017	2018	Total	Raw time to removal (d)
A	Madison Valley	active reduction	7	3	10	2.1 ± 0.6
B	Gallatin Valley	no reduction	30	21	51	3.5 ± 0.6
C	Madison Valley	active reduction	8	8	16	4.0 ± 0.5
D	Gravelly Range	USFS	4	14	18	3.3 ± 0.9
E	Paradise Valley	no reduction	12	0	12	2.2 ± 0.6
F	Madison Valley	active reduction	8	7	15	6.3 ± 1.8
G	Paradise Valley	no reduction	0	21	21	3.7 ± 0.7
H	Gardiner	USFS	0	3	3	1.1 ± 0.1
I	Ruby Valley	no reduction	12	13	25	3.9 ± 0.8
J	Madison Valley	no reduction	17	0	17	1.6 ± 0.4
K	Tobacco Root	USFS	2	17	19	4.3 ± 0.8
L	Madison Valley	active reduction	9	8	17	6.5 ± 1.7
M	West Yellowstone	USFS	0	9	9	0.8 ± 0.2

Notes: Management types include private ranches with no scavenger reduction (no reduction), private ranches with active scavenger reduction (active reduction), and U.S. Forest Service lands (USFS). Out of the 264 cameras deployed, 233 resulted in usable data and the number of usable sites is displayed for 2017, 2018, and the total.

material before it was placed in the field to mimic an actual abortion event.

We used ArcGIS software (ESRI 2015) to randomly select sites in our study area. Sites were ≥1 km apart from one another during each 30-d period. All sites were >800 m from buildings and campgrounds and were located across varying degrees of human activity from low to high activity depending on the distance to the nearest road (from 0.2 to 5.4 km).

We placed bovine fetuses and placentas on the landscape within the brucellosis risk transmission period from February 1 to June 15 (Cross et al. 2015) in 2017 and 2018. At each site, we placed one fetus and one placenta (hereafter, fetal unit) on the ground and attached a remote, motion-detecting camera (Browning Dark Ops Elite HD) to a tree, fencepost, or metal T-post 10 m away from the fetal unit. To decrease human scent contamination that may have influenced scavenger behavior at sites, we transferred fetal units directly to the ground from the storage bags and wore latex gloves when processing the fetal units. Remote cameras were activated by infrared and movement and were used to monitor the scavenger community as well as the time to removal of the fetal units by scavengers.

We investigated each site after 2–4 weeks had passed and collected the camera if no sign of the fetal unit could be found. If portions of the fetal unit remained on-site, we left the camera in place and continued monitoring the site. We evaluated camera data to determine time to removal, defined as the amount of time from the deployment of the fetal unit in the field until it was completely removed by scavengers. We considered a fetal unit to be removed if it was consumed in view of the camera or if scavengers removed the fetal unit from view of the camera. If the fetal unit was moved off-camera, we assumed it was consumed shortly after or moved to an area where brucellosis transmission risk was minimal (e.g., fox den, eagle nest). We deployed VHF transmitters (Advanced Telemetry Systems, model A4050) on 30 fetuses distributed across habitat and management types to test the assumption of consumption upon removal of the fetal unit off-camera. We checked the VHF transmitters every 3–5 d to investigate distances moved and off-camera consumption times.

We deployed cameras at 264 sites and 233 of those sites resulted in usable time to removal data (no camera failure and camera remained in position). For cases when the exact time of removal was not photographed, we used the midpoint between the time the fetal unit was last seen in a photograph and the first time the fetal unit was missing. There were 36 occasions when the last time the fetal unit was seen on camera was over 24 h later than the first time it was documented as missing and 12 of those occasions the time difference was over 80 h. We explored whether dropping these 36 occasions made a difference in the analysis and found the parameter estimates of the full data and the data with the 36 occasions removed were very similar with slightly wider confidence intervals (Appendix S1: Table S1).

We defined primary scavengers as those that ended up removing ≥50% of the fetal unit and secondary scavengers as those that removed <50% of the fetal unit. The primary scavenger that was the first to arrive and consume the fetal unit at each site was used in species-specific analyses of the camera data (n = 205). In 71 occasions, there was another primary scavenger who arrived second at the site and consumed ≥50% of the fetal unit, but these were not used in the species-specific analyses.

Statistical analyses

The time to removal data we collected naturally fit into a time-to-event survival model. We initially used a parametric accelerated failure time survival analysis framework implemented in R version 3.6.1 (R Development Core Team 2019) using the package *survreg* (version 3.1-12; Therneau 2015, Therneau and Grambsch 2000) and included a random effect of the 13 study locations. We first investigated whether the exponential, Weibull, logistic, lognormal, log-logistic, or Gaussian error distribution was the best fit based on Akaike information criteria (AIC). We also used AIC to evaluate whether potential confounding effects of year, day of year, elevation, snow depth (collected on site), or distance to road (Montana State Library 2017) should be included when assessing the effects of habitat type (grassland, sagebrush, and forest) and management type (private ranches with no scavenger reduction, private ranches with active scavenger reduction, and USFS land). We assessed model fit using the marginal and conditional R^2 calculations of Nakagawa and Schielzeth (2013).

After removing two sites deployed in June where the fetuses quickly decomposed and were not consumed by vertebrate scavengers, our data had no left or right censoring, making our survival analyses the same as a generalized linear mixed-effects model with a log link function. To assess the statistical significance of both habitat and management, we implemented a fully Bayesian modeling approach in order to facilitate probabilistic statements and derive aggregate parameters without relying on the asymptotic properties of the delta method or potential issues with p-values in hierarchical models.

Based upon preliminary analyses outlined above, we modeled the natural logarithm of time-to-remove, τ_{ij}, for deployment i at study location j as a function of habitat type (h_k for $k = 1$ or 2 for grassland and sagebrush, respectively), management type (m_l for $l = 1$ or 2 for no scavenger reduction and USFS, respectively), and a random effect δ_j of the 13 study locations. We considered forest habitats with active scavenger reduction to be the baseline. Thus, our model was of the form: $\log(\tau_{ij}) \sim \text{Normal}(\alpha + h_{k[i]} + m_{l[i]} + \delta_j, \sigma^2)$, where $\delta_j \sim \text{Normal}(0, \psi^2)$. For prior distributions, we assumed relatively uninformative priors for the log scale where α, h, m, were Normal (0, 1000) and σ^2 and ψ^2 were Uniform (0, 4). We ran the models in R using *R2jags* (version 0.5-7; Su and Yajima 2020) and *JAGS* (version 4.3.0; Plummer 2019) for 50,000 Markov chain Monte Carlo iterations on three chains with 25,000 burn-in iterations. We assessed convergence using trace plots and R_{hat} values, which were <1.0001 (Brooks and Gelman 1998). Our parameter estimates were very similar to those produced by *lme4* (version 1.1-23; Bates et al. 2015), so we are confident that our results are not strongly influenced by our choice of prior distributions. We back-calculated the predicted mean time to removal using $E(\tau_{ij}) = \exp(\alpha + h_{k[i]} + m_{l[i]} + \delta_j + \sigma^2/2 + \psi^2/2)$.

Results

We recorded 15 species (Fig. 1a) of primary scavengers (consuming ≥50% of a fetal unit) including coyotes (*Canis latrans*), golden eagles (*Aquila chrysaetos*), *Corvus* spp. (ravens; *Corvus corax* and American crows; *Corvus brachyrhynchos*), red foxes (*Vulpes vulpes*), bald eagles (*Haliaeetus leucocephalus)*, turkey vultures (*Cathartes aura*), black bears (*Ursus americanus*), red-tailed hawks (*Buteo jamaicensis*), gray wolves (*Canis lupus*), mountain lions (*Puma concolor*), American martens (*Martes americana*), bobcats (*Lynx rufus*), great horned owls (*Bubo virginianus*), black-billed magpies (*Pica hudsonia*), and striped skunks (*Mephitis mephitis*). Species-specific data were comparable for the primary scavengers that were

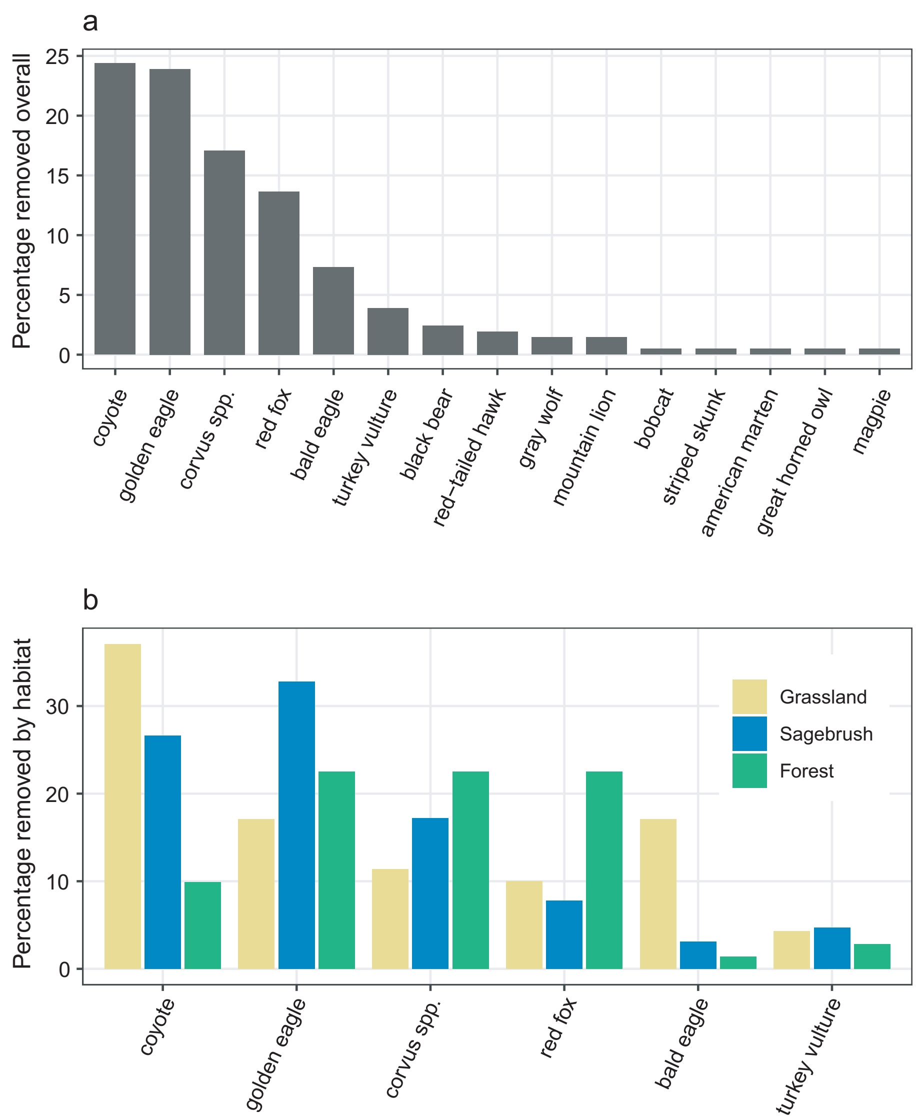

Fig. 1. (a) The percentage of fetal units removed by individual scavenger species (first-to-consume primary scavenger) for all study sites (n = 205) in southwest Montana in 2017 and 2018 and (b) the percentage of fetal units removed by the top six most common scavenger species (first-to-consume primary scavenger) across all study sites, displayed by habitat type (yellow, grassland n = 79; blue, sagebrush n = 70, green; forest n = 84). The remaining species from "a" are not included in "b" (i.e., the percentage removed for each habitat type does not sum to one across the six species presented).

first-to-consume and second-to-consume, so here we present the first-to-consume data (n = 205) and we include the second-to-consume data (n = 71) in Appendix S1: Fig. S1. Coyotes and golden eagles were the two most dominant scavengers, each consuming 24% of the total fetal units (48% of fetal units combined; Fig. 1a). The composition of species that were the most common dominant scavengers of fetal units shifted across habitat types (Fig. 1b). Corvids, including *Corvus* spp. and magpies, were the first scavenger species to discover the fetal unit at 58% of the sites, but they usually removed a minor portion of the fetal unit before a mammalian species or large bird of prey discovered the fetal unit. Avian species generally scavenged during the daylight hours (97%), whereas mammalian species scavenged in both day (39%) and night (61%).

The raw mean time to removal of fetal materials by scavengers across all sites was 3.6 d (±0.3 SE, range = 0.1–27 d, n = 233; Figs 2, 3a). The predicted mean time to removal averaged across all management types was faster in grassland habitats ($\bar{x}$ = 2.9 d, 95% credible interval = [1.8–5.0]) compared to sagebrush (5.4 d, 95% credible interval = [3.4–9.3]) and forest (5.2 d, 95% credible interval = [3.3–9.0]; Fig. 3b). Relative to management types, the predicted mean time to removal was faster on USFS land (3.0 d, 95% credible interval = [1.4–6.0]) and ranches with no scavenger reduction (4.1 d, 95% credible interval = [2.3–7.8]) in comparison to ranches with active scavenger reduction (6.5 d, 95% credible interval = [3.4–12.8]; Fig. 3b).

Out of the 30 fetuses that we tracked using radio telemetry, 28 resulted in usable data. Scavengers consumed seven fetuses on camera at the deployment location and scavengers moved 21 fetuses away from the deployment location. In the instances where scavengers moved the fetuses, they were moved a mean distance of 604 m (±162 SE, range = 7–2814 m). Of the fetuses that were moved, 19 were consumed within a few days of the removal event and two remained on the landscape for 1–1.5 months. Although fetuses remained on the landscape longer than the camera indicated in those two cases, one fetus was buried

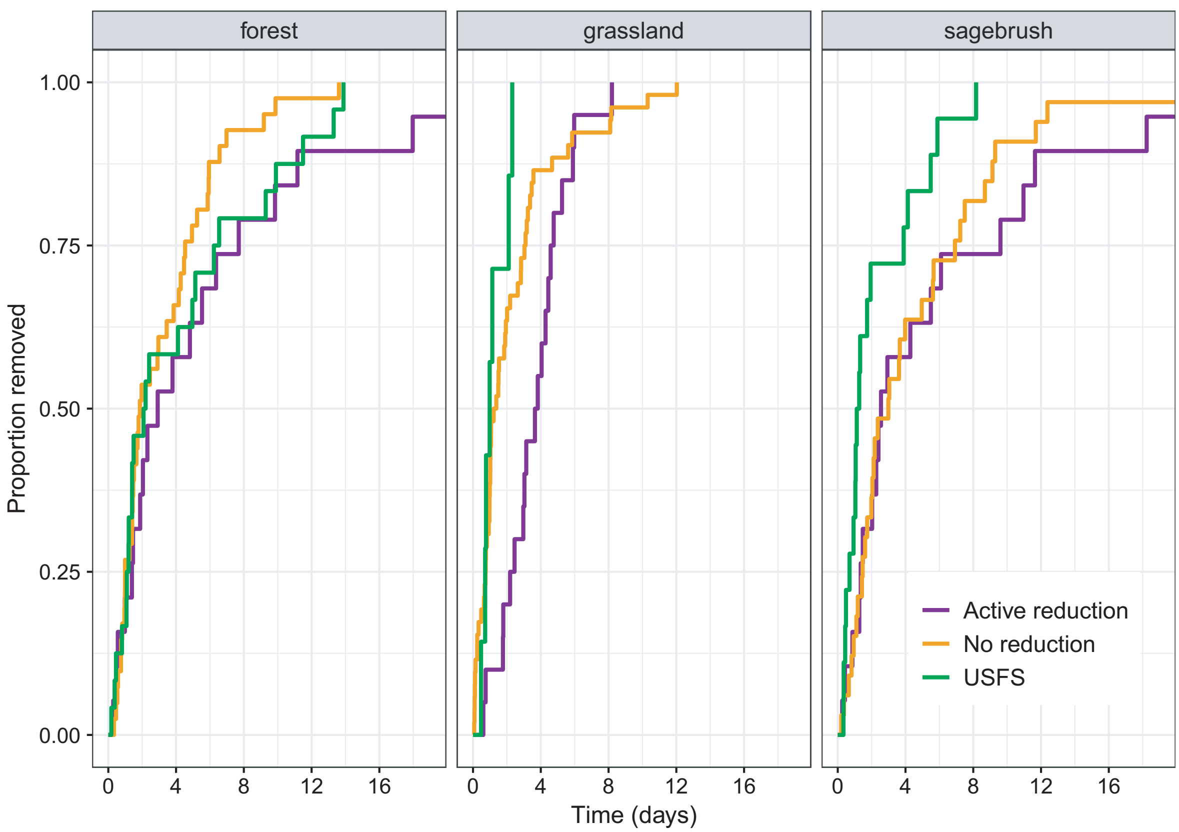

Fig. 2. The proportion of fetal units removed by scavengers (first-to-consume primary scavenger) over time in days across habitat types (forest n = 84, grassland n = 79, sagebrush n = 70) for each management type in southwest Montana in 2017 and 2018. Management types include private ranches with active scavenger reduction (active reduction, purple), private ranches with no scavenger reduction (no reduction, orange), and U.S. Forest Service land (USFS, green).

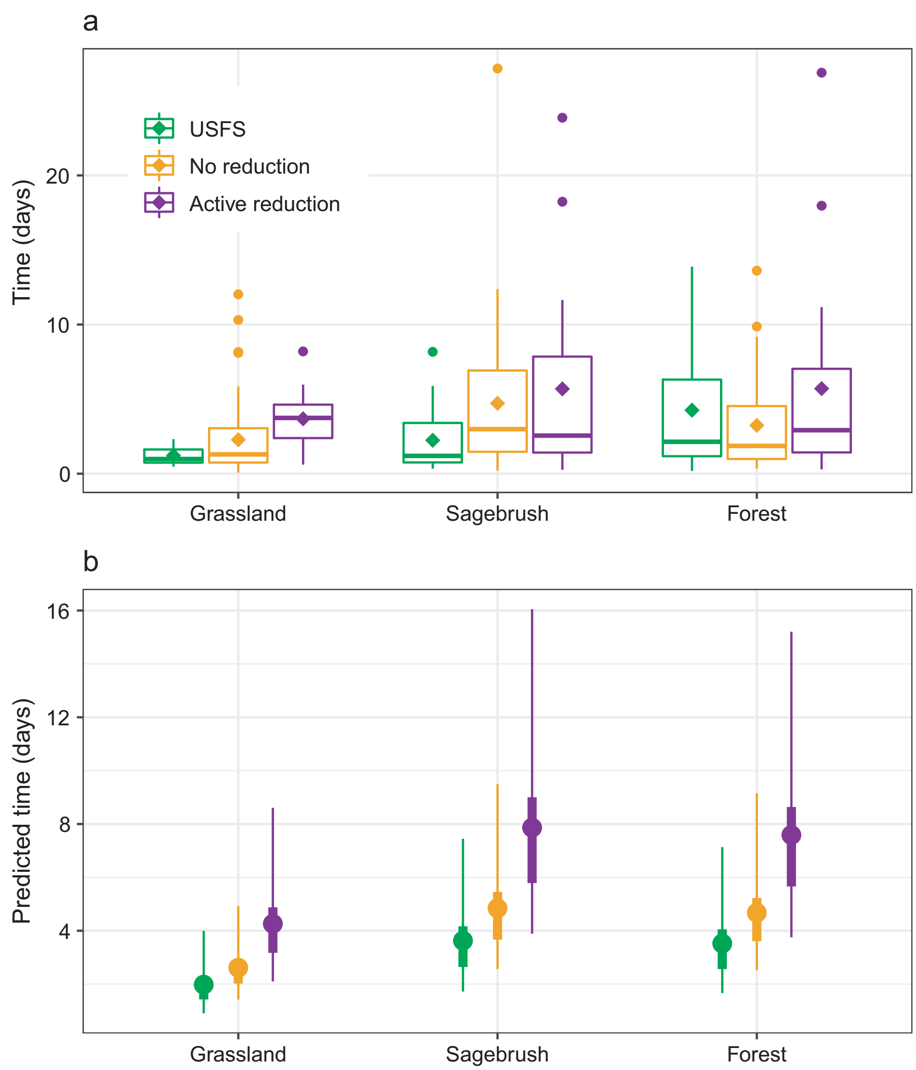

Fig. 3. The time to removal (in days) of fetal units from the time of deployment until removal by a scavenger across all sites (n = 233) in southwest Montana in 2017 and 2018. Management types include U.S. Forest Service land (USFS), private ranches with no scavenger reduction (no reduction), and private ranches with active scavenger reduction (active reduction). The box plots (a) display the raw data with the line indicating the median (50th percentile of the data) and the diamond indicating the mean. The box displays the inter-quartile range (IQR), which goes from the 25th to 75th percentile of the data and the whiskers extend to the furthest data point within 1.5 times the IQR. The line plots (b) display the predicted time to removal from a time-to-event survival model using a fully Bayesian modeling approach. The wide lines display the 50% credible interval, and the thin lines display the 95% credible interval.

under ~20 cm of snow and one fetus was stashed under grass near a fox den and as a result, the hypothetical risk of brucellosis transmission to elk or cattle was negligible at the cached locations. We tracked the fetuses within 2–5 d after removal from camera, so while we are unable to know the exact number of days between removal on camera and consumption of the fetuses, 19/21 (90%) were consumed within the same general timeframe as those fetuses that remained on camera.

Six grazing species including elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), pronghorn (*Antilocapra americana*), American bison

(*Bison bison*), and cattle (*Bos taurus*) investigated the fetal units by sniffing and making contact; however, they appeared to not participate in scavenging. Elk contacted the fetal units at 32 out of 245 sites (13%). We documented a minimum of 142 individual elk contacting fetal units, including two events where ~20 individual elk contacted a fetal unit over the course of one hour.

Our preliminary statistical modeling results suggested that a lognormal error distribution was the best model among those explored based on AIC (Appendix S1: Table S2). Fetus size did not improve the model fit based upon AIC, so we did not include fetus size in the final model (Appendix S1: Table S3). The covariates year, day of year, elevation, snow depth, and distance to road did not improve the model fit based upon AIC and so were dropped from later analyses (Appendix S1: Table S4). Our final model related time to removal as a function of management and habitat as well as a site-specific random effect (Appendix S1: Tables S1, S4). The marginal R^2 and conditional R^2 of this model were 0.15 and 0.33, respectively, indicating that there remains a large fraction of the variation in the time to removal to be explained (Fig. 3). Based on the posterior probability distribution; however, there was over a 99% probability that scavenging occurred more quickly in grassland habitats compared to forest or sagebrush habitats ($h_{\text{grassland}} = -0.58$, 95% credible interval = [−0.96, −0.22] relative to forest; Fig. 3b; Appendix S1: Table S1). In addition, there was an 88% probability that time to removal in areas with no scavenger reduction was faster than in areas with active scavenger reduction ($m_{\text{no reduction}} = -0.49$ [−1.34, 0.31] relative to active scavenger reduction; Fig. 3b; Appendix S1: Table S1). Time to removal on USFS land was the fastest (Fig. 3). On private rangelands, the predicted mean time to removal at sites with active scavenger reduction in grassland habitats was 4.2 [2.1–8.1] d and in sagebrush habitats was 7.8 [3.9–15.8] d (Fig. 3 b). In comparison, the predicted mean time to removal at sites without scavenger reduction in grassland habitats was 2.6 [1.5–5.0] d and in sagebrush habitats was 4.9 [2.6–9.6] d (Fig. 3b). For a given site, we estimated 90% of fetuses disappeared within 9.7 d if it was on USFS land, 13.2 d from a ranch with no scavenger reduction, and 20.9 d from a ranch with active scavenger reduction. We estimated 90% of fetuses disappeared within 11.8 d from grassland, 21.7 d from sagebrush, and 20.9 d from forest.

Discussion

Scavengers can play an important role in ecosystems by removing carcasses from the landscape that may harbor infectious diseases, yet they face significant threats from the effects of habitat disruption and disturbance as well as recreational and management removals by humans. Our study is the first to explicitly explore habitat and management effects on time to removal of fetal materials by scavengers on rangelands used for cattle grazing in southwest Montana, where the potential transmission of brucellosis from elk to cattle is most likely. We documented 15 scavenger species and of those, coyotes, red foxes, golden and bald eagles, *Corvus* spp., and turkey vultures consumed 90% of the fetal units. The mean time to removal was between three to five days and 90% of the sites were scavenged within 10–20 d depending on the habitat and management type. We determined there was a high probability (88%) that ranches with active scavenger reduction have slower removal time of abortion materials, potentially exposing those ranches to higher spillover risk given the same background rate of brucellosis prevalence in elk. We also detected time to removal was faster in grassland habitats than sagebrush and forested habitats, which is important given that elk congregate in open habitats where cattle are likely to be present (Proffitt et al. 2011, Brennan et al. 2015). These findings are relevant within the designated brucellosis surveillance area where scavenger communities' impact on the removal of abortion materials is important in the context of better understanding how brucellosis spreads and increases prevalence, as well as for reducing disease transmission risk. Our results may also have general implications for other diseases that can be indirectly transmitted through carcasses, such as chronic wasting disease (Miller et al. 2004) and anthrax (Hugh-Jones and de Vos 2002, Turner et al. 2014), where scavengers may play a sanitizing role. Beyond brucellosis, carcasses can be vectors for many wildlife diseases, so the role of scavengers is likely significant for other disease systems as well. Our study highlights the need for further research on the relationship between scavengers and disease to assess whether scavengers facilitate or decrease disease spread for each disease system.

We observed time to removal was 1.6 and 2.2 times faster on private ranches with no scavenger reduction and USFS lands, respectively, compared to private ranches with active scavenger reduction. It is possible that removal rates are faster on USFS land and ranches with no scavenger reduction given that there may be a greater abundance and density of mammalian scavengers on these landscapes. It is also possible that mammalian scavenger behavior may change on ranches with active scavenger reduction, leading to mammalian scavengers that are more skittish and less likely to take risks at a site where a fetal unit was deployed. It was unexpected that USFS lands and ranches with no scavenger reduction had similar removal rates, given that dominant mammalian scavengers can be harvested without quotas across USFS lands in Montana, although scavenger reduction on USFS lands is for recreational purposes and is likely to be sporadic in comparison to private ranches who are protecting livestock operations. Plus, harvest on USFS lands is likely more limited than on private ranches due to accessibility restrictions on USFS lands in our study area for much of the year and the potential for harvest by humans is likely to be offset by the sheer amount of habitat USFS lands provide for scavenger species. Because of these factors, the abundance and density of dominant mammalian scavenger species may be similar on USFS lands and ranches with no scavenger reduction, which may be responsible for the similar time to removal we observed in these two management types. Rayl et al. (2019) estimated that in areas with the potential of commingling between livestock and elk in the designated brucellosis surveillance area, 98% of the relative risk of elk abortion events occurred on private ranchlands and therefore the greatest risk of disease spillover was on private ranchlands (Rayl et al. 2019). Our research indicates that promoting, or at least not actively reducing, scavengers in these areas could serve as management practices that decrease the likelihood that cattle will encounter abortion materials on the landscape.

Time to removal was 1.8 and 1.9 times faster in grassland habitats compared to forest and sagebrush habitats, respectively. The faster time to removal we observed in grasslands may be due to better visibility of the fetal units for avian scavengers and better scent detection of fetal units for mammalian scavengers as scent likely travels further in open areas. Furthermore, mammalian scavengers may use birds as a visual cue to locate food sources (Kane and Kendall 2017) and the congregations of birds are visible at a longer distance in open habitats as opposed to closed, forest habitats. Proffitt et al. (2011) found that elk prefer forest and shrublands during the transmission risk period, but this selection decreases as snowpack increases, pushing elk into lower elevation grassland habitats. Elk congregating in large groups in grasslands during periods of high snowpack (Brennan et al. 2015, Proffitt et al. 2015, Rayl et al. 2019) likely increases brucellosis transmission risk because these also tend to be areas where cattle are located.

Our estimated time to removal was notably faster than the mean of 18.2 d observed by Aune et al. (2012) who conducted a removal study in a similar area as two of our study locations in the Custer Gallatin National Forest surrounding Yellowstone National Park ($\bar{x}$ = 21 h ± 3.2 SE; Table 1). It is possible the deviation from Aune et al. (2012) was due to differences in sampling methodologies or the density and composition of scavenger species may have shifted since the early 2000s when their fieldwork was conducted. Fetal units averaged across our study area were removed at a slower rate ($\bar{x}$ = 3.6 d) than on supplemental elk feedgrounds in Wyoming (<2 d; Cook et al. 2004, Maichak et al. 2009). This is not surprising considering the high abundance of scavengers that are associated with elk feedgrounds (Cook et al. 2004, Maichak et al. 2009).

We documented numerous instances of elk, bison, and cattle investigating and contacting fetal units, which is the dominant transmission mechanism of brucellosis and creates the possibility of a spillover event between elk and cattle. Recorded elk contacts were relatively uniformly distributed over time (Appendix S1: Fig. S2), suggesting that quicker removal times are likely to reduce contacts and subsequently decrease disease transmission risk. It is difficult to relate our results to the total reduction in contacts with fetal units because it is unclear how many contacts and transmission events occur within minutes of an abortion event. This would be hard to simulate or measure in a natural setting since elk are displaced by the presence of people setting up sampling sites.

Scavengers are encountering a mosaic of management strategies as they move across the landscape, including a patchwork of landownership, and it is not clear at what spatial scale impacts from the management actions of adjacent properties influence scavenger abundance, density, and behavior. There could be potential annual variability of mammalian scavenger reduction as well depending on the timing of livestock calving seasons and grazing system rotations. Additionally, our classification of management types was the level of detail available for the scope of this study; however, we acknowledge that there is variation within each type and our simplified classification may not have truly captured the discrepancy of impacts to scavengers on the landscape. While there are counts available for the number of furbearer species trapped in Montana (Giddings 2014) and the number of coyotes removed for damage complaints in the United States (USDA APHIS 2018), we were not able to determine the intensity or spatial distribution of limitless recreational hunting on USFS lands or the exact removal numbers on private lands.

Regardless of habitat type or management strategies, the amount of time fetal units remained on the landscape before they were removed by scavengers in our study area was less than the estimated time *B. abortus* remains viable on the landscape (several days to weeks; Cook et al. 2004, Aune et al. 2012). Because the amount of time *B. abortus* remains on the landscape is directly tied to transmission risk (Aune et al. 2012, Cross et al. 2015), our research indicates scavengers, particularly coyotes, eagles, and foxes, are important species on the landscape for removing brucellosis transmission risk, especially on private rangelands. Limited research on canids and brucellosis provides some evidence that canids might become exposed to *B. abortus* (Scanlan et al. 1984, Davis et al. 1988, Tessaro and Forbes 2004), but are unlikely to transmit brucellosis or facilitate disease transmission and thus serve an important ecosystem function by reducing disease risk. While mammalian scavengers have been demonstrated to be important components of the scavenger community (Cook et al. 2004, Maichak et al. 2009), our results also highlight the critical role avian scavengers, especially golden eagles, play in removing potentially infected materials.

This study has direct implications for livestock producers whose land overlaps with elk during the brucellosis transmission period. Our results suggest that if ranchers are moving livestock to grazing land where elk have been present during the likely brucellosis-induced abortion period, there is a 90% probability across all sites that fetuses will be removed by scavengers within 16 d. We recognize that although mammalian scavengers can help reduce disease transmission risk, there is a balance for ranchers to consider between the costs of negative impacts to livestock operations from mammalian scavengers and the benefits they provide in removing abortion materials from rangelands. Studies suggest that livestock losses to predators appear to be relatively low on a landscape scale (Graham et al. 2005), but losses are not uniform spatially and small losses can represent a significant burden to ranchers which may lead to more aggressive scavenger removal actions.

In areas where mammalian reduction is an important management action for working landscapes, avian scavengers are also effective at removing carcasses and therefore may help offset the reduction of mammalian scavengers in an area. However, there are prominent threats for avian scavengers with the impacts of collisions with power lines and wind turbines, electrocutions, and habitat disturbance (Harness and Wilson 2001, Kochert and Steenhof 2002, Smallwood and Thelander 2008) being some of the primary drivers of struggling populations. Lead poisoning is an increasingly well-studied threat to raptors globally (Church et al. 2006, Herring et al. 2017, Pain et al. 2019) that causes mortality and a wide range of physiological and neurological issues (Finkelstein et al. 2012, Haig et al. 2014, Ecke et al. 2017), which could reduce their capacity to remove carcasses effectively and efficiently from the landscape. Lead poisoning is prevalent in golden eagles in southwest Montana with lead being detected in the blood of 97% of wild-caught eagles in southwest Montana, with 45% of those showing acute lead levels (Harmata and Restani 2013). Much of this lead poisoning likely comes from hunter-killed carcasses (Craighead and Bedrosian 2008, Bedrosian et al. 2012, Cruz-Martinez et al. 2012) and from recreational shooting of ground squirrels (McTee et al. 2019), coyotes, and other unregulated species. These studies highlight the potential importance of carcass removal programs and using more wildlife-friendly non-lead ammunition for hunting and demonstrate the role state game agencies, conservation groups, and the hunting public can play in reducing the amount of lead available to scavengers on the landscape while educating others on the potentially harmful effects of lead-based ammunition.

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Data Availability Statement

Data are available from the U.S. Geological Survey: https://doi.org/10.5066/P9QVWB3D

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3783/full