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Context dependence of elk (*Cervus elaphus*) vigilance and wolf (*Canis lupus*) predation risk

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Abstract: To assess the relationship between predation risk perceived by elk (*Cervus elaphus* L., 1758) as evidenced by vigilance, we conducted focal animal observations in elk winter range. We stratified our observations in Glacier National Park, Montana, USA, and Waterton Lakes National Park, Alberta, Canada, in valleys with three wolf (*Canis lupus* L., 1758) population levels (Saint Mary Valley: no wolf; Waterton Valley: moderate wolf; North Fork Valley: high wolf). Although the lowest elk vigilance occurred in Saint Mary and the highest in the North Fork, our analysis revealed a complex picture. Our model included distance to forest edge, group size, distance to road, social class, and impediments to detecting and escaping wolves. In Saint Mary, none of the variables were significant. In Waterton, vigilance decreased as elk group size increased ($p < 0.00001$) and increased as impediments increased ($p = 0.0005$). In the North Fork, vigilance increased as group size increased ($p = 0.03$), bulls were more vigilant ($p = 0.02$), and the interaction between group size and impediments was significant ($p = 0.03$). Where a high wolf population existed, elk did not exhibit uniform or expected response to predation risk factors. High wolf presence may necessitate adaptive elk behaviour that differs from response to moderate wolf presence.

Key words: elk, *Cervus elaphus*, focal sampling, predation risk, vigilance, wolves, *Canis lupus*.

Résumé : Afin d'évaluer le lien entre le risque de prédation perçu par les wapitis (*Cervus elaphus* L., 1758) tel qu'il est reflété par la vigilance, nous avons recueilli des observations sur des individus précis dans l'aire de distribution hivernale de l'espèce. Nous avons stratifié nos observations dans le parc national Glacier (Montana, États-Unis) et dans le parc national des Lacs-Waterton (Alberta, Canada) dans des vallées présentant trois niveaux de population de loups (*Canis lupus* L., 1758) (vallée de Saint Mary, aucun loup; vallée de Waterton, population modérée de loups; vallée de la North Fork, forte population de loups). Si la vigilance des wapitis la plus faible a été observée dans la vallée de Saint Mary, et la plus forte, dans la vallée de la North Fork, le portrait qui ressort de notre analyse n'en est pas moins complexe. Le modèle intègre la distance jusqu'à la lisière de la forêt, la taille du groupe, la distance jusqu'à un chemin, la classe sociale et les entraves à la détection des loups et à la fuite pour échapper à ces derniers. Aucune de ces variables n'était significative pour la vallée de Saint Mary. Dans la vallée de Waterton, plus la taille du groupe de wapitis était grande, plus la vigilance était faible ($p < 0,00001$), et plus les entraves étaient importantes, plus la vigilance était grande ($p = 0,0005$). Dans la vallée de la North Fork, plus la taille du groupe était grande, plus la vigilance était grande ($p = 0,03$), les mâles étaient plus vigilants ($p = 0,02$), et la relation entre la taille du groupe et les entraves était significative ($p = 0,03$). En présence d'une forte population de loups, les wapitis ne présentaient pas des réactions uniformes ou prévisibles aux facteurs de risque de prédation. Une forte présence de loups pourrait exiger des wapitis l'adoption d'un comportement adaptatif qui diffère de la réaction à une présence de loups modérée. [Traduit par la Rédaction]

Mots-clés : wapiti, *Cervus elaphus*, échantillonnage individuel, risque de prédation, vigilance, loups, *Canis lupus*.

Introduction

In addition to density-mediated effects on their prey (e.g., predators killing prey), predator presence can have behaviourally mediated effects (e.g., predators causing prey to alter foraging behaviour) (Schmitz et al. 2004). Avoidance of predation shapes herbivore behaviour (Abrams 1991; Altendorf et al. 2001). Optimal foraging by prey involves balancing risk avoidance with energy expenditure and food needs (Lima and Dill 1990; Illius and Fitzgibbons 1994). Vigilance represents a compromise between perceived risk and meeting other survival needs. Behaviourally mediated effects of predators on their herbivore prey can lead to trait-mediated indirect effects (e.g., where one species alters the interaction between two other species) on plant communities, termed trophic cascades (Beckerman et al. 1997).

Elk (*Cervus elaphus* L., 1758) and their primary predator, the wolf (*Canis lupus* L., 1758) (Mech and Peterson 2003), have been the subjects of several studies of behavioural response to predation risk. Vigilance, defined in terrestrial mammals as the proportion of time an individual spends with its head raised above its shoulders, scanning for predators, is the measure commonly used to assess elk response to the threat of predation (Childress and Lung 2003).

Ecological context influences elk vigilance (Brown et al. 1999). Landscape features that create impediments to detecting or escaping wolves may increase vulnerability to predation (Laundré et al. 2001). Elk (*i*) may avoid sites with high impediments, (*ii*) demonstrate higher vigilance in these sites, and (or) (*iii*) browse less intensively in them (Ripple and Beschta 2006). Group size also influences vulnerability to predation (Hebblewhite and Pletscher 2002), with elk in larger groups commonly thought to be less vulnerable to predation (Hamilton 1971; Geist 2002). Other factors that influence elk vigilance include social class, distance to road, and distance to forest edge (Lung and Childress 2007). Of all elk

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social classes, adult cows with calves are said to be the most vigilant (Wolff and Van Horn 2003). Elk tend to avoid roads due to the human presence roads represent (Rost and Bailey 1979). Elk use forest cover primarily for food and protection from predators (Fortin et al. 2005; Liley and Creel 2008). However, elk may be more vulnerable to predation inside and near forests, due to the impediments to seeing or escaping wolves created by trees and large dead wood (Halofsky and Ripple 2008).

The ecological effectiveness of wolves in influencing elk behaviour may be a function of wolf population and distribution (Mao et al. 2005). Long-term risk is the landscape-scale probability of an elk encountering a wolf; however, risk can be measured on a finer spatiotemporal scale, termed short-term risk (Creel et al. 2008). Prey vigilance may reflect assessment of long-term risk level (Kauffman et al. 2007).

To investigate the role of long-term predation risk and environmental factors in influencing elk vigilance, we observed elk vigilance in this species' winter range in three valleys that differed in wolf density. We hypothesized that elk would be more vigilant where there were more wolves. We also hypothesized that elk would spend more time with their heads above their shoulders (vigilant) in places with more impediments to detecting or escaping wolves.

Materials and methods

Study area

The study setting spans the US–Canada border within Glacier National Park (GNP), Montana, USA, and Waterton Lakes National Park (WLNP), Alberta, Canada, in the Crown of the Continent Ecosystem. GNP contains 4047 km^2 of forest, alpine meadows, and lakes; WLNP encompasses 520 km^2 of forest, alpine meadows, and lakes. Biotic communities of the two parks are similar (Achuff et al. 2005; Hop et al. 2007).

We studied three geographically separate valleys (Fig. 1), all of which are elk winter range: (1) the Saint Mary Valley, which covers 1392 ha in southeastern GNP; (2) the Waterton Valley, which covers 2741 ha in WLNP; and (3) the North Fork Valley, which covers 5705 ha in northwestern GNP. Ecological resources are comparable in all valleys (e.g., climate, soil, elevation), as is precipitation quantity and temporal distribution (Achuff et al. 2005; Hop et al. 2007). The valleys consist of low-elevation (1024–1700 m) grasslands dominated by rough fescue (*Festuca altaica* Trin.) that offer elk snow depth <0.7 m and wind protection. Secondary foods include quaking aspen (*Populus tremuloides* Michx.), shrubs, and conifers (Singer 1979; Achuff et al. 2005). While all valleys offer similar wolf habitat, past wildlife management policies and practices have varied, resulting in a range of wolf population sizes among the valleys. Thus, the three valleys differed in long-term predation risk.

Wolf abundance in the Crown of the Continent Ecosystem was very low overall from the 1880s until the mid-1970s, due to wolf extirpation policies and actions. In the mid-1970s, wolves from Canada began to recolonize the ecosystem naturally and were confirmed denning in the North Fork in 1986 (Ream et al. 1989). Wolves have continued to den in the North Fork since then (Sime et al. 2010). They were not confirmed denning in WLNP until 1992 (Fox and Van Tieghem 1994). Wolves had not recolonized Saint Mary at the time of our study (2007–2009) because of human intolerance (Sime et al. 2010).

The three valleys had three different wolf populations. We characterize wolf density via agency reports and field observations that took place during the course of our study. We also based our assessment of wolf population status on Fuller et al. (2002), who characterized an established population as one that dens and produces pups that survive through December of the breeding year. During our study, Saint Mary had no wolves denning, with lone wolves and wolf sign observed on 2–3 occasions/year (Sime et al. 2010). Accordingly, we characterized Saint Mary as having a wolf density of 0 wolves/100 km^2, termed no relative wolf density for our analysis. Waterton had a single pack that denned and produced pups and averaged 6 wolves, equivalent to an estimated wolf density of 7 wolves/100 km^2 (Watt 2009), termed moderate relative wolf density for our analysis. The North Fork had two packs that produced multiple litters each per year, a total of 38 individual wolves, equivalent to an estimated wolf density of 22 wolves/100 km^2 (Sime et al. 2010), termed high relative wolf density for our analysis.

We determined elk density via agency reports and field data (e.g., Parks Canada aerial surveys, pellet counts, field observations of herd size and distribution) collected during 2007–2009. Saint Mary had an estimated elk density of 1050 elk/100 km^2; Waterton had an estimated elk density of 1200 elk/100 km^2; the North Fork had an estimated elk density of 400 elk/100 km^2.

Based on the above estimated densities of wolves and elk, the ratio of wolves to elk was 1:171 in Waterton and 1:18 in the North Fork. These ratios represent no wolf predation risk in Saint Mary, moderate wolf predation risk in Waterton, and high wolf predation risk in the North Fork.

Elk vigilance could be influenced by other large carnivores. In our study sites, these include cougar (*Puma concolor* (L., 1771)), grizzly bear (*Ursus arctos horribilis* Ord, 1815), and black bear (*Ursus americanus* Pallas, 1780). Bears did not have a large impact on elk in our study, because bears hibernate when elk are on their winter range, and cougars prey mostly on deer in WLNP (Kunkel and Pletscher 2001; Banfield 2010). Furthermore, there is no evidence that cougar numbers differed widely among the three valleys. Thus, wolves were the leading elk predator in our study.

Field methods

Focal sampling involves observing a single individual continuously for a specified period of time (Laundré et al. 2001). Focal sampling is an established method in ecology to measure prey response to predator presence. We conducted a total of 622 focal observations of free-ranging elk actively feeding over a 2-year period (11 April 2007 through 17 March 2009), avoiding observations during the rut (Wolff and Van Horn 2003). The sampling unit was the individual elk. We stratified observations by valley and by social class (bull, spike bull, adult cow, adult cow with calf) (Wolff and Van Horn 2003). We haphazardly selected individuals engaged in feeding to sample as evenly as possible across all social classes (Table 1). The observation period ran from 28 October to 11 April, when elk were reliably present in their winter range.

We defined a group as ≥3 elk not more than 100 m apart, and observed individual elk until a group was no longer observable (Childress and Lung 2003). To avoid observing the same individual more than once, we only observed 1–4 focal individuals in each group per day and only revisited groups at a particular location on additional days if they contained >10 individuals (Childress and Lung 2003).

Observations took place from park roads and in natural blinds away from roads, using binoculars (10 mm × 50 mm) and a spotting scope (20–60 mm × 65 mm) when the animals were visible and active between the hours of 0415 and 1940. Observation sites were selected to provide best viewing access to elk without disturbing them. All observations were made at a distance of ≥50 m from each focal animal. We waited 5 min from arrival at an observation site before beginning the first observation period. To address bias potentially created by road adaptation, we included distance to road as an explanatory variable.

Each observation was 3–20 min long and ended when the focal animal walked out of sight, ended a feeding bout, or the time limit was reached. During this interval, we used a tape recorder to continuously observe and record behaviour. Data were transcribed afterward by listening to the audio recording and timing intervals with a stopwatch. Behaviour was classified into feeding,

Fig. 1. Map of study areas in Glacier National Park (GNP), Montana, USA, and Waterton Lakes National Park (WLNP), Alberta, Canada.

Table 1. Categorical explanatory variables used multivariate analysis in three valleys.

	Impediments (no. of observations)			Social class (no. of observations)				
Valley	Low	Moderate	High	Bull	Spike bull	Adult cow	Adult cow with calf	Total sample
Saint Mary	17	82	115	28	50	67	69	214
Waterton	194	27	21	57	68	53	64	242
North Fork	62	54	50	46	34	49	37	166

Note: For definition of the variable "impediments" see Table 3.

raised head, and other behaviour (e.g., grooming and interacting with conspecifics). We subdivided raised head into (*i*) vigilant and (*ii*) locating food or moving to another feeding location. Because of differences in observation length, vigilance was normalized as a proportion (percentage of time spent vigilant). We obtained the azimuth from the observation point to the focal animal, observer location coordinates (in metres; error is ±2–6 m), and distance to focal animal (using a Leica laser rangefinder, in metres; error is ±1 m).

Variables assessed included group size (number of individuals), position within group (peripheral, intermediate, central), topography (valley, upland, gully), distance to forest edge, distance to road (nearest primary), view impediments (low, moderate, high), debris (low, moderate, high), snow depth, and social class (Tables 1, 2). All observations took place in grassland habitat that had similar type and height of vegetation, so we did not include vegetation type or biomass as a variable (Fortin et al. 2005).

We determined the position of an animal in a group per methods established by Bednekoff and Ritter (1994). We used visual observation and topographic maps to identify landscape characteristics (valley, upland, and gulley) that pertain to the types of topography encountered by elk. We used topography, rather than plant community, because it allowed for finer-scale evaluation of landscape features that could affect elk behaviour. We used a laser rangefinder to measure distance to forest edge, primary road, and view impediments. We used a leveling rod to measure escape impediment height and snow depth. Impediments to the ability of an elk to detect wolves (view) and escape wolves (debris) (Table 2) were collinear, so we created a new variable (impediments) that combined the effects of view and debris (Table 3).

Table 2. Definition of predation risk variables "debris" and "view".

Variable	No to low (1)	Moderate (2)	High (3)
Debris	Grass cover, debris found <100 m of the focal animal consisting of shrub cover <15 cm in height, and no downed wood or rocks ≥15 cm in diameter. No landscape characteristics that represent escape impediments for an elk	Debris found ≥50 < 100 m of the focal animal consisting of low shrubs, occasional pieces of downed wood, trees, and occasional rocks ≥15 < 30 cm in height or diameter. Mild slopes (<5%) and drop-offs that represent moderate escape impediments for an elk	Debris found <50 m of the focal animal consisting of shrubs, trees, and rocks ≥30 cm in height or diameter. Sharp slopes (≥5%), sharp drop-offs, and ravines that represent severe escape impediments for an elk
View	No landscape features, such as hills, within 100 m of the focal animal that can impede the ability of that animal to detect a predator by eyesight	Landscape features, such as hills, in <180° of the viewshed of the focal animal, located ≥50 < 100 m from the focal animal, which can impede the ability of that animal to detect a predator by eyesight	Landscape features, such as hills, in ≥180° of the viewshed of the focal animal, located <50 m from the focal animal, which can impede the ability of that animal to detect a predator by eyesight

Table 3. Definition of the variable "impediments".

Impediments	Debris	View
Low (1)	1	1
	1	2
	2	1
Moderate (2)	1	3
	2	2
	3	1
High (3)	3	2
	2	3
	3	3

Note: Predation risk variables "debris", e.g., impediments to escape for an elk (*Cervus elaphus*) in three levels (low (1), moderate (2), high (3)), and "view", e.g., impediments to visually detecting a predator in three levels (low (1), moderate (2), high (3)), and all of their possible combinations have been used to create the variable "impediments" in three levels (low (1), moderate (2), high (3)).

Hunting of elk by humans can influence elk vigilance (Proffitt et al. 2008). During our study, hunting took place immediately outside the study areas, on public and private lands. Elk hunting seasons were similar, with the exception of Waterton, which had a late winter antlerless elk hunt outside the Park. This may have increased vigilance in Waterton elk, although late season harvest was low (20 permits/20% successful harvest rate) (Alberta ESRD 2010). Collectively, hunting seasons caused elk to stay inside both Parks, which may have influenced group size.

Analysis

We examined elk mean vigilance, treating each valley as a case study, because we had no replication of wolf density. We did not include wolf GPS-collar data in our analysis, due to lack of parallel data (e.g., no collared wolves in Waterton or Saint Mary). In the past decade, GPS collars have been deployed on wolves as part of elk focal animal studies to determine predation risk. However, more recently, researchers have determined that studies which rely on GPS-collar data to identify wolf encounters with prey often underestimate the frequency and strength of antipredator responses (Creel et al. 2013). We used wolf density to indicate long-term predation risk instead of GPS-collar data on wolves.

We evaluated normality for the response variable, vigilance, by observing its distribution, and by observing residual plots. For the purpose of graphical presentation of data, we transformed group size, distance to forest edge, and distance to road into categorical variables (Figs. 2*a*, 2*d*, 2*f*). We defined these categories based on our field observations and on the scientific literature (Childress and Lung 2003). However, for all multivariate analyses, we used these as continuous variables (Table 4).

We created a correlation matrix and discarded from further analysis one of each pair of variables that were collinear. Position in group was correlated to group size; we kept group size, the variable used most often in analyses of elk vigilance (Brown 1999). Topography was correlated to impediments; we kept impediments, the finer scale of the two variables. We discarded the variable snow depth due to an insufficient range of values, which did not reliably represent the potential effect of snow depth on elk foraging (Hobbs et al. 1981).

We fitted a general linear model to describe Y_i, elk mean vigilance, and expressed the mean proportion of elk vigilance with the mixed linear model: $E(Y_i) = \beta_0 + \beta_1 X_{1i} + \beta_2 X_{2i} + \beta_3 X_{3i} + \beta_4 X_{4ijkl} + \beta_5 X_{5ijk} + \beta_2 X_{2i} \times \beta_5 X_{5ijk}$, where Y is arcsine of elk vigilance, X_1 is distance to forest edge (m), X_2 is group size, X_3 is distance to road (m), X_{4ijkl} is social class (where $ijkl$ is adult bull, spike bull, adult cow, and adult cow with calf, respectively), X_{5ijk} is impediments (where ijk is low, moderate, and high, respectively), and $X_2 \times X_{5ijk}$ is interaction of group size and impediments.

We included the interaction between impediments and group size. We wanted to determine whether a relationship existed between impediments and the increased safety that elk perceive when in larger groups (Geist 2002; Halofsky and Ripple 2008). It is possible that elk may feel safer in larger groups and this may influence their response to impediments, when all other factors in the model are considered. We did not include other interactions because of a lack of biological significance. We performed all analyses using the PROC MIXED function in SAS version 9.1 (SAS Institute, Cary, North Carolina, USA).

Results

Mean elk group size for the three valleys are reported in Table 4, with Waterton having the largest group size, followed by Saint Mary then North Fork. Overall mean (±95% confidence interval (CI)) elk vigilance was 9.41% ± 1.45% in Saint Mary, 13.74% ± 2.33% in Waterton, and 19.72% ± 3.33% in the North Fork. Simple bivariate analysis indicated that elk vigilance did not differ within each valley by group size, position in group, social class, distance to forest edge, impediments, or distance to road (Figs. 2*a*–2*f*).

Using multivariate analysis, we found no significant effect of any of these variables on elk vigilance in Saint Mary (Table 5). In Waterton, vigilance was negatively related to group size ($p < 0.0001$) (the larger the group, the less vigilant the focal animal) and positively related to impediments ($p = 0.0005$) (the greater the impediments, the more vigilant the focal animal). None of the other variables were significant (Table 5). In the North Fork, vigilance was positively related to group size ($p = 0.03$) (the larger the group, the more vigilant the focal animal) and bull elk were more vigilant than the other social classes ($p = 0.02$). The interaction of group

Fig. 2. (*a*–*f*) Influence of predation risk variables on mean vigilance of elk (*Cervus elaphus*). The error bars represent 95% confidence intervals. We define group size categories as small (≤25 elk), moderate (>25 ≤ 75 elk), and large (>75 elk). We define position in group categories as peripheral (animals in a group as those with no neighbors in one direction; Periph), central (animals in a group as those with neighbors on all sides that were located in the center of the group), and intermediate (animals intermediately located between the center of the group and its periphery; Interm). We define social class categories as per Table 1. We treated the distance to forest edge as a categorical variable, defined as close (≤50 m), moderate (>50 ≤ 100 m; Mod), and far (>100 m). We defined impediments as per Table 3. We treated distance to road as a categorical variable, defined as close (≤150 m), moderate (>150 ≤ 300 m), and far (>300 m). Mod is moderate in all panels.

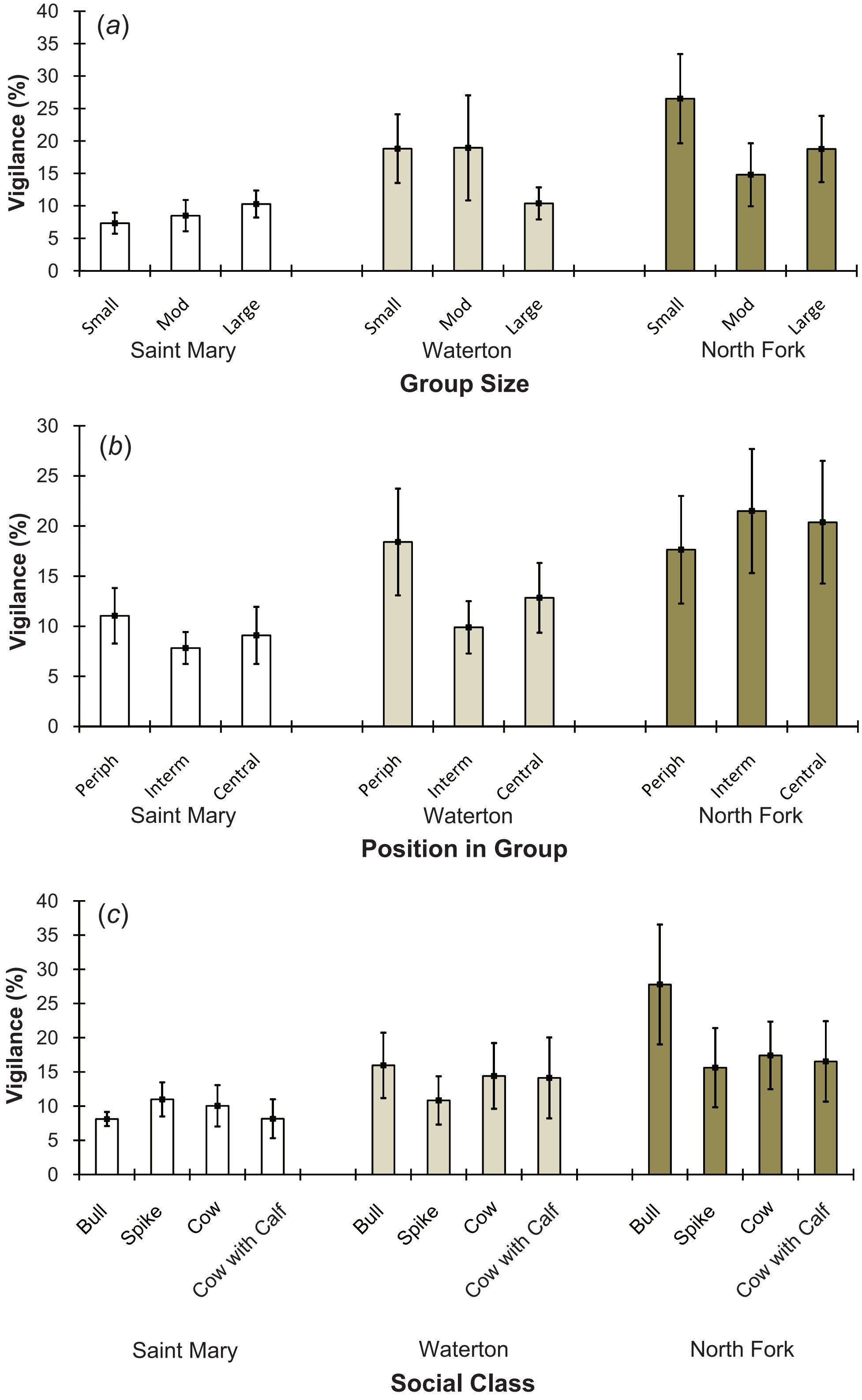


Fig. 2 (*concluded*).

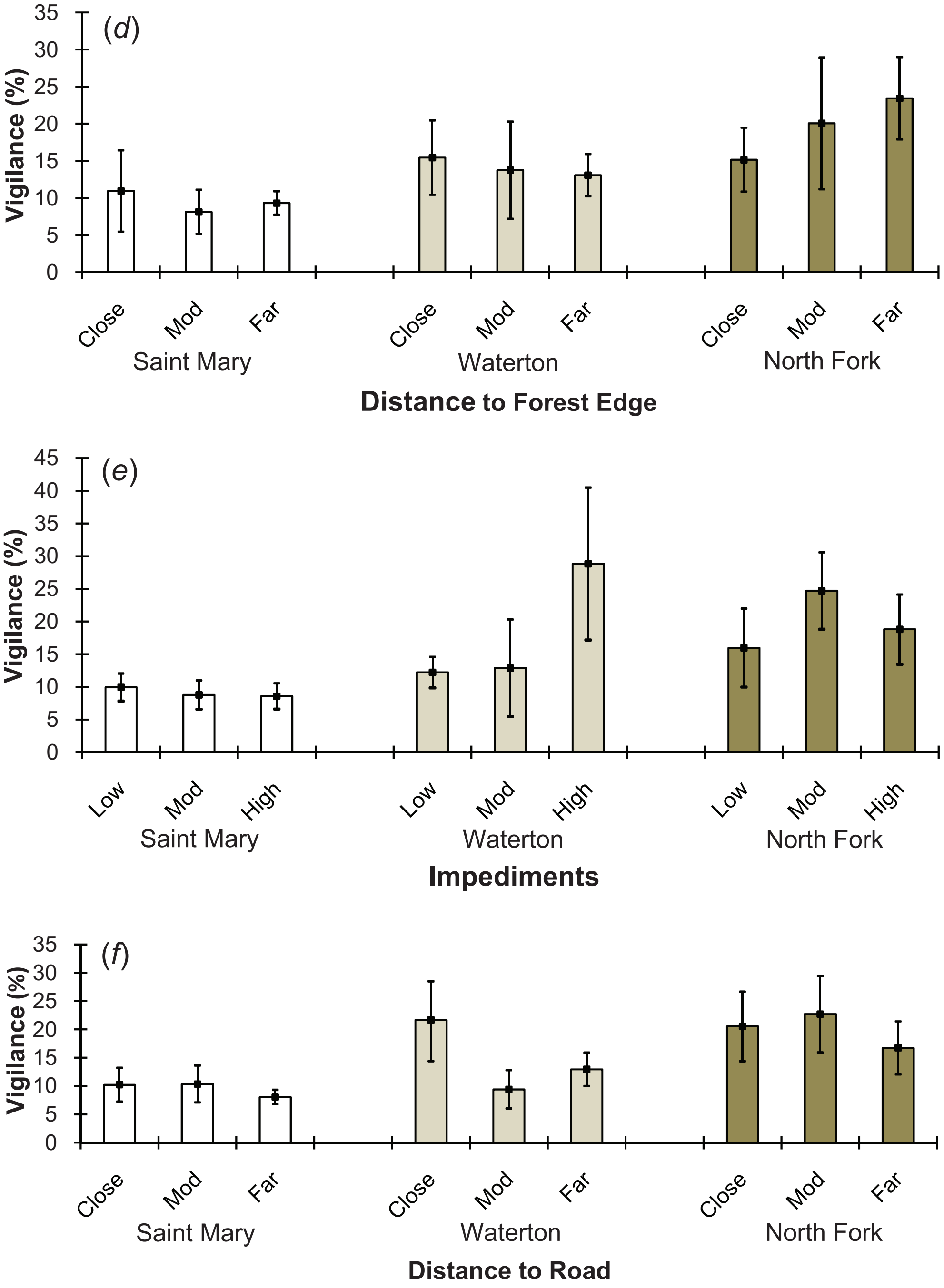


Table 4. Summary statistics of continuous variables.

	Group (no. of individuals)			Distance to forest edge (m)			Distance to road (m)		
Valley	Mean	±95% CI	Range	Mean	±95% CI	Range	Mean	±95% CI	Range
Saint Mary	91	6.5	6–193	257	22.0	1–633	269	22.0	15–711
Waterton	341	39.0	6–700	142	13.0	2–537	494	55.5	2–1730
North Fork	76	7.5	6–149	133	19.5	0–800	302	32.5	1–1114

Note: CI, confidence interval.

size and impediments was significant ($p = 0.03$); initially, vigilance increased as group size and impediments increased. However, as impediments increased from moderate to high and group size continued to increase, vigilance declined (Table 5, Fig. 3).

Discussion

Vigilance is a multidimensional behaviour influenced by a variety of environmental factors. Past research has shown that vigilance can increase as group size diminishes (Frid 1997), is greater

Table 5. Results of fitting a general linear model to describe the mean vigilance of elk (*Cervus elaphus*).

Valley	Variable	Variable type	Variable levels	Effect	*p*
Saint Mary	Distance to forest edge	Continuous	NA	–	0.12
	Group	Continuous	NA	–	0.35
	Distance to road	Continuous	NA	–	0.27
	Social class	Categorical	Bull	–	0.06
			Cow	–	
			Cow with calf	–	
			Spike bull	Reference level	
	Impediments	Categorical	Low	Reference level	0.68
			Medium	+	
			High	+	
	Group × impediments	Categorical	Low	Reference level	0.38
			Medium	+	
			High	+	
Waterton	Distance to forest edge	Continuous	NA	+	0.85
	Group	Continuous	NA	–	<0.0001
	Distance to road	Continuous	NA	–	0.49
	Social class	Categorical	Bull	–	0.17
			Cow	–	
			Cow with calf	–	
			Spike bull	Reference level	
	Impediments	Categorical	Low	Reference level	0.0005
			Medium	+	
			High	+	
	Group × impediments	Categorical	Low	Reference level	0.07
			Medium	–	
			High	–	
North Fork	Distance to forest edge	Continuous	NA	–	0.59
	Group	Continuous	NA	+	0.03
	Distance to road	Continuous	NA	–	0.15
	Social class	Categorical	Bull	+	0.02
			Cow	–	
			Cow with calf	–	
			Spike bull	Reference level	
	Impediments	Categorical	Low	Reference level	0.46
			Medium	–	
			High	+	
	Group × impediments	Categorical	Low	Reference level	0.03
			Medium	+	
			High	–	

Note: The Effect column indicates a positive or negative effect, based on the sign of *b* values obtained by fitting the model. For categorical variables, the reference level is indicated in the Effect column. NA, not available.

for cows with calves (Wolff and Van Horn 2003), is greater where there are impediments to detecting and escaping wolves (Halofsky and Ripple 2008), and increases with proximity to road (St. Clair and Forrest 2009).

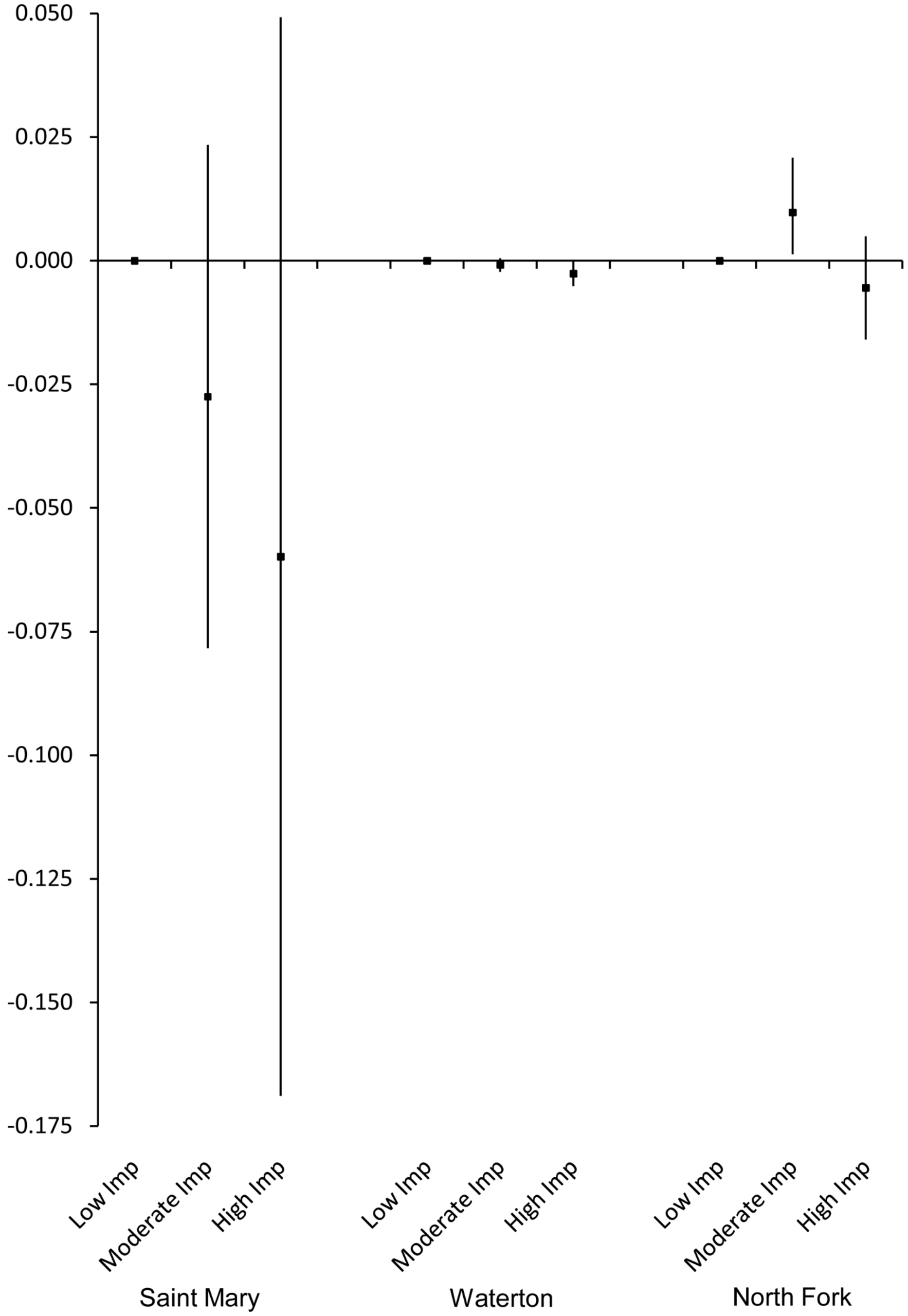
In our study of elk winter range vigilance behaviour in valleys that had different levels of wolf density, we expected to find relationships as described above. We also expected that elk would spend more time vigilant in places where there were more wolves. However, when we deconstructed vigilance by examining the variables that comprised predation risk in these valleys, we found some surprising relationships.

In Saint Mary, where no well-established wolf population existed and transient wolves were sporadically present during the time of the study, we found the lowest elk vigilance of all three valleys and no significant effects on vigilance of any explanatory variable (Table 5). This suggests that in Saint Mary, in the absence of an established wolf population, elk did not perceive the occasional wolf passing through as a threat and that these transient wolves did not exert an ecosystem-level effect (Soulé et al. 2003; Mao et al. 2005).

In Waterton, a well-established, moderate wolf population had denned within the park since 1994, with numbers and spatial distribution that were highly variable temporally (Watt 2009). Waterton elk were more vigilant than Saint Mary elk. As we expected, in Waterton, elk response to factors such as group size and impediments was similar to that found by Childress and Lung (2003) and Halofsky and Ripple (2008). As group size increased, vigilance decreased; as impediments increased, vigilance increased. However, elk in this valley failed to respond to predation risk variables such as distance to road and social class, which have been identified as important (Frair et al. 2005; Halofsky and Ripple 2008). Therefore, in a landscape with a moderate and variable wolf population, as well as a moderate ratio of wolves to elk, behavioural compensation by elk to predator presence was only significant when it came to group size and vigilance.

The North Fork had a high, well-distributed wolf population, a high wolf density, and a high ratio of wolves to elk (Sime et al. 2010). Elk in this valley were more vigilant than in Waterton, but responded to predation risk factors in ways that were not fully consistent with other findings in the scientific literature. For example, North Fork elk did not respond to the predation risk variable impediments alone (Halofsky and Ripple 2008) and they became more vigilant as group size increased (Childress and Lung 2003). When we examined the interaction between group size and impediments, we found what may have been an adaptive response, where initially vigilance increased as group size and

Fig. 3. The interaction of group size and impediments in North Fork. Group is a continuous variable, while impediments (Imp) is a variable consisting of three categories (low, moderate, and high), as defined in Table 3. We used low as the reference level of this variable. Group size increases as impediments levels increase. The *y* axis represents the coefficient values of this interaction. The response variable in the model is the proportion of time that elk (*Cervus elaphus*) spent being vigilant. Error bars represent 95% confidence intervals.



impediments increased, but then declined as group size and impediments continued to increase.

Some studies have found adaptive responses by elk to wolf presence. Hebblewhite et al. (2005) found that wolf encounter and attack rates may increase for large groups. Creel and Winnie (2005) found group size formation to be an adaptive behaviour; when wolves are immediately present, group sizes remain small, but when wolves are absent, group sizes increase, perhaps as a foraging response. Our findings suggest that in a high wolf density system, such as the North Fork, elk are using adaptive strategies to avoid wolf predation.

North Fork elk vigilance that was the reverse of expectations may have been related to how wolves detect prey. Wolves detect prey via sight and smell (Harrington and Asa 2002). If wolves rely on olfaction to detect elk, they could detect a large group of elk from a greater distance than a small group of elk. Thus, in a high wolf area where wolves are well-distributed (Sime et al. 2010) and where a high wolf to elk ratio exists, as elk group size increases, elk can be detected more easily (Hebblewhite et al. 2005). It is possible that the lack of a positive relationship between vigilance and group in Waterton compared with the North Fork may have been due to the lower wolf population in Waterton. Such findings are consistent with the findings of Hebblewhite and Pletscher (2002), in which elk found larger groups more risky in areas with a high wolf population because of the higher detectability of such groups.

It is not fully clear to us why in the North fork elk did not respond to impediments alone, a factor identified as having an important effect on elk vigilance (Halofsky and Ripple 2008), but did respond to it in the context of its interaction with group size. There was such a high wolf population and density in this valley (Sime et al. 2010) that it was very difficult for an elk to avoid wolves. In such a system, high and frequent wolf presence may necessitate adaptive elk behaviour that differs from elk response to a more moderate and variable wolf presence.

The North Fork was the only valley in which there was a difference in vigilance among social classes. Here, bulls were more vigilant than all the other social classes. This finding counters studies in which adult cows with calves demonstrate the highest levels of vigilance (Childress and Lung 2003; Halofsky and Ripple 2008). This may be explained by the fact that in the North Fork, wolf predation on male elk was higher than for other social classes of healthy individuals (Kunkel et al. 2004). Parallel data on wolf predation on elk by social class did not exist for the other valleys.

There is a rich body of literature on the complexity of prey response to predator presence. In the Greater Yellowstone Ecosystem, elk demonstrated heightened vigilance upon wolf reintroduction, but these effects diminished for some social classes over the next 5 years, as elk adjusted their vigilance levels and reassessed predator lethality (Laundré et al. 2001). Here, Creel et al. (2008) found elk vigilance lower at a site with a higher proportion of time spent at risk (higher number of wolves) and higher at a site with fewer wolves, whether predators were immediately present or absent.

Empirical studies have attributed reduced vigilance in systems with a high predator population to prey differential adaptive decision-making in response to complex cues (Barros et al. 2008; Ferraria et al. 2010). What we observed in the North Fork, where elk response to impediments alone was not significant (Table 5), was similar to the above studies. Taken as a whole, in this valley, behavioural compensation by elk to predator presence by group size and impediments suggests elk adaptive behaviour.

We had further unexpected findings. Distance to forest edge has been identified as an important driver of elk vigilance (Hernández and Laundré 2005). This variable had no effect in our study, nor did distance to road. However, a study in WLNP found elk avoidance of roads (St. Clair and Forrest 2009). Our findings may differ because the St. Clair and Forrest (2009) study took place during the rut.

We have established that the three valleys we studied were ecologically similar, but differed by wolf long-term predation risk. These valleys provide compelling landscape-scale case studies of the complexity of elk behavioural responses to the threat of predation. Not all differences in elk vigilance that we found could be attributable to differences in the probability of an elk encountering a wolf (Creel et al. 2008). Taken together, our findings suggest that while there appears to be an association between vigilance and wolf population level, the apparent association between vigilance and predation risk variables, including wolf density, may, in some cases, be weak, nonuniform, and nonlinear. Deeper investigation is warranted to better understand the many dimensions of these relationships. Understanding the trait-mediated indirect effects of predators on their prey and the plants their prey consume has high conservation relevance due to the link between such dynamics and trophic cascades in a variety of communities (Schmitz et al. 2004; Beschta and Ripple 2009). Awareness of the complexity and nonlinear nature of these interactions has management implications, if the objective is to restore plant communities via trophic cascades mechanisms.

In summation, we found that in an area with no established wolf population and a resulting nonexistent level of long-term predation risk (Saint Mary), elk did not respond to commonly identified drivers of vigilance. At an intermediate level of long-term predation risk (Waterton), some drivers (group size, impediments) appeared to be important while others were not. At high levels of long-term predation risk (North Fork), vigilance was high but not driven by some of these common factors. Even more interestingly, in some cases, the relationship between vigilance and risk factors was reversed compared with other valleys as wolf density increased, which countered our expectations. While the transient wolves in Saint Mary did not exert an ecosystem-level effect (Soulé et al. 2003; Berger 2007) as evidenced by lack of response elk to behaviourally mediated drivers of vigilance (e.g., impediments), in the other valleys, some of these drivers (e.g., distance to forest, distance to road) had no effect regardless of wolf population. Elk reduce predation risk via a variety of strategies. While wolves drive elk vigilance, other factors may be modifying this multidimensional relationship in complex ways.

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