Human impact on deer use is greater than predators and competitors in a multiuse recreation area

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The spatiotemporal behaviour of animals may be determined by interactions with competitors, predators and humans. Nonconsumptive effects, or risk effects of predation, whereby predators induce behaviour changes in prey through their perceived risk, are increasingly seen as important determinants of prey behaviour and spatiotemporal landscape use, which may scale to have population and ecosystem level consequences. Similarly, human disturbance, even that from recreational activity, may result in behavioural changes analogous to the risk effects of predation. As landscapes steadily urbanize, these effects are likely to become common and understanding behavioural responses to human activity may be a crucial component of conservation and management of species in the Anthropocene. We propose using time-to-event analysis based on remote camera images as a behavioural indicator to compare the influence of competitors, predators and humans on the length of time between successive deer events (i.e. deer return times), by season, as a case study. We found that the mere presence of humans was the most important determinant of deer return times in spring and autumn, whereas in summer, competitor (i.e. moose and elk) presence was most important. In winter, a combination of human presence and the number of predators (i.e. canids) was the strongest determinant of deer return times. We suggest human recreation is a major driver of fine-scale, spatiotemporal behavioural responses of deer and that using time-to-event analyses provides a novel framework to identify these behavioural responses. Understanding an animal's behavioural response to humans, competitors and predators has important implications for conservation areas and multiuse landscapes in urbanizing landscapes.
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The consumptive effects of predation are well studied, however, the nonconsumptive effects of predation have increasingly been shown to have population and ecosystem level consequences due to trade-offs arising from altered prey behaviour, resulting in changes to activity patterns, habitat selection and foraging opportunities (Creel & Christianson, 2009). Indeed, these risk effects may be as important as or more important than the consumptive effects of predation (DeWitt et al., 2019). However, the relative importance of nonconsumptive effects in a system may depend on prey, predator or environmental characteristics (Wirsing et al., 2021) with few studies linking nonconsumptive effects of prey responses to appreciable changes in their population (Sheriff et al., 2020).

Similarly, anthropogenic effects such as habitat alteration, loss or fragmentation are well known to impact animal populations, but ecologists are becoming increasingly aware that human disturbance influences animal behaviour in ways that may be analogous to nonconsumptive effects of predation (Frid & Dill, 2002). Human disturbance can influence animal space use (Marzano & Dandy, 2012; Musiani et al., 2010; Taylor & Knight, 2003), behavioural patterns (Murray & St Clair, 2015; Schlacher et al., 2013; Sibbald et al., 2011), predator–prey dynamics (Magle et al., 2014) as well as the species richness and abundance of a site (Ficetola et al., 2007; Reed & Merenlender, 2008). In some systems, it has been suggested that the behavioural response of wildlife to human disturbance may exceed that of natural predators (Ciuti et al., 2012).

In many cases, human disturbance is measured based on the proximity and density of infrastructure development, but recreational activities such as tourism, hiking, skiing and biking have also been linked to changes in animal behaviour, the effects of which

may scale up to population and ecosystem level consequences and, as such, constitute a nonconsumptive effect or risk effect (George & Crooks, 2006; Little et al., 2014; Phillips & Alldredge, 2000; Reed & Merenlender, 2008). As human populations and the demand for recreational opportunities continue to grow, the risk effects of human recreational behaviour on wildlife will only increase (Balmford et al., 2009). This is of particular concern in areas and landscapes that have been explicitly set aside as nature reserves and parks for conservation purposes while also promoting recreative human use (Knight & Gutzwiller, 1995). Additionally, the infrastructure development to facilitate human use in these parks, particularly recreational trails, may produce a similar type of behavioural effect on wildlife as paved roads, although perhaps not of the same magnitude (Forman et al., 2003). Therefore, understanding the effects of human recreational behaviour on wildlife behaviour within the context of natural competition and predation may be an important consideration for the continued management of conservation areas and urbanizing landscapes (Berger-Tal et al., 2011; Gallo et al., 2019; Lewis et al., 2021).

Remote cameras are increasingly being used to assess occupancy, intensity of use, activity patterns and to estimate animal density (Burton et al., 2015; Carbone et al., 2002; Chandler & Royle, 2013; Cusack et al., 2015; Frey et al., 2017; Jennelle et al., 2002; Moeller et al., 2018) and may be particularly suited for research of conservation behaviour (Caravaggi et al., 2017). Remote cameras have been used to understand how animals alter their spatial or temporal behaviour and whether their use of areas is dependent on competitors and the risks associated with predator or human presence (Flowers, 2019; Keim et al., 2019). However, the scale at which this occurs may be partly obscured by pooling observations over days and seasons (Little et al., 2014). It may be that behavioural responses are local in time and reflected in the time between revisits (if individuals can be identified) or reuse (if individuals cannot be identified) of an area rather than an overall intensity of use (number of observations) of a particular location (Flowers, 2019). Additionally, changing fitness goals may result in differing seasonal perceptions of risk from different sources, resulting in a behavioural trade-off (Mangel & Clark, 1986).

In this paper, we used a novel application of time-to-event analyses for remote camera data (Flowers, 2019) in a hypothesis-testing framework to compare the risk effects associated with human recreation behaviour, predators and competitors on a prey species in a protected multiuse area, as a case study. Our purpose was two-fold. First, we determined the relative importance of human, competitor and predator activity on deer during four biologically derived seasons: spring, summer, autumn and winter. We predicted that deer would show longer return times to the multiuse area in response to the recreational behaviour of humans than in response to the behaviour of predators or competitor species across all seasons, based on the assumption that the recreational behaviour of humans has a nonconsumptive effect on deer in this multiuse area. Second, we evaluated whether return times and time-to-event analysis can be used as a behavioural indicator (sensu Berger-Tal et al., 2011) for understanding human impacts on animal behaviour and provide a metric by which behaviour-based management options could be tested or compared.

METHODS

Study Area

The Cooking Lake − Blackfoot Provincial Recreation Area (BPRA) is a provincially protected area located approximately 40 km east of Edmonton in central Alberta, Canada (Fig. 1). The BPRA has glacial moraine topography with a mix of deciduous forests, lakes, wetlands and grasslands. Forested areas are primarily deciduous and predominantly trembling aspen, *Populus tremuloides*, with patches of conifers. Mean (± SD) annual precipitation in the BRPA is 440 ± 79 mm, with a mean (± SD) January temperature of $-10.25 \pm 3.30\,°C$ and a mean (± SD) July temperature of $16.91 \pm 1.43\,°C$; 1999−2018, Environment Canada, https://climate.weather.gc.ca/historical_data/search_historic_data_e.html,
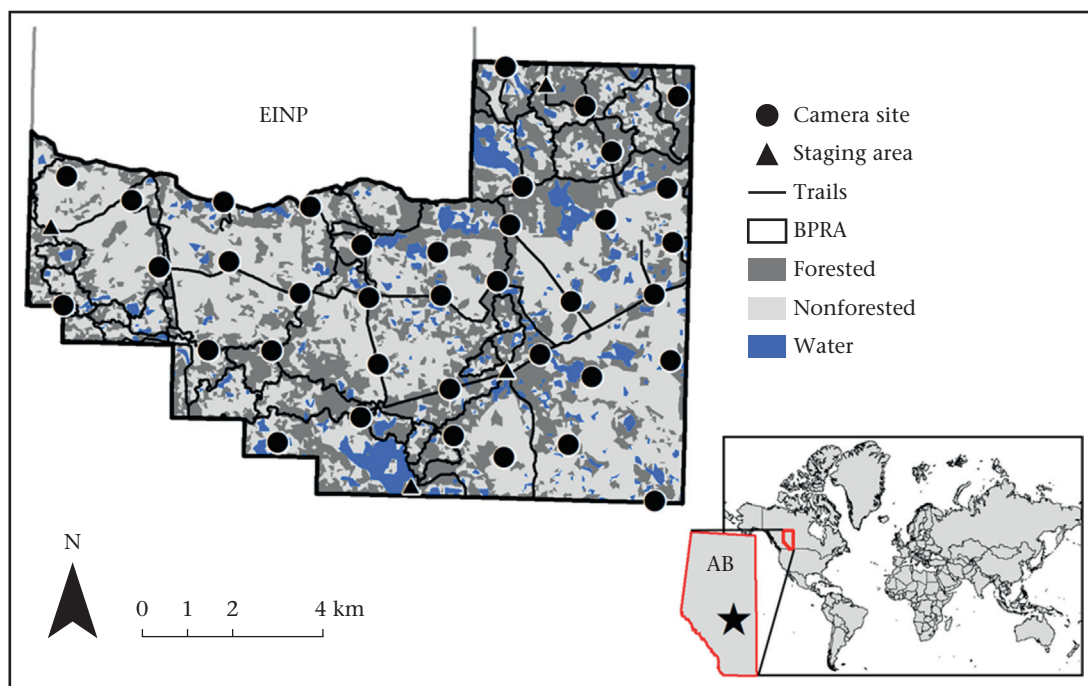

Figure 1. Locations of 37 remote camera-traps distributed across the Blackfoot Provincial Recreation Area, Alberta (AB), Canada from 2017−2018, which is directly below Elk Island National Park (EINP).

accessed 6 October 2021). The BPRA is approximately 97 km^2 and enclosed by a 2.2 m high fence, which restricts wildlife movement in and out of the park to adjacent agricultural land and human settlements. While nearly half of the area is managed as seasonal grazing pasture for cattle, the BPRA is a multiuse landscape with Indigenous and licenced hunting, maintained gas wells and a variety of opportunities for nonmotorized recreation, with approximately 170 km of maintained trails (G. Elzinga, personal communication). There are four staging (parking) areas that provide access to the BPRA. Elk, *Cervus canadensis*, moose, *Alces alces*, mule deer, *Odocoileus hemionus*, and white-tailed deer, *Odocoileus virginianus*, are common in the park, and predators include low numbers of black bears, *Ursus americanus*, cougars, *Puma concolor*, and grey wolves, *Canis lupus*, as well as more common coyotes, *Canis latrans*.

Camera Trapping

We deployed 37 camera traps (Reconyx Hyperfire: H500, P800, P900; Reconyx, Holmen, WI, U.S.A.) randomly within a 1600 m grid, with locations being constrained to be no closer than 800 m from the nearest camera and accessible for regular checking (Fig. 1). Cameras were installed on trees or fenceposts approximately 1 m off the ground and placed facing areas where detections would be maximized, such as trails or open areas. Cameras were set to take three photos with each motion-triggered event and were serviced approximately every 3 months to replace batteries and the SD cards as needed and to clear vegetation within the field of view. We collected camera trap data from June 2017 to July 2018. The EventFinder suite was used to facilitate the removal of nontarget (i.e. vegetation and empty frames) images and then used to collapse individual images into independent events for classification (for full details see Janzen et al., 2019). Photographic metadata, including camera name, location, date and temperature, were recorded as were the species name, age class, sex and number of individuals.

Ethical Note

This study used noninvasive remote cameras to observe animals in their natural conditions. Researchers were at each site for approximately 15 min approximately every 3 months to conduct maintenance and retrieve stored images. Research and collection permits were granted for the work from Alberta Parks and the work followed the expectations of The King's University Research Ethics Board.

Data Analysis

For the proceeding analyses, we combined mule deer and white-tailed deer (hereafter deer), moose and elk (hereafter large ungulates) and coyotes and wolves (hereafter canids; wolves accounted for only 1.3% of all canid events). At each camera, we calculated the number of hours between sequential deer events (i.e. the time-to-event). Time-to-event records were grouped into four biological seasons: spring (May–June, which coincides with the deer calving season), summer (July–September), autumn (October–November, which coincides with the deer breeding season and the licensed archery and rifle hunting season) and winter (December–April).

We used a Cox proportional hazard model with mixed effects to evaluate the influence of covariates on the return times (i.e. time-to-event) for deer at each camera. Camera identity (ID) was included as a random intercept. Return times were left-censored to 1 h and right-censored to 72 h to meet the assumptions of

proportional hazard. Covariates included in the Cox proportional hazard model were classified as either environmental or biological. Environmental covariates included the proportion of forested and nonforested area and the proportion of water around each camera, whether a camera was located on a human trail as a Boolean factor (0 = not on trail, 1 = on trail) and the distance (m) to grazing fields and staging areas. We reclassified the 19 land cover types from the 2015 North America Land Change Monitoring System land cover map (http://www.cec.org/north-american-environmental-atlas/land-cover-30m-2015-landsat-and-rapideye/; Canadian extent developed by Latifovic et al., 2017) to forested, nonforested and water cover types. For each land cover type (forested, closed canopy; nonforested, open canopy; water), we calculated the proportion around each camera at three buffer sizes (100 m, 250 m, 500 m) and evaluated each buffer size in a univariate Cox proportional hazard model where deer return times across all seasons was the response variable. We selected the buffer size based on the univariate Cox proportional hazard model that had the highest log likelihood value for each land cover class. This buffer size was then used for each seasonal model.

Biological covariates included the number of large ungulate, canid and human events documented between the two deer-to-deer events (used to calculate the return time), as well as each biological covariate as a Boolean factor (0 = no event, 1 = at least one event). For each season and each biological covariate, we first ran univariate Cox proportional hazard models to select either the continuous covariate (number of large ungulates, canids or humans) or Boolean factor based on the model with the highest log likelihood value, which was then included in the subsequent model selection. Due to lack of variation, we were unable to model deer return time as a function of the group size of deer present during an event (mean ± SD = 1.1 ± 0.4 deer/event).

Using the above covariates, we used Akaike's information criterion (AIC) to evaluate nine candidate models for each biological season (Appendix, Table A1). There was no correlation between covariates included in the same model (Pearson's correlation coefficient: | r | > 0.6). The proportions of forested and nonforested cover were highly correlated ($r = 0.93$) and, therefore, we evaluated only the proportion of forested cover. The top model for each season was based on a ΔAIC < 2. We also evaluated the assumption of proportional hazard for each top model using the Schoenfeld residual test ($P < 0.05$). Because Schoenfeld residual tests are sensitive to large sample sizes and we had large sample sizes for some seasonal models ($N > 100$), we subsampled our time-to-events ($N = 100$) and report mean P values with confidence intervals for the Schoenfeld residual test after 1000 iterations. All analysis was conducted using the statistical computing program R (version 3.6.3; R Core Team, 2021) with Cox proportional hazard models fitted using the 'coxme' package, AIC model selection using the 'MuNin' package and Schoenfeld residual tests conducted using the 'survival' package.

RESULTS

Thirty-two per cent of the 37 camera traps were predominantly surrounded (>67%) by forested land cover (based on a 100 m buffer around each camera trap), whereas 49% of camera traps were surrounded by nonforested land cover and 19% of the camera traps were surrounded by a mixture (33–67%) of forested and nonforested land cover (Appendix, Table A2).

Across all cameras, we identified 3505 canid events, 3339 deer events, 8102 human events and 4672 large ungulate events, with the greatest proportion of canid and human events occurring in the winter and the greatest proportion of deer and large ungulate events occurring in the spring and summer (Table 1).

Table 1
Total number (*N*) and intensity (events per camera trap day) of events for each species group identified at 37 remote cameras in the Blackfoot Provincial Recreation Area in Alberta, Canada, during spring (May–June), summer (July–September), autumn (October–November) and winter (December–April), 2017–2018

Species	Spring		Summer		Autumn		Winter		Total	
	N	Intensity	N	Intensity	N	Intensity	N	Intensity	N	Intensity
Canids	738	8.89	683	6.38	508	8.47	1576	10.58	3505	8.65
Deer	1388	16.72	1317	12.31	457	7.62	177	1.19	3339	8.24
Humans	2090	25.18	1912	17.87	1270	21.17	2834	19.02	8106	20.01
Large ungulates	1444	17.40	1773	16.57	747	12.45	708	4.75	4672	11.54
Total	5660	68.19	5685	53.13	2982	49.70	5295	35.54	19622	48.45

The top buffer radius for forested and nonforested stands based on a univariate Cox proportional hazard model was 250 m, whereas the top model for water included the 500 m buffer size (Appendix, Table A3). Therefore, we included the proportion of forested stands at 250 m and the proportion of water at 500 m in all seasonal models. Additionally, across all seasons, Boolean factors of humans and large ungulates provided a better model fit (i.e. higher log likelihood) compared to the continuous metric and were included in all seasonal models (Appendix, Table A4). In contrast, canids as a Boolean factor had a higher log likelihood for spring and summer but not for autumn and winter, and, therefore, canids as a Boolean factor were only included in the spring and summer Cox proportional hazard models, whereas number of canids were included in the autumn and winter Cox proportional hazard models.

Spring

During the spring season (May–June), 763 deer return times were calculated. The top Cox proportional hazard model identified for the spring season included humans as a Boolean factor (Table 2). The mean (± confidence interval, CI) bootstrapped *P* value from the 1000 Schoenfeld residual tests was 0.13 ± 0.01, indicating that our top Cox proportional hazard model passed the assumption of proportional hazard. As indicated by the hazard ratio, the return times across sites increased by 55% when humans occurred between deer events (hazard ratio = 0.45; CI = 0.35–0.57; Table 3).

Summer

During the summer season (July–September), 635 deer return times were calculated. The top Cox proportional hazard model for the summer season included large ungulates as a Boolean factor (Table 4). The mean (± CI) bootstrapped *P* value from the 1000 Schoenfeld residual tests was 0.21 ± 0.02, indicating that our top Cox proportional hazard model passed the assumption of proportional hazard. Return time of deer increased by 46% when large ungulates were present between deer events (hazard ratio = 0.54; CI = 0.45–0.65; Table 3).

Autumn

During the autumn season (October–November), 216 deer return times were calculated. The top Cox proportional hazard model for the autumn season included humans as a Boolean factor (Table 5). The mean (± CI) bootstrapped *P* value from the 1000 Schoenfeld residual tests was 0.30 ± 0.02, indicating that our top Cox proportional hazard model passed the assumption of proportional hazard. In the autumn hunting season, the presence of humans resulted in a 68% increase in deer return times (hazard ratio = 0.32; CI = 0.21–0.49; Table 3). During the autumn, the effect of humans appeared to be the strongest of all seasons and lasted the longest, as indicated by the time before (~70 h) the confidence intervals began to overlap (Fig. 2).

Winter

During the winter season (December–April), 53 deer return times were calculated. We identified two top Cox proportional hazard models for the winter season, which included canids as a continuous factor and humans as a Boolean factor (Table 6). The Schoenfeld residual tests for the Cox proportional hazard models with number of canids and humans as a Boolean factor had *P* values of 0.27 and 0.60, respectively, indicating that both models passed the assumption of proportional hazard. Human presence increased the return time of deer by 63% (hazard ratio = 0.37; CI = 0.09–0.76; Table 3), although the small sample size and overlapping confidence intervals suggest that this effect did not last as long as in other seasons (Fig. 2). During winter, we found that the number of intervening canids, as an index of predator activity, increased return times for deer by approximately 20% per additional canid observed between deer events (hazard ratio = 0.81; CI = 0.68–0.96; Table 3; Fig. 2).

Table 2
Model coefficients, number of model parameters (*K*), Akaike's information criterion (AIC), change in AIC from best model (ΔAIC) and model weights calculated from AIC (*w_i*) for competing mixed effect Cox proportional hazard models predicting return times (h) of deer at remote cameras (*N* = 37) in the Blackfoot Provincial Recreation Area in Alberta, Canada, during the spring season (2017–2018)

Model	Trail	Staging area	Grazing field	Forested	Water	Large ungulate_b	Canid_b	Human_b	K	AIC	ΔAIC	w_i
Human_b								−0.81	2	8538.86	0.00	0.83
Large ungulate_b						−0.61			2	8541.99	3.13	0.17
Canid_b							−0.63		2	8553.98	15.12	0.00
Water					1.80				2	8585.20	46.34	0.00
Null									1	8586.82	47.96	0.00
Staging area		0.00006							2	8586.84	47.98	0.00
Trail	0.10								2	8587.09	48.23	0.00
Forested				0.21					2	8587.19	48.33	0.00
Grazing field			−0.00004						2	8587.41	48.54	0.00

Return times were related to large ungulate, canid and human events as Boolean factors (_b), whether the camera was located on a human trail as a Boolean factor, distance to staging areas and grazing fields (m) and the proportion of forested land cover and water around each camera buffered at 250 m and 500 m, respectively.

Table 3
Hazard ratios (HR) and 95% confidence intervals (CI) for each covariate (large ungulates and humans as Boolean factors ($_b$) and number of canids ($_n$)) in the top mixed effect Cox proportional hazard model for each season (spring, summer, autumn, winter)

Covariate	Spring		Summer		Autumn		Winter	
	HR	95% CI	HR	95% CI	HR	95% CI	HR	95% CI
Canid$_n$	–	–	–	–	–	–	0.81	0.68–0.96
Human$_b$	0.45	0.35–0.57	–	–	0.32	0.21–0.49	0.37	0.09–0.76
Large ungulate$_b$	–	–	0.54	0.45–0.65	–	–	–	–

DISCUSSION

Animal behaviour is increasingly seen as an important component of conservation and management, and in particular, the incorporation of behavioural indicators of anthropogenic impacts (Berger-Tal et al., 2011). We used remote cameras, an emerging tool for the quantification of behavioural impacts (Caravaggi et al., 2017), to monitor the risk effects of human recreational activity in relation to both competitors and predators. We show via the results of our case study of deer in a multiuse recreation area, that fine-scale return times, as measured using time-to-event analysis, are a useful behavioural indicator and that human activity and disturbance influenced return times more than predators in most biologically relevant seasons. Below we first describe the results of our case study, then discuss the relevance of describing human recreational activity as a risk effect akin to predation, and lastly describe how our analysis framework might be used to quantify the behavioural responses of animals as indicators that can be used to monitor and compare management decisions within the framework of conservation behaviour (Berger-Tal et al., 2011).

Using a hypothesis-driven univariate approach, we found little evidence for landscape variables to be informative in predicting return times of deer, often not outperforming the null model and almost never ranking above the covariates for competitors, predators and humans. Human presence, however, was shown to be the most important determinant of deer return times throughout much of the year. While human presence had the greatest influence on the time between deer events during both spring and autumn, the presence of competitors (i.e. moose and elk) was the most important determinant of increasing return times in summer. In the winter, however, a combination of human presence and the number of canids (potential predators) was the most important determinant of deer return times. Thus, in three out of four seasons (spring, autumn, winter), human presence significantly affected deer behaviour and altered their spatiotemporal use of the BPRA, and the impact of human disturbance exceeded that of natural predators (based on a ΔAIC > 2).

During the spring calving period (May–June), we found evidence that human disturbance influenced deer return times but little support for the influence of competitors or predators. During this time, mothers adopt a hiding strategy for their fawns (Lent, 1974) and may be particularly susceptible to disturbance events (Lingle et al., 2008). For example, increased human disturbance during the calving period was documented to decrease reproductive success (i.e. calf:cow ratios) of elk in Colorado, U.S.A. (Phillips & Alldredge, 2000). We also observed the highest intensity (events/day) of human use during the spring season compared to the other seasons, which may further exacerbate the disturbance caused by humans during this sensitive season. In summer, when available forage is most abundant, we noted competitors having the biggest impact on deer return times. Under high resource availability, individuals typically become more tolerant of heterospecifics and conspecifics (red deer, *Cervus elaphus*: Thouless, 1990; Veiberg et al., 2004). However, there may be dominance interactions over access to higher-quality forage, whereby smaller-bodied ungulates (i.e. deer) are displaced by larger elk or moose (Stewart et al., 2002). Unsurprisingly, autumn deer return times were influenced most strongly by the presence of humans, since this season was a priori constructed to correspond to the licenced hunting season (46% of human events were classified as hunting during this period). Hunting, as both a consumptive and nonconsumptive effect, is well known to influence deer and ungulate spatiotemporal patterns of use and vigilance behaviour (Benhaiem et al., 2008; Little et al., 2014; Root et al., 1988; Visscher et al., 2017). Indeed, it appears that ungulates can rapidly alter their spatiotemporal behaviour with the onset of hunting by seeking refuge or becoming increasingly nocturnal to access foraging habitats at less risky times (Said et al., 2012; Visscher et al., 2017).

In almost all seasons, we found that the mere presence or occurrence, rather than the intensity of use (number of individuals) of competitors, predators and humans was enough to elicit a behavioural response resulting in longer return times to a site. The only exception to this pattern was during the winter season, when the number of canids between deer events was selected as a more

Table 4
Model coefficients, number of model parameters (K), Akaike's information criterion (AIC), change in AIC from best model (ΔAIC) and model weights calculated from AIC (w_i) for competing mixed effect Cox proportional hazard models predicting return times (h) of deer at remote cameras ($N = 37$) in the Blackfoot Provincial Recreation Area in Alberta, Canada, during the summer season (2017–2018)

Model	Trail	Staging area	Grazing field	Forested	Water	Large ungulate$_b$	Canid$_b$	Human$_b$	K	AIC	ΔAIC	w_i
Large ungulate$_b$						−0.62			2	6891.05	0.00	0.98
Human$_b$								−0.66	2	6898.40	7.35	0.02
Canid$_b$							−0.46		2	6920.39	29.34	0.00
Forested				0.50					2	6927.73	36.68	0.00
Trail	0.22								2	6928.32	37.27	0.00
Grazing field			0.0001						2	6929.21	38.16	0.00
Null									1	6932.14	41.09	0.00
Water					0.70				2	6933.05	42.00	0.00
Staging area		−0.00001							2	6933.40	42.35	0.00

Return times were related to large ungulate, canid and human events as Boolean factors ($_b$), whether the camera was located on a human trail as a Boolean factor, distance to staging areas and grazing fields (m) and the proportion of forested land cover and water around each camera buffered at 250 m and 500 m, respectively.

Table 5
Model coefficients, number of model parameters (K), Akaike's information criterion (AIC), change in AIC from best model (ΔAIC) and model weights calculated from AIC (w_i) for competing mixed effect Cox proportional hazard models predicting return times (hours) of deer at remote cameras ($N = 37$) in the Blackfoot Provincial Recreation Area in Alberta, Canada, during the autumn season (2017−2018)

Model	Trail	Staging area	Grazing field	Forested	Water	Large ungulate$_b$	Canid$_n$	Human$_b$	K	AIC	ΔAIC	w_i
Human$_b$								−1.13	2	1868.40	0.00	1.00
Large ungulate$_b$						−0.72			2	1887.12	18.72	0.00
Canid$_n$							−0.26		2	1888.62	20.21	0.00
Trail	0.32								2	1894.86	26.46	0.00
Null									1	1896.81	28.40	0.00
Forested				0.26					2	1897.47	29.06	0.00
Staging area		0.00005							2	1897.67	29.26	0.00
Grazing field			−0.00004						2	1897.75	29.34	0.00
Water					−0.80				2	1898.02	29.62	0.00

Return times were related to large ungulates and humans, as Boolean factors ($_b$), number of canids ($_n$), whether the camera was located on a human trail as a Boolean factor, distance to staging areas and grazing fields (m) and the proportion of forested land cover and water around each camera buffered at 250 m and 500 m, respectively.

informative metric compared to only their presence. This may be a result of the increased potential for predation that occurs as snow levels increase (wolves: Nelson & Mech, 1986; wolves and coyotes: Olson et al., 2021). Coyotes (the numerically dominant canid in our study; 99% of canid events) can form packs during winter, which in other systems resulted in an increased proportion of ungulates in their diet (Gese et al., 1988; D. R. Visscher, personal observation). Additionally, the model with canids was only marginally better (ΔAIC = 0.67) than the model that included human presence, suggesting that both are important determinants of deer return times in winter. Winter human activity in the BPRA includes a substantial amount of cross-country skiing (65% of human events), which has been shown to alter moose and elk space use by displacing them from areas along trails in Yellowstone National Park, U.S.A., as well as Elk Island National Park, Alberta, Canada, which is adjacent to BPRA (Cassirer et al., 1992; Ferguson & Keith, 1982).

Our results suggest that return times may be a useful behavioural indicator for understanding anthropogenic impacts on behaviour and, as such, help inform behaviour-based management (Berger-Tal et al., 2011). In particular, our finding that return times increased the most in the presence of humans may have important implications for the management of conservation areas where

restricted access may be insufficient to mitigate the behavioural responses of ungulates to the mere presence of humans. This may limit the capacity of these multiuse landscapes to provide refuge for ungulates, as behavioural responses to human disturbance can result in reduced population growth (Reed & Merenlender, 2008). If human disturbance is analogous to predation risk, this reduction in population growth may occur through the nutritional cost associated with behavioural changes rather than as a result of stress (Creel et al., 2007, 2009). Our results also appear to suggest that deer behaviour, at least in this landscape, is not oriented towards humans in order to gain some benefit from predator avoidance (i.e. predator shield; Berger, 2007; Muhly et al., 2011), but rather human activity is a significant deterrent of deer reuse of an area and forms a trade-off with the risks associated with predation. Deer overabundance is an increasingly common situation and may result in negative ecological implications (Cote et al., 2004). Within the context of managing conservation areas, it may be possible to alter the impact of ungulates on the ecosystem using both consumptive (hunting for fear: sensu Cromsigt et al., 2013) and increased recreational activities, through selective trail access, as potential management tools. Indeed, return times could be used as a useful behavioural metric to monitor the efficacy of various behaviour-
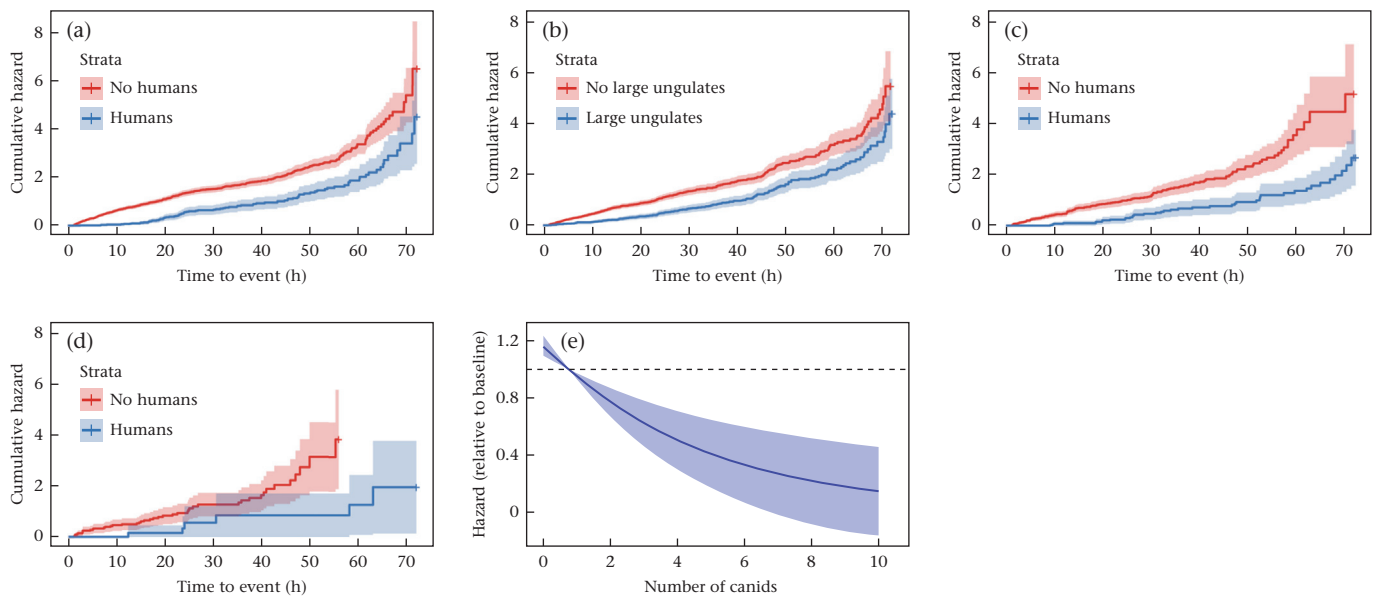

Figure 2. Cumulative hazard and 95% confidence intervals for deer return times (a) during spring when a human was observed or not observed between deer events, (b) during summer when a large ungulate was observed or not observed between deer events, (c) during autumn when a human was observed or not observed between deer events and (d) during winter when a human was observed or not observed between deer events. (e) Hazard (relative to baseline; $y = 1$) and 95% confidence intervals of deer returning to a camera site during the winter relative to the number of canids identified between deer events. Note that in (d), there were no return times >55 h when no humans were present.

Table 6
Model coefficients, number of model parameters (K), Akaike's information criterion (AIC), change in AIC from best model (ΔAIC) and model weights calculated from AIC (w_i) for competing mixed effect Cox proportional hazard models predicting return times (h) of deer at remote cameras ($N = 37$) in the Blackfoot Provincial Recreation Area in Alberta, Canada, during the winter season (2017–2018)

Model	Trail	Staging area	Grazing field	Forested	Water	Large ungulate$_b$	Canid$_n$	Human$_b$	K	AIC	ΔAIC	w_i
Canid$_n$							−0.21		2	313.57	0.00	0.54
Human$_b$								−1.13	2	314.24	0.67	0.39
Null									1	320.69	7.12	0.02
Staging area		−0.0002							2	321.31	7.74	0.01
Large ungulate$_b$						−0.72			2	321.48	7.91	0.01
Forested				−0.66					2	321.72	8.16	0.01
Grazing field			0.0001						2	321.98	8.41	0.01
Water					0.86				2	322.65	9.08	0.01
Trail	0.32								2	322.76	9.19	0.01

Return times were related to large ungulates and humans, as Boolean factors ($_b$), number of canids ($_n$), whether the camera was located on a human trail as a Boolean factor, distance to staging areas and grazing fields (m) and the proportion of forested land cover and water around each camera buffered at 250 m and 500 m, respectively.

based management in a conservation behaviour framework (Berger-Tal et al., 2011).

Although the response of animals to human disturbance is species specific (Lewis et al., 2021), deer, and in particular, white-tailed deer, are known to adapt to urbanizing environments (McCleery, 2010). As such, we might assume they are resistant to human disturbance relative to predation, yet we have shown in a multiuse landscape (with white-tailed deer representing 81% of all deer events) that this may not always be the case. It is likely that deer behavioural responses to human disturbance, like other animals, may differ along an urbanization gradient (Carlen et al., 2021; Knopff et al., 2014; Ritzel & Gallo, 2020). Additionally, although we did not differentiate between sex and age classes in our analysis to maintain robust sample sizes, behavioural responses to predation and disturbance vary for different groups depending on fitness consequences and individual personality (Bonnot et al., 2015; Kie, 1999; Said et al., 2012; Visscher et al., 2017).

Although nonconsumptive effects, or risk effects, have been well studied in experimental systems, debate still surrounds their importance in natural systems, particularly debate on whether the behavioural responses measured over small timescales do, in fact, scale up to population and ecosystem level consequences (Sherrif et al., 2020). Although our present study offers behavioural evidence for the potential of risk effects on deer from both predation and human activity, we were not able to link deer return times to population level consequences. However, human disturbance has been implicated in simulations and in field studies looking at population level impacts on ungulates (Bennett et al., 2009; Phillips & Alldredge, 2000).

In conclusion, we found that human disturbance from recreational activities in this study area appears to be an important determinant of deer behaviour, as assessed by a time-to-event analysis. We found that the mere presence of humans increased deer return times to an area and that this effect generally exceeded that of predators or competitors in most seasons. These results suggest that the behavioural consequences of recreational human activities on deer may be an important factor to mitigate in conservation areas with potential population and ecosystem level consequences. We suggest that our time-to-event analysis framework and return times can be used as a behavioural indicator linking behavioural responses of animals to risk trade-offs and help evaluate behaviour-based management.

Author Contributions

Darcy R. Visscher: conceptualization, investigation, resources, data curation, methodology, writing- original draft, writing- review & editing, visualization, supervision, project administration, funding acquisition. **Philip D. Walker**: conceptualization, methodology, formal analysis, writing- original draft, writing- review & editing, visualization. **Mitchell Flowers:** conceptualization, methodology, writing- original draft, writing- review & editing. **Colborne Kemna:** investigation, data curation, writing- review & editing, **Jesse Pattison:** investigation, data curation, writing- original draft, writing- review & editing, **Brandon Kushnerick:** investigation, data curation, writing- original draft, and writing- review & editing.

Data Availability

The raw data for this study is available upon request from the corresponding author.

Declaration of Interest

None.

Acknowledgments

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Appendix

Table A1
List of 13 candidate mixed effect Cox proportional hazard models used to model deer return times (RT) as a function of large ungulates, canids, humans (either continuous or Boolean factor), camera located on a human trail as a Boolean factor, the distance to staging areas and grazing fields and the proportion of forested land cover and water around each camera buffered at 250 m and 500 m, respectively

Model name	Model structure
Null	RT ~ 1
Trail	RT ~ trail
Staging area	RT ~ staging area
Grazing field	RT ~ grazing field
Forested	RT ~ forested 250 m
Water	RT ~ water 500 m
Large ungulate	RT ~ large ungulate
Canid	RT ~ canid
Human	RT ~ human

Table A2
Number of cameras within binned land cover classes (<33%, 33–66%, >67%) based on the percentage of land cover within a 100 m around each camera

Land cover	<33%	33–67%	>67%
Forested	18	7	12
Nonforested	12	7	18
Water	37	0	0

Table A3
Log likelihood values for competing univariate mixed effect Cox proportional hazard models with returns times modelled as a function of the proportion of forested cover, nonforested cover and water buffered at 100 m, 250 m and 500 m around each camera

Model	100 m	250 m	500 m	Log likelihood
Forested 250 m		0.19		−10670.86
Forested 100 m	0.10			−10670.83
Forested 500 m			0.09	−10670.84
Nonforested 250 m		−0.23		−10670.82
Nonforested 100 m	−0.12			−10670.85
Nonforested 500 m			−0.25	−10670.95
Water 500 m			1.22	−10670.08
Water 100 m	0.76			−10670.60
Water 250 m		0.66		−10670.52

Table A4
Log likelihood values for competing univariate mixed effect Cox proportional hazard models with returns times modelled as a function of continuous and Boolean covariates for large ungulates, canids and humans identified between deer return times

Season	Model	Boolean	Log likelihood	Continuous	Log likelihood
Spring	Large ungulates	+	−4250.70	−0.13	−4256.97
	Canids	+	−4259.08	−0.26	−4262.65
	Humans	+	−4249.69	−0.09	−4260.50
Summer	Large ungulates	+	−3432.31	−0.06	−3445.45
	Canids	+	−3448.78	−0.20	−3449.36
	Humans	+	−3436.44	−0.07	−3442.59
Autumn	Large ungulates	+	−928.60	−0.09	−932.64
	Canids	+	−936.72	−0.26	−934.80
	Humans	+	−922.47	−0.10	−926.31
Winter	Large ungulates	+	−159.25	−0.04	−159.89
	Canids	+	−156.15	−0.21	−155.74
	Humans	+	−156.06	−0.17	−157.34