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Daniel Kinka
Utah State University

Jeffrey T. Schultz
USDA-National Wildlife Research Center

Julie K. Young
USDA-National Wildlife Research Center, julie.k.young@usda.gov

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Wildlife responses to livestock guard dogs and domestic sheep on open range

Daniel Kinka^{a,b,1}, Jeffrey T. Schultz^c, Julie K. Young^{c,*}^a Department of Wildland Resources, Utah State University, Logan, UT 84322, USA^b American Prairie Reserve, P.O. Box 908, Bozeman, MT 59771, USA^c USDA-National Wildlife Research Center, Predator Research Facility, 4200 South 600 East Cache County Rd., Millville, UT 84326, USA

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ABSTRACT

Domestic sheep (*Ovis aries*) are an attractant to carnivores; however, sheep are often accompanied by humans and livestock guardian dogs (LGDs; *Canis familiaris*), which defend sheep from depredation. Sheep also compete directly with wildlife for grazing resources. Although practiced for millennia in much of the world outside North America, the effect that transhumance has on wildlife is poorly understood. To test the effect of sheep bands (sheep, humans, and LGDs) on wildlife, we modeled the detection probability of wild mammals relative to the presence of sheep bands in the Northwestern United States. Sheep band presence was associated with a reduction of about half in the likelihood of detecting large carnivores (*Ursus americanus*, *Ursus arctos*, *Canis lupus*, and *Puma concolor*, $p < 0.05$) and deer (*Odocoileus* spp., $p < 0.01$), both while the band was present and after it left the area. Contrastingly, coyotes (*Canis latrans*) were more than three times as likely to be detected when sheep bands were present ($p < 0.001$), and twice as likely after sheep bands left ($p < 0.01$). Coyotes were the only species we modeled that was more likely to be detected when a sheep band was present. It is unclear how long these effects persist after a sheep band has moved through an area, but our results suggest that transhumance temporarily displaces many large mammals, which results in mesopredator release of coyotes. This study suggests there is a tradeoff between the conservation benefits provided by LGDs and humans protecting sheep and the costs of displacement to some wild mammals.

1. Introduction

How animals impact the space use of one another is generally determined by their relative position in a trophic hierarchy, and the level of territoriality between conspecifics and intraguild competitors. Prey respond to risk effects imposed on them by predators (Moll et al., 2017), with predators imposing both consumptive and non-consumptive effects on prey (Sih, 1980; Abrams, 1984). The finding that prey experience a landscape of fear, where non-consumptive effects shape behavior, space use, and demography more than consumptive effects, has been exhibited in natural systems (Brown et al., 1999; Creel and Christianson, 2008; Laundré et al., 2014) and proposed as a theory to explain and inform wildlife management and conservation decisions (Atkins et al., 2017).

Whereas dominant predators, including humans (*Homo sapiens*), suppress and compete for resources with subordinate competitors

* Corresponding author.

E-mail address: julie.k.young@usda.gov (J.K. Young).¹ Current address: American Prairie Reserve, P.O. Box 908<https://doi.org/10.1016/j.gecco.2021.e01823>

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(Darimont et al., 2015; Gunther and Smith, 2004; Prugh et al., 2021) and conspecific predators often protect resources from competing individuals by defending a territory (Mech, 1993; Gese, 2001), non-consumptive effects are also influencing predators. The non-consumptive effects of assemblages containing humans, multiple predators, and multiple prey has recently been identified as existing in a 'landscape of coexistence' (Rio-Maior et al., 2019; Oriol-Cotterill et al., 2015). Assessing these assemblages is important to understanding prey spatial responses that enable a landscape of coexistence yet remains understudied (Kohl et al., 2019; Say-Sallaz et al., 2019), especially when these assemblages include domestic animals. There remains a need for an ecological framework that explains systems in which humans, livestock, and wildlife interact (Chapron and López-Bao, 2016; Bagchi, 2019; Miller and Schmitz, 2019). Beyond improving our ecological understanding, this is also important because there is a growing concern over the potential negative impacts of domestic animals, such as livestock guardian dogs (LGDs; *Canis familiaris*), on endemic wildlife (Drouilly et al., 2020; Smith et al., 2020; Whitehouse-Tedd et al., 2020) alongside mounting social pressure for utilizing non-lethal measures to reduce conflict between humans and carnivores, even though research is relatively limited on the efficacy of such measures (Eklund et al., 2017).

Uniquely anthropogenic, sheep bands are dynamic assemblages of domestic sheep (*Ovis aries*), dogs, and people that travel throughout landscapes in search of sheep forage. Following a global practice known as transhumance (Starrs, 2018), domestic sheep are herded to higher altitude pastures each summer to take advantage of forage resources. In North America, this tradition is typically practiced with sheep, shepherds, herding dogs, and LGDs. This assemblage (henceforth "sheep band") travels through and between undeveloped public lands each summer.

A sheep band does not have a direct analogue in natural large-mammal systems but represents a unique type of defended prey. Defended prey generally refers to a species which defends itself through weapon-like adaptations (Stankowich, 2012; Stankowich and Campbell, 2016), aposematism (Gittleman et al., 1980; Mappes et al., 2005), or sociality (i.e., advanced group vigilance; Rood 1986, Krause and Ruxton, 2002). A less common but more analogous type of defended prey occurs when one species actively guards prey against another predator species. For example, certain varieties of ants (e.g., *Lasius niger*) guard food-producing aphids from predators (Oliver et al., 2008) and multiple species of damselfish (e.g., *Plectroglyphidodon lacrymatus*) defend algae patches from other herbivorous fish (Paola et al., 2012). In these cases, the guarding species successfully alters the behavior and space use of a predator (Jones, 2005; Oliver et al., 2008). Despite the fact that invertebrates and fish may seem disparate examples of defended prey, there is no a priori reason to assume the basic ecological theory should not hold for a sheep band and native predators (Young and Shivik, 2006). In fact, like aphids and algae, domestic sheep are largely defenseless to a host of potential predators and commonly killed when undefended (Klebanow and McAdoo, 1976).

Domestic sheep compete with other herbivorous and omnivorous wildlife for food resources, although the degree to which this competition manifests in terms of wildlife space use varies by species (Jorgensen, 1983; Schieltz and Rubenstein, 2016; Steen et al., 2005). Within the sheep band, shepherds, LGDs, and even herding dogs defend sheep from depredation (Gehring et al., 2010). While shepherds and herding dogs are generally only within the flock during the day, LGDs are present within the flock 24-hours a day and offer the first line of defense against predation. Pastoralists have utilized LGDs to mitigate depredation of livestock for at least 5000 years (Gehring et al., 2010; Ivaşcu and Biro, 2020). Contemporary research on LGDs indicates they are effective for reducing livestock loss (Green et al., 1984; Andelt, 1992; Andelt and Hopper, 2000; Smith et al., 2000; van Bommel and Johnson, 2012; Kinka and Young, 2019). However, one recent meta-analysis found that their effectiveness may be weak relative to other non-lethal methods, at least when protecting lambs from coyotes, cougars, and black bears (Eklund et al., 2017). Only recently domesticated from wolves (Coppinger and Coppinger, 2002; Gehring et al., 2021), people have selectively bred LGDs to defend livestock from predators. LGDs are bonded to livestock when they are young, which enforces their natural instinct to protect (Rigg, 2001). Thus, LGDs may act as intraguild competitors to sheep predators even though they do not kill and consume sheep.

Temporal or spatial avoidance of predators is a commonly observed non-consumptive effect that is also observed in cases where domestic dogs or humans may be considered as the predator. Many large mammals, especially large carnivores, temporally avoid areas of human activity (Nickel et al., 2020) and areas with dogs (Zapata-Ríos and Branch, 2018). This extends to mesopredators, as foxes have also been shown to avoid free-roaming dogs (Mitchell and Banks, 2005; Krauze-Gryz et al., 2012) despite being more detectable in areas frequented by dogs (Lenth et al., 2008). van Bommel and Johnson (2016) showed that red foxes (*Vulpes vulpes*) avoided areas where LGDs were present. Bobcats (*Lynx rufus*) and a host of ungulates have also been shown to avoid areas frequented by dogs (Lenth et al., 2008; Young et al., 2011). Bobcats were the only mesopredator to show potentially negative impacts of the presence of LGDs in one study of a ranch in Texas, USA (Bromen et al., 2019).

A host of carnivores depredate sheep, including wolves (*Canis lupus*, 1.3% of total domestic sheep depredations), bears (*Ursus* sp., 5.0%), and cougars (*Puma concolor*, 5.6%, (U.S. Department of Agriculture, 2015). Even so, coyotes (*Canis latrans*) remain the most common predator to kill sheep throughout the United States. Coyotes were identified as the predator in 54.3% of all reported depredations events in 2014 (U.S. Department of Agriculture, 2015) and most previous research on LGDs focused on sheep depredation by coyotes. While some of these large carnivores have been shown to depredate free-roaming dogs (Butler et al., 2004), the effect of LGDs on the space-use of large carnivores and mesopredators is unknown (but see Vanak and Gompfer, 2009).

Limited research on the ecological impacts of LGDs makes it difficult to predict how LGDs might interact with native carnivores. Is an LGD simply a free-roaming dog or an intraguild competitor, and does this vary with the size of the native carnivore? It has been shown that distance to brown bears and other wolves is inversely related to the establishment of a new wolf pair (Ordiz et al., 2015), even though intraspecific competition among wolves does not seem to affect home-range size (Mattisson et al., 2013). If LGDs moving through the landscape as part of a sheep band are seen as competitors by nearby wolves, they could provoke intraspecific aggression just as an invading wolf pack might (but see Lescaureux and Linnell, 2014). However, because of the large number of animals in a sheep band and the presence of humans, wolves may respond to the sheep band as they would a more dominant pack (Parsons et al., 2016).

Allen et al. (2017) showed that LGDs permitted many intrusions by other wild canids into sheep pastures while still preventing fine-scale interactions between predators and sheep, but whether this applies to sheep bands on open range or in areas with a suite of large carnivores is unclear. Wolves appear to avoid brown bears to some extent (Ordiz et al., 2015) even though they often outcompete brown bears for food resources (Gunther and Smith, 2004). Dogs, on the other hand, displace brown bears (Hansen, 2014). This displacement may be related to the association between dogs and humans (Hansen, 2014; Støen et al., 2015; Piédallu et al., 2017); a scenario similar to LGDs with shepherds. Further, while LGDs can successfully defend livestock from black bears (Smith et al., 2000) and cougars (González et al., 2012), it is unclear whether this is accomplished via displacement or more direct interactions.

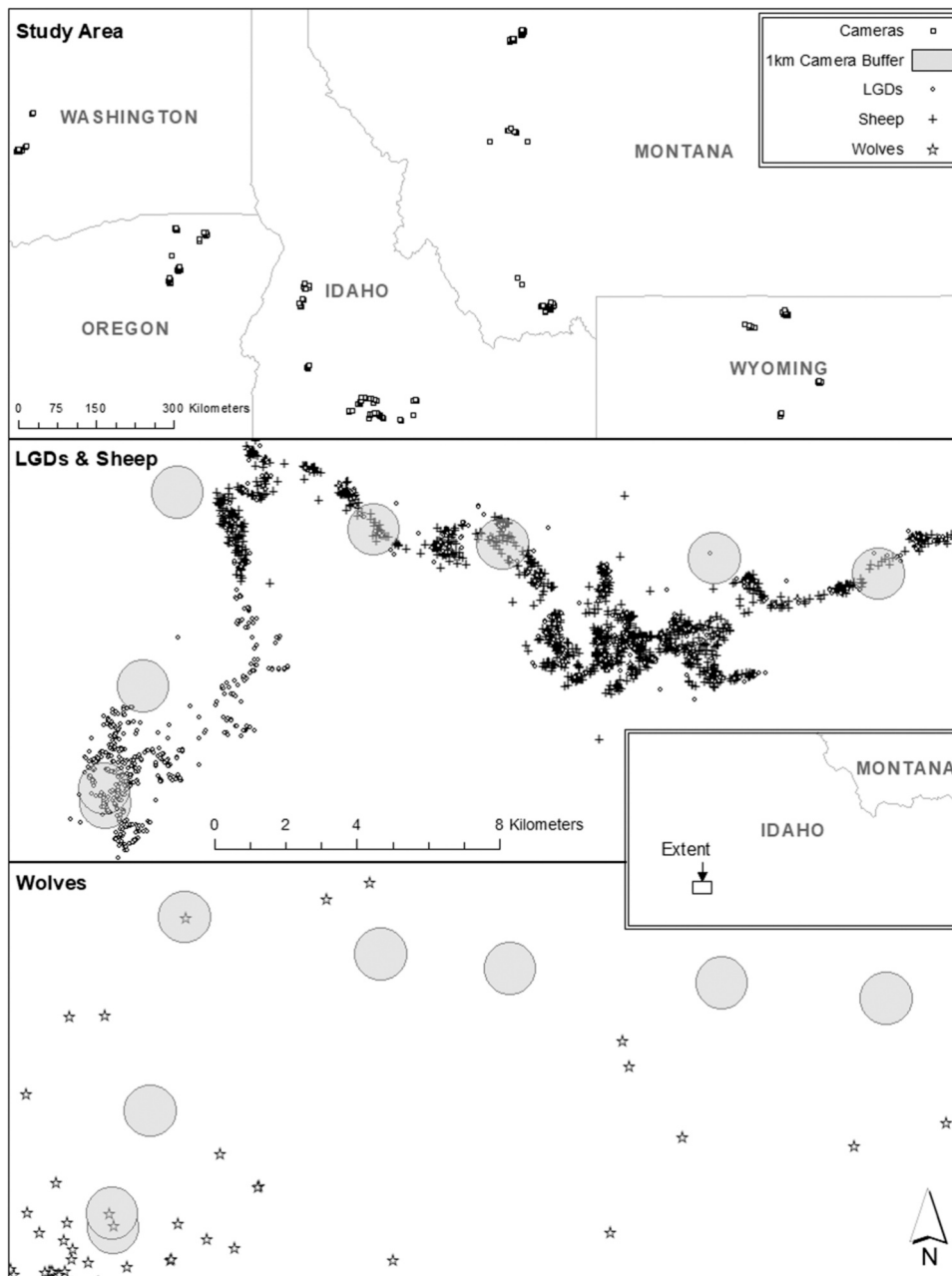


Fig. 1. Map of field sites and camera trap design. The top panel shows the location of all camera traps deployed during May – October, 2014 – 2016. The middle and lower panels show the same trapping grid from Idaho's Sawtooth National Forest in 2014. Grey circles indicate 1-km radius buffers around any camera trap active within the extent during the 2014 field season. Note that the overlapping buffers in the bottom left corner of the map indicate two sequential deployments of the same camera; they did not overlap temporally. The middle panel shows the locations of LGDs and sheep collected by GPS collar in relation to the camera trap buffers. The lower panel shows the locations of collared wolves collected via GPS and radio telemetry, as well as verified sightings of wolves, in relation to the camera trap buffers.

There has been an emergence of research to understand effects of dogs (*Canis familiaris*) and humans on wildlife (e.g., Hansen, 2014, Lescureux and Linnell, 2014, Young et al., 2011, Parsons et al., 2016, Gehr et al., 2017, Gaynor et al., 2018), which has recently extended to livestock guardian dogs (Drouilly et al., 2020; Smith et al., 2020; Whitehouse-Tedd et al., 2020). Concerns have been recently raised that LGDs within a sheep band may impose severe negative impacts on wildlife, but this is disputed (Allen et al., 2019a, 2019b; Johnson et al., 2019). This dispute may be driven in part by the disparity between human-attended and un-attended LGDs in that when LGDs are attended by people, impacts to wildlife are minimized relative to LGDs without humans present (Drouilly et al., 2020). The suggestion being that a human handler can curb some of the domestic dog behavior that results in negative consequences to wildlife. The effect that assemblages which include livestock and the people and domestic animals protecting them have on predatory wildlife is less understood, and our study aims to fill this gap.

This study focuses on how transhumance affects localized space use of endemic carnivores and native ungulates preyed upon by endemic carnivores. We used detection probability as our metric of localized space use because camera-trap spacing optimized for sheep-band home range is too close to ensure spatial independence for animals with large home ranges (MacKenzie et al., 2006; van Bommel and Johnson, 2016; Ramesh et al., 2017). Probability of detection can serve as a proxy for localized space use to the extent that species do not change their behavior when sheep bands are present in a way that makes them more or less detectable by camera (van Bommel and Johnson, 2016; Ramesh et al., 2017). In other words, there is no a priori reason to suspect that the wildlife species in this study would be more or less detectable by unmanned camera traps when a sheep band is present. To test the effect of a sheep band on the detection probability of medium- to large-bodied North American carnivores and ungulates, we deployed trail cameras in grazed areas across the Northwestern United States. As sheep, shepherds, and LGDs all remain closely proximate throughout the grazing season, the sheep band became the unit of analysis, but we assume LGDs are the dominant deterrent to carnivores within the sheep band. We hypothesize that LGDs, through their association with shepherds and as part of a sheep band, serve as intraguild competitors to, and temporarily displace brown bears, wolves, black bears, and cougars on the landscape. We predict the effect is the same for herbivores and mesopredators, driven primarily by non-consumptive effects or a kind of anthropocentric landscape of fear. Results of this study inform the ongoing debate about the ecological impacts of LGDs as part of transhumant ecosystems.

2. Materials and methods

2.1. Study area

We collected data from May to October of 2014 – 2016 in areas with a suite of large carnivores and herbivores overlapping and adjacent to grazing sheep bands in five US states: Oregon, Washington, Montana, Idaho, and Wyoming. Study sites are detailed in Kinka and Young (2018, 2019) and included remote areas where livestock are grazed on public land, as well as fenced and unfenced private land (Fig. 1).

2.2. Livestock guardian dogs and sheep

The unit of interest for analysis is the sheep band, which typically consists of approximately 1000 adult ewes, with 1–2 lambs each, and 2–8 LGDs at all times (Young et al., 2019). A shepherd, 1–2 herding dogs, and 0–2 horses are also present during most daylight hours. The specific make-up of sheep bands is dynamic, so we were unable to control for the exact number of LGDs with the band, LGD breed, or sheep breed in analysis. LGD and sheep breeds are described in Kinka and Young (2018, 2019).

2.3. Camera trapping

To measure the space use of wildlife in relation to LGDs and sheep, we deployed camera traps to collect presence/absence data for medium- to large-bodied mammals before, during, and after a sheep band was grazed through a given area (Fig. 1). Bushnell Trophy Cam HD motion-triggered cameras were set-up along grazing routes or around grazed areas of private land between 615 and 2917 m in elevation (most between 1200–1400 m). Night vision was enabled on each camera with the infrared flash set to low. We spaced camera traps 2–4 km apart based on field observations that 4-km² roughly approximates the space used by a grazing sheep band within any 7-day period. We set cameras at a height of approximately 90–100 cm above the ground, generally along a path or game trail. A maximum of one photograph per second was captured when motion was detected in front of the camera. While camera traps were set along a transect roughly approximating the anticipated route of the sheep band, presence/absence of the sheep band within any particular grid cell was determined by the camera data, and thus varied by location and date. There was not a predetermined duration and the length of deployment for any specific camera varied based on location.

2.4. Additional location data

All LGDs associated with the camera grid were outfitted with store-on-board GPS collars (Telonics or ATS), which recorded GPS locations for the LGDs every 2.5 or 5 h throughout the grazing season. Three to five sheep from each sheep band were also fitted with store-on-board GPS collars (i-gotU GT-600) for 3–6 weeks at a time throughout the grazing season. If ranchers preferred that we not collar their sheep, we asked herders to carry handheld GPS devices and record locations for the sheep band three-times a day. Due to collar failure, collar loss, or the occasional relocation of LGDs from one band to another, there were gaps in the location data for certain individual LGDs at certain times. However, as LGDs generally work as a unit, and are always proximate to the sheep (see Young et al.,

2019 for a further investigation of LGD-sheep spatial interactions), there was no reason to believe that these gaps in individual records biased the data for the entire sheep band. State wildlife agencies provided location data for 20 wolves and 5 brown bears in the vicinity of sheep bands in Montana, and for 20 wolves in the vicinity of sheep bands in Idaho. By also incorporating wolf and brown bear sightings and triangulating the location of VHF-collared wolves and brown bears, we incorporated an additional 6 brown bear and 25 wolf locations.

2.5. Data preparation

To model the probability of detection for multiple species in the presence of sheep bands, we first created occupancy matrices for all species of interest based upon data collected from trail cameras. We defined surveys as a 7-day period in which a camera was deployed with each species either present or absent during the survey period. We then used information from wolf and brown bear sightings, as well as locations from LGDs, sheep, wolves, and brown bears fitted with GPS collars to fill-in gaps in occupancy matrices for these species. If a collar location or sighting fell within a 1-km radius of a trail camera during its deployment, we marked the species as present for the 7-day survey period in which the location was recorded (if the species had not already been detected by a camera trap) to create robust occupancy matrices. We combined robust occupancy data for LGDs and sheep to create a single encounter history for sheep bands. Cougar, black bear, coyote, red fox, bobcat, moose, elk, deer (we combined mule deer and whitetail data), and pronghorn occupancy matrices were based on camera data alone. In cases where cameras were deployed < 1 km of one another during overlapping trapping periods, the camera with the shorter deployment was excluded from analysis. We only included Montana study sites in occupancy models for brown bears as we never detected brown bears outside of Montana and they were not known to exist within other parts of our study area during the time of the study. Similarly, we removed Oregon and Washington field sites from the red fox data set as we never detected them at those field sites and they were not known to exist in the Eastern parts of those states during the time of the study (Hoffmann and Sillero-Zubiri, 2016).

2.6. Statistical analysis

We analyzed brown bear, wolf, cougar, black bear, coyote, red fox, bobcat, moose, elk, deer, and pronghorn data using single-species, single-season occupancy models (MacKenzie et al., 2006). Concerned about a small number of detections in our overall dataset for large carnivores, we also modeled occupancy for brown bears, wolves, cougars, and black bears combined into a single category. We used the encounter history of the sheep band as a survey-level covariate for probability of detection to account for sheep bands moving in and out of a trapping area (Farris et al., 2015). We coded this variable to have three levels (before, during, and after sheep band presence) to examine the relative impacts of sheep band presence on wildlife detection probability both during and immediately after the band moved through an area, relative to baseline detection probabilities before the band arrived. We defined sheep band presence as any 7-day trap period where LGDs or sheep were identified as present within a 1-km radius of a camera location (via trail camera or GPS collar). The before and after conditions were determined post hoc, so that any 7-day trap period before LGDs or sheep were identified were classified as “before,” and any 7-day trap period after the last LGD or sheep detection in the series was classified as “after.” As such, the precise dates and length of any of the three conditions varied for each camera location. We also included state and year as possible predictors of occupancy and detection probability in our modeling exercise to account for differences in species densities over space and time. Although we did allow occupancy probability to vary by year in brown bear models, and state and year in all other species models, we chose not to report on occupancy probabilities since we did not space camera traps far enough apart to ensure spatial independence (MacKenzie et al., 2006; van Bommel and Johnson, 2016; Ramesh et al., 2017).

Table 1

Total number of seven-day camera trap surveys with at least one detection (Survey Detections), camera trapping sites with at least one detection (Site Detections), total number of relevant trap sites (Sites), and raw occupancy estimates (Naïve Occupancy) by species based on camera trap and VHF- and GPS-collar data collected in the Northwest, U.S., from 2014 to 2016. Survey and site detections for brown bears and wolves include data gathered from GPS and VHF collars, sightings, and camera traps. Only the Montana study sites were considered in occupancy models for brown bears, while Oregon and Washington field sites were not considered in occupancy models for red fox. We did not attempt to model bighorn sheep occupancy as only one detection was recorded.

Species	Survey detections	Site detections	Sites	Naïve occupancy
Deer	411	130	185	0.703
Coyote	179	85	185	0.459
Elk	190	77	185	0.416
Red fox	52	27	137	0.197
Black bear	56	36	185	0.195
Domestic Cow	51	24	185	0.130
Brown Bear	11	6	51	0.118
Bobcat	25	13	185	0.070
Pronghorn	24	13	185	0.070
Wolf	17	13	185	0.070
Moose	15	8	185	0.043
Cougar	7	4	185	0.022
Bighorn Sheep	1	1	185	0.005

We used an all-combinations approach to model creation and selection, given the small number of variables considered and our a priori decision to collect data on and include those variables. We ranked our candidate models using AIC from the all-combinations model set for each species. Only those models with a delta AIC value ≤ 2.00 were considered “top models” and reported. In reporting and discussing the results of the top model set for each species, we relied on the calculated significance ($\alpha = 0.05$) of the individual parameters within each top model.

All models were constructed and analyzed using the RPresence package V 2.13.6 (MacKenzie and Hines, 2018) in program R V 4.0.2 Patched (R Core Team, 2020). We considered any models whose parameter estimates were not identical to three or more significant digits to have inadequately converged (Hines and MacKenzie, 2019). We interpreted such model results with skepticism and make note of any such occurrences in our results. We did not consider any model producing a warning about the legitimacy of the estimated standard errors in the variance-covariance matrix to have sufficiently converged and have chosen not to attempt any interpretation of those model results (Hines and MacKenzie, 2019). We also performed goodness of fit tests on each species’ global models to obtain estimated \hat{c} values using the ‘modfitboot’ option in the RPresence package (MacKenzie and Hines, 2018) by applying 10,000 parametric bootstrap simulations. For more precise reporting, we chose not to employ model averaging. Instead, we evaluated all models with a delta AIC value less than or equal to 2.00 in the context of the set.

3. Results

We collected photographs from 185 camera locations over 992 trap surveys and detected all species of interest (Table 1). Our cameras also detected vehicle and other human activity infrequently. GPS data added 239 unique survey detections of LGDs and 93 of sheep for a total of 372 additional surveys where a band (i.e., LGD, sheep, or both) was detected using GPS data. GPS data, VHF triangulation, and live sightings combined added three additional survey detections for wolves and one additional survey detection for brown bears.

3.1. Affected species

For all large carnivores combined (i.e., wolves, brown bears, black bears, and cougars), both band presence and state were significant predictors of detection probability in the highest-ranking occupancy model, which was the only large carnivore model with a delta AIC ≤ 2.00 (Fig. 2). Across years, large carnivores were about half as likely to be detected when a band was present (odds = 0.46; 95% CI = 0.25 – 0.87; $p = 0.02$) as well as after the band left the area (odds = 0.43; 95% CI = 0.23 – 0.81; $p < 0.01$) compared to before the band arrived. State was also included as a predictor of detection probability, indicating that detection probability for large carnivores varied significantly between certain states (see Fig. 2). Five of the 32 large carnivore models did not adequately converge, but none with a delta AIC value ≤ 2.00 or a model weight greater than 0.06. Parametric bootstrapping indicated overdispersion in the global large carnivore model ($\hat{c} = 3.36$).

For black bears alone, band presence was a significant predictor of detection probability in the highest ranked model ($p < 0.05$,

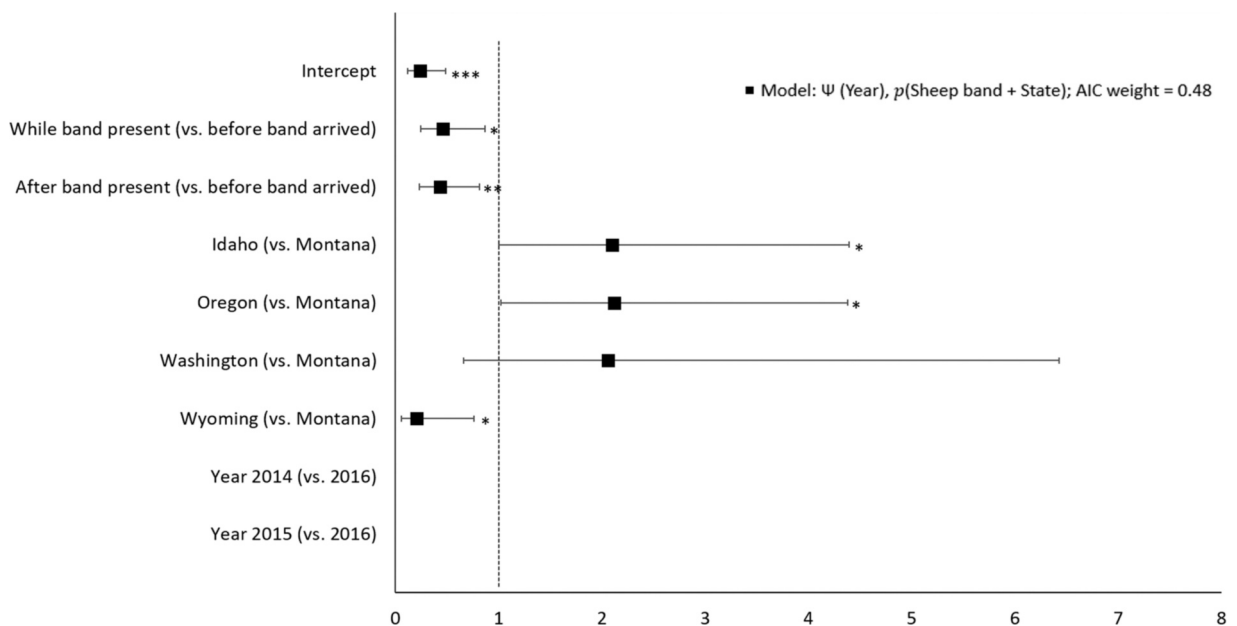


Fig. 2. Odds ratios for probability of detection (p) for the highest-ranking occupancy models ($\Delta AIC \leq 2.0$) of large predator species (brown bears, wolves, cougars, and black bears). Error bars represent 95% confidence intervals, and the dotted line signifies 1:1 odds of detection. Statistically significant odds ratios are represented with level of significance denoted by asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

model weight = 0.32), but the term was not included in the only other model with a delta AIC ≤ 2.0 ($\Delta AIC = 0.96$, model weight = 0.20; Fig. 3). According to the top-ranked model, black bears were 0.46 times less likely to be detected in an area after a band left than before it arrived (95% CI = 0.21 – 0.99, $p < 0.05$). Black bears also appear to have been less likely to be detected while a band was present, but the effect is not significant (odds = 0.47, 95% CI = 0.22 – 1.02, $p = 0.06$). State was also included as a predictor in both top models, indicating that detection probability for black bears varied from state to state (see Fig. 3). Three of the 32 black bear models did not adequately converge, but none with a delta AIC value ≤ 2.00 or a model weight greater than 0.04. Goodness of fit for the global black bear model was within the normal range ($c\text{-hat} = 1.08$).

For brown bears, although the highest-ranking model was the null model (model weight = 0.33), band presence was a significant predictor of detection probability in the second highest-rated model ($p < 0.05$, $\Delta AIC = 0.79$, model weight = 0.22). The only other brown bear model with a delta AIC values ≤ 2.0 (model weight = 0.16) also did not include band presence (Fig. 4). According to the second highest ranking model, brown bears, like black bears, were far less likely to be detected in an area after a band left (odds = 0.04, 95% CI = 0.00 – 0.80, $p = 0.04$). Also like black bears, brown bears appear to have been less likely to be detected while a band was present, but the effect was not significant (odds = 0.13, 95% CI = 0.01 – 1.67, $p = 0.12$). Year was also included as a predictor in the second- and third-highest ranked models, but did not significantly impact detection probability from brown bears in any case. Two of the eight brown bear models did not adequately converge, but none with a delta AIC value ≤ 2.00 or a model weight greater than 0.05. Parametric bootstrapping indicated overdispersion in the global brown bear model ($c\text{-hat} = 6.88$).

For wolves, both band presence and year were significant predictors of detection probability in the highest-ranking occupancy model, which was the only model with a delta AIC ≤ 2.00 (model weight = 0.52) but which only converged to 0.87 significant digits. Although likely specious due to inadequate convergence, this model did indicate that across years, wolves were significantly less likely to be detected when a band was present than before the band arrived (odds = 0.19; 95% CI = 0.04 – 0.91; $p = 0.04$). Including the top-ranked model, a total of 12 of the 32 wolf models failed to adequately converge. Goodness of fit for the global wolf model was within the normal range ($c\text{-hat} = 0.55$).

For coyotes, band presence, state, and year were all significant predictors of detection probability in the highest-ranking occupancy model (model weight = 0.43). The only other coyote model with a delta AIC ≤ 2.00 ($\Delta AIC = 1.64$; model weight = 0.19) also included band presence and state as significant predictors of detection probability (Fig. 5). Considering the results of both of these models, coyotes were more than three times as likely to be detected when a band was present than before the band arrived (odds > 3.00 , $p < 0.001$, Fig. 5). Even after a band left the area, probability of detection for coyotes was still more than two times as likely than before the band arrived (odds > 2.00 , $p < 0.01$, Fig. 5). State was included as a predictor of detection probability in both top coyote models, indicating that detection probability for coyotes varied from state to state (see Fig. 5). Year was also included as a predictor of detection probability, but only in the highest-ranked model and only significant for differences between 2015 and 2016. Detection probability for coyotes was significantly higher in 2015 than 2016 (odds = 2.07; 95% CI = 1.33 – 3.23; $p < 0.01$). All 32 coyote models converged properly; however, parametric bootstrapping indicated overdispersion in the global coyote model ($c\text{-hat} = 7.16$).

For deer, band presence, state, and year were all significant predictors of detection probability in the three highest-ranking ($\Delta AIC \leq 2.00$) occupancy models (cumulative model weights = 0.75, Fig. 6). These three models only varied in the parameterization of the

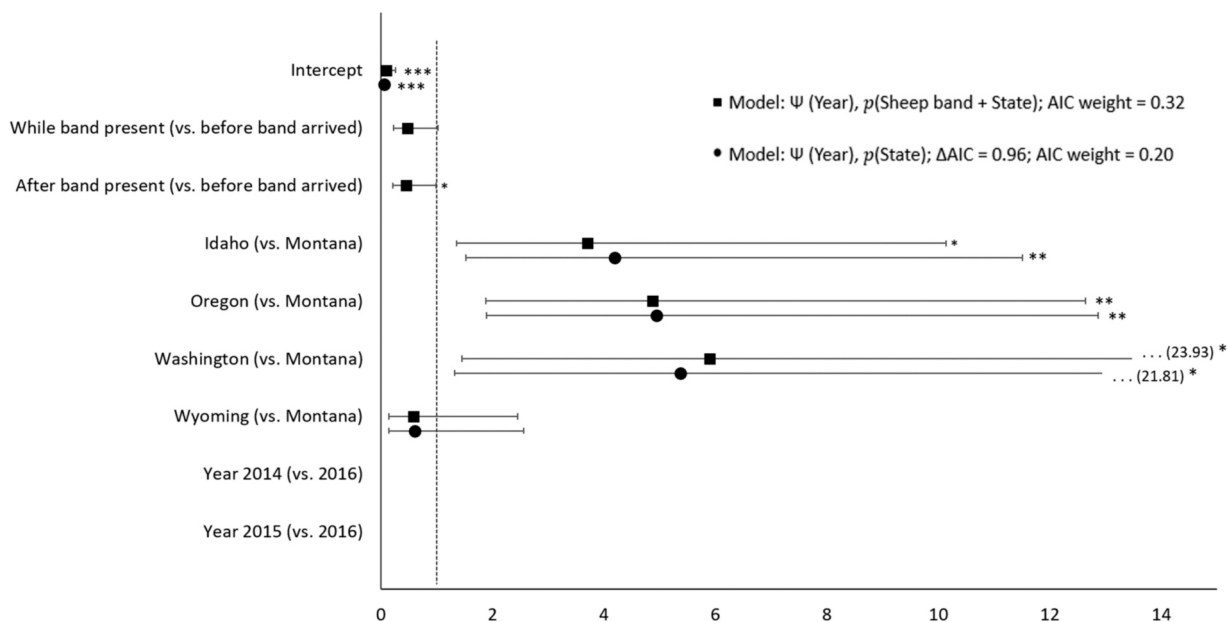


Fig. 3. Odds ratios for probability of detection (p) for the highest-ranking occupancy models ($\Delta AIC \leq 2.0$) of black bears. Error bars represent 95% confidence intervals, and the dotted line signifies 1:1 odds of detection. Statistically significant odds ratios are represented with level of significance denoted by asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

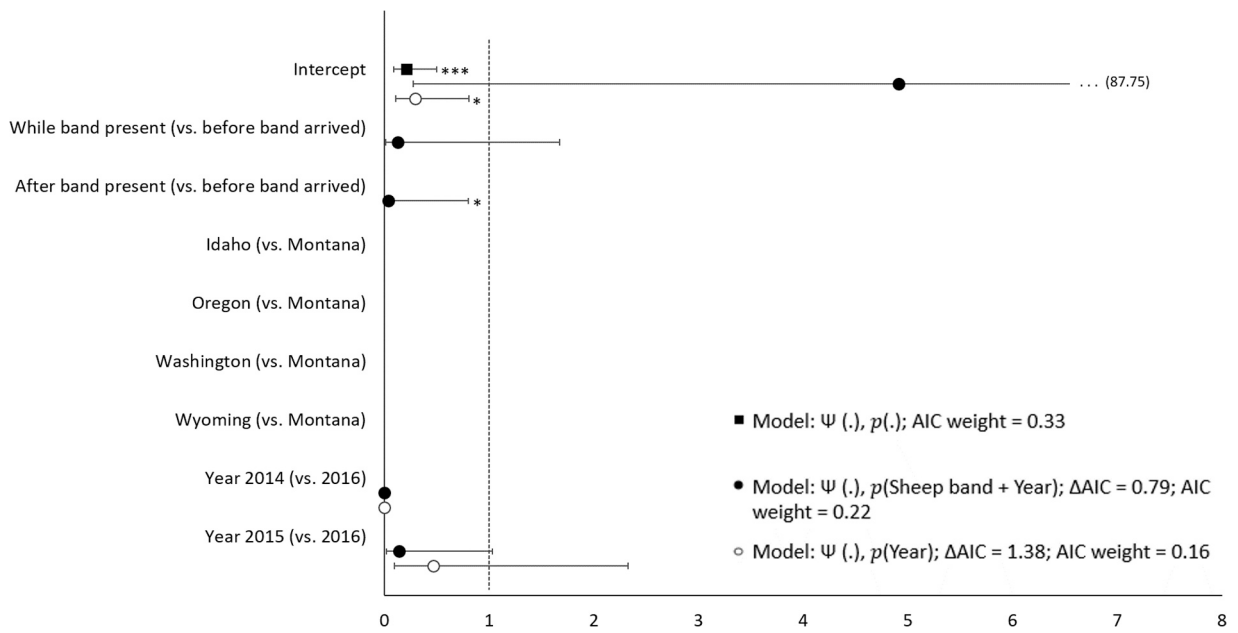


Fig. 4. Odds ratios for probability of detection (p) for the highest-ranking occupancy models ($\Delta AIC \leq 2.0$) of brown bears. Error bars represent 95% confidence intervals, and the dotted line signifies 1:1 odds of detection. Statistically significant odds ratios are represented with level of significance denoted by asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

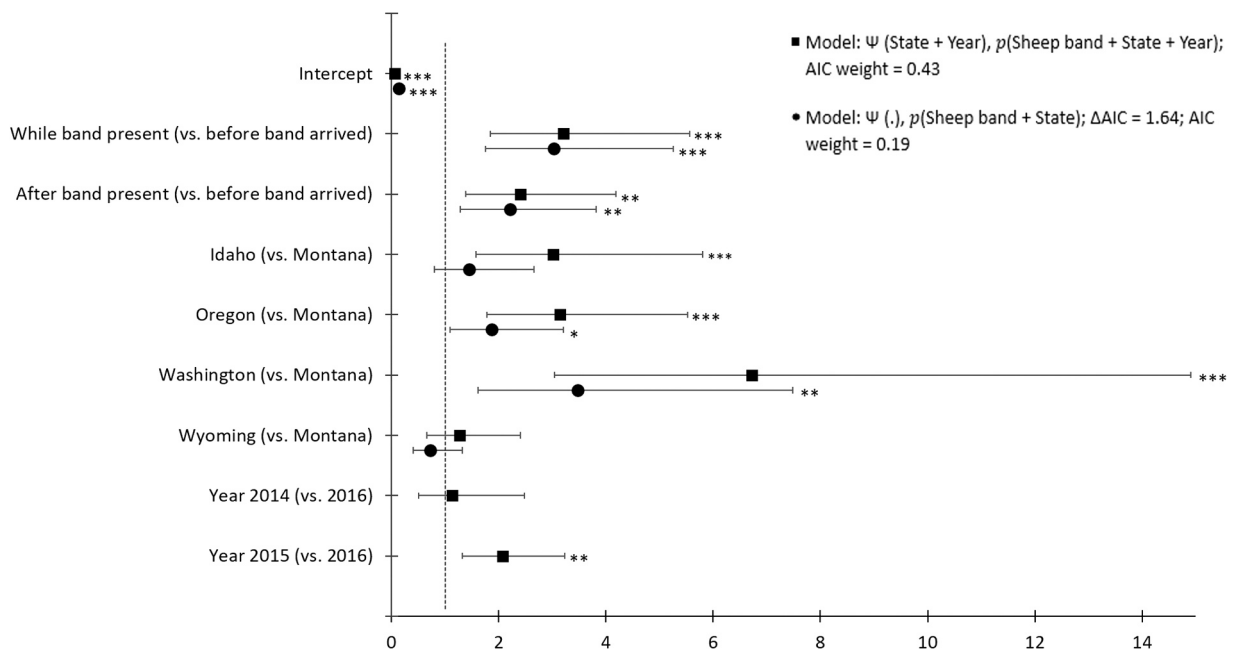


Fig. 5. Odds ratios for probability of detection (p) for the highest-ranking occupancy models ($\Delta AIC \leq 2.0$) of coyotes. Error bars represent 95% confidence intervals, and the dotted line signifies 1:1 odds of detection. Statistically significant odds ratios are represented with level of significance denoted by asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

occupancy probability term (not reported). All three models indicate that deer were about half as likely to be detected when a band was present than before the band arrived ($p < 0.01$, Fig. 6). This effect persisted even after the band left the immediate area ($p < 0.001$, Fig. 6). Detection probability for deer varied from state to state, particularly in Idaho and Washington (see Fig. 6). All three models indicate that deer were about twice as likely to be detected in 2014 as they were in 2016 ($p < 0.05$, Fig. 6). No significant differences in detection probability of deer was identified between 2015 and 2016. The sixth-ranked of the 32 deer models ($\Delta AIC = 3.35$, weight =

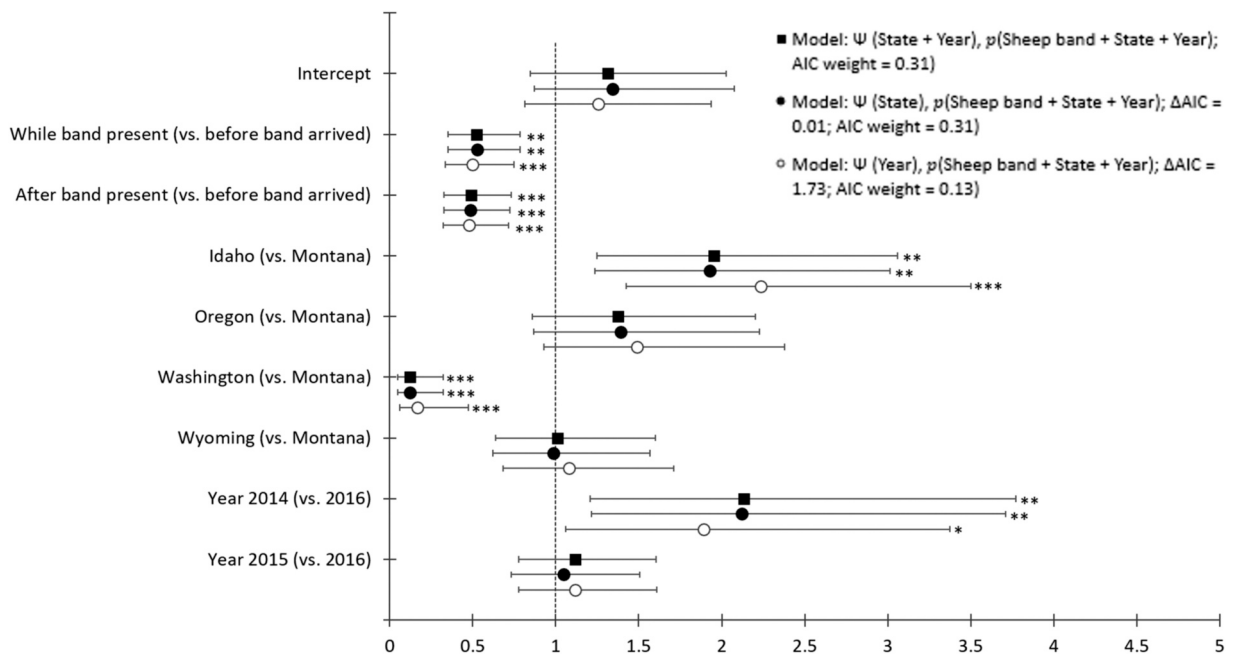


Fig. 6. Odds ratios for probability of detection (p) for the highest-ranking occupancy models (Δ AIC \leq 2.0) of deer (whitetail and mule deer combined). Error bars represent 95% confidence intervals, and the dotted line signifies 1:1 odds of detection. Statistically significant odds ratios are represented with level of significance denoted by asterisks (* p < 0.05, ** p < 0.01, *** p < 0.001).

0.06) did not converge to three or more significant digits. Goodness of fit for the global deer model was within the normal range (c -hat = 0.97).

3.2. Unaffected species

For red foxes, three of the five highest ranking models (Δ AIC \leq 2.00) included band presence as a predictor of detection probability, but in no case was its effect statistically significant (p > 0.05). The two highest-ranked models (cumulative weight = 0.31) indicate significantly higher probabilities of detection for red foxes in 2014 than in 2016 (p < 0.05), but no significant differences were found between 2015 and 2016, as was seen for deer. All 32 red fox models converged properly, and goodness of fit for the global model was within the normal range (c -hat = 1.04).

For elk, the two highest-ranked models (Δ AIC \leq 2.0) did not include band presence as a predictor of detection probability. Both indicate that elk were significantly more likely to be detected in 2015 than 2016 (p < 0.001), as was seen for coyotes, and that detection probability varied by state. All 32 elk models converged properly, although there was some evidence of overdispersion in the global model (c -hat = 1.42).

3.3. Species with inconclusive results

For cougars, the highest-ranking model was the null-model, and the second and third highest ranked models failed to converge to three or more significant digits. In none of the four top-ranked models for cougars (Δ AIC \leq 2.00) was band presence included as a predictor. Most of the cougar models failed to adequately converge and the global model indicated an under-dispersed data set (c -hat = 0.002).

For bobcats, there were eight models with delta AIC values \leq 2.00 and the five highest-ranking models all failed to adequately converge to three or more significant digits or correctly estimate standard error values. Four of the eight top models included band presence as a predictor of detection probability, but in no case was it found to be statistically significant.

Both moose and pronghorn included models that failed to converge among the top-ranked models (Δ AIC \leq 2.0), although neither species' model sets included band presence as a predictor of detection probability among its top-ranked models (Δ AIC \leq 2.0). Only one bighorn sheep photograph was captured in the dataset, so we did not attempt to model its occupancy.

4. Discussion

Our findings describe how defended sheep herds moving across a landscape affect the space use of a number of endemic large- and medium-sized mammals. We found that sheep bands in the Northwestern U.S. may cause a non-consumptive effect in large carnivores, exhibited as displacement. The presence of a sheep band was associated with a reduction in the probability of detection for large

carnivores by about half (Fig. 2), both during and after a sheep band was present. This result supports our theorizing that domestic sheep in a sheep band are a defended prey and that sheep bands (presumed as a function of LGDs), in turn, serve as intraguild competitors to large carnivores. The avoidance of the sheep band by large carnivores suggests that sheep bands constitute a dominant competitor on the landscape. How this effect on large carnivore behavior relates to actual loss prevention will require further study (but see Kinka and Young, 2019), but these findings may highlight a behavioral effect on large carnivores which contributes to understanding ecological impacts of LGDs and their success as a non-lethal management tool (Andelt and Hopper, 2000; Gehring et al., 2010).

While our results provide evidence that large carnivores as a group are less likely to use small habitat patches occupied by sheep bands, the effect is less clear at the species level. For black bears, brown bears, and wolves, there is at least some evidence to suggest that the effect of a sheep band on the space use of large carnivores is also evident at the species-level. Wolf data show a clear pattern of avoidance to a sheep band, but failure of the top model to adequately converge to a sufficient number of significant digits draws the validity of this species-specific finding into question. For brown bears, we likely lacked sufficient data for a clear effect to be observed. However for black bears, we were able to document more than 50 detections throughout our study; enough to be fairly confident in our model outcomes. The clear pattern of black bears avoiding areas previously visited by a sheep band (top model only) may serve as corroborating evidence of the same effect in their larger ursid cousin. Bears are omnivorous; thus, the displacing effect of a sheep band, particularly after the band left an area, could be driven both by non-consumptive effects of LGDs and humans, as well as resource competition with sheep (Jorgensen, 1983). With brown bear populations expanding in the Northern Rocky Mountains (Mace and Carney, 2012), larger sample sizes may be attainable in the future. Cougars however, showed inconclusive results with no change in probability of detection as a result of sheep band presence. Our small sample of cougar detections may have limited our ability to properly model or detect an effect of sheep bands. Cougars, being an ambush predator, are presumably less conspicuous than canids and ursids, and a more rigorous detection methodology might have been necessary to attain a large sample size for such a cryptic species.

Counter to our original hypothesis, coyotes were more detectable when a sheep band was present. For coyotes – the primary predators of domestic sheep (U.S. Department of Agriculture, 2015) – it may have been that the attracting force of a vulnerable prey species like domestic sheep overwhelmed any displacing effect of LGDs or shepherds. However, coyotes also have smaller home ranges (Lindstedt et al., 1986), and unlike wolves they may not be able to move to a different part of their territory when a sheep band arrives. Subsequently, coyotes may have fewer response options than larger carnivores, instead attempting to take advantage of the abundant food resource when sheep became available. Further, avoidance of sheep bands by large carnivores, particularly wolves, may also induce a temporal mesopredator release for coyotes (Prugh et al., 2009; Sivy et al., 2017; Haswell et al., 2018), further incentivizing them to attempt to capitalize on the food resources presented by a sheep band. A mesopredator, like the coyote, may perceive humans as less dangerous than apex predators, like wolves, and therefore shifted behavior when sheep bands were present because of the local absence of wolves despite the added presence of humans (Shores et al., 2019). Although we did not set out to investigate a potential mesopredator release imposed by sheep bands, these results highlight how novel anthropogenic scenarios may facilitate mesopredator release and the need for future work focused on this ecological framework (e.g., Shores et al., 2019).

Red foxes and bobcats are less common predators of domestic sheep (U.S. Department of Agriculture, 2015) but both have previously been shown to avoid LGDs (Bromen et al., 2019; van Bommel and Johnson, 2016). The presence of a sheep band that included LGDs in our study system had no effect on red foxes and results for bobcats were inconclusive. These differences may be because of the abundance of large carnivores in our system compared to other study systems. That is, compared to places like Australia and Texas, where mesopredators do not have to adapt their behavior to avoid conflict with larger carnivores, throughout the Northwestern U.S. a host of large carnivore species impose non-consumptive effects on mesopredators. For red foxes in the Northwestern U.S., LGDs may serve as a surrogate for other endemic large carnivores that foxes have adapted to coexist with in other ways.

Similar to the large carnivore group, deer avoided areas occupied by a sheep band. This effect persisted even after a sheep band left the area. Much like how reduced detectability of bears after a sheep band had grazed an area may be driven by competition for food resources from the sheep (Jorgensen, 1983), the same may be causing displacement of deer. However, the absence of any significant effect of the sheep band on elk is reason to suspect that humans and LGDs may be affecting deer space use as well. Elk may be a more dominant competitor to sheep than whitetail or mule deer, but the well-documented impact of LGD predation on native grazers (Drouilly et al., 2020; Smith et al., 2020; Whitehouse-Tedd et al., 2020) and the finding that elk are more responsive to humans than potential predators (Proffitt et al., 2009), combine to suggest that this displacement of deer may be exacerbated by deer perceiving LGDs as potential predators. Deer may be responding to the presence of herders with LGDs, in addition to resource competition from domestic sheep. Indeed, the presence of LGDs and herders in a sheep band adds a layer of complication to the underlying cause of any displacing effect, but studies of livestock competition on wild ungulates tend to show more negative impacts to mule deer and white tail deer than elk (Schieltz and Rubenstein, 2016). Because both deer and elk are hunted by humans and previous studies suggest they show a spatial response to hunters (e.g., Brown et al., 2020; Proffitt et al., 2009), it is possible that deer were responding to the presence of LGDs or LGDs with herders than the presence of sheep in these assemblages. For both competition and predation, elk should be assumed to be more robust than deer due to their size and herding behavior, but lack of data prohibited us from identifying corroborating evidence for other ungulates, such as moose, bighorn sheep, or pronghorn.

In addition to sheep-band presence, we modeled for a potential effect of year and state on probability of detection for all species (except state for brown bears). Year was a significant predictor in top models for coyote, red fox, elk, and deer detectability. Coyotes and elk exhibited a similar increase in detectability in 2015, while red foxes and deer instead exhibited their highest detectability in 2014. There were also significant differences in detectability for large carnivores as a group, black bears, coyotes, elk, and deer by state. Considering the very large scale of our study, the inclusion of state and year was only meant to capture uncontrollable variance in

ecological factors and management regimes between study regions and over time. Significant differences in detectability of certain species in a given state or year was presumably driven by fluctuations in ecological conditions, like primary productivity and prey abundance, or different management actions and hunting quotas from state to state. However, we did not set out to explicitly study baseline variations in detectability of mammal species across the Northwestern U.S. There is no post hoc reason to suspect that any species was more conspicuous in a given year or state, as an increased probability of detection might suggest. Our camera trapping protocol was well established and reinforced across sites throughout each field season, so it is unlikely that variation in specific placement by different study personnel explains yearly or regional differences. Instead, these differences likely reflect differences in relative abundance of these species throughout space and time, as was intended.

Large carnivores as a group, brown bears, black bears, and deer all showed at least some evidence of continued avoidance of areas grazed by a sheep band, sometimes for several weeks, after the sheep band had left. Coyotes also showed a lingering response to sheep band presence, even after a band had left, but unlike for the other species mentioned, coyote detectability remained higher than baseline after sheep left. For coyotes, the logical conclusion for increased detectability during and after the occupancy of a sheep band is the temptation to capitalize on a large pulse of potential food resources, especially under conditions of mesopredator release. Although we are unable to estimate the duration of this effect – our methodology did not allow us to examine the rate of decay of the effect of sheep band occupancy on wildlife space use – it is not necessarily concerning. Coyotes would have to eventually redistribute themselves, presumably to something similar to baseline. Potentially more concerning is the potential long-term avoidance by large carnivores as a group, brown bears, black bears, and deer. Coupled with other evidence of the negative ecological impacts of LGDs (Drouilly et al., 2020; Smith et al., 2020; Whitehouse-Tedd et al., 2020), any evidence of long-term displacement of wildlife by LGDs would have implications on the ethics and sustainability of LGD use, regardless of their effectiveness at non-lethally mitigating livestock depredation. Contrastingly, temporal displacement may be considered an acceptable cost when compared to the benefit of reduced livestock depredation and subsequent reduction in demand for lethal removal of carnivore species. Indeed, our results provide support to the scientific literature that LGDs benefit carnivore conservation (Whitehouse-Tedd et al., 2020). Considering that for LGDs to be successful in reducing livestock depredations they must either passively displace carnivores when livestock are present or physically chase, fight, and potentially kill attacking predators, displacement may be the preferable mechanism from conflict reduction and conservation perspectives.

It is possible that decreased detection rates resulted from altered fine-scale space use patterns of the terrestrial mammals we analyzed. For example, if large carnivores killed livestock and were therefore less active because of time spent feeding or scavenging, they may have been less likely to be detected by our camera traps. While fine-scale movement data would be necessary to assess this alternative hypothesis, we suspect it to be highly unlikely because LGDs prevent sheep from being killed by carnivores (Andelt, 1992; Andelt and Hopper, 2000; Kinka and Young, 2019), so any decrease in carnivore movement while a sheep band is present, as a function of feeding behavior at a carcass site, would be lessened if LGDs were present to reduce the total number of depredations. Even so, our results cannot offer definitive conclusions here, because we did not measure the length of displacement or fine-scale movement of carnivores. Thus, we emphasize the utility of more deliberative investigations of potential long-term effects of LGDs on wildlife space use.

The near ubiquity of shepherds, herding dogs, and LGDs among grazing sheep in North America makes their unique contributions to defense difficult to disambiguate. Miller and Schmitz (2019) created a predictive framework about livestock-carnivore conflicts that considered livestock and humans as discrete components because they can affect multispecies systems differently. The role of humans in dictating carnivore behavior has been a recent topic of study (Dorresteijn et al., 2015) with some suggesting that humans may impose a landscape of fear on carnivores (Lodberg-Holm et al., 2019; Støen et al., 2015; Suraci et al., 2019) and serve as a super predator (Smith et al., 2017; Moll et al., 2018) with reverberating effects throughout the ecosystem (Wilson et al., 2020). Ultimately, our data do not allow us to untangle the singular effects of humans, herding dogs, and LGDs, but transhumance is a system that embeds all of these components in the ecological landscape. It is worth mentioning that LGDs outnumbered people in every one of our monitored sheep bands and LGDs were active during the day and night, while shepherds and herding dogs were only active during the day. Further, the use of humans alone, typically called range riders, does not appear to significantly impact wolf space-use (Parks and Messmer, 2016), accumulatively suggesting the presence of LGDs drove the responses of wildlife we observed in this study. While more research will be needed to identify the unique contributions of humans and LGDs on carnivore behavior and space use, our study offers an important insight into the ecological role of sheep bands and non-consumptive mechanisms that prevent depredation of sheep by endemic carnivores during transhumant grazing.

CRedit authorship contribution statement

Daniel Kinka: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Jeffrey T. Schultz:** Data curation, Formal analysis, Visualization, Writing – review & editing. **Julie K. Young:** Conceptualization, Data curation, Funding acquisition, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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