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WILDLIFE RESEARCH

Spatiotemporal responses of ungulates to hunting in a fenced multi-use area

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ABSTRACT

Context. Human activities, such as tourism and hunting, affect the spatiotemporal behaviour of wildlife. For example, it is well documented that ungulates change their spatiotemporal behaviour as a response to hunting pressure, but less is known about ungulate responses to hunting in areas where human activity is common throughout the year and ungulates are constrained by fences. **Aims.** In this camera-trap study, we analysed the change in spatiotemporal behaviour of wild ungulates (elk, *Cervus canadensis* (3519 events), moose, *Alces alces* (1153 events), and white-tailed deer, *Odocoileus virginianus* (2708 events)) in response to the hunting period in a recreational and fenced park, the Cooking Lake–Blackfoot Provincial Area, Canada. **Methods.** We used general linear models to compare species-specific patterns of intensity of use, calculated as events per week, in response to changes in the nature of human disturbance, namely a shift from recreation to hunting activity. In particular, we compared intensity of use in and out of the hunting season to determine whether species engaged in spatial patterns of avoidance with respect to hunting. We used daily and seasonal patterns of activity to determine how ungulates shifted their temporal use in response to hunting activity and whether they became more nocturnal as a result. **Key results.** We found that ungulates responded temporally to the hunting period by generally shifting their activity to more nocturnal hours, with white-tailed deer showing the biggest temporal shift, suggesting that the ungulates distinguish between consumptive and non-consumptive human activities. Nevertheless, temporal overlap between humans and all ungulate species increased during the hunting period as humans targeted times of increased ungulate activity. Spatially, the response was less distinctive and was species-specific. Elk showed little change in spatial behaviour in response to the hunting period. In contrast, moose decreased the use of trail areas and other areas frequented by humans, whereas deer, counterintuitively, increased the use of trail areas, albeit their use became much more nocturnal. **Conclusions.** We have shown that responses of ungulates to hunting exceed those to non-consumptive recreational use, and whereas temporal responses (increased nocturnality) were consistent across ungulate species, spatial responses were species-specific. **Implications.** Management in small fenced multi-use areas needs to account for shifts in the intensity of disturbance resulting from a change in human disturbance from recreational activity to hunting. Providing spatial opportunities for avoidance of humans is key for most species if hours of operation in these areas already limit the timing of human activity.

Keywords: animal activity, camera traps, human disturbance, hunting, recreation, spatiotemporal behaviour, ungulate, wildlife management.

Introduction

As human populations grow, there is increasing pressure on natural areas to support opportunities for recreation (Balmford *et al.* 2019). Human activity and its consequences for animal behaviour, conservation, and management have received increasing attention. Recreation, even at low levels, is understood to cause risk effects (or non-consumptive effects) in a directly analogous way to predation, which may have cascading effects for individuals and populations of affected wildlife and, indeed, ecosystems

(Phillips and Alldredge 2000; George and Crooks 2006; Reed and Merenlender 2008; Lewis *et al.* 2021; Sytsma *et al.* 2022). Particularly problematic is when human activity seasonally shifts from being non-consumptive (e.g. recreation) to consumptive (e.g. hunting), causing mismatched behavioural responses of wildlife, resulting in the death of individuals (Frair *et al.* 2007; Smith *et al.* 2021).

In response to human disturbance, wildlife increase vigilance, flight behaviour (Manor and Saltz, 2003; Brown *et al.* 2012) and changed their use of habitat and activity time (e.g. spatiotemporal behaviour; Wakefield and Attum 2006; Baker and Leberg 2018; Gaynor *et al.* 2018). A meta-analysis of 76 studies of 62 species from six continents found a shift towards nocturnality in response to increased human disturbance, with a similar effect size for lethal and non-lethal human activities, suggesting that the mere presence of humans is the determinant, and not its activity (Gaynor *et al.* 2018). Indeed, in natural populations, avoiding human activity may result in a trade-off with avoiding natural predators, and may even exceed the response to predation (Proffitt *et al.* 2009; Ciuti *et al.* 2012; Crosmary *et al.* 2012; Visscher *et al.* 2023).

Human hunting results in well-documented changes in ungulate behaviour. Spatially, ungulates respond to hunting pressure by selecting for habitats that offer concealment and reduce movement rates, decisions that have been linked to increased survival (Bonnot *et al.* 2013; Lone *et al.* 2015; Little *et al.* 2016; Parsons *et al.* 2022). Hunting risk can also be minimised by modifying the temporal patterns of space use to safe times, while benefiting from locations that may be otherwise risky (Bonnot *et al.* 2013; Visscher *et al.* 2017). At finer scales, hunting pressure increases vigilance, flight initiation distance, and return times to a site (Benhaiem *et al.* 2008; Stankowich 2008; Visscher *et al.* 2023). However, the response may be species- and context-dependent, resulting from the interplay of both the temporal and spatial predictability of risk (Sih 1984; Mitchell and Lima 2002; Laundré 2010; Saïd *et al.* 2012; Dröge *et al.* 2017), and may be additionally constrained in small fenced conservation areas (Xu *et al.* 2021).

Understanding the potentially contrasting effects of human recreation and hunting on wildlife behaviour is an important consideration for the continued management of multi-use and urbanising landscapes (Berger-Tal *et al.* 2011; Gallo *et al.* 2019; Lewis *et al.* 2021). In this study, we analysed whether wild ungulates species (elk, moose, and deer) change their spatiotemporal behaviour as a response to human hunting activity relative to recreation activity at the Cooking Lake–Blackfoot Provincial Recreational Area (BPRA), a fenced multi-use recreation area near Edmonton, Canada. We predicted that the presence of hunting activity by humans would (1) elicit a temporal shift towards more nocturnal activity and (2) the ungulates will frequent areas with more concealed habitat and locations further away from centres of human activities, such as trails or parking lots.

Methods

Study area

The Cooking Lake–Blackfoot Provincial Recreational Area (hereafter BPRA), is an approximately 97 km^2 park located about 40 km east of Edmonton, central Alberta, Canada. The area is fenced with a 2.2 m high fence to restrict animals from crossing towards the adjacent Elk Island National Park, neighbouring agriculture, and human settlements. The BPRA contains grazing pastures for seasonal cattle grazing. The BPRA has a wide variety of large wild mammals, with elk (*Cervus canadensis*), moose (*Alces alces*), mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*) as the most common herbivores, and coyote (*Canis latrans*) as the most common carnivore. Other less common large predators present are black bears (*Ursus americanus*), cougars (*Puma concolor*) and wolves (*Canis lupus*). The BPRA is open from 07:00 am until 11:00 pm daily for non-motorised recreational activities and contains an extensive and maintained 170 km^2 multi-use trail system to facilitate human activities year-round, including hiking, horse riding, cycling, and cross-country skiing. Licensed hunting of ungulates is allowed in the BPRA during November (but not on Sundays). Ungulates other than white-tailed deer are subject to a limited entry-draw system and Indigenous hunting occurs throughout the year, and overlaps with recreation activity, but is most concentrated in the fall (Hedley *et al.* 2022).

Data collection

In total, 37 Reconyx (HC500, HC600, PC900) remote cameras were systematically placed throughout the BPRA, with each camera being at least 800 m from one another (Fig. 1). Cameras were attached to a tree approximately 1 m above the ground facing the areas where the chance of detection was highest. The latitude, longitude, elevation, distance to parking lots, and location relative to trails were noted for each camera. We also quantified the amount of open habitat (grass, wetland, and shrubland), forested habitat and water within a 100-m radius in the surroundings by using Geographic Information Systems (GIS). In total (but not mutually exclusively) 27 of 37 cameras were associated with recreation trails, roads, or trails used for cattle movement, 14 of 37 were located on the edge of a grazing field, and 14 of 37 cameras had over 50% forested habitat within a 100-m buffer. On detection of any motion-triggered event, the cameras took three photos. Later, the 'EventFinder' (Janzen *et al.* 2019) suite was used to remove non-target photos and collapse individual images to independent events by a temporal cut-off. Between 7 June 2017 and 17 July 2018, 28,401 events were identified, and metadata including the camera name, location, date, time, moon phase, temperature, species name, number of individuals, age class, and sex were assigned to

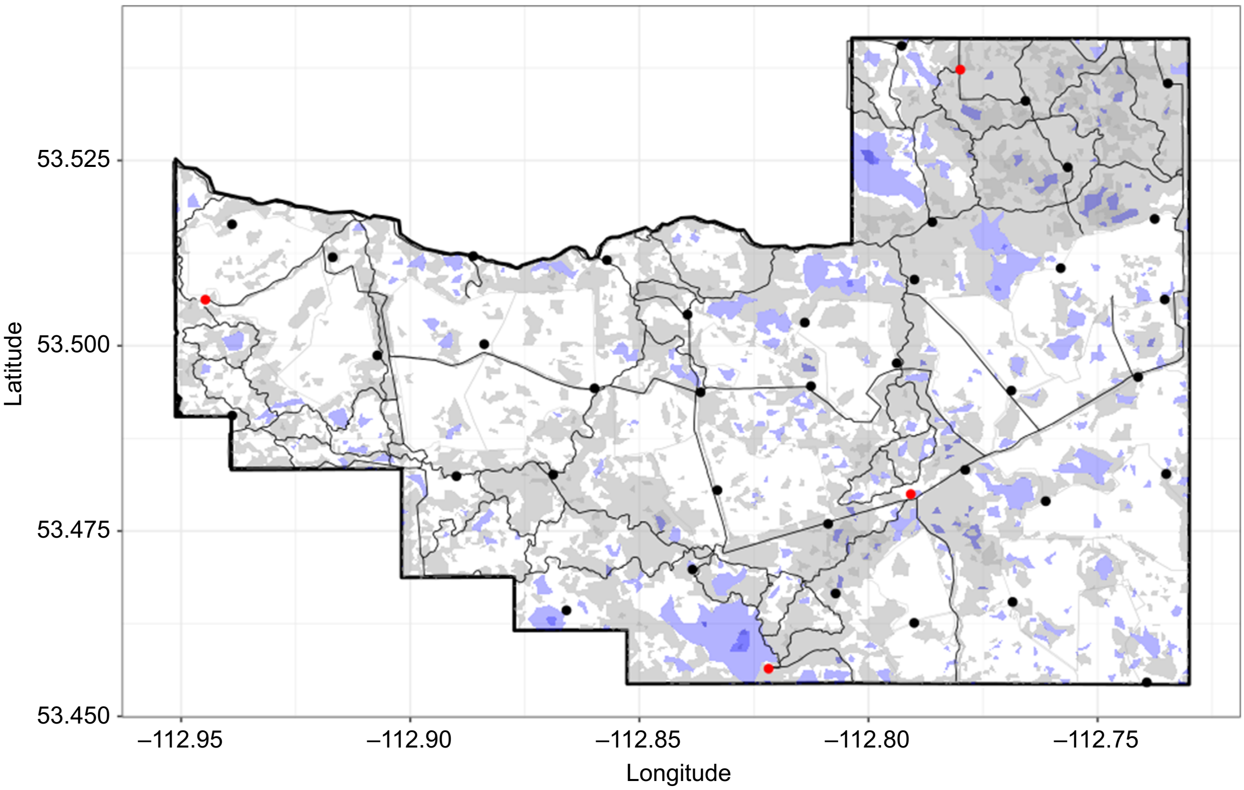

Fig. 1. Map of the Cooking Lake–Blackfoot Provincial Area (BPRA) in Canada in 2017–2018. The black dots represent the 37 camera sites, and the red dots represent the four parking lots. The main roads are indicated by black lines. Forested area is represented by grey and water by blue.

each event. We also noted the behaviour or activity for all events including humans. Sunrise and sunset times for the closest city (Edmonton) for each day were recorded.

Statistical analysis

First, for each event, it was determined whether it took place during the hunting period (November) or during the non-hunting period (December–October). To test whether species changed their temporal activity in response to hunting presence, we created daily activity graphs for each species, on the basis of the camera-trap detection times, for both the hunting and non-hunting period and estimated the coefficient of temporal overlap ($\Delta = 0$, no overlap; $\Delta = 1$, total overlap; Ridout and Linkie 2009) between the two periods with the package 'overlap' (ver. 0.3.9; https://CRAN.R-project.org/package=overlap; Meredith and Ridout 2014) in R (ver. 4.0.4; https://cran.r-project.org; R Core Team 2021). Dependent on sample size, two estimators could be used to estimate the overlap, namely, Δ_4 when both the sample sizes of the pairwise comparison were larger than 50 and Δ_1 when sample sizes were smaller (Meredith and Ridout 2014). We ranked the overlap estimates in three levels, considering a low overlap with $\Delta < 0.50$, a moderate overlap with $0.50 < \Delta < 0.75$, and a high overlap with $\Delta > 0.75$ (Monterroso *et al.* 2014; Viviano *et al.* 2021). The 95% confidence intervals (95% CI) of the overlap estimate were calculated with 10,000 bootstrap replicates (Havmøller *et al.* 2020; Viviano *et al.* 2021). We used these temporal activity data to analyse whether a significant shift in temporal activity was present by testing the probability that the two sets of circular distributions are in fact different by using the package 'activity' (ver. 1.3.4; https://CRAN.R-project.org/package=activity; Rowcliffe *et al.* 2014). We performed a Hermans–Rasson test for each species to analyse whether the daily activity differed from random (Landler *et al.* 2019). We analysed whether the temporal activity overlap between species changed as a result of the hunting period by using a permutation test (10,000 permutations) with the same overlap estimates and 95% CIs used as in the previous analysis.

Furthermore, to analyse whether the animals' activity shifted towards more nocturnal behaviour, we calculated the risk ratio (RR) following the methods of Gaynor *et al.* (2018). Here, we assessed whether each event was taken at day or night on the basis of the sunrise and sunset data (https://www.sunrise-and-sunset.com/en/sun/canada/edmonton/2017/june/1). Hereafter, we calculated the RR by comparing the percentage of activity at night during the hunting period (X_{H}) and non-hunting period (X_{NH}), with $\mathrm{RR} = (X_{\mathrm{H}} / X_{\mathrm{NH}})$. A positive RR indicates an increase in nocturnal activity, whereas a negative RR indicates an increase in diurnal activity during the hunting period.

To test spatial responses to human hunting activity, we analysed the effects of human use and environmental factors on deer, elk, and moose intensity of use (*sensu* Keim *et al.* 2019) at camera locations during (or not) the hunting period. We produced a pair of common *a priori* models for each species to determine (1) the variables associated with a species intensity of use, (2), specifically, whether or not the switch in human activity from recreation to hunting resulted in a change in the variables associated with a species intensity of use, and (3) to compare across species. Candidate models consisted of temperature (temp), features that promote avoidance of humans, namely, the amount of closed hiding vegetation and water within a 100-m radius of the camera (closed habitat and water respectively), variables associated with potential and realized human activity, including whether the camera was located on or off a maintained trail (trail), and the distance from the camera to the nearest parking lot (parking lots), and the number of human events (human; Supplementary Table S1). To determine whether hunting activity by humans resulted in a shift in the variables associated with a species intensity of use relative to human recreational activity, we included information on whether the data represented the hunting period (hunting). For each species, we created two candidate models, the first with hunting included as an additive effect, simply as another variable in the model, and second as an interaction with both the habitat and human grouping of variables. This second set of models allowed us to determine whether human hunting activity results in a change in the variables associated with a species intensity of use. In all models, the camera site was included as a random effect because of the repeated measurements taken at a cameras site. We used a zero-inflated generalised linear mixed model from the package 'glmmTMB' (family = negative binomial) to account for overdispersion (ver. 1.1.9; https://CRAN.R-project.org/package=glmmTMB). Akaike's information criterion (AIC) was used to identify the most parsimonious model from an *a priori* candidate set (Akaike 1998; Burnham and Anderson 1998). Model coefficient of determination (r^2) was calculated according to Nakagawa *et al.* (2017), using the package 'performance' (ver. 0.12.3; https://CRAN.R-project.org/package=performance). We make the assumption that our intensity of use measure reflects patterns of overall habitat use on the basis of the density of camera coverage in the BPRA, although we cannot discount a shift away from our cameras or measure changing intensity of use where we do not have cameras; likewise, we assume that intensity of use is not conflated with temporal patterns of use at a site, but rather reflects changing behavioural preference of a camera site (and its context) with regards to the perceived risk of the site.

Ethics statement

This study complied with all ethics requirements for the collection of remote data by using camera-traps.

Results

In total, 28,401 events were recorded, including 3519 elk events, 1153 moose events, 2708 white-tailed deer (hereafter, deer) events, and 8106 human events (Table S2). Non-human events were predominantly single individuals (81.8% of events, median number of individuals per event is 1.00) but could include multiple individuals.

Temporal response

During both the hunting and non-hunting periods, each species' activity patterns significantly differed from random (Hermans–Rasson test, Table S3). All species showed a change in diel activity (increased nocturnality) during the hunting period compared with the non-hunting period (Tables 1, S3, Fig. 2). Compared to the non-hunting period, humans showed more activity in the early morning and less during noon. Elk increased their activity in the early evening and decreased their early morning activity. Likewise, moose became more active during the early evening and less active after midnight. Deer shifted their activity more closely to midnight and became relatively less active during the early morning and early evening. Overall, all species changed their activity to more nocturnal hours during the hunting period (Table 1). The change in human temporal behaviour during the hunting season relative to that during recreational activity the rest of the year resulted in significantly increased human temporal overlap with elk and deer during the hunting period, and there was a non-significant shift to increasing temporal overlap between humans and moose (Table 2, Fig. 2).

Spatial response

The spatial response of ungulates to hunting as measured by changes in their intensity of use was species-specific (Fig. 3). However, for all species, the model that included an interaction term for hunting period and the habitat- and

Table 1. Risk ratio (RR) calculated by comparing the percentage of activity at night during the hunting (X_H) and non-hunting (X_{NH}) periods, with RR = X_H / X_{NH}.

Species	X_H	X_{NH}	Increase in nocturnal activity (RR)
Elk	0.87	0.65	1.40
Moose	0.85	0.69	1.23
Deer	0.76	0.33	2.34
Human	0.26	0.02	10.93

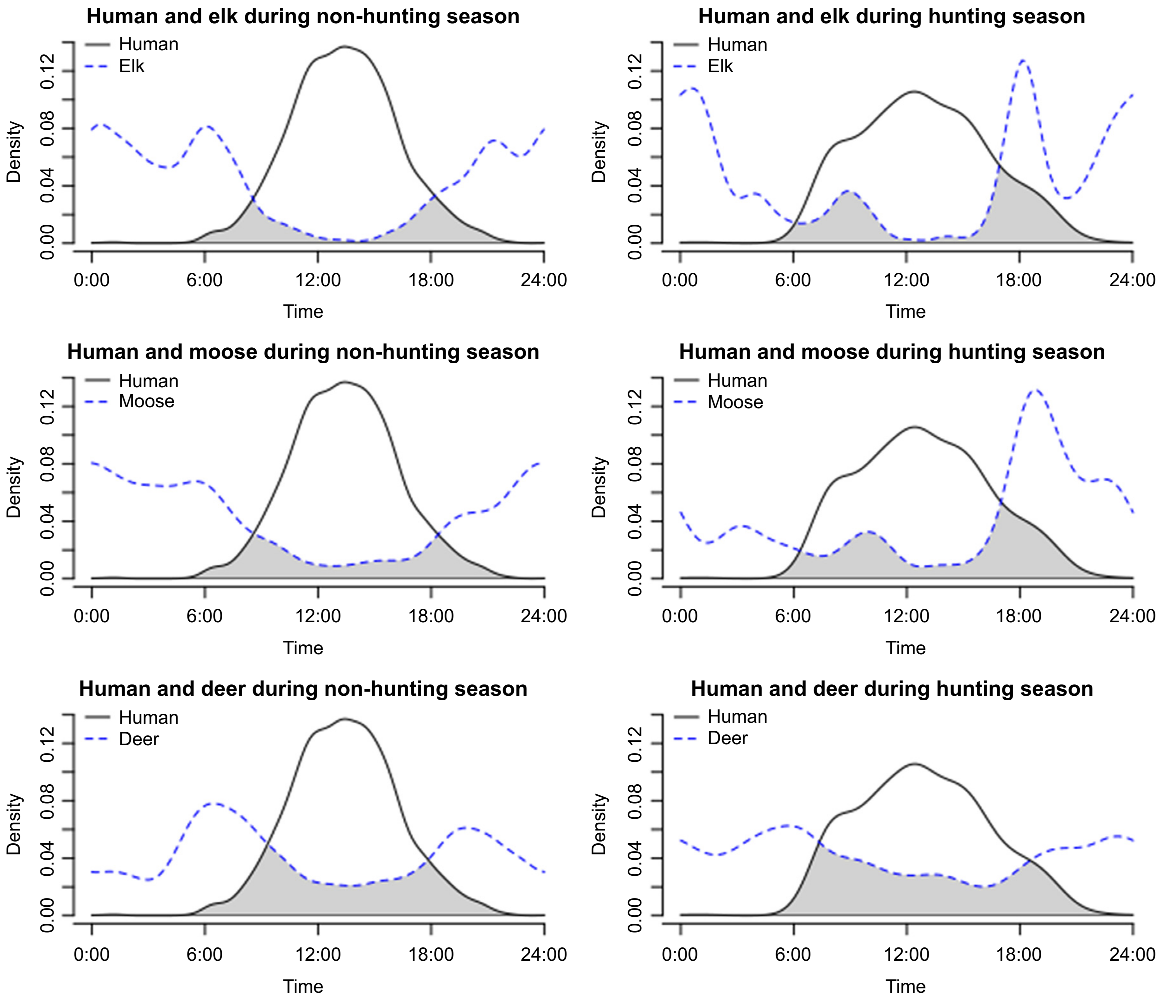

Fig. 2. Human overlap activity graphs with all species (elk, moose, and deer) during hunting and non-hunting seasons in Cooking Lake–Blackfoot Provincial Area, Canada, 2017–2018.

Table 2. Coefficients of overlap (Δ, estimate of overlap; 95% CI, 95% confidence interval) between humans and ungulate species for both the hunting and non-hunting periods captured in Cooking Lake–Blackfoot Provincial Area, Canada, 2017–2018, and the *P*-value of the permutation test between the overlap values.

Species	Non-hunting season		Hunting season		*P*
	Δ	95% CI	Δ	95% CI	
Human–elk	0.19	0.18–0.20	0.28	0.24–0.33	**0.0082**
Human–moose	0.23	0.21–0.25	0.34	0.24–0.46	*0.0869*
Human–deer	0.37	0.35–0.38	0.45	0.39–0.51	**0.0268**

Significant *P*-values are highlighted in bold, trends are highlighted in italics.

human-related variables was selected as the most parsimonious model compared to when hunting did not interact with the other habitat- and human-related variables (AICc weights of 0.96, 0.80, and 0.93 for deer, elk, and moose respectively). The interaction model fit the data reasonably well for each species (conditional r^2 of 0.54, 0.36, and 0.36 for deer, elk, and moose respectively). All species had a higher intensity of use when temperatures were, on average, higher. The intensity of use by deer was significantly higher when there was increased water within 100 m of the camera, and on trails during the hunting period (Table 3). The only significant variable (besides temperature) associated with the intensity of use by elk was increased closed habitat during the hunting period (Table 3). The intensity of use by moose was significantly increased with increased water and closed habitat within 100 m of the cameras and there was a reduction in the use of maintained trails during the hunting season (Table 3).

Discussion

In a fenced multi-use recreation area, we found that, as predicted, ungulates (elk, moose, and deer) responded

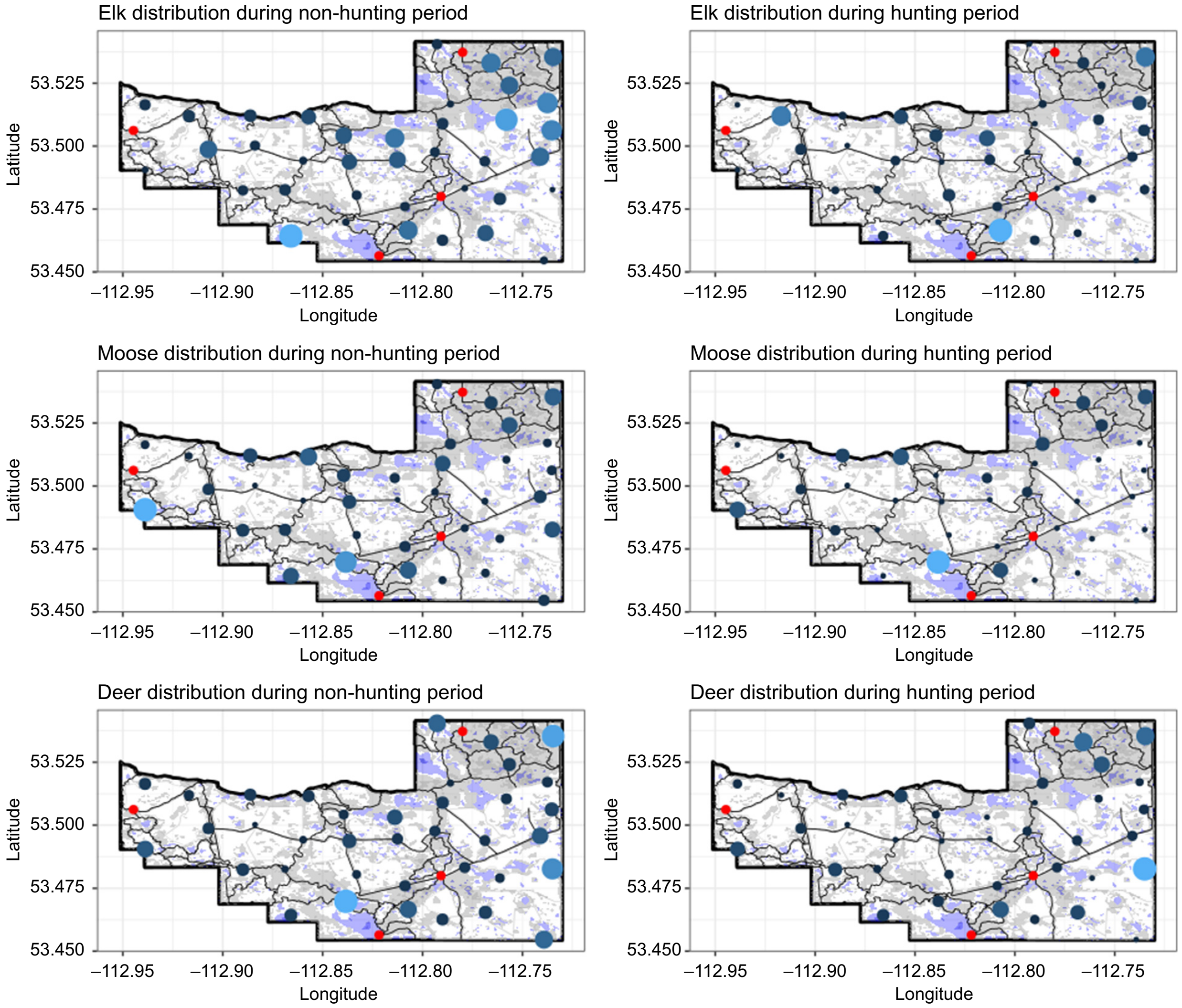

Fig. 3. Distribution of the three ungulate species (elk, moose, deer) during the non-hunting and hunting periods in Cooking Lake–Blackfoot Provincial Area, Canada, 2017–2018. The blue dots represent the camera sites, with the colour (from dark to lighter blue) and increasing size indicating an increasing mean number of events per month. The red dots represent the parking lots. The main trails are indicated by black lines. Forested area is represented by grey and water by blue.

temporally to human hunting relative to recreational use, by generally shifting to more nocturnal behaviour. However, humans also shifted to more nocturnal behaviour during the hunting season, resulting in an overall increased overlap in activity. Changes in spatial intensity of area use in response to hunting season were more species-specific than were the temporal changes. Elk increased their use of sites with closed canopies, whereas moose avoided the trails during the hunting period and were found generally closer to water and in closed habitats. Deer, contrary to predictions, used trail sites more intensely during the hunting period; however, of all the ungulates, they had the strongest shift to nocturnal behaviour at this time.

The shift to increased nocturnal behaviour has been observed before in ungulates as a way to become temporally segregated from human activity and hunting (Crosmary *et al.* 2012; Visscher *et al.* 2017; Gaynor *et al.* 2018), and the degree of the response may be reflective of the species perceived risk (Crosmary *et al.* 2012; Norum *et al.* 2015). However, this shift towards nocturnality was not accompanied with the predicted decrease in temporal overlap between ungulates and humans, primarily because human hunting activity is reactive and attempts to match the perceived time of ungulate activity (Hedley *et al.* 2022).

Human disturbance can influence the space-use (Taylor and Knight 2003; Marzano and Dandy 2012) and behavioural patterns (Sibbald *et al.* 2011) of the ungulates, and, in some systems, the behavioural response to human disturbances may exceed that of predators (Ciuti *et al.* 2012; Visscher *et al.* 2023). Although it is well known that hunting

Table 3. Parameter estimates for the best zero-inflated models for the intensity of use (i.e. events per camera location per week) of each of the three ungulate species: elk, moose and deer.

Parameter	Elk	Moose	Deer
Fixed effects			
Intercept	0.177	**−3.784**	**−1.100**
Temp	**0.037**	**0.031**	**0.101**
Hunting = yes	−0.038	0.834	0.522
Human	0.003	0.007	0.003
Water	1.834	**8.991**	**8.705**
Closed habitat	−0.349	**1.623**	0.448
Trail	−0.471	**1.203**	−0.214
Parking lots	0.0001	*0.0002*	0.000002
Hunting × Human	−0.051	−0.039	*0.024*
Hunting × Water	−0.777	5.663	−2.723
Hunting × Closed habitat	**1.860**	0.276	0.604
Hunting × Trail	−0.195	**−1.807**	**1.180**
Hunting × Parking lots	−0.00003	0.0001	0.00002
Zero-inflated model			
Intercept	−3.162	−18.225	−17.823

Variables that were included in all models included hunting period (hunting: yes/no), week number (week, fitted as a second-order polynomial), mean temperature (temp), the proportion of water (water) and vegetation (closed habitat) within a 100-m radius of the camera, location of the camera on or off a trail (trail), the distance to the nearest parking lot (parking lots), as well as interactions between hunting and closed habitat, trail or parking lots. Camera site was included as a random variable. Significant estimates are formatted in bold and trend effects ($0.1 < P > 0.05$) in italic.

modifies the spatial and temporal use patterns of animals (Swenson 1982; Crosmary *et al.* 2012; Bonnot *et al.* 2013; Lone *et al.* 2015; Little *et al.* 2016; Visscher *et al.* 2017; Gaynor *et al.* 2018; Smith *et al.* 2018), we found significant but only small spatial effects in this study. Recreational activities such as tourism, hiking, skiing, and biking are also linked to changes in animal behaviour, the effects of which may scale up to population- and ecosystem-level consequences (Phillips and Alldredge 2000; Reed and Merenlender 2008; Lewis *et al.* 2021). It is likely that the fully fenced BPRA, with its high recreational use by humans throughout the year, may limit the ungulates' abilities to further respond spatially to hunting (Tablado and Jenni 2017; Gaynor *et al.* 2018; Xu *et al.* 2021). Ungulates are spatially limited in their ability to engage in a sort of shell game with humans (Mitchell and Lima 2002) because of the confines of the perimeter fence, which may preclude complete spatial segregation and the use of refuge land (Sergeyev *et al.* 2022).

Elk, in our study system, appear to respond to hunting only with an increased use of closed habitats. Anecdotally, these elk, along with those in adjacent Elk Island National Park, originated from stock that were historically hunted (prior to park establishment) and remain wary of humans and show no signs of habituation (Frair *et al.* 2007). Our results suggest that this wariness exists through both hunting and non-hunting periods and results in little change in behaviour. This is different from elk in other regions, which are less spatially constrained and therefore show marked responses to human activity and hunting (Paton *et al.* 2017; Visscher *et al.* 2017). Moose showed more change in spatial use during the hunting period; however, moose events constituted a limited sample size for the hunting period. Throughout the year, moose frequent areas that are typically less human-disturbed, such as closed and wetland habitats, with a tendency to visit sites near water. In a wetland-dominated park such as the BPRA, these areas may provide refuge areas to avoid humans, owing to their relative inaccessability. During the hunting period, the intensity of use of areas near trails by moose decreased (Neumann *et al.* 2011). Moose thus appear to increase their human avoidance spatially, corresponding to the behavioural response race model, which predicts that prey use spatial partitioning (Sih 1984; Laundré 2010). Deer appear to use temporal partitioning to reduce encounters with humans during hunting season. Deer had the highest increase in nocturnality while seemingly increasing their intensity of use along trails and in proximity to human activity. Increased vigilance, which we did not measure, may be an important behavioural response in deer, potentially compensating for the lack of spatial partitioning, allowing them to use risky places during less risky times (Benhaiem *et al.* 2008; Stankowich 2008; Clare *et al.* 2023).

Conclusions

The management of small, fenced parks remains problematic, particularly when the goals of multiple user groups must be balanced against the park's ecological integrity (Apollonio *et al.* 2017; Dressel *et al.* 2018; DaRugna *et al.* 2022). Ungulates have been shown to respond to hunting over and above their responses to human recreational activities, with consistent trends across all species resulting in temporal partitioning between themselves and humans; however, we found more inconsistent, species-specific partterns of spatial partitioning. The number and arrangement of our camera locations may have been insufficient to resolve shifts in spatial use by ungulates between hunting and non-hunting seasons. It remains unclear whether the non-consumptive effects of these behaviours will have population- and ecosystem-level repercussions (Phillips and Alldredge 2000; Reed and Merenlender 2008; Sheriff *et al.* 2020; Lewis *et al.* 2021). Because the BPRA is a small, fenced area and human hunters are reactive and attempt to match the ungulate activity patterns, the behavioural responses of the ungulates might not be sufficient to adjust to the hunting pressure and may result in population-level consequences. If ungulate numbers decline, managers may consider further access control to reduce human recreational activity or hunting to certain areas of the park and create refuge areas, because evidence suggests that ungulates would respond to these locations relatively quickly (Visscher *et al.* 2017).

Supplementary material

Supplementary material is available online.

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

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