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RESEARCH ARTICLE

Integrating human trail use in montane landscapes reveals larger zones of human influence for wary carnivores

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Abstract

1. Coexistence between humans and wildlife is necessary for many conservation goals but is difficult to achieve in landscapes with increasing human populations and species that are often wary of people and may also threaten human safety. In these contexts, coexistence may be enhanced by identifying geographic areas where animal movement is particularly important and changes to human use via trail design could support both wildlife conservation and human safety.
2. We used camera trap data to monitor the spatial distribution of grizzly bears (*Ursus arctos*), grey wolves (*Canis lupus*), and humans within the central Canadian Rocky Mountains, where anthropogenic development and human activity have gradually encroached on limited wildlife habitat. We quantified spatial variation in human use and then incorporated this output into models for the detection rates of bears and wolves. We interpolated metrics of human use throughout the study area using inverse distance weighted averages of human detection rates from cameras. This approach supported a novel estimate of the cumulative effects of human use at all nearby trails on animal space use. We used our models to estimate the zone of influence of human use on bears and wolves, determining the distance at which human use on nearby trails no longer exhibited a measurable change in detection rates for each of grizzly bears and wolves.
3. The negative effects of human use on wildlife declined steeply with distance such that 50% of the decrease in detection rates immediately adjacent to trails would be expected to occur at 267 m for grizzly bears and 576 m for wolves. Weak effects, 5% as strong as the effect adjacent to trails, extended up to 1.8 and 6.1 km for grizzly bears and wolves, revealing the importance of cumulative measures of human use.
4. *Synthesis and applications*. Our work shows how human activity over entire landscapes can alter wildlife detection rates. Our results identify target buffer distances for protected areas near trails, and the modelling framework could be used by land managers to predict how altering trail networks and modifying human activity could affect wary wildlife species and advance coexistence.

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KEYWORDS
camera traps, grey wolf, grizzly bear, habitat selection, human disturbance, human–wildlife coexistence, Poisson process, zone of influence

1 | INTRODUCTION

Inevitable consequences of anthropogenic development across the world include natural habitat loss, degradation, and fragmentation that negatively affect diverse species of wildlife (Tucker et al., 2018; Vitousek et al., 1997). Maintaining natural, healthy, and connected landscapes is a central theme for wildlife management and human–wildlife coexistence, a paradigm for sustainable persistence of humans and wildlife in the same broader area (Bergstrom, 2017; König et al., 2020). Human–wildlife coexistence is increasingly challenging in natural areas that attract recreationalists whose presence might inadvertently reduce habitat quality and landscape connectivity (Hammitt & Cole, 2015), particularly for wary carnivorous species with low tolerance for human disturbance (Pineda-Munoz et al., 2021; Suraci et al., 2021). Reducing the likelihood of interactions between people and large carnivores that could injure people is also important. For these reasons, land-use planners and wildlife managers with a mandate to support coexistence urgently need tools to determine how to identify and regulate effects of humans on wildlife while supporting public safety.

A metric with increasing prevalence in the context of human–wildlife coexistence is the estimation of a zone of influence, the distance at which individuals of a focal species or group exhibit a change in behaviour, typically a change in habitat use, in response to human activity (Boulanger et al., 2012). Zones of influence can be measured in a variety of ways (Ford et al., 2020), but estimates are complicated by the spatiotemporal variability underlying the behaviour of both humans and wildlife and the expected scale of these interactions. Animal responses to human features often vary with time of the day (Richter et al., 2020; Shuai et al., 2022) and season of the year (Novčić & Parača, 2021; Uboni et al., 2015) with similar sources of variation in human activity (Anderson et al., 2023; Gaynor et al., 2018). Moreover, animal reactions to human activities may occur at variable distances from their sources (Stankowich, 2008) or in response to subtle changes in the environment (Boyle & Samson, 1985). And yet, if these spatial and temporal patterns are well understood, land managers may be able to optimize the timing and locations of restrictions on human access to natural areas in ways that minimize inconvenience to people while maximizing benefits to wildlife. For example, closing a high-use road at night in Banff National Park, Canada, increased the road's nocturnal use by ungulates and carnivores by a factor of two in less than a year (Whittington et al., 2019). Estimating zones of influence can be especially useful when land managers hope to identify the amount of space necessary to buffer focal, sensitive species from human use (Ford et al., 2020), including small-scale disturbances like trails for non-motorized recreation, where they could inform fine-scale placement and restrictions on human use (Bow Corridor Ecosystem Advisory Group, 1999; Dertien et al., 2021).

Estimating a zone of influence typically requires collecting data on the spatiotemporal distribution of the focal wildlife species as well as the information about human disturbance throughout the target landscape (Ford et al., 2020). Ideally, such measures encompass all forms of potential displacement by human activities, but many studies estimate zones of influence by analysing only the single nearest human feature as a predictor for wildlife occurrence (e.g. Coleman et al., 2013; Kite et al., 2016; Malcolm et al., 2020; Pigeon et al., 2014; Rogala et al., 2011). This technique is likely accurate at identifying the direction of human influence (i.e. attraction or repulsion), but it overlooks the intensity of use at the feature, as well as effects of more distant anthropogenic features that potentially exert a cumulative effect on wildlife behaviour and habitat use, underestimating the zone for wary species. Generating a landscape-level index of human use could refine and improve zone of influence estimates for focal wildlife species, particularly for wary species in landscapes where human use has multiple footprints that vary in both space and time.

Camera traps are an ideal tool for estimating zones of influence of human use on trails for wary species such as grizzly bears (*Ursus arctos*) and grey wolves (*Canis lupus*; hereafter 'wolves'). They have been used extensively to monitor these and many other carnivore species because they are inexpensive, non-invasive, and can simultaneously and accurately monitor entire communities of large animals, including humans (Burton et al., 2015; Marion et al., 2020; Naidoo & Burton, 2020). Like other large terrestrial carnivores, grizzly bears and wolves exhibit extensive home ranges (Benson & Patterson, 2015; McLellan & Hovey, 2001) that require connected landscapes with large amounts of secure habitat. Both species are also typically wary of people (Gibeau et al., 2002; Zanni et al., 2023), but they are capable of habituation (Wam et al., 2014; Wheat & Wilmers, 2016) and make use of anthropogenic linear features as travel corridors (Dickie et al., 2017; Pollock et al., 2019; Roever et al., 2010; Zimmermann et al., 2014), which may be reflected as attraction or repulsion on camera traps.

The purpose of this work was to use cameras traps to estimate zones of influence of non-motorized human recreation, typically on or near trails, in the surrounding landscape for grizzly bears and wolves in and around the Bow Valley of the central Rocky Mountains of Alberta. There, grizzly bears are listed as threatened and a recovery plan for them promotes landscape connectivity and access to secure habitat patches (Alberta Environment and Parks, 2020). Wolves have recently recolonized this landscape after decades of persecution (Paquet et al., 1996a, 1996b) and appear to exhibit considerable sensitivity to human disturbance (Muhly et al., 2011; Paquet et al., 1996a, 1996b; Whittington et al., 2019). Our study included

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the tourist towns of Canmore and Banff, Alberta, where visitation has rapidly increased (Alberta Government, 2023).

To achieve this purpose, we fit Poisson process models that assessed spatial variation in the camera detection rates of grizzly bears, wolves, and humans in our study area. First, we fit the model for human detection rates, which allowed us to simultaneously assess environmental factors that are correlated with recreation hotspots and predict human density at locations we were unable to survey. Next, we used the predictions from this model as a covariate (in association with other environmental variables) in our models for grizzly bears and wolves to assess the cumulative impact of human use at and surrounding the site where these species were detected. We estimated zones of influence for grizzly bears and wolves based on the strength of these effects from nearby camera sites, relative to the strength of effect at the focal site. Our results rigorously quantify human–carnivore interactions in an area that is important to carnivore conservation in the broader region and inform management of people, wildlife, and land to facilitate coexistence.

2 | MATERIALS AND METHODS

2.1 | Study area and design

We collected and analysed a camera trap dataset that documented the occurrence patterns of humans and wildlife in southwestern Alberta and southeastern British Columbia, in the central Canadian Rocky Mountains (Figure S1). The study area contained high elevational variation and the lower-altitude montane ecoregion contains most of the biodiversity (Holland & Coen, 1983). The area included Banff, Yoho, and Kootenay National Parks and adjacent provincial lands in Alberta that contained towns, Provincial Parks, and Wildland Provincial Parks. People are attracted to the natural beauty of this area, particularly tourists interested in outdoor recreation (Draper, 2000). The study area contained arterial routes for human transportation including the Trans-Canada Highway (Chruszcz et al., 2003), a major railway (St. Clair et al., 2019), and four towns, including Canmore, Alberta. The permanent resident population in Canmore has increased by 30% from 11,089 residents in 2001 to 14,450 residents in 2022, and Banff has experienced similar growth (31% from 7347 residents to 9656; Alberta Government, 2023). Tourism has concurrently increased, with over 5 million people visiting the region each year (Alberta Government, 2019).

We monitored the spatiotemporal distributions of wildlife and humans using camera traps deployed throughout the study area and activated by a combination of motion and infrared detection when an animal entered the field of view (Welbourne et al., 2016). Agency personnel and volunteers deployed cameras at 1699 sites (Figure S1) using a variety of models (Reconyx models HC600, HC800, HC900, PC85, RM30) between 2007 and 2022, with active time for each camera ranging from 3 days to 14 years (mean = 772 days; standard deviation = 1098 days). Our data come from multiple datasets that were intended to address several purposes, including monitoring the presence of wary species, assessing the frequency of human use, and identifying locations for wildlife crossing structures adjacent to highways. Volunteers and staff classified camera images to species and recorded independent detections only when animals of the same species at the same location were separated by at least 10 min. The size of this temporal window for separating detections is shorter than many studies (Burton et al., 2015) but recent work has suggested that model parameter estimates are not extremely sensitive to this choice (Holinda et al., 2020; Koetke et al., 2024). Our study did not require ethical approval and no permission was required for fieldwork.

We quantified abiotic and biotic variation in the study area with a variety of data sources. We used a digital elevation model (DEM), a raster with 30 × 30 m spatial resolution, to quantify the region's topography. We used elevations from the DEM and the 'terrain' function from the 'terra' R package (Hijmans, 2023) to calculate slope and aspect. We used a landcover model developed by McDermid et al. (2009) that converted Landsat satellite imagery into major landcover classes in the study area. We retained the following landcover types for our study area: non-vegetated, barren, or recently burned, closed coniferous forest, open coniferous or deciduous forest, herbaceous or wetland, shrub, and water (as in Whittington et al., 2022). Landcover did not change throughout most of the study area, although some areas classified as burned and barren developed early seral vegetation. However, we lacked annual estimates of landcover and considered it static for our analyses. We estimated average annual snow cover using 500 m resolution MODIS MYD10A1 data, averaged from 2010 to 2021, and converted both GIS layers to rasters with the same 30 × 30 m spatial resolution as the topographic data. Parts of our study area are at high enough elevations for snow to remain throughout the year, rendering this covariate important even for hibernating species like bears. We expected lower wildlife detection rates in areas with high annual snow cover because those areas would be associated with high elevations, deeper snows, rugged terrain, and poorer quality habitat (Pedersen et al., 2021; Whittington et al., 2022). We obtained vector shapefiles indicating the location of human recreational trails from Parks Canada (for all trails within National Park boundaries) and the Government of Alberta (for all areas outside National Parks). Each trail was classified as designated (constructed intentionally by the provincial or federal government for recreational use) or undesignated (constructed illegally or unauthorized for recreation). We obtained a similar vector shapefile for all roads in the study area by downloading National Road Network data for the provinces of Alberta and British Columbia (Government of Canada, 2022).

2.2 | Modelling framework for camera trap data

Our goal of estimating the cumulative effects of human use across a complex network of trails on wildlife required us to accurately estimate human use at every trail in the study area, not just the small subset of trails where we deployed camera traps. Thus, we first

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designed a model with human detections as the response variable of interest. This 'human model' generated predictions for the density of human use throughout the study area, which became a predictor variable in our 'wildlife models'. Both models are derived from the Poisson process statistical framework to support comparison and tandem interpretation.

For both the human and wildlife models, we assessed second-order habitat selection (i.e. selection within the range of the study population; Johnson, 1980) from camera trap detection data using the following modelling techniques, which allowed us to predict camera detection rates at unsurveyed locations. We used non-homogeneous Poisson point process models that evaluated the expected rate of 'events' (i.e. number of events per unit of time) occurring along our chosen spatial axes (Cox & Isham, 1980; Illian et al., 2007). Our events were camera detections and the spatial axes were the covariates described above. This modelling approach has three advantages. First, Poisson process models can be applied to presence-only data and do not require any sort of coordinated or systematic sampling design (Fithian & Hastie, 2013; Warton & Shepherd, 2010). The models estimate rates of detection without equating non-detections to non-use, as in their applications to animal telemetry data (Aarts et al., 2012; Hooten et al., 2017; Northrup et al., 2022). By estimating detection rates as an indicator of relative density, rather than absolute density, constraints on where and how cameras are placed on the landscape are relaxed. Second, Poisson process models do not summarize detections into discrete 'sampling units' as is typically done for occupancy models (Burton et al., 2015), thereby eliminating the problem of zero-inflation where and when animals are not detected. Instead, continuous time models can leverage more information because camera traps are always on and can detect animals at any time (Borchers et al., 2014; Kellner et al., 2022). It is mainly for this reason that Poisson processes have been applied previously to camera trap data for estimating animal density (Royle et al., 2009; van Dam-Bates et al., 2024), habitat selection (Keim et al., 2019), and occupancy (Kellner et al., 2022). A third advantage is that the response variable in our application of these models is the detection rate of the focal species, which simplifies biological interpretations of the fitted values for covariates and resulting model predictions.

To fit our Poisson process model, we used four types of data:

1. the spatial locations, $\mathbf{x}_1, \ldots, \mathbf{x}_N$, where cameras were deployed (N is the total number of cameras in the dataset);
2. a list of sampling intervals representing times at which each camera was active, $T_{L1}, \ldots, T_{LN}$;
3. for each camera i, a list of J_i detection times $\{t_{i,1}, \ldots, t_{i,J_i}\}$, where $J_i = 0$ implies that camera i had no detections and this list is empty;
4. for each camera i, a list of $P + 1$ covariate values, $\{r_0(\mathbf{x}_i), \ldots, r_P(\mathbf{x}_i)\}$ associated with the location $\mathbf{x}_i$ where camera i was deployed.

Our modelling process accommodated sampling intervals that were not composed of consecutive time periods (e.g. a camera may have been active for two separate periods separated by a period of inactivity). The first covariate, r_0, is always equal to 1 and corresponds to the model intercept (the predicted detection rate when all other covariates are 0). In general, Poisson process models can incorporate detection rates that vary in time as well as in space, but we only focused on the spatial variation in detection rates here. Thus, a simple functional form for the detection rate at any location $\mathbf{x}_i$, $\Lambda(\mathbf{x}_i)$, might assume that detection depends linearly on all the covariates:

$$\Lambda(\mathbf{x}_i) = \exp\left[\sum_{p=0}^{P} \lambda_p r_p(\mathbf{x}_i)\right].$$

Exponentiating the linear combination of the covariates multiplied by their respective coefficients (λ_p) ensured $\Lambda(\mathbf{x}_i) > 0$ always. As long as $\Lambda(\mathbf{x})$ is greater than or equal to 0 everywhere, any functional form could be used to express the effect of a covariate on the response variable.

Because the likelihood function L for a non-homogeneous Poisson process depends on the value of Λ at all observed detections, it must be normalized by an integral representing the average value of Λ across the study period. Integrating over time is not necessary because our detection function was assumed to be temporally constant (i.e. the integral evaluates to the detection function $\Lambda(\mathbf{x}_i)$ multiplied by the length of the sampling period $\| T_{Li} \|$), and since the camera trap array represented a spatially discrete sample of the study area, we changed the spatial dimension of the integral to a sum:

$$L(\lambda_0, \ldots, \lambda_P) = \prod_{i=1}^{N}\left[\prod_{j=1}^{J_i} \Lambda(\mathbf{x}_i)\exp(-\| T_{Li} \| \Lambda(\mathbf{x}_i))\right].$$

An additional step to simplify model fitting was to maximize the log-likelihood, formulated as follows, rather than the true likelihood. The 'linear' form of the log-likelihood function is as follows:

$$\log L(\lambda_0, \ldots, \lambda_P) = \sum_{i=1}^{N}\left[\sum_{j=1}^{J_i}\sum_{p=0}^{P} \lambda_p r_p(\mathbf{x}_i) - \| T_{Li} \| \exp\left(\sum_{p=0}^{P} r_p(\mathbf{x}_i)\right)\right].$$

2.3 | Quantifying human use in the study area

We designed our human model as a Poisson process model for the detection rate of humans on our camera traps to facilitate informed and accurate predictions about how human use varied throughout the study area. This model estimated how humans select for an optimal recreation experience akin to animal habitat selection studies (Meekan et al., 2017; Sidder et al., 2023). We compared human use at camera sites to relevant environmental variables that may correlate with aesthetic or functional benefits of recreating in different parts of the study area (Pauli et al., 2019). These covariates included slope (with both a linear and quadratic term, to account for potential selection for intermediate slopes) and aspect (specifically, the cosine and sine of aspect), both derived from a digital elevation model (DEM). The cosine of aspect represents an index of 'eastness' and the sine represents an index of 'northness', which are relevant to snow cover,

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forest type, and temperature in our montane, northern study area. We included four covariates representing landcover classes ('open coniferous or deciduous forest', 'barren/nonvegetated/burned', 'herbaceous/wetland', and 'shrub'), with 'closed coniferous forest' as the reference category. We chose this as the reference category because it was the most frequent landcover type in the study area, making up 49% of the landscape. None of our cameras were located in the 'water' landcover class, but since humans often use natural areas adjacent to water (Kakoyannis & Stankey, 2002), we included 'distance to nearest water body' as a covariate. As anthropogenic variables indicative of human access to the camera location, we included distance from the nearest town, distance to the nearest road and a categorical variable indicating the trail context of the camera (i.e. placed within 50 m of a designated trail, within 50 m of an undesignated trail, within 50 m of a road, or farther than those distances from either feature).

In addition to the covariates named above, we included an autoregressive component in the model to account for the attraction of people to locations with other people (and trails), which was necessarily spatially autocorrelated. Specifically, we incorporated the detection rate (detections per day) of humans ($H(\mathbf{x})$) at nearby cameras as additional model covariates and weighted their contribution by their distance d from the focal camera. We used an inverse distance weighting to calculate $f_H(\mathbf{x}_i)$, an interpolated average of human use at cameras near $\mathbf{x}_i$. We assumed that at locations close to other cameras, interpolated human use estimates would be quite accurate, and covariate information would not be needed, whereas covariate data (rather than autoregressive information) would better explain human use at locations without other cameras nearby. We represented the amount of such information using $w_H(\mathbf{x}_i)$, which we calculated from on the number of cameras near $\mathbf{x}_i$. We generated f_H and for each location using only cameras with the same trail/road designation, which is represented mathematically by F_{same}, a function that is 1 if two locations are on the same kind of trail or road. This revised model for detection takes the following form:

$$
\begin{aligned}
f_H(\mathbf{x}_i) &= \frac{\sum_{j\neq i} d(\mathbf{x}_i,\mathbf{x}_j)^{-\alpha} H(\mathbf{x}_j) F_{\text{same}}(\mathbf{x}_i,\mathbf{x}_j)}{\sum_{j\neq i} d(\mathbf{x}_i,\mathbf{x}_j)^{-\alpha} F_{\text{same}}(\mathbf{x}_i,\mathbf{x}_j)} \\
w_H(\mathbf{x}_i) &= 1-\exp\left(-\nu \sum_{j\neq i} d(\mathbf{x}_i,\mathbf{x}_j)^{-\alpha} F_{\text{same}}(\mathbf{x}_i,\mathbf{x}_j)\right) \\
\Lambda_H(\mathbf{x}_i) &= \exp\left[(1-w_H(\mathbf{x}_i))\sum_{p=0}^{P}\lambda_p r_p(\mathbf{x}_i) + w_H(\mathbf{x}_i)\log f_H(\mathbf{x}_i)\right].
\end{aligned}
$$

The model parameter $\alpha > 0$ measures the strength of the inverse distance decay. Smaller values indicate that human use at a trail is predicted well by trails that are farther away, suggesting a wider scale of spatial autocorrelation. The model parameter $\nu > 0$ quantifies how much information about nearby human use (quantified based on the distance between the focal camera and other cameras) is necessary to accurately predict the density of human use.

To ensure that the predictions were accurate, we performed a leave-one-out cross-validation on the model. This technique involves predicting each data point using the parameters from the model, but assuming that the focal data point has been removed from the dataset. In other words, our interpolation of human use would not include the focal location. We acquired our predictions by calculating the detection rate according to the model equations and median posterior estimates. Then, we calculated the root median squared error (using median over mean because there were some outlier sites with hundreds of visitors per day) across the set of camera locations to assess how close the average predicted human use value was to the true value.

2.4 | Statistical analysis of wildlife detections

We modelled the detection rate of grizzly bears and wolves as a function of environmental and anthropogenic covariates in the study area. We included linear and quadratic terms for elevation and slope, as well as sine and cosine of aspect, as calculated from our DEM. We included average annual snow cover (linear and quadratic) as an additional abiotic covariate. We also included habitat information using the same landcover variables (closed conifer, open conifer or deciduous, shrub, herbaceous or wetland, barren or burned) as outlined above.

We did not include an autocorrelation component in this model, as we did for the human model, for two reasons: (1) while we expected human use to be autocorrelated in ways that could not be explained by our covariates, including the sharing of popular recreation destinations, we did not expect such patterns on the same magnitude for wildlife, for which trail networks are not as defined or contiguous, and (2) we anticipate that the observed human detection rates are closer to the 'true' average density of humans on the landscape because they were detected so much more often, as opposed to the wildlife species that were undetected at a majority of cameras, which reduces the accuracy of interpolating observed detection rates as exact estimates of relative density.

We included the density of human use, also as calculated above, at focal and nearby areas as covariates in our wildlife models. We assumed that the effect of human use at a nearby location depended directly on the density of human use at that location as well as the distance between that location and the focal camera, with the strength of this effect decreasing with distance. We used our estimate of α for this model to quantify the zone of influence for wildlife of human use on trails. We used an exponential decay function to represent this relationship, which decays faster than an inverse distance function, to minimize the effects of human use outside the estimated zone of influence on wildlife. We incorporated human use at each raster cell $(c_1, c_2, \ldots)$ in the study area into Λ as follows:

$$
\Lambda(\mathbf{x}_i,t) = \exp\left[\sum_{p=0}^{P}\lambda_p r_p(\mathbf{x}_i,t) + \lambda_H \sum_j d(\mathbf{x}_i,c_j)^{-\alpha}\Lambda_H(c_j)\right].
$$

In this context, the value of the second sum serves as a 'disturbance index' for human use (with comparable meaning to Hojnowski, 2017),

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TABLE 1 The components of the Web of Science search term used to review the literature on wildlife responses to anthropogenic features and/or disturbance.

Component	Intended purpose
('grizzly bear*' or 'brown bear*' or wolf or wolves or '*Canis lupus*' or '*Ursus arctos*')…	English and scientific names of our two focal species, accounting for pluralizations
AND [(human* or anthropogenic) AND (develop* or residen* or disturb* or interact*) OR…	Citations with the words 'develop', 'residence', 'disturb', 'interact', or their derivations needed to also include either 'human' or 'anthropogenic', since these terms could be used widely in non-anthropogenic contexts
(recreat* or trail* or hik* or bik*)]	Citations with any of these words did not explicitly need to include the words 'human' or 'anthropogenic' because these terms already imply an anthropogenic context

Note: Each of the components, listed here as rows, were linked through a series of 'AND' and 'OR' operators that required any citations to meet multiple criteria for consideration in our review.

generated from the predicted human use values. Calculating the second sum over all raster cells is computationally intensive, so we rounded all distance values ($d(\mathbf{x}_i, c_j)$) up to the nearest 30 m interval (except for the cell containing $\mathbf{x}_i$, which was rounded down to 0 m). We did not include any raster cells further than 12 km from $\mathbf{x}_i$ in the sum. This produced 400 discrete increments of distance to sum over. These steps supported a simplified formulation of the detection rate:

$$\Lambda(\mathbf{x}_i, t) = \exp\left[\sum_{p=0}^{P} \lambda_p r_p(\mathbf{x}_i, t) + \lambda_H \sum_{d=0}^{400} d^{-\alpha} \sum_{j \in J_d} \Lambda_H(c_j)\right].$$

Here, J_d is the set of raster cells that are approximately (as determined by the rounding rule described above) d meters from $\mathbf{x}_i$. The value of the third sum did not depend on the parameters so we computed it ahead of time for each value of d and each site $\mathbf{x}_i$.

In the grizzly bear model, we slightly modified the model structure above to account for time periods when grizzly bears were hibernating and would consequentially be undetectable. Grizzly bear den phenology has been studied extensively in the Rocky Mountains and surrounding areas (Ciarniello et al., 2005; Pigeon et al., 2016; Vroom et al., 1980), so we did not feel it necessary to model this explicitly. Instead, we determined the proportion of bears hibernating at any given time of year a priori (Appendix S1) from a dataset of global positioning system (GPS) locations of grizzly bears collared in the study area during the sampling period.

2.5 | Model fitting and parameter estimation

We estimated parameters for all three (human, grizzly bear, and wolf) models using Bayesian methods to better acknowledge the uncertainty in our parameter estimates. We used the No U-Turn (NUTS) sampler (Hoffman & Gelman, 2014) implemented by the Stan software library (Stan Development Team, 2023). For each species, we ran five independent chains and excluded the first half of each chain from inference as warmup iterations (Carpenter et al., 2017). More complex models require more iterations, so we re-ran the samplers until the number of iterations was sufficient for model convergence. We assessed convergence using $\hat{R}$ values, which are estimated for each parameter, and are below 1.01 for all parameters in models that have converged (Vehtari et al., 2021). After verifying proper chain convergence using $\hat{R}$ values, we obtained posterior medians and 95% credible intervals for each parameter.

2.6 | Comparing our zones of influence to others

We conducted a literature review to identify other studies that have estimated zones of influence of non-motorized human use on grizzly bears and wolves. We systematically searched the Web of Science citation database for peer-reviewed articles that included as keywords at least one of our study species (including 'brown bear' or 'grizzly bear') along with a suite of terms that could be associated with human use in natural areas (Table 1). We manually screened all citations that fit these criteria, retaining only the articles that (a) specifically identified a relationship between distance from humans and effect size of human disturbance, (b) explicitly considered the density of human use or recreation rather than only distance from trails or other features, and (c) estimated this process using data rather than estimating a value a priori via expert opinion or other non-quantitative estimates. The studies that estimated a zone of influence, according to these criteria, either did so using a threshold-based analysis (e.g., by demonstrating that the effects of humans are negligible after some distance) or by fitting a smooth curve to the effect of human use as a function of distance (similar to our models, but often with only the nearest feature). We qualitatively compared our results to existing work by visualizing both the smooth curves and the discrete thresholds, which we mapped onto a continuous plane as step functions.

3 | RESULTS

Our 1699 camera traps were active for a total of over 3000 camera-years and captured over 11,000 images of grizzly bears, 18,000 images of wolves, and one million images of human recreationalists. Our Poisson process models quantified human use throughout the study area, estimated wildlife responses to several ecological

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variables, and integrated the effects of human use and ecological variables on detection rates for grizzly bears and wolves across the same study area. The purpose of these steps was to estimate zones of influence for both species and then compare them with values from the literature. Effect sizes for various selection relationships are represented by posterior medians, with 95% credible intervals depicted in brackets.

Every covariate we included in the model for human use was a significant predictor for human detection rates, with 95% credible intervals excluding 0 (Figure 1). Human recreationalists were frequently detected on our network of cameras and more often along trails that were close to towns, roads, and waterbodies (Figures 1 and 2). Recreationalists were detected 3.6 times as often (95% credible interval: [3.54, 3.59]) at locations 1 km from the nearest road, relative to locations 10 km from the nearest road. We observed similarly positive relationships for towns (1.1 times as often; 95% CI: [1.07, 1.13]) and waterbodies (3.1 times as often; 95% CI: [3.02, 3.16]). Humans selected strongly for east-facing slopes (or slopes where the cosine of aspect was larger), visiting those areas 2.3 (95% CI: [2.24, 2.28]) times as often as west-facing slopes. They were also detected more often at intermediate, but not steep (~15°) slopes (Figure 1). The human use model revealed extensive human use of both designated trails (1.7 visitors per day; 95% CI: [1.72, 1.73]) and undesignated trails (1.1 visitors per day; 95% CI: [1.11, 1.13]), with undesignated trail use approximately 35% (95% CI: [0.346, 0.356]) lower than at designated trails with similar habitat qualities. Off-trail sites had very low human use, with the model predicting 34.5 detections/year (95% CI: [34.1, 35.1]) at locations more than 50 m from trails. After 2500 iterations per chain (1250 of these were excluded as warmup iterations), the human model appeared to converge, with all parameters registering $\hat{R}$ values below 1.0017, well below the recommended value of 1.01 (Vehtari et al., 2021). The human model appeared to predict human use quite accurately, as the root median squared error for the dataset was 0.879 humans/day. Therefore, the predicted human use at 50% of camera sites would be 0.879 humans/day more or less than the observed value if we removed that site from the dataset.

The wildlife models revealed differences in how grizzly bears and wolves used the ecological landscape. Grizzly bears were detected most frequently at intermediate elevations (approximately 2000 m), while wolves displayed an opposite trend, with the lowest predicted detection rate at approximately 1750 m (Figure 3). Both species avoided steep terrain (>45°; Figure 3). Grizzly bears and wolves were 2.2 (95% CI: [2.08, 2.42]) and 5.0 (95% CI: [4.65, 5.39]) times as likely, respectively, to be detected in flat terrain than at 25° slopes. Wolves displayed strong selection for southwest facing slopes, being detected there 2.3 (95% CI: [2.14, 2.42]) times as often as at northeast-facing slopes (Figure 3). Both species avoided areas with relatively high snow cover, but grizzlies appeared to select for habitat that had intermediate levels of snow cover (Figure 3; Table S1). Grizzly bears selected strongly for barren or burned areas (including gravel pits, recently burned, and alpine areas); the model indicates that their detection rate in this habitat type was 1.4 times as high (95% CI: [1.36, 1.52]) as in closed coniferous forest (the reference category; Table S1; Figure 4). They exhibited slight selection against herbaceous habitats (relative to closed coniferous forests). Wolves preferred herbaceous wetlands, shrubs, open coniferous forest, and barren or burned habitats over closed coniferous forests, but none of these effects were as strong as grizzly bear selection for barren or burned habitat. Maximum $\hat{R}$ values for both models were well below the 1.01 threshold (1.0036 for grizzly bears and 1.0062 for wolves) after 1250 iterations (625 were excluded as warmup iterations), suggesting convergence.

Use of Poisson process models made it possible to integrate the effects of human use with ecological variables to show that grizzly bears and wolves were detected much less frequently in areas with higher rates of human use (Table S1). For example, comparing a site with relatively high human disturbance (e.g., the

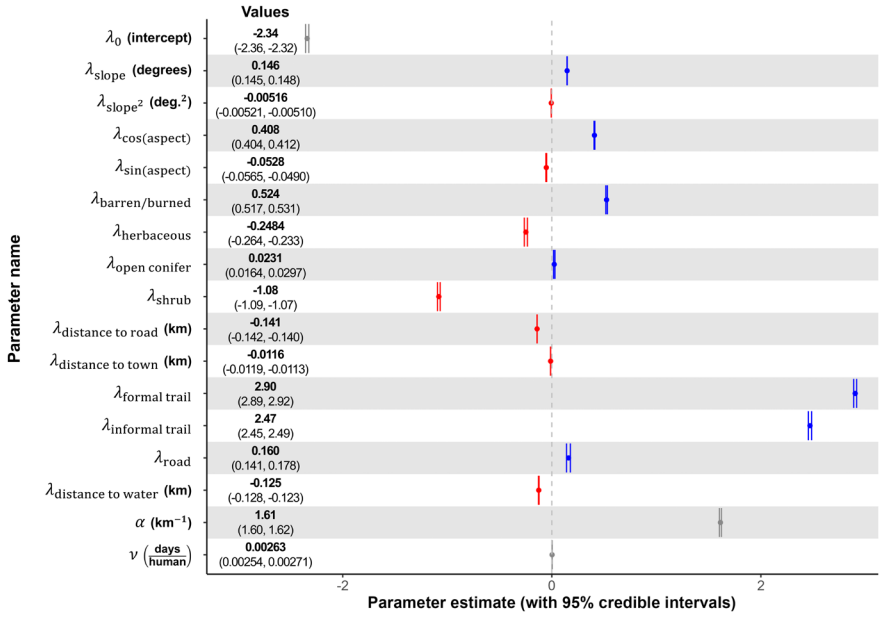

FIGURE 1 Coefficient plot for the human Poisson process model, with median posterior estimates and 95% credible intervals indicated on the left side of the plot. Units for the parameters are indicated on the *y*-axis label when relevant. Selection coefficients are coloured based on their directional significance (red = significantly negative selection; blue = significantly positive selection). Parameters that are not selection coefficients (and for which a value of 0 is not meaningful) are coloured in grey.

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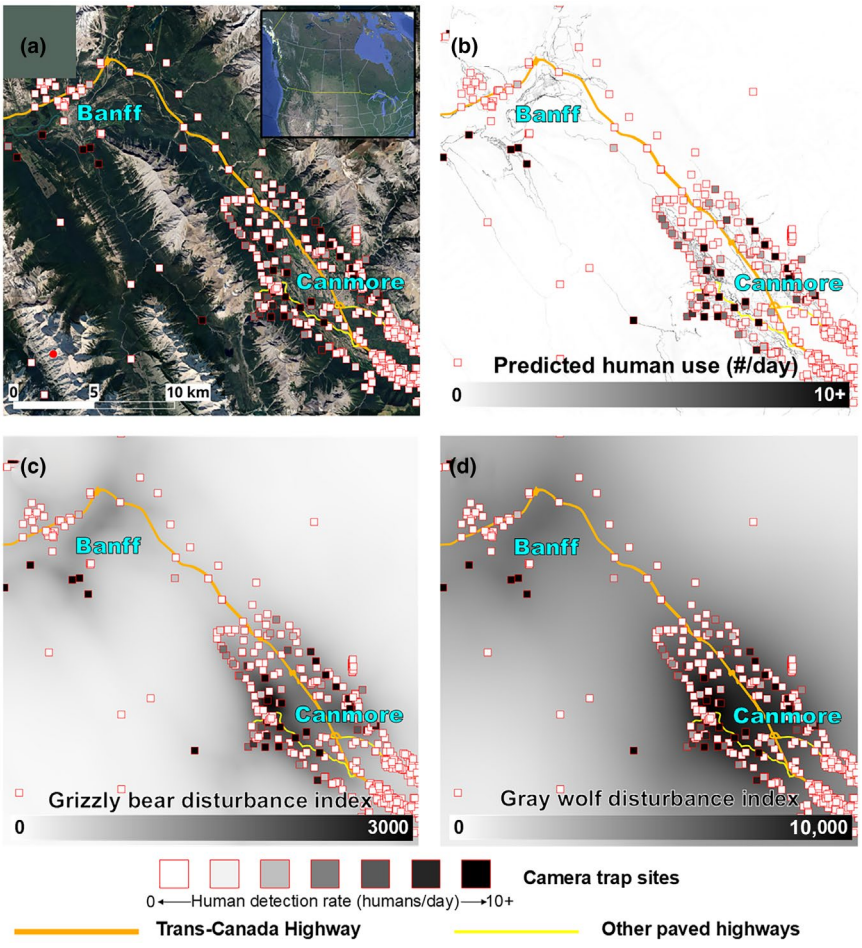

FIGURE 2 Human disturbance indices for grizzly bears and wolves, as estimated by our model, for a subset of the study area that includes Banff, Alberta and Canmore, Alberta, the area's two largest towns. Panel (a) depicts the satellite imagery of the region. Panel (b) depicts the predicted levels of non-motorized human recreation. Panels (c) and (d) display the human disturbance indices as estimated by the wildlife models. Major roadways and camera trap sites are included in all four panels as landmarks.

75th quantile disturbance index for each species) to a site with relatively low disturbance (25th quantile among all cameras) produced 67% fewer detections of wolves (95% CI: [0.617, 0.720]) and 51% fewer detections for grizzlies (95% CI: [0.405, 0.620]). Our estimated zone of influence was larger (smaller α) for wolves than for grizzly bears, meaning the effects of human disturbance for wolves extended further away from locations with human use (Figures 2 and 5).

Based on our criteria for estimating an explicit zone of influence, our literature search revealed only four studies for grizzly bears (Coleman et al., 2013; Hojnowski, 2017; Kasworm & Manley, 1990; Ladle et al., 2019) and three for wolves (Hebblewhite & Merrill, 2008; Malcolm et al., 2020; Rogala et al., 2011). These studies corroborated our finding that wolves have a wider zone of influence than grizzly bears, but the zones of influence we calculated were larger than the other studies for both species (Figure 6). At a distance of 1 km, our model's relative strength of influence was 40% higher than the average value from the literature for grizzly bears and 97% higher for wolves. Our calculated zones of influence estimated that some displacing effect (at least 5% as strong as the effect directly on the trail) of human recreationalists extended as far as 1.8 km (95% CI: [1.51, 2.12]) for grizzly bears and 6.1 km (95% CI: [5.41, 7.06]) for wolves, again exceeding the values, especially for wolves, of other estimates for zones of influence that do not acknowledge effects of human displacement at faraway distances (Figure 5). Our estimated zones declined rapidly with distance such that 50% of the displacing effect immediately adjacent to trails would occur at 267 m (95% CI: [238, 301]) for grizzly bears and 576 m for wolves (95% CI: [537, 621]). Appendix S2 contains a link to an interactive tool that can estimate the zone of influence corresponding to any relative strength of influence (e.g. 50%) and can also make the inverse calculation to derive the strength of influence at any distance.

4 | DISCUSSION

As human populations rise globally, it is increasingly difficult to predict and mitigate the effects of human use on the persistence of wildlife populations. We introduce a framework for doing so using camera traps that detected both people and wildlife throughout the central Rocky Mountains of Canada. We used Poisson process models to build and incorporate a predictive map of human use intensity to show how the cumulative effects of human use on trail networks influenced detections of grizzly bears and wolves along the same trail networks and surrounding areas. Our results suggest that these carnivores avoid areas with consistently high human use with a zone of influence for this activity that is larger for wolves than bears and exceeds previous estimates.

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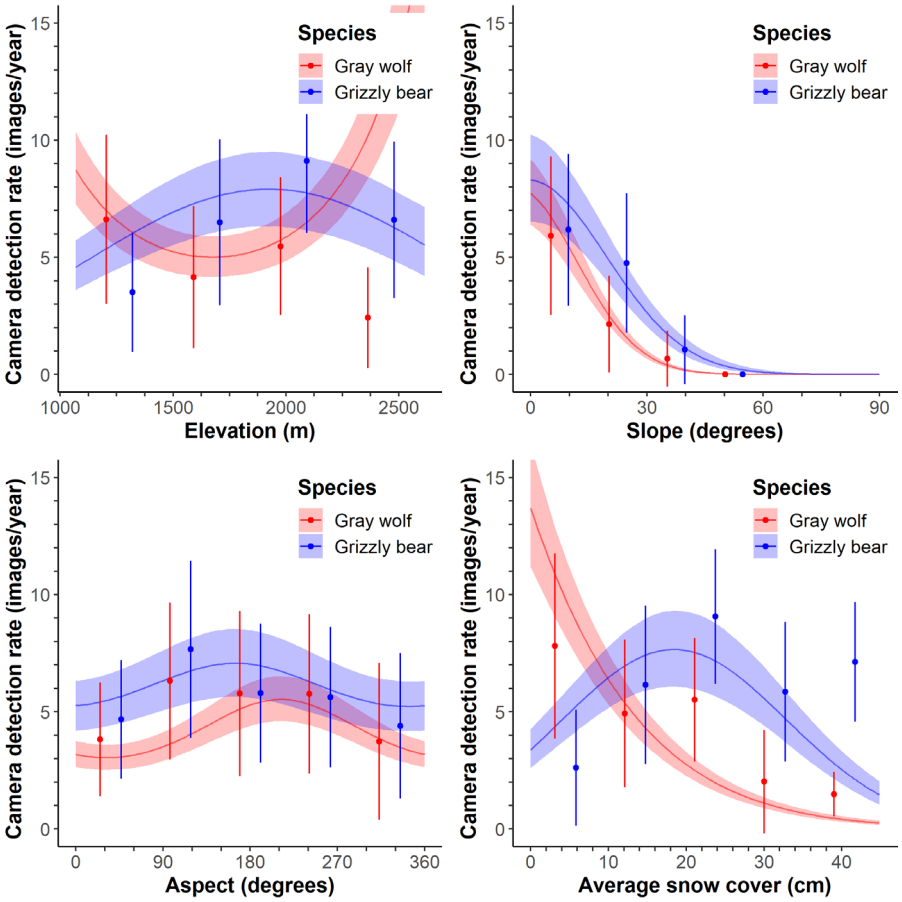

FIGURE 3 Relationships between topographic covariates (elevation, slope, aspect, and average snow cover) and camera detection rates for grizzly bears and wolves. Smooth curves represent predicted detection rates from the wildlife models, assuming constant values for all non-focal covariates. The shaded areas around each line represent the 95% credible interval around the median posterior estimate. Model predictions were generated by setting all other covariates equal to their mean value across all cameras, and the landcover type was set to the reference category (closed coniferous forest). The dot-and-line plots represent the observed detection rate (weighted mean ± weighted standard deviation) of each species at our cameras for different 'binned' values of each covariate. Grizzly bear detection rates have been adjusted to account for hibernation (units are images/365 active bear days).

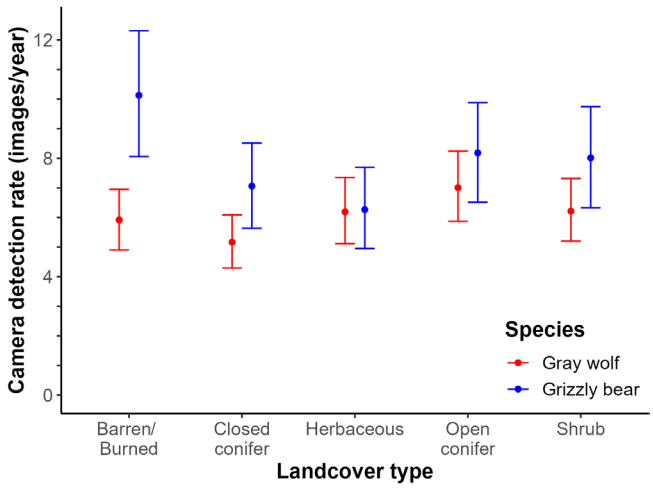

FIGURE 4 Predicted detection rates, assuming average values for all other covariates, for grizzly bears (blue) and wolves (red) in different landcover types. Model predictions were generated by setting all other covariates equal to their mean value across all cameras. Dots represent median predictions from the wildlife models and error bars represent 95% credible intervals. Grizzly bear detection rates have been adjusted to account for hibernation (units are images/365 active bear days).

The camera traps we used in this study measured the density of human use at each camera site, leaving most of the study area unmeasured, so we interpolated the camera-derived estimates of human use through the remainder of the study area. There are few alternatives to estimating human use because obtaining a true census of human activity everywhere on any landscape is impossible, and even large-scale tracking datasets (e.g., Strava; Corradini et al., 2021) are potentially biased in the types of recreation and recreationalists they track (Venter et al., 2023). Our interpolated estimates of human use incorporated such covariates as slope, aspect, land cover class, and distance to trails, roads, towns, and water, that we expected to influence the movements of humans and wildlife. Our results build on the growing body of literature concerning human 'habitat selection' (Pauli et al., 2019; Peterson et al., 2020; Sidder et al., 2023) to identify the environmental and anthropogenic covariates that recreationalists preferred in our study area (Figure 1). For example, our camera dataset documented widespread use of undesignated trails that was only 35% lower than use on designated trails, highlighting the magnitude of undesignated trail use in the study area. The purpose of our human model was to produce a covariate predicting the intensity of human use throughout the study area, which was necessary for understanding the cumulative effects of human use (across multiple features) on wildlife.

We included environmental covariates in our wildlife models (Figures 3 and 4; Table S1) for two reasons. First, it was necessary to ensure that any relationship between wildlife use and human use was not a result of confounding environmental covariates. Indeed, we found some similar selection coefficients for human use (Figure 1) and carnivore use (Table S1), including avoidance of highly

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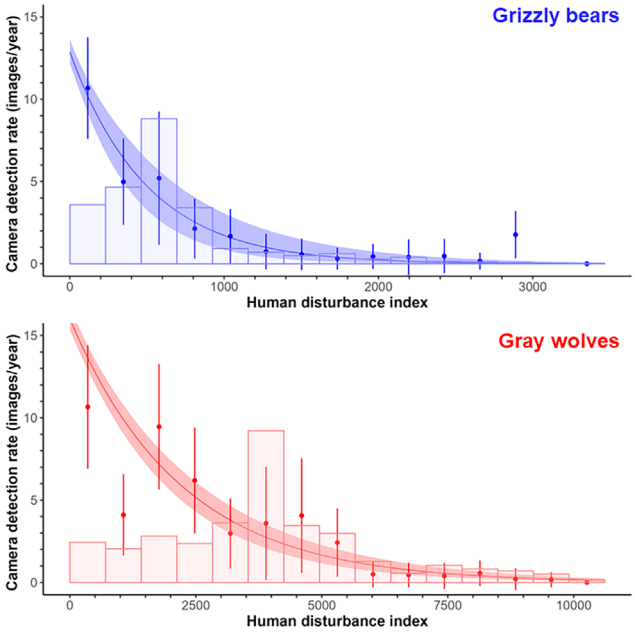

FIGURE 5 Predicted detection rates, assuming average value for all other covariates, for grizzly bears (blue) and wolves (red) at different levels of human disturbance. Shaded ribbons represent 95% credible intervals around the median posterior estimate (solid line) for detection rate. Model predictions were generated by setting all other covariates equal to their mean value across all cameras, and the landcover type was set to the reference category (closed coniferous forest). Dot-and-line plots represent observed detection rates (weighted mean ± weighted standard deviation) at camera sites within binned human disturbance indices. The histogram represents the total distribution of disturbance indices across camera sites for each species. Grizzly bear detection rates have been adjusted to account for hibernation (units are images/365 active bear days).

sloped terrain with north-facing aspects. A second purpose was to determine if and how the selection we measured differed from other studies of habitat selection by these species in the Canadian Rockies. For example, our models identified weak, albeit significant, selection by wolves for open coniferous, herbaceous, shrub and barren or recently burned habitats, relative to closed coniferous forest. This weak selection corroborates conclusions in the literature about wolves using a wide range of habitats, apart from their stark avoidance of humans (Arjo & Peltscher, 2004; Ehlers et al., 2014; Mech, 2017; Paquet et al., 1996a, 1996b). We also found that avoidance of steep slopes was commonly observed in existing studies on wolf and grizzly bear habitat selection (Hebblewhite & Merrill, 2008; Milakovic et al., 2011; Peterson et al., 2021). Conversely, our results revealed a pattern of very strong selection for barren or burned habitats by grizzly bears. Previous work in the region suggests that grizzly bears usually avoid non-vegetated areas (Chetkiewicz & Boyce, 2009; Milakovic et al., 2012; Nielsen et al., 2002, 2006). Our temporally static landcover model could not capture successional revegetation at mine sites, gravel pits or burned areas, all of which have been identified as key grizzly bear food sources during succession (Apps et al., 2004; Cristescu et al., 2015; McLellan & Hovey, 2001; Milakovic et al., 2012). Inaccuracy in designating landcover types is a recurrent problem in studies of habitat selection (Behney, 2020). Even without errors, different techniques for measuring landcover variables introduce variation that makes it difficult to compare environmental variables among datasets. Our model predictions aligned well with observed habitat use patterns for topographic variables, except for predicting unrealistically high use by wolves at high elevations (Figure 3), likely because elevation was correlated other variables (e.g., snow cover or slope) that wolves selected against. These correlations are not accounted for in marginal effects plots that attempt to isolate the effect of one variable, but when predicting detection rates at real locations with correlated covariates, the apparent selection for high elevations is effectively cancelled by selection against snowy, sloped terrain.

By integrating our interpolated model of human use with various ecological covariates, we were able to determine how detections of grizzly bears and wolves were affected by both the proximity of anthropogenic features, as well as the amount of human use on them. This approach was inspired by Hojnowski (2017) who calculated a 'disturbance index' for her study area based on the distance to the nearest recreational trail and the intensity of use on that trail. Separating feature footprints from associated human use is important because low-use linear features appear to attract both grizzly bears (Roever et al., 2010) and wolves (Dickie et al., 2017; Whittington et al., 2005), owing to the more efficient movement they afford (Dickie et al., 2020). Our disturbance index was calculated in such a way that low-use trails are not expected to deter grizzly bears or wolves. Although our model does not account for attraction to these features, this could be achieved in subsequent work by adding environmental covariates.

Our wildlife models integrated human and wildlife selection to show that areas with frequent human use reduced the detection rates of grizzly bears and wolves, with diminishing effects that were still evident up to 6 km away. Our estimated zones of influence were higher than other rates that have been estimated for both grizzly bears (Coleman et al., 2013; Hojnowski, 2017; Kasworm & Manley, 1990; Ladle et al., 2019) and wolves (Hebblewhite & Merrill, 2008; Malcolm et al., 2020; Rogala et al., 2011; Figure 6). In particular, we documented how human use at sites nearly 2 km (for grizzly bears) and 6 km (for wolves) away can slightly, but measurably, reduce habitat quality for these wary species, which has not been found in previous studies. The larger zones of influence we estimated stem logically from the method we used. By incorporating the additive effects of all nearby features and estimating the human use they attracted, we estimated a cumulative effect of recreationalists on wary carnivores. Previous studies have primarily focused on only the nearest feature to any location, rather than all nearby locations (e.g., Coleman et al., 2013; Hojnowski, 2017), and necessarily omit the effects of faraway features on animal space use. Some studies also estimated selection using a series of discrete bins (e.g., Kasworm & Manley, 1990; Rogala et al., 2011), which may obfuscate some of the variation in how wildlife respond to human use from different distances.

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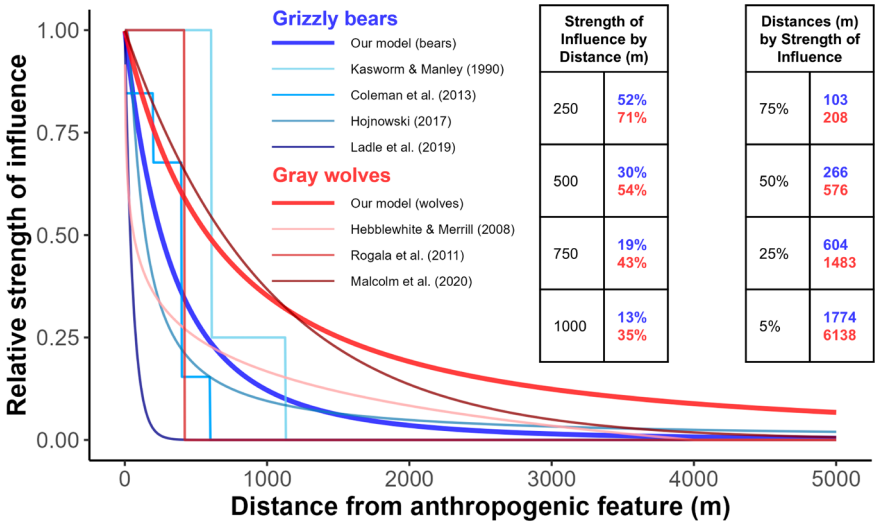

FIGURE 6 Zones of influence estimated for grizzly bears (shades of blue) and wolves (shades of red) from various studies (including our work, displayed with thicker lines). Studies were selected from a systematic review of the human–wildlife interaction literature and were only included if they explicitly analysed the relationship between distance to anthropogenic features, intensity of human use at those features, and wildlife disturbance, as we did with our models. The tables in the inset can be used either for determining how much the influence of human activity is reduced at different distances (the table on the left) or how wide a buffer would have to be to exclude areas exceeding some strength of influence (the table on the right).

Many of the studies we compared our results to have influenced guidelines regarding the extent to which protected areas should be 'buffered' from trails (Ford et al., 2020), and conservation practitioners in our study area have recommended buffering critical wildlife habitat accordingly (Bow Corridor Ecosystem Advisory Group, 1999, 2012). By estimating the relationship between distance and strength of effect as a smooth curve, rather than identifying a threshold, our results expand on existing management recommendations to highlight the potential for human use to affect wildlife at large distances, especially in areas with high-use trails or dense networks of trails. Land managers can use our results to generate optimal buffer distances for excluding land within some undesirable influence of human use, or they can calculate the strength of such an influence at any distance away from a trail (Figure 6). We hope that the tool accessible via the link in Appendix S2 can facilitate these types of management decisions in the Canadian Rockies and beyond.

Our methods for examining the effects of human use on wildlife detections in a developing landscape overlooked some details that might be incorporated into future studies. First, we ignored seasonal variation in wildlife detections, even though forage availability and reproductive demands cause habitat selection to vary seasonally for both grizzly bears (Milakovic et al., 2012; Nielsen et al., 2010) and wolves (Uboni et al., 2015). Our results represent an average of these different seasonal behaviours since each season was represented roughly equally, but given that human use varies seasonally in our study area, wildlife may adjust their selection patterns for areas near human use seasonally. Future work could assess seasonal effects of human use on carnivore detection rates and the zone of influence. We also ignored diel variation in detections, even though many large mammals avoid humans by becoming more nocturnal (Gaynor et al., 2018) in what is sometimes called 'temporal partitioning' of a landscape (Kronfeld-Schor & Dayan, 2003). This phenomenon has been directly observed elsewhere for both grizzly bears (Coltrane & Sinnott, 2015; Northrup et al., 2012) and wolves (Frey et al., 2020; Sytsma et al., 2022). The relationship between distance from human features and avoidance (which we quantified with the model parameter α) might also vary based on environmental covariates, because certain habitat types may facilitate wider perceptual ranges for wildlife (Elmeligi & Shultis, 2015). It is possible to expand on our Poisson process framework to incorporate such a relationship, and we recommend this as a topic for future work. Finally, our models could not evaluate the effects of specific types of recreationalists in real time, which would be better estimated with the flight initiation distances that have been performed extensively for our study species (Karlsson et al., 2007; Moen et al., 2012; Versluijs et al., 2022; Wilker & Barnes, 1998).

Despite the lacking sensitivity to variation among seasons, time of day, and type of recreational activity, the average effects of human use on carnivore detections we calculated could be used to advance human–wildlife coexistence in landscapes devoted to both wildlife conservation and human recreation. Because our models quantified the changes in carnivore detections associated with variation in human use, they could be used to predict the effects of future changes in human use, which could include trail expansions as well as decommissioning of existing trails. Specifically, the human use layer we generated as a model covariate (Figure 2b) could be altered to inform hypothetical disturbance index layers (as in Figure 2c,d) with greater or lesser disturbance to estimate associated changes in detection rates. Such projections would be

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even more useful if they incorporated the variation we omitted in both human use and wildlife use associated with season, time of day, and type of recreation (e.g. with or without off-leash dogs).

Our study reinforces the opinion of others that understanding zones (or rather, patterns) of influence of human use on wildlife is complex, but necessary for coexistence (Ford et al., 2020; Lamb et al., 2020; Suraci et al., 2021). Enduring interest in estimating zones of influence has produced a wide variety of results arising from different methods (Figure 6). By incorporating all nearby anthropogenic features and accounting for variation in human use along these features, our models suggested that these zones are larger than has previously been estimated, with human use on trails exerting small, but measurable, influence as far as 1.8 km for grizzly bears and 6.1 km for wolves. A plausible management target for areas like wildlife corridors might be to limit that influence to no more than 50% of the maximum impact of human use adjacent to trails, which we calculated to be approximately 300 m for grizzly bears and 600 m for wolves. Alternatively, managers may wish to use our models more precisely to estimate the decaying response to human use as a function of distance from trails with various levels of human use to target site- or scenario-specific detection rates for carnivores. In our landscape and many others, continued human population growth increases the challenge of balancing natural experiences for human recreationalists while also conserving healthy wildlife populations (Pooley et al., 2021), especially for wary carnivores like grizzly bears and wolves. Meeting this balance requires an interdisciplinary approach in which understanding the behaviour of humans is as important as understanding the behaviour of wildlife (Arias, 2015; Kollmuss & Agyeman, 2002). Much of the disturbance experienced by wary wildlife in our study area took place on undesignated trails, which could be mitigated with effective public engagement. We hope that our efforts can be synthesized in a collaborative manner to facilitate coexistence between people and wildlife in the Canadian Rockies and beyond.

AUTHOR CONTRIBUTIONS

John Paczkowski and Jesse Whittington organized efforts to collect and classify all camera images used in this analysis. Peter R. Thompson, John Paczkowski, Jesse Whittington, and Colleen Cassady St. Clair conceived the idea for analysis. Peter R. Thompson carried out the analysis with some assistance from the three other coauthors. Peter R. Thompson wrote the first draft of the manuscript which was subsequently revised and edited by John Paczkowski, Jesse Whittington, and Colleen Cassady St. Clair.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.s7h44j1h8 (Thompson et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Quantifying grizzly bear denning patterns.

Appendix S2: Interactive tool for calculating zones of influence.

Figure S1: Map of study area and camera locations.

Table S1: Wildlife model parameter estimates.

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