Differential risk effects of wolves on wild versus domestic prey have consequences for conservation

Tyler B. Muhly, Mike Alexander, Mark S. Boyce, Roger Creasey, Mark Hebblewhite, Dale Paton, Justin A. Pitt and Marco Musiani

T. B. Muhly (tmuhly@ucalgary.ca), Faculty of Environmental Design, Univ. of Calgary, Calgary, Alberta, T2N 1N4, Canada. – M. Alexander, Alberta Sustainable Resource Development, Lands Division, Pincher Creek, Alberta, T0K 1W0, Canada. – M. S. Boyce and J. A. Pitt, Dept of Biological Sciences, Univ. of Alberta, Edmonton, Alberta, T6G 2E9, Canada. – R. Creasey, TerrainFX, 101 - no. 2 Strathlea Crescent SW, Calgary, Alberta, T3H 5A8, Canada. – M. Hebblewhite, Dept of Ecosystem and Conservation Sciences, Univ. of Montana, Missoula, MO 59812, USA. – D. Paton and M. Musiani, Faculty of Environmental Design, Univ. of Calgary, Calgary, Alberta, T2N 1N4, Canada.

Predators play integral roles in shaping ecosystems through cascading effects to prey and vegetation. Such effects occur when prey species alter their behavior to avoid predators, a phenomenon called the risk effects of predators. Risk effects of wild predators such as wolves are well documented for wild prey, but not for free ranging domestic animals such as cattle despite their importance for ecosystem function and conservation. We compared risk effects of satellite-collared wolves (n = 16) on habitat selection by global-positioning-system-collared elk (n = 10) and cattle (n = 31). We calculated resource selection functions (RSFs) in periods before, during and after wolf visits in elk home ranges or cattle pastures. The habitat variables tested included: distance to roads and trails, terrain ruggedness, food-quality and distance to forest. When wolves were present, elk stayed closer to forest cover and selected less for high-quality-food habitat. Thus, the risk effects of wolf presence on elk produced a change in the tradeoff between food and cover selection. Cattle responded by avoiding high-quality-food habitat and selecting areas closer to roads and trails (where people likely provided security), but these effects manifested only after wolves had left. Artificial selection in cattle may have attenuated natural anti-predator behaviors. The effects of predators on ecosystems are likely different when mediated through risk effects on domestic compared to wild animals. Furthermore, predator control in response to livestock predation, an important conservation issue, may produce broad ecosystem effects triggered by decrease of an important predator species. Conservation planners should consider these effects where domestic herbivores are dominant species in the ecosystem.

The influence of predators on prey are not limited to killing of prey (i.e. lethal or density-mediated effects) but include the risk effects (Creel and Christianson 2008) of prey avoiding predators, also called non-consumptive (Preisser and Bolnick 2008) or trait-mediated (Abrams 1995) effects. Risk effects manifest as changes in behavior adopted by prey to avoid being killed, and they ultimately can affect prey fitness (Creel and Christianson 2008, Preisser and Bolnick 2008). Risk effects can propagate throughout food webs via indirect effects (Agrawal et al. 2001), which are defined as a species' influences on another species via an intermediate species (Abrams 1995). The effects of predators may be vital to ecosystem integrity (Estes 1996) and are therefore of significant importance to ecosystem conservation and management.

Risk effects of canids on ungulates appear strong, particularly relative to other predators such as mountain lions *Puma concolor* (Laundré et al. 2001, Kluever et al. 2009). Through their interaction with ungulates, canids may influence whole ecosystems via-indirect effects, and wolves *Canis lupus* may be a good sample case (Crête and

Manseau 1996). Wolves are the main predator of ungulates in many parts of the world and the risk effects on elk *Cervus elaphus* are notable because of the relatively wide distribution and overlap between these species, and because it has well documented implications for other components of the ecosystem, such as riparian vegetation, beavers *Castor canadensis* and songbirds via indirect effects (Ripple et al. 2001, Hebblewhite et al. 2005a). Management considerations for wolves, elk and their interactions have therefore implications for conservation of the whole ecosystem.

In many ecosystems where wolves and elk co-occur (including our study area), domestic cattle *Bos taurus* are also present and are killed by wolves. In fact domestic animals such as cattle are the dominant herbivore (both in terms of numerical abundance and biomass) in many ecosystems and might also play a significant role in mediating the effects of predators on ecosystems. In addition, predation and harassment of domestic animals by wolves creates conflict with humans in many parts of the world (Fritts et al. 2003).

Resolution of such conflicts requires adequate understanding of the ecological context of predator–prey interactions (Ormerod 2002). In these ecosystems it might therefore be important to understand risk effects of predators on domestic as well as wild animals. However, the risk effects of wolves on free-ranging domesticated large ungulate livestock are relatively unknown (but see Kluever et al. 2009). Livestock might respond differently to predators than wild prey because of behavioral (e.g. flight response) and morphological (e.g. horn size) changes caused by artificial selection by humans. In livestock, production traits (e.g. weight gain) are favored, which diverts resources from other traits (Mignon-Grasteau et al. 2005), some of which might be important in predator avoidance. Domestic animals typically have smaller brains and less acute sense organs than do their wild ancestors (Diamond 2002). In general, domestic animals express a lower incidence of anti-predator traits (Mignon-Grasteau et al. 2005).

Risk effects of predation are a function of the hunting mode of the predator, anti-predator tactics of the prey and the landscape (Heithaus et al. 2009). Disentangling the contribution of landscape from anti-predator behaviors in risk effects is challenging. Wolves, elk and cattle would be ideal species to compare risk effects of a predator on domestic and wild herbivores. In fact, elk responses to wolves are often dependent on landscape features such as security cover provided by terrain (Frair et al. 2005), forest (Fortin et al. 2005) and humans (Hebblewhite et al. 2005a). However, the direction of such risk effects might be difficult to predict. For example, elk might select open habitats so they can detect wolves from afar (Hebblewhite et al. 2005b) or they might select forest cover to hide from wolves (Creel et al. 2005). Similar habitat-mediated risk effects might be evident in cattle, or they might be absent due to artificial selection by humans that de-emphasizes anti-predator behaviors. The risk effects of predators on domestic animals may have different consequences for ecosystems compared to risk effects on wild prey. These effects should be accounted for by ecosystem managers where wild predators and domestic prey are sympatric and domestic prey are the dominant herbivore.

The purpose of this study was to test for and compare risk effects of wolves, as measured by habitat selection of wild (elk) and domestic (cattle) ungulate species. Our objectives were to determine whether (1) the presence of wolves within elk home ranges and cattle pastures caused changes in selection of security cover and food-quality habitat patches, and (2) such risk effects were different in cattle compared to elk. For elk, our hypothesis was that wolves would have a significant and immediate risk effect, as the majority of sources report elk selection for security cover and a switch to habitats characterized by sub-optimal food quality during wolf presence. Conversely, we hypothesized that cattle would not switch habitat during wolf presence periods, because of poor anti-predator behavior. We compared risk effects of satellite-collared wolves on habitat selection by global-positioning-system-collared elk and cattle in southwest Alberta, Canada by using generalized linear mixed models (GLMM) to calculate resource selection functions (RSF) in periods before, during and after wolf visits in elk home ranges or cattle pastures.

Methods

Study area

The study occurred within a montane ecosystem along the eastern slopes of the Rocky Mountains in southwest Alberta, Canada (Fig. 1). The continental divide bounds the western edge of the study area. Towards the east, topography is less rugged, with rolling foothills that eventually level to flat prairie and agricultural lands. Forested lands occur in the western half of the study area and open into grasslands to the east. Wild ungulates in the area, in addition to elk, include white-tailed deer *Odocoileus virginianus*, mule deer *O. hemionus* and moose *Alces alces*. Cattle are the predominant domestic herbivore, but domestic sheep *Ovis aries* also occur in a few areas. Carnivores (in addition to wolves) such as grizzly bears *Ursus arctos horribilis*, black bears *U. americanus*, mountain lions and coyotes *Canis latrans* frequent the study area, but wolves are the predominant predator of elk (Hebblewhite et al. 2005b) and cattle (Musiani et al. 2003). There are several small towns (populations of 300 to 3665 people) located within the study area. Agriculture (primarily livestock grazing), forestry, natural gas development and recreational activities are the prevailing human land uses. Lands to the west are predominantly public, and to the east are predominantly private. Livestock grazing occurs on private lands throughout the year and on public lands in the summer (May to October).

Wolf, elk and cattle telemetry data

Sixteen wolves from four known wolf packs in the study area (Fig. 1) were fitted with ARGOS satellite-radiotelemetry collars in southwest Alberta between 2004 and 2007 by Alberta Sustainable Resource Development (ASRD), using either modified foot-hold traps or helicopter netgunning. There was at least one ARGOS collar maintained in each pack during the study. ARGOS collars were programmed to provide three locations per day. In all wolf visits to elk and cattle no more than one wolf was monitored and different individuals were monitored in the same pack in different years. Therefore the absence of a radio collared wolf does not necessarily mean an absence of wolves, because other wolves in the study area might have been present although un-collared. Thus, the analyses that follow are conservative because the pre- and post-wolf phases may be contaminated with some wolf presence. However, if a prey response signal is found, this has to rise above the background 'noise' of possible presence of other predators throughout the study.

Forty-eight female elk were captured in January 2007 using helicopter netgunning and fitted with a global-positioning-system (GPS)-radiotelemetry collar programmed with a two-hour relocation schedule. On average 1111 locations were used to create home ranges and mean elk home range size was 112 km². Cattle GPS-radiotelemetry data were collected over three summers (2004–2006) from cattle in three large fenced cattle pastures (12 km², 23 km² and 23 km²) within the study area (Fig. 1). In 2004, GPS-radiotelemetry collars programmed with a 20-min relocation schedule were placed on nine randomly chosen cattle from 1 July to 14 September. In 2005, eleven cattle were fitted with the
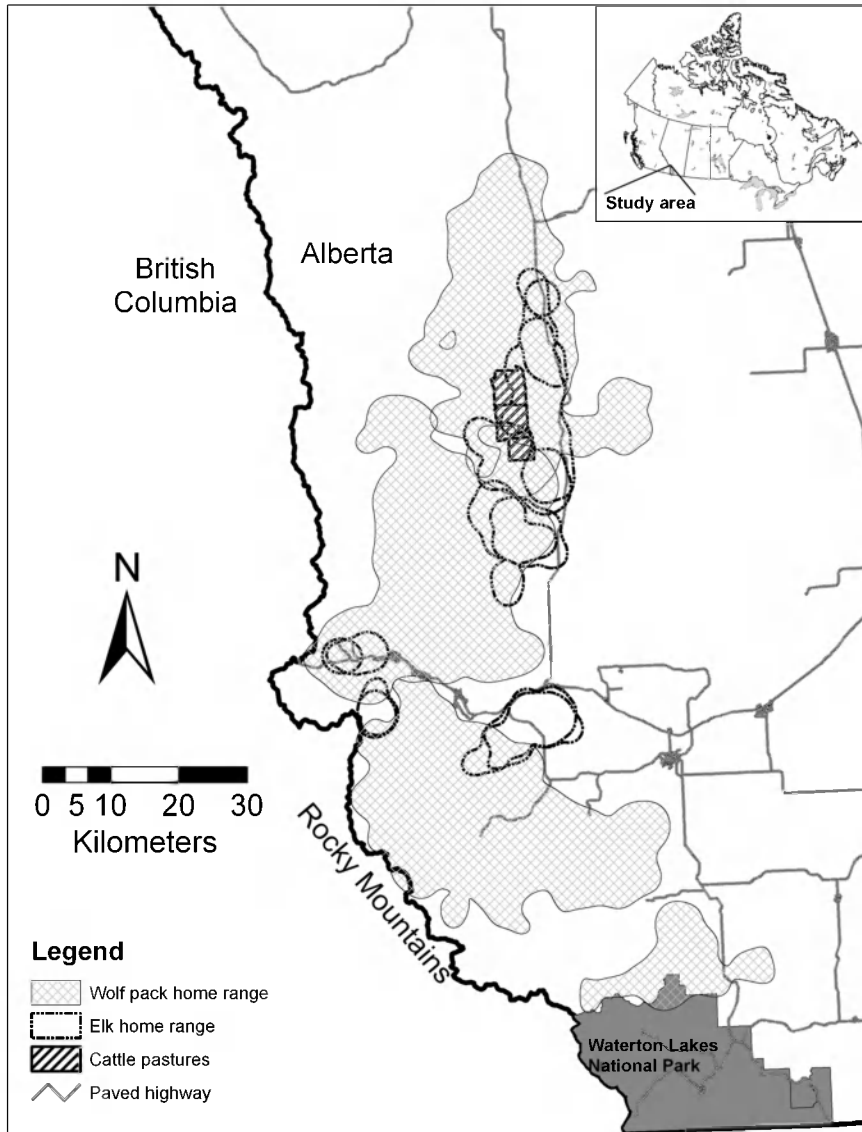
Figure 1. Map of the study area in southwest Alberta, Canada with home ranges of wolf packs (n = 4, total of 16 wolves collared) and of elk (n = 10 collared), and with cattle pastures (n = 3, total of 31 cattle collared) where wolf–prey interactions were studied in 2004–2007. Home ranges were determined using a 95% kernel density estimator.
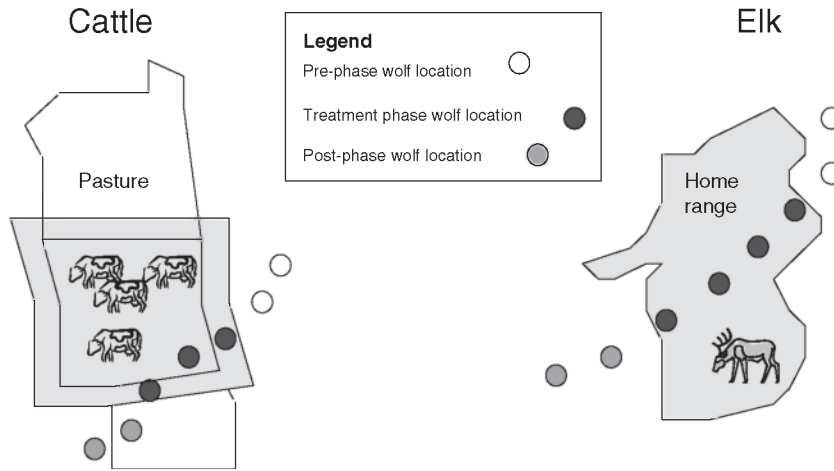
same collars from 1 April to 1 May and from 1 July to 10 September. The same sampling design was employed in 2006, with the exception that no radiotelemetry collars were deployed from 1 April to 1 May. Cattle collared were year-ling males and females.

Study design

We compared habitat selection by elk and cattle between three phases (Fig. 2): before wolf visit (pre-phase), during wolf visit (treatment phase) and after wolf visit (post-phase). A post-treatment phase was included as there can be a lag in prey responses to predators (McGarigal and Cushman 2002). We used radiotelemetry data to document wolf vis-its. Cattle with radiotelemetry collars were confined to one of three pastures (Fig. 1, 2). We categorized wolves as pres-ent (i.e. the treatment phase) when a collared wolf occurred within the cattle pasture or a 1.5 kilometer buffer around the

pasture (Fig. 2). It should be considered that wolves often travel in packs and that prey species are adapted to detect presence of packs through scent, hearing and visual clues. A detection distance of one to two kilometers has also been assumed to identify short-term predation risk response by prey in other studies of large mammal predator–prey inter-actions (Creel et al. 2005, Gude et al. 2006). We included this buffer as a conservative means to account for detection distance of predators by prey. We identified wolf presence periods by their presence in elk home ranges or cattle pas-tures, rather than proximity to collared animals, because elk and cattle live in herds and thus the behaviour of uncollared animals using other parts of the home range or pasture could influence the behaviour of the collared animals.

For elk, which range freely throughout the study area, wolf presence was considered when a wolf with a radiotelem-etry collar entered an elk home range (Fig. 2). We estimated a winter and a summer home range for each radiotelemetry

Figure 2. Experimental design used to test for the effects of wolves on elk and cattle habitat selection in southwest Alberta in 2004–2007. The treatment phase was the period when wolves were located within buffered cattle pastures or elk home ranges, plus a period to account for temporal precision of the wolf relocation data, whereas pre- and post-phases were 18 h long (the average treatment phase length). Also indicated are the hierarchical strata of the data controlled for including total number of wolf visits (level 3 stratum), prey animals with radiotelemetry collars involved (level 2 stratum), and their radiotelmetry locations (level 1 stratum; Methods).

	Before (pre-phase)	During (treatment phase)	After (post-phase)	Number of wolf visits (level 3)	Number of collared animals (level 2)	Number of radiotelemetry locations (level 1)
Cattle	18 h	Time wolf in pasture plus 4.5 h before and after	18 h	19	31	20 961
Elk	18 h	Time wolf in home range plus 4.5 h before and after	18 h	51	10	1908

collared elk, as elk in the Rocky Mountains have different seasonal home ranges (Hebblewhite et al. 2006). Winter was defined as 12 January (when the study began) to 31 May and summer as 1 June to 13 October (when the study ended), comparable to previous studies on elk (Creel et al. 2005, Hebblewhite et al. 2006). We estimated elk home ranges using a 95% kernel density estimator (Seaman and Powell 1996) with a smoothing parameter (h = 3000 m) determined based on our knowledge of elk distribution in the study area. We did not buffer the home ranges because visual inspection of the kernels indicated that the 95% contour extended 1 to 2 km outside the actual telemetry locations, a length comparable to the buffer we used around cattle pastures.

Although more temporally resolved than previous predation risk studies (Creel et al. 2005), the temporal precision of our wolf relocation data (one location every nine hours) made it difficult to determine exactly when a wolf entered and left elk home ranges and cattle pastures. As a conservative means to account for this uncertainty we added 4.5 h (i.e. half of the average duration between locations) before and 4.5 h after the time wolves occurred in the elk home range or cattle pasture. A uniform pre- and post-phase duration was used to ensure experimental phases were consistent and thus comparable to each other. Pre- and post-phases were defined as 18-hour periods before and after the treatment phase, because 18 h was the average length of all treatment phases. Furthermore, an 18-hour period was appropriate to minimize the effects of daily patterns in resource selection

on the results. Patterns in habitat selection typically occur over a 24-hour (i.e. daily) cycle (Alcock 2005). These daily patterns occur in wolves (Merrill and Mech 2003) and elk (Godvik et al. 2009) and may occur in cattle too. Thus, tests comparing behaviors occurring in shorter time-frames may show significant differences that are simply due to changes in daily patterns in activity – i.e. not due to other 'treatments' such as for example a predators' visit.

Habitat selection by elk and cattle

We used RSFs (Manly et al. 2002, Johnson et al. 2006, Lele 2009) to quantify elk and cattle habitat selection before, during and after wolf visits. We followed RSF 'sampling protocol A' (Manly et al. 2002) where used (i.e. elk and cattle radiotelemetry locations) and available resource units were sampled (Johnson et al. 2006). Available resource units were sampled at one random location km^{-2} in each home range (for elk) or pasture (for cattle). Thus for this analysis, we considered resource selection within the home-range (third order of selection; Johnson 1980). This approach may underestimate rare habitats within the home range that are used by elk and cattle as refugia from prey, therefore our approach is conservative for detecting habitat switches by prey in response to predator presence.

We considered spatial covariates for elk and cattle RSF calculation and measured the following at each used and available location: distance to nearest road or trail, distance to nearest forest cover, terrain ruggedness and food quality (high or low).

Covariates were quantified using Geographic Information Systems (GIS) datasets. We identified three measures of security cover (human activity, forest and topography). The use of human activity as a measure of security for animals might seem paradoxical. However, wolves are known to avoid humans more than elk, which may use human activity areas as a refuge from predation (Hebblewhite et al. 2005a). A similar difference can be hypothesized between wolves and cattle, which might also seek humans for 'security cover'. We used a GIS dataset of roads and trails obtained from ASRD. We defined forest security cover for ungulates as forested areas with a canopy closure above 75% (Lyon 1979, Skovlin et al. 2002) and using a GIS model of canopy closure (McDermid et al. 2009) we calculated the distance of each location to forest cover with 75% canopy closure. We calculated terrain ruggedness (Riley et al. 1999) from a 30-m² spatial resolution digital elevation model (DEM). We obtained a 30-m² spatial resolution GIS map of vegetation cover derived from Landsat data (McDermid et al. 2009) and collapsed it into two ungulate food quality classes, high and low. Herbaceous, shrub, regenerating cutblocks, and deciduous forest cover types were defined as high-food quality and coniferous forest and barren ground cover types were defined as low-food quality. We identified high-food quality habitats based on the preferred food types of elk and cattle where they co-occur (Stewart et al. 2002, Beck and Peek 2005). Overall, classification accuracy of the vegetation cover map was 80%, as calculated from a ground-truthing approach using 245 independent, randomly selected test sites surveyed in the field (McDermid et al. 2009). All GIS work was conducted in ArcGIS 9.2 (ESRI Inc.). Habitat present in elk home ranges (n = 10) had the following characteristics: mean terrain ruggedness index = 13, mean distance from roads and trails = 394 m, mean distance from forest cover = 157 m, proportion of high-food quality habitat = 83%. Habitat present in the three cattle pastures was characterized by mean terrain ruggedness index = 16, mean distance from roads and trails = 245 m, mean distance from forest cover = 42 m, proportion of high-food quality habitat = 60%.

We also tested for interactions between proximity to security cover and high-food quality habitat made by ungulates when wolves were present compared to when they were absent. We tested for the following three interactions as covariates in the RSF: distance to road or trail × food quality, distance to forest cover × food quality and terrain ruggedness × food quality. A significant interaction coefficient in the RSF implies that selection for high-food quality habitat is a function of proximity to security cover.

To test our hypotheses for elk and cattle response to wolves, we produced one RSF model for each herbivore species and for each experimental phase that included all covariates. We tested the strength of covariates in each RSF using a z-test (StataCorp 2009, rel. 10.1) and examined whether there was a clear change in the sign (positive or negative) and significance of coefficients when wolves were present compared to when they were absent.

We validated each of our RSF models using k-fold cross validation (Boyce et al. 2002) at the population level (i.e. including all animals and visits). The k-fold cross validation procedure was performed five times withholding 20% of the data at each iteration. The area-adjusted frequency of animal locations was compared to the predicted RSF scores using a Spearman rank correlation. A predictive model has a significant positive correlation.

Hierarchical modeling of habitat selection

We used generalized linear mixed models (GLMMs) to include random effects in our RSFs because they account for autocorrelation of longitudinal telemetry data, correlation within hierarchical strata of the data and between-strata variance, which allows for robust inference and appropriate estimation of marginal (i.e. population) and conditional (i.e. visit) responses (Skrondal and Rabe-Hesketh 2004, Gillies et al. 2006). GLMMs are increasingly used in ecology (Bolker et al. 2009) and RSF modelling (Koper and Manseau 2009) for these reasons. The hierarchical strata of the data (Fig. 2) were radiotelemetry locations (level 1) within individual animals (level 2) within wolf visits (level 3). We therefore used a three-level GLMM to model cattle habitat selection and included: (1) a random intercept at the individual level (level 2) to accommodate variation in sample size of telemetry locations (level 1) among individual cattle; (2) a random intercept at the visit level (level 3) to accommodate for unbalanced sample size of GPS-radiocollared cattle (level 2) between visits; and, (3) a random coefficient at the visit (level 3) to examine conditional variability in prey use of resources in the presence of predators. We used a two-level GLMM to model elk habitat selection and included: (1) a random intercept at the visit level (level 3) to accommodate unbalanced sample size of telemetry locations between visits; and, (2) a random coefficient at the visit level (level 3) to examine conditional variability in prey use of resources in the presence of predators. Compared to cattle, a random intercept at the individual level was not necessary in the elk RSFs because only one elk was involved in each visit and thus there was no level 2 stratum.

Two GLMMS were calculated for each experimental phase, one with a conditional level 3 coefficient for distance to forest cover and one with a conditional level 3 coefficient for food habitat quality. We calculated the conditional value of these covariates specifically because our initial analysis found that they were significant fixed effects in both the elk and cattle GLMMs and that the coefficients differed between phases of a visit (i.e. before, during and after wolf visits) indicating they were important habitat covariates to prey in the presence of predators. We tested whether there was a difference in the conditional coefficients for distance to forest cover or food habitat quality between each experimental phase using a paired sample Wilcoxon signed-ranks test (Sokal and Rholf 2000). GLMMs were calculated using STATA 10.1 (StataCorp 2009) and the GLLAMM function with a logit link (<www.gllamm.org>; Skrondal and Rabe-Hesketh 2004). We derived maximum-likelihood estimates using adaptive quadrature with 20 integration points (Rabe-Hesketh et al. 2005).

Results

Occurrence of wolf visits to elk home ranges and cattle pastures

We documented 51 independent wolf visits (i.e. presence events) to elk home ranges that involved ten different elk
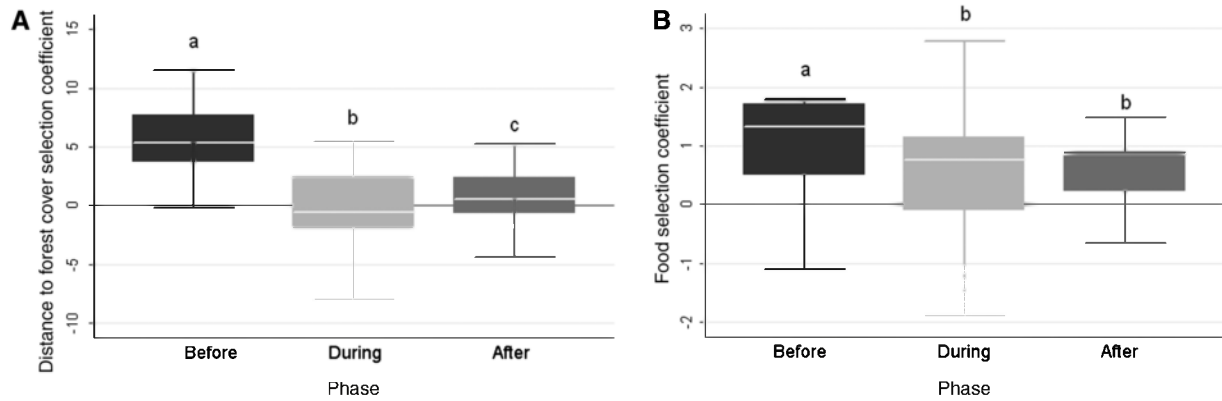
Figure 3. Box plots for elk selection coefficients for distance to forest cover (A), and high-food quality habitat (B) assessed in phases before, during and after wolf visits to elk home ranges in southwest Alberta 2004–2007. Conditional coefficients across wolf visits were estimated with generalized linear mixed models (GLMMs). Phases with different coefficients (p < 0.05) are marked by different letters above the box plot, whereas box plots with same letter are not different. Also indicated are the median value (white line within the box), 25th and 75th percentiles (bounds), and 10th and 90th percentiles (whiskers).

(Fig. 2). Wolf visits (i.e. the treatment phase) were initiated at various periods of the day. Twenty-nine visits were initiated between 12:01 a.m. and 6:00 a.m., six were initiated between 6:01 a.m. and 12:00 p.m., ten were initiated between 12:01 p.m. and 6:00 p.m. and six were initiated between 6:01 p.m. and 12:00 a.m. We also documented 19 wolf visits to cattle pastures, involving 31 different cattle and these visits were also initiated throughout the day. Seven visits were initiated between 12:01 a.m. and 6:00 a.m., three were initiated between 6:01 a.m. and 12:00 p.m., five were initiated between 12:01 p.m. and 6:00 p.m. and four were initiated between 6:01 p.m. and 12:00 a.m.

Changes in habitat selection by elk

We found a change in selection of high-food quality habitat and security cover by elk when wolves were present in elk home ranges compared to when they were absent. Elk avoided forest cover prior to wolf visits (z = 2.970, p < 0.01). According to the marginal RSF model, before wolf presence, elk had a 95% probability of selecting areas up to 600 m distant from forest cover (all other covariates at their mean value). Elk neither selected nor avoided forest cover during and after wolf presence suggesting that they used forest cover as it was available: average distance 157 m (Table 1; we direct readers to Appendix 1, Table A1 and A2 for actual RSF coefficient values for elk and cattle GLMMs, respectively). The conditional (individual treatment) coefficients for distance to forest cover dropped during wolf visits compared to before wolf visits (Fig. 3A; z = 7.082, p < 0.001) and increased after wolf visits compared to during wolf visits (Fig. 3A; z = –3.196, p < 0.01). There was also a lag effect, because conditional coefficients were lower after wolf visits compared to before wolf visits (Fig. 3A; z = 7.027, p < 0.001). Elk selected high-food quality habitat before (z = 1.993, p < 0.05) and after (z = 2.182, p < 0.05) wolf visits, but not during wolf visits (Table 1). According to the marginal RSF model, before wolf presence elk had a 70% probability of occurring in high-food quality habitat versus 30% in low-quality. During wolf presence there was neither selection nor avoidance of high-food quality habitat suggesting

elk occurred in high-food quality habitat as it was available. As observed in the period 'before', after wolf presence elk had again a higher probability of occurring in high-food quality habitat (84%). Similar to what we found for forest cover, the conditional coefficients for high-food quality habitat dropped during wolf visits compared to before wolf visits (Fig. 3B, z = 4.454, p < 0.001), indicating high-food quality habitats were less important to elk when wolves were present. There was also a lag effect, as conditional coefficient values were significantly lower after wolf visits compared to before wolf visits (Fig. 3B, z = 5.338, p < 0.001). Out of all the interactions tested between environmental covariates, the coefficient for distance to road or trail and food was the only one that changed across experimental phases and it switched from being not significant to negative during (z =

Table 1. Changes in habitat resource selection by elk and cattle before, during and after wolf visits to home ranges and pastures, respectively, in southwest Alberta in 2004–2007.

Resource	Elk			Cattle		
	Before	During	After	Before	During	After
Distance to road or trail	ns	ns	ns	+***	+***	−***
Distance to forest cover	+*	ns	ns	+***	+***	+***
High-food quality habitat	+*	ns	+*	+***	+***	−***
Distance to road or trail × high-food quality habitat	ns	−*	−*	−***	−***	+***
Distance to forest cover × high-food quality habitat	−***	−**	−***	−***	−***	−***
Terrain ruggedness × high-food quality habitat	+*	+***	+*	+***	+***	+***

* = significant p < 0.05; ** = significant p < 0.01; *** = significant p < 0.001; ns = p > 0.05.

–2.010, p < 0.05) and after (z = –2.746, p < 0.01) wolf visits (Table 1). This indicated that when wolves were present, and after wolves left elk home ranges (i.e. a lag effect), elk preferred high-food quality habitat close to roads and trails. In all phases, the coefficients of the interaction between distance to forest cover and food was negative (before: z = –5.366, p < 0.001, during: z = –1.789, p = 0.074, after: z = –2.824, p < 0.01) and between terrain ruggedness and food was positive (before: z = 2.071, p < 0.05, during: z = 3.634, p < 0.001, after: z = 2.335, p < 0.05) with similar trade off mechanisms, which in this case did not change with wolf visits (Table 1). This indicated that elk were more likely to select high-food quality habitat when close to the security provided by forest cover and terrain ruggedness.

Changes in habitat selection by cattle

Cattle response to wolves was detectable in the period after wolf visits, consistent with a lagged effect. Cattle selected for roads and trails after wolves left pastures (z = –12.555, p < 0.001), whereas before (z = 8.633, p < 0.001) and during (z = 8.113, p < 0.001) wolf visits they avoided them (Table 1). According to the marginal RSF model, before wolf presence, cattle had a 95% probability of selecting areas up to 1200 m from a road or trail. During wolf presence, cattle had a 95% probability of selecting areas just up to 900 m from a road or trail. This distance further dropped in the period after wolf presence when cattle had a 95% probability of selecting areas right on roads and trails. Similarly, high-food quality habitat was selected before (z = 8.401, p < 0.001) and during (z = 11.324, p < 0.001) wolf visits, but avoided after wolves left pastures (z = –12.721, p < 0.001; Table 1, Fig. 4B). According to the marginal RSF model, before and during wolf presence cattle had a 65% and 75% probability (respectively) of selecting high-food quality habitat. However, after wolf presence the probability of selecting high-food quality habitat dropped to 37%. Cattle always avoided forest cover and did so incrementally before, during and after wolf visits (Table 1, Fig. 4A). The interaction between food and distance to forest cover (before: z =

–7.451, p < 0.001, during: z = –6.355, p < 0.001, after: z = –6.974, p < 0.001) and food and terrain ruggedness (before: z = 11.364, p < 0.001, during: z = 8.524, p < 0.001, after: z = 7.172, p < 0.001) were negative and positive across all phases, respectively (Table 1). Similar to elk, cattle preferred high-food quality habitat close to forest cover and in more rugged terrain. The interaction between high-food quality habitat and distance to roads and trails switched from negative before (z = –11.222, p < 0.001) and during (z = –1.972, p < 0.05) wolf visits to positive after (z = 15.223, p < 0.001) wolf visits. Cattle preferred high-food quality habitat close to roads and trails prior to and during wolf visits, but switched to avoiding high-food quality habitat close to roads or trails after wolf visits.

Elk and cattle RSF model validation

Elk RSFs during and after wolf visits were valid for population level inferences (r_s = 0.76, p = 0.018 and r_s = 0.75, p = 0.028, respectively), consistent with the notion that habitat selection was predictable when influenced by predation risk. The elk RSF before wolf visits did not validate (r_s = 0.67, p = 0.071) due to lack of correlation in one of the test groups (r_s = 0.37, p = 0.285). The variability of the relationship between elk presence and habitat variables that are important in anti-predator strategies, as exemplified by lack of validation of our RSF, might also be due to random presence of uncollared wolves as well as other predators in the period before the wolf visits detected in this study. The cattle RSFs were valid for population level inferences in all periods (r_s = 0.991, p < 0.001, r_s = 0.922, p < 0.001 and r_s = 0.752, p = 0.018, before, during and after wolf visits, respectively).

Discussion

We identified a habitat-mediated risk effect of wolf presence on elk selection for forest cover and avoidance of quality food patches. Elk immediately responded to wolf visits, and there was a persistence of the response immediately after wolves
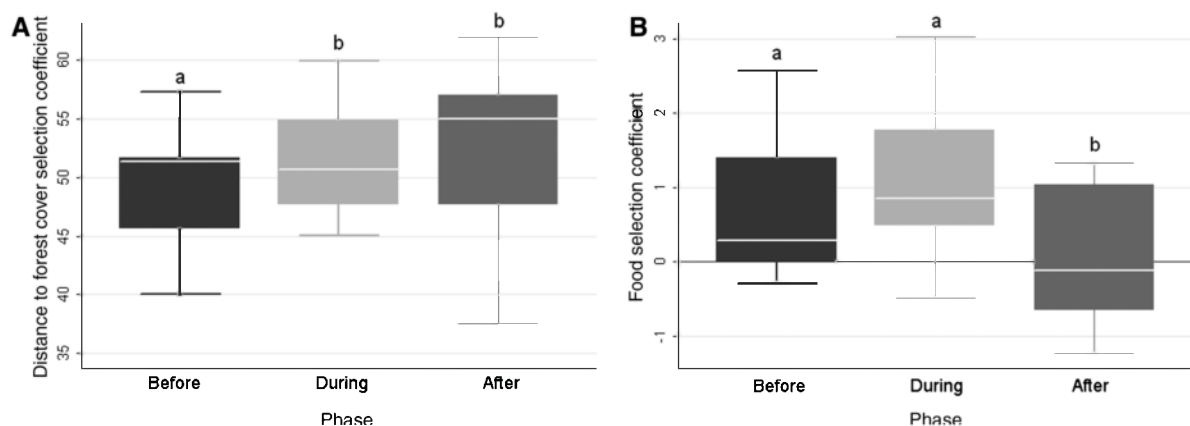
Figure 4. Box plots for cattle selection coefficients for distance to forest cover (A), and high-food quality habitat (B) assessed in phases before, during and after wolf visits to cattle pastures in southwest Alberta 2004–2007. Conditional coefficients across wolf visits were estimated with generalized linear mixed models (GLMMs). Phases with different coefficients (p < 0.05) are marked by different letters above the box plot, whereas box plots with same letter are not different. Also indicated are the median value (white line within the box), 25th and 75th percentiles (bounds), and 10th and 90th percentiles (whiskers).

left the home range. Our results were consistent with the notion broadly presented in other studies in North America that elk increase their selection of forest cover and decrease selection of high-food quality habitat types in the presence of predators (Morgantini and Hudson 1985, Creel et al. 2005, Fortin et al. 2005). We also found that after wolves visited home ranges elk may have used human activity as refugia from predation. Such behavior is not unusual in wild ungulates (Berger 2007). Human activity has been implicated in creating a low predation risk scenario for non-migratory elk in a similar area of Alberta (Hebblewhite et al. 2005a).

Similar to elk, cattle made tradeoffs between forest cover and food quality of the habitat patches used. This suggested that cattle might not have been able to select for the best food patch available and the best available forest cover scenario at the same time. Such tradeoffs presented whether wolves were present or absent. However, unlike elk, when wolves entered pastures cattle did not respond by selecting for forest cover. It is possible that the range of habitats available to cattle to select from during wolf visits was limited by fencing – i.e. cattle could use habitats within pastures only. However, cattle pastures were of comparable size to elk home ranges (Fig. 1) and encompassed a similar array of habitats.

Wolves caused cattle to switch to low-food quality habitat and use roads and trails after wolves had left the pastures. Cattle selection for areas farther from forest was a constant tendency across phases that become stronger during and after wolf visits. Thus, instead of forest, cattle selected roads and trails indicating they perceived human infrastructure and activity as a form of security cover from predation. Cattle may have remained in open areas during predator presence because they relied on grouping as an anti-predator strategy (Laporte 2009), like some large wild bovids (Hunter and Skinner 1997).

The lagged responses to wolf visits indicated cattle responded less promptly than elk to wolves, and suggested that anti-predator behaviors in cattle could have been blunted by domestication and artificial selection. Alternatively, the lack of an immediate anti-predator response might be due to lack of experience, instead of being the result of artificial selection and domestication. As suggested in other behavioral studies conducted on cattle (Kluever et al. 2009) and sheep (Romeyer and Bouissou 1992), artificial selection has likely resulted in attenuated anti-predator behaviors in livestock that might make them more vulnerable than wild ancestors to predation.

As is typical in ecological studies, our results might have been confounded by a number of variables that could not be measured or controlled for in complex environments, and that can still affect results. For example, snow accumulation might contribute to the outcome of predator-prey interaction on certain days (Nelson and Mech 1986). Similarly, age of prey might be a factor, as younger animals might be more vulnerable (Husseman et al. 2003). Sample sizes for our study animals and events, and the data available on the ecosystems were all limited, which precluded from controlling for a number of factors and variables. Therefore, our findings are limited to correlative patterns between certain variables or factors (example, occurrence of a visit by collared wolves) and other variables or factors (example, a change in habitat selection by prey). Overall, we found a clear signal of a change in habitat selection by prey correlated to visits by collared wolves, despite a conservative methodology designed to minimize type I errors, i.e. identifying a prey response when one did not exist.

Finally, our methodologies did not account for the possibility of wolf responses to elk and cattle behaviour and habitat use. In theory, it is possible that wolves approach prey animals only when these move to certain habitats, instead of prey responding to wolves by moving in these same habitats. However, we made the reasonable assumption that wolves had not detected the exact location of individual prey animals prior to entering the elk home ranges or cattle pastures, and thus the type of habitat 'used' by prey did not influence a wolf's decision to enter the home range or pasture. Our assumption seems supported by our finding that in the period after wolf visits various animals (elk) returned to habitat used prior to wolf visits. Thus, it seems that a prey response was elicited by the 'wolf-treatment', rather than vice versa.

Conservation implications and conclusions

How livestock respond to predator presence has significant implications for predator conservation in livestock production areas. Wolf predation on livestock causes a significant human–wolf conflict, and the lethal control of wolves by humans is the typical management response (Fritts et al. 2003). However, complete removal of wolves from cattle range, or vice versa, are unrealistic or unlikely without significant political repercussions (Kellert et al. 1996). Thus, conflict between humans and wolves is likely to continue, unless other means to break the cycle of depredation and lethal control of wolves are identified. Various non-lethal approaches to livestock protection have been tried (Shivik 2006), but none have been universally applied. The attenuated anti-predator response by cattle to wolves surely contributes to the cycle of livestock killed by wolves and wolves killed by people as a consequence (Musiani et al. 2003). Fluctuations in densities of important predators such as wolves might have implications for risk effects on prey and for the indirect effects on other species in ecosystems. Our study indicates similar considerations apply to scenarios where wolves are culled in response to livestock depredation. Under these circumstances, people should be aware that changes in wolf numbers might produce changes in the strength of ecosystem effects, and also in the type of effects if wild or domestic prey are dominant. Our results on cattle selection for roads and trails suggest livestock might perceive roads and trails as safe areas from predators because they associate roads and trails with humans. A potential solution for protecting livestock from wolves might therefore be to increase human presence on the landscape. However, the efficacy of such a management action on livestock survival requires experimental testing. Furthermore, increased human presence over large areas may ultimately have negative effects on wolves and the ecosystem in general by excluding wolves from those areas.

Another matter of consideration is that livestock producers are concerned about the fitness consequences of the risk effects of predators in general on livestock, such as increased stress and reduced foraging time (Howery and DeLiberto

2004). Further research is required using quantitative techniques (Lind and Cresswell 2005) to assess the energetic consequences of wolf visits to cattle: for example, whether risk effects that we detected result in decreased weight gain. Our results suggest that the economic impacts of wolf-triggered risk effects on cattle could be considered while planning compensation programs.

We conclude that wolves have habitat-dependent risk effects on elk and to a weaker extent on cattle. Both elk and cattle adjusted their use of high-food quality habitat and security cover in response to wolves and therefore both species can mediate the effect of predators on the food web where they co-occur. The types of risk effects were different for each prey species, however, and likely reflected the consequences of domestication and artificial selection on anti-predator behavior. The ecological effects of predators such as wolves may be different in areas where domestic animals such as cattle are the dominant herbivore in the ecosystem, if compared to areas frequented by wild prey only. Mechanisms of predator–prey interactions and the indirect effects on other species in ecosystems are well documented and considered in conservation of wild animals and ecosystems (Hebblewhite et al. 2005a). However, conservation groups as well as wildlife and rangeland managers should consider that such effects may manifest differently in ecosystems where domestic animals are dominant species.

References

Abrams, P. A. 1995. Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. – Am. Nat. 146: 112–134.

Agrawal, A. A. 2001. Phenotypic plasticity in the interactions and evolution of species. – Science 294: 321–326.

Alcock, J. 2005. Animal behavior. – Sinauer.

Beck, J. L. and Peek, J. M. 2005. Diet composition, forage selection, and potential for forage competition among elk, deer, and livestock on aspen–sagebrush summer range. – Rangeland Ecol. Manage. 58: 135–147.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. – Biol. Lett. 3: 620–623.

Bolker, B. M. et al. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. – Trends Ecol. Evol. 24: 127–135.

Boyce, M. S. et al. 2002. Evaluating resource selection functions. – Ecol. Modell. 157: 281–300.

Creel, S. and Christianson, D. 2008. Relationships between direct predation and risk effects. – Trends Ecol. Evol. 23: 194–201.

Creel, S. et al. 2005. Elk alter habitat selection as an antipredator response to wolves. – Ecology 86: 3387–3397.

Crête, M. and Manseau, M. 1996. Natural regulation of cervidae along a 1000 km latitudinal gradient, change in trophic dominance. – Evol. Ecol. 10: 51–62.

Diamond, J. 2002. Evolution: consequences and future of plant and animal domestication. – Nature 418: 700–707.

Estes, J. A. 1996. Predators and ecosystem management. – Wildlife Soc. Bull. 24: 390–396.

Fortin, D. et al. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. – Ecology 86: 1320–1330.

Frair, J. L. et al. 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. – Landscape Ecol. 20: 273–287.

Fritts, S. H. et al. 2003. Wolves and humans. – In: Mech, L. D. and Boitani, L. (eds), Wolves: behavior, ecology and conservation. Univ. of Chicago Press, pp. 289–340.

Gillies, C. et al. 2006. Application of random effects to the study of resource selection by animals. – J. Anim. Ecol. 75: 887–898.

Godvik, I. M. R. et al. 2009. Temporal scales, tradeoffs, and functional responses in red deer habitat selection. – Ecology 90: 699–710.

Gude, J. A. et al. 2006. Prey risk allocation in a grazing ecosystem. – Ecol. Appl. 16: 285–298.

Hebblewhite, M. et al. 2005a. Human activity mediates a trophic cascade caused by wolves. – Ecology 86: 2135–2144.

Hebblewhite, M. et al. 2005b. Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk predator–prey system. – Oikos 111: 101–111.

Hebblewhite, M. et al. 2006. Is the migratory behavior of montane elk herds in peril? The case of Alberta's Ya Ha Tinda elk herd. – Wildlife Soc. Bull. 34: 1280–1294.

Heithaus, M. R. et al. 2009. Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. – J. Anim. Ecol. 78: 556–562.

Howery, L. D. and DeLiberto, T. J. 2004. Indirect effects of carnivores on livestock foraging behavior and production. – Sheep Goat Res. J. 19: 53–57.

Hunter, L. T. B. and Skinner, J. D. 1997. Vigilance behaviour in African ungulates: the role of predation pressure. – Behaviour 135: 195–211.

Husseman, J. S. et al. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. – Oikos 101: 591–601.

Johnson, C. J. et al. 2006. Resource selection functions based on use–availability data: theoretical motivation and evaluation methods. – J. Wildlife Manage. 70: 347–357.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. – Ecology 61: 65–71.

Kellert, S. R. et al. 1996. Human culture and large carnivore conservation in North America. – Conserv. Biol. 10: 977–990.

Kluever, B. M. et al. 2009. Predator and heterospecific stimuli alter behaviour in cattle. – Behav. Process. 81: 85–91.

Koper, N. and Manseau, M. 2009. Generalized estimating equations and generalized linear mixed-effects models for modelling resource selection. – J. Appl. Ecol. 46: 590–599.

Laporte, I. 2009. Behavioural effects of wolf presence: responses of cattle and elk. MS thesis. – Univ. of Calgary.

Laundré, J. W. et al. 2001. Wolves, elk, and bison: reestablishing the 'landscape of fear' in Yellowstone National Park, USA. – Can. J. Zool. 79: 1401–1409.

Lele, S. R. 2009. A new method for estimation of resource selection probability function. – J. Wildlife Manage. 73: 122–127.

Lind, J. and Cresswell, W. 2005. Determining the fitness consequences of antipredation behavior. – Behav. Ecol. 16: 945–956.

Lyon, L. J. 1979. Habitat effectiveness for elk as influenced by roads and cover. – J. For. 77: 658–660.

Manly, B. F. J. et al. 2002. Resource selection by animals (2nd ed.). – Kluwer Academic Publishers.

McDermid, G. J. et al. 2009. Remote sensing and forest inventory for wildlife habitat assessment. – For. Ecol. Manage. 257: 2262–2269.

McGarigal, K. and Cushman, S. A. 2002. Comparative evaluation of experimental approach to the study of habitat fragmentation effects. – Ecol. Appl. 12: 335–345.

Merrill, S. B. and Mech, L. D. 2003. The usefulness of GPS telemetry to study wolf circadian and social activity. – Wildlife Soc. Bull. 31: 947–960.

Mignon-Grasteau, S. et al. 2005. Genetics of adaptation and domestication in livestock. – Livestock Production Sci. 93: 3–14.

Morgantini, L. E. and Hudson, R. J. 1985. Changes in diets of wapiti during a hunting season. – J. Range Manage. 38: 77–79.

Musiani, M. et al. 2003. Wolf depredation trends and the use of fladry barriers to protect livestock in western North America. – Conserv. Biol. 17: 1538–1547.

Nelson, M. E. and Mech, L. D. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. – J. Wildlife Manage. 50: 471–474.

Ormerod, S. J. 2002. Applied issues with predators and predation: editor's introduction. – J. Appl. Ecol. 39: 181–188.

Preisser, E. L. and Bolnick, D. I. 2008. The many faces of fear: comparing the pathways and impacts of nonconsumptive predator effects on prey populations. – PLoS One 3: e2465.

Rabe-Hesketh, S. et al. 2005. Maximum likelihood estimation of limited and discrete dependent variable models with nested random effects. – J. Econometrics 128: 301–323.

Riley, S. J. et al. 1999. A terrain ruggedness index that quantifies topographic heterogeneity. – Intermountain J. Sci. 5: 1–4.

Ripple, W. J. et al. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. – Biol. Conserv. 102: 227–234.

Romeyer, A. and Bouissou, M. F. 1992. Assessment of fear reactions in domestic sheep and influence of breed and rearing conditions. – Appl. Anim. Behav. Sci. 34: 93–119.

Seaman, D. E. and Powell, R. A. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. – Ecology 77: 2075–2085.

Shivik, J. A. 2006. Tools for the edge: what's new for conserving carnivores. – BioScience 56: 253–259.

Skovlin, J. M. et al. 2002. Elk habitat selection and evaluation. – In: Toweill, D. E. and Thomas, J. W. (eds), North American elk: ecology and management. Smithsonian Inst. Press, pp. 531–555.

Skrondal, A. and Rabe-Hesketh, S. 2004. Generalized latent variable modeling: multilevel, longitudinal, and structural equation models. – Chapman and Hall.

Sokal, R. R. and Rohlf, F. S. 2000. Biometry. – Freeman.

Stewart, K. M. et al. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. – J. Mammal. 83: 229–244.

Appendix 1

Resource selection function coefficients and standard errors for elk and cattle before, during and after wolf visits calculated from generalized linear mixed models

Table A1. Elk resource selection function coefficients (β) and standard errors in periods before, during and after wolf visits to elk home ranges calculated from two generalized linear mixed models (GLMMs) with distance to forest cover or food habitat quality as conditional coefficient, respectively.

Covariate		Random coefficient = distance to forest cover			Random coefficient = food habitat quality		
		Before	During	After	Before	During	After
Fixed effects							
Terrain ruggedness	β	–0.026*	–0.030*	–0.022*	–0.032**	–0.041***	–0.023**
	SE	0.012	0.012	0.009	0.013	0.012	0.009
Distance to road or trail (km)	β	–0.008	0.094	0.063	0.087	0.576	0.150
	SE	0.263	0.250	0.186	0.309	0.296	0.183
Distance to forest cover (km)	β	5.469***	0.329	0.803	2.576***	1.768***	1.353***
	SE	1.034	0.533	0.434	0.867	0.315	0.222
Food habitat quality	β	0.559*	0.156	0.426*	1.025**	0.495	0.574*
	SE	0.281	0.248	0.195	0.398	0.402	0.240
Terrain ruggedness × food habitat quality	β	0.027*	0.045***	0.021*	0.031*	0.059***	0.024**
	SE	0.013	0.012	0.009	0.014	0.013	0.009
Distance to road or trail (km) × food habitat quality	β	–0.450	–0.494*	–0.457*	–0.393	–0.968***	–0.553***
	SE	0.279	0.246	0.166	0.329	0.297	0.170
Distance to forest cover (km) × food habitat quality	β	–5.286***	–0.205	–0.253**	–2.365**	–0.613**	–0.357***
	SE	0.985	0.115	0.089	0.873	0.231	0.100
Random effects							
$\gamma_k^{(visit)}$	intercept	0.930	1.259	0.745	1.943	2.253	0.986
	SE	0.209	0.275	0.174	0.819	0.835	0.347
$\gamma_{1k}^{(visit)} x_{1jk}$	coefficient	8.648	11.297	7.341	1.341	2.251	0.303
	SE	2.122	2.952	2.071	0.752	0.886	0.215
Covariance		–2.652	–2.631	–1.625	–1.592	–1.890	–0.546
	SE	0.614	0.759	0.499	0.781	0.818	0.284
Correlation		–0.935	–0.698	–0.695	–0.987	–0.840	–1.000

* = significant p < 0.05; ** = significant p < 0.01; *** = significant p < 0.001.

Table A2. Cattle resource selection function coefficients (β) and standard errors in periods before, during and after wolf visits to cattle pastures calculated from two generalized linear mixed models (GLMMs) with distance to forest cover or food habitat quality as conditional coefficient, respectively.

Covariate		Random coefficient = distance to forest cover			Random coefficient = food habitat quality		
		Before	During	After	Before	During	After
Fixed effects							
Terrain ruggedness	β	−0.040***	−0.047***	−0.021***	−0.037***	−0.038***	−0.023***
	SE	0.003	0.004	0.003	0.003	0.004	0.003
Distance to road or trail (km)	β	1.059***	1.150***	−1.725***	1.032***	1.183***	−1.731***
	SE	0.123	0.142	0.136	0.123	0.139	0.138
Distance to forest cover (km)	β	48.600***	52.516***	50.774***	50.765***	55.386***	51.821***
	SE	6.009	7.911	6.898	7.108	8.369	7.138
Food habitat quality	β	0.544***	0.585***	−0.189**	0.696***	1.130***	−0.381***
	SE	0.081	0.095	0.068	0.083	0.010	0.076
Terrain ruggedness × food habitat quality	β	0.043***	0.039***	0.023***	0.038***	0.027***	0.024***
	SE	0.004	0.005	0.003	0.004	0.005	0.003
Distance to road or trail (km) × food habitat quality	β	−1.709***	−0.276	2.359***	−1.626***	−0.312***	2.328***
	SE	0.145	0.160	0.151	0.145	0.158	0.153
Distance to forest cover (km) × food habitat quality	β	−44.747***	−50.833***	−50.993***	−46.941***	−53.221***	−49.741***
	SE	6.008	7.912	6.901	7.109	8.370	7.139
Random effects							
$\gamma_{jk}^{(cow)}$	intercept	0.004	0.018	0.241	0.000	0.120	0.232
	SE	0.003	0.008	0.014	0.000	0.021	0.020
$\gamma_{k}^{(visit)}$	intercept	0.069	0.195	0.071	0.491	1.398	0.410
	SE	0.008	0.016	0.005	0.053	0.146	0.021
$\gamma_{1jk}^{(visit)} x_{1ijk}$	coefficient	6.916	8.178	20.902	0.581	0.437	0.336
	SE	0.627	0.675	1.289	0.059	0.036	0.022
Covariance		−0.486	−0.151	−0.341	−0.518	−0.283	−0.352
	SE	0.046	0.063	0.041	0.055	0.090	0.021
Correlation		−0.703	−0.119	−0.280	−0.970	−0.362	−0.947

* = significant $p < 0.05$; ** = significant $p < 0.01$; *** = significant $p < 0.001$.