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Fine-scale predation risk on elk after wolf reintroduction in Yellowstone National Park, USA

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Abstract While patterns from trophic cascade studies have largely focused on density-mediated effects of predators on prey, there is increasing recognition that behaviorally mediated indirect effects of predators on prey can, at least in part, explain trophic cascade patterns. To determine if a relationship exists between predation risk perceived by elk (*Cervus elaphus*) while browsing and elk position within the landscape, we observed a total of 56 female elk during two summers and 29 female elk during one winter. At a fine spatial (0–187 m) and temporal scale (145–300 s), results from our model selection indicated summer vigilance levels were greater for females with calves than for females without calves, with vigilance levels greater for all females at closer escape-impediment distances. Winter results also suggested greater female vigilance levels at closer escape-impediment distances, but further indicated an increase in vigilance levels with closer conifer-edge distances. Placed within the context of other studies, the results were consistent with a behaviorally mediated trophic cascade and provide a potential mechanism to explain the variability in observed woody plant release from browsing in Yellowstone National Park, Wyoming, USA.

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Introduction

An animal's landscape can be described by surrounding vegetation, topography, and climate. Another lens through which an animal's landscape can be viewed and defined is by varying levels of predation risk, also known as the "landscape of fear" (Laundré et al. 2001). Peaks and valleys in a landscape of fear can be related to relatively greater and lesser risks from predation. Such a landscape can be explicitly measured and defined through an animal's behavior, and also by the animal's location within the landscape at any given moment. Consequences of anti-predator behavior will also partially dictate the duration, frequency, and location of food acquisition. Therefore, outcomes of behavioral decisions related to predation risk could in part influence present and future prey fitness, as well as modify plant communities (Brown et al. 1999; Schmitz et al. 2004; Ray et al. 2005).

According to foraging theory, prey should balance resource acquisition (food, shelter, and mates) and safety, demands that can conflict with one another (Sih 1980; Lima and Dill 1990; Brown et al. 1999). Whether prey decide to seek food in a risky patch over a safe patch depends on many factors including: the physical state of the forager (starving or satiated); the potential energy gain from the food source; direct and indirect indicators of predation risk such as frequency with which prey encounters a predator; time since last predator encounter; and forager and predator species size (Berger and Cunningham 1988; Brown 1999).

Prey have various methods of decreasing their individual predation risk. Although not always observed (Laundré et al. 2001), an anti-predator strategy often described in ungulate literature relates to group size. While predator detectability of prey might increase with prey herd size (Hebblewhite and Pletscher 2002), several anti-predator advantages of larger group sizes potentially exist including the decreasing probability that any single individual will be killed (dilution effect), and the possibility of more "eyes" to scan the environment for predators (many eyes effect) (Dehn 1990; Geist 2002). Hence, the amount of scanning done by a given individual could decrease with increasing group size. With decreased scanning time, the amount of time spent on other activities, such as foraging, can increase for an individual.

While behavioral predator–prey studies involving large predators are limited in Yellowstone National Park (YNP), Wyoming, USA, the reintroduction of gray wolves (*Canis lupus*) into the park in the winters of 1995 and 1996 offered researchers an opportunity to study behavioral changes in this species' primary prey: elk (*Cervus elaphus*). When an ungulate is killed by a wolf, studies have observed the occurrence of kills to be greater in certain landscape locations than others. In YNP, Bergman et al. (2006) found greater elk vulnerability to wolf predation when elk were closer to edges, defined as changes to the forest structure that could impede animal movement, suggesting speed, maneuverability, and escape potential decreased around these structural elements of the landscape. Gula (2004) in Poland and Kunkel and Pletscher (2001) in Glacier National Park, Montana, USA, observed greater wolf kill success near riparian areas and in ravines, with the latter study further detecting greater wolf kill success near ice. Geist (2002) noted running elk tended to avoid impediments, such as slash, deep snow, and swampy grounds.

Vigilance represents a frequent behavioral measure of elk response to predation risk (Hunter and Skinner 1998), a behavior described by an alert posture where the animal is erect with its head above shoulder height (Geist 2002). To date, research on elk within YNP has documented increased average female elk vigilance levels following wolf reintroduction, greater female elk vigilance levels in high wolf-encounter regions, and lower female elk vigilance in low wolf-encounter regions (Laundré et al. 2001; Childress and Lung 2003). Other post-wolf reintroduction studies have observed seasonal changes in habitat preference by elk (Mao et al. 2005) and changes in habitat preference by elk dependent upon wolf presence or absence (Wolff and Van Horn 2003; Creel et al. 2005; Fortin et al. 2005; Gude et al. 2006). Concurrently, plant research in YNP has tested the theory of trophic cascades, defined as the indirect effects of carnivores on plants. Correlative evidence has documented decreases in aspen (*Populus tremuloides*), cottonwood (*Populus* spp.), and willow (*Salix* spp.) regeneration following wolf extirpation in 1926 (Larsen and Ripple 2003; Ripple and Beschta 2004; Beschta 2005), and a patchy release of these three species following wolf reintroduction (Beyer 2006; Ripple and Beschta 2006, 2007), in some areas of the park.

Collectively, recent research in YNP broadly indicates that: (1) elk vigilance behavior and movement patterns have changed since wolf reintroduction; and (2) certain woody browse species preferred by elk are beginning to release in some locations within elk winter ranges throughout the park for the first time in several decades. The overall research goal is to improve our understanding of elk vigilance behavior and fine scale foraging patterns as they relate to ongoing patterns of woody plant release. The specific question we addressed was: does elk vigilance while foraging vary across the landscape?

Materials and methods

Field methods

We observed elk vigilance in YNP through binoculars (8 mm × 23 mm) from roads in the park. We studied summering female elk observed along the paved road corridor between West Yellowstone and Madison Junction, and from Madison Junction to Mammoth Hot Springs, and wintering female elk observed along the road corridor from Tower Junction to Buffalo Ranch in the Lamar Valley. Elk vigilance was defined as the proportion of time an elk had its head above shoulder height as compared to browsing and grooming. Because not all elk were observed for the same length of time, we calculated the ratio of the amount of time an elk was vigilant to the total observation time thereby standardizing all observations for comparative purposes. We observed female elk from 1 August to 10 August 2005, and from 7 June to 15 June 2006, between 0530 and 2100 hours. Winter elk observations were made between 15 November and 26 November 2005 from 0900 to 1630 hours.

Once we located an elk herd, a focal female elk was haphazardly chosen based on herd position and if she was in a bout of feeding (Childress and Lung 2003). We defined an elk herd as a collection of elk whose members were within 100 m of each other and separated by at least 100 m from neighboring elk (Childress and Lung 2003). We defined a feeding bout as an active feeding period for an individual and only female elk in the midst of a feeding bout were selected for observation.

To reduce the likelihood of observing the same individual more than once, we only observed one to three focal individuals in each herd, and only revisited herds at a particular location if they contained more than ten individuals (Childress and Lung 2003). Like Fortin et al. (2004), each focal observation ended after 5 min or if the animal lay down. Because we were interested in the distance between the observed animal and fine-scale features in the landscape, observations also ceased if the animal moved more than six steps. For summer observations, the female social status of each focal elk was further noted as either females with calves or females without calves. Because 2006 summer observations were conducted during the birthing season when newborn calves are often hiding, some mothers were likely misclassified as females without calves. Due to large winter herd sizes, we were unable to measure female social status during winter observations. For all herds, we recorded the group size, or total number of animals in a herd. All observations were recorded using a tape recorder and later transcribed.

Any observation <120 s long was discarded. We also discarded observations if the behavior was compromised due to road noise, the presence of the observer, or the presence of other park visitors. All elk had to be >75 m from the primary road (mean summer road distance ± SE = 216 ± 23 m, mean winter road distance ± SE = 535 ± 58 m). To lessen the impact an observer might have on elk behavior, we initiated observations only after the observer was situated in a vehicle for 5 min.

We recorded the position of each observation point with a global positioning system receiver, noting the distance and azimuth from the observation point to the focal elk with a laser range finder and compass. Once the herd was no longer present, we moved to the location of the focal elk based on azimuth and distance from observation point and recorded fine-scale spatial information in each of four 90° quadrants defined by the cardinal directions. We noted escape impediment type (downed woody debris >15 cm in diameter at breast height, $\geq$0.5 m in height above the ground, and >3 m in length; boulders >1 m in height, width, and length; scree), distance to each escape impediment, distance to conifer edge, and distance to primary road. All distance measurements were made with a laser range finder that had a maximum search radius of 999 m. For escape impediments, we measured the distance to the nearest four impediments within each quadrant that were also within the search radius of the laser range finder. We also recorded visibility within a quadrant, defining visibility as the distance to an object or landform that blocked more than 1/4 of the potential view within the quadrant. Visibility evaluation was based on the assumption that an elk is approximately 2 m tall.

Data analyses

Because both the response variable (elk vigilance) and the majority of measured landscape variables were continuous, we developed multiple regression models and conducted model selection using Aikaike's information criteria (AIC$_c$) (Burnham and Anderson 2002). We used AIC$_c$ to account for potential bias when the sample size is small relative to the number of parameters in the candidate models (Burnham and Anderson 2002).

We generated a set of a priori hypotheses to guide the development of biologically reasonable one-, two- and three-factor regression models explaining elk vigilance. We hypothesized vigilance to be inversely related to visibility distances (Visibility), structural-impediment distances (Impediment), conifer-edge distances (Conifer Edge), and group size (Group Size). We also hypothesized that vigilance would increase with impediment number, and that females with calves would be more vigilant than females without calves (Social Status). As elk vigilance is a proportion between 0 and 1, we applied a logit transformation [$\log(Y/1 - Y)$] to our response variable (Ramsey and Schafer 2002). We found high correlations ($r > 0.90$) between the distance to the nearest escape impediment and average distance to the nearest two and three escape impediments. Because explanatory variables with correlations >0.90 can inflate the amount of variation explained if placed in the same model (Burnham and Anderson 2002), we included only the distance to the nearest escape impediment, rather than the average distance to the nearest two and three escape impediments, as an explanatory variable in all further analyses.

All candidate models were created from some combination of the explanatory variables (Table 1). To better meet the assumptions of regression, we log-transformed Visibility, Impediment, and Conifer Edge (Ramsey and Schafer 2002). As we collected data over two summers, the summer analysis was blocked by year. Winter data were analyzed separately from summer data because observations were conducted in different portions of the park and factors associated with elk behavior could differ seasonally. Seven winter observations were beyond the search radius of our laser range finder for impediment distance and were therefore discarded from the AIC$_c$ analysis although we were able to include those observations in our post hoc analyses (see below for details).

We ran the AIC$_c$ analyses using the PROC MIXED function with maximum likelihood estimation methods in SAS version 9.1 (SAS Institute, Cary, N.C.), ranking the 21 summer and 13 winter candidate models from lowest to highest AIC$_c$ values. The difference in AIC$_c$ values between the model with the lowest AIC$_c$ value and each successive model, known as Δ_i, was used to help determine the best set of candidate models. Δ_i values between 0 and 2 indicate strong support for the model being the best approximate model, Δ_i between 4 and 7 indicate moderate support for the model being the best approximate model, and $\Delta_i > 10$ indicate weak support for that particular model (Burnham and Anderson 2002). We also generated Akaike's weights to further help determine the strength of evidence for each

Table 1 List of summer candidate models[a]

Null model
Intercept only
Vigilance models
One-factor models
Visibility
Social Status
Impediment
Group Size
Conifer Edge
Two-factor models
Visibility + Social Status
Visibility + Impediment
Visibility + Group Size
Visibility + Conifer Edge
Social Status + Impediment
Social Status + Group Size
Social Status + Conifer Edge
Impediment + Group Size
Impediment + Conifer Edge
Group Size + Conifer Edge
Three factor models
Visibility × Social Status + Visibility + Social Status
Visibility × Impediment + Visibility + Impediment
Social Status × Impediment + Social Status + Impediment
Social Status × Conifer Edge + Social Status + Conifer Edge
Impediment × Conifer Edge + Impediment + Conifer Edge

[a] Winter candidate models are identical to summer models except Social Status is not included in the winter analysis

model, given a specific set of candidate models (Burnham and Anderson 2002). Akaike's weights are normalized to be a set of positive weights that sum to 1. We examined negative 2 log-likelihood values (k) when choosing the set of best models. Negative 2 log-likelihood values reflect the overall fit of each model, where smaller values indicate a better fit. Evidence ratios based on Akaike weights were calculated to assess the likelihood of different models relative to the top a priori models. We also applied Welch's two-sample t-tests with unequal variances to determine if differences at the 0.05 level were present in our explanatory variables by social status, year, or season.

Previous research on willow recruitment and elk browsing (Ripple and Beschta 2006) noted less browsing on willow ≤30 m from escape impediments. As post hoc analyses, we therefore examined the relationships between vigilance levels ≤30 m to the nearest escape impediment to vigilance levels beyond 30 m from the nearest impediment using Welch's two-sample t-tests with unequal variances. All analyses were conducted with logit-transformed vigilance and log-transformed impediment distances to better meet the assumptions of t-tests. Although seven winter observations were discarded from the AIC_c analysis (the closest impediment was beyond the 999 m maximum distance of our laser range finder), those seven observations were included in our post hoc analyses because all seven observations were >30 m from the nearest impediment.

Results

Summer elk vigilance

We collected a total of 56 summer elk observations ($n = 26$ in summer 2005, and 30 in summer 2006). On average, elk were observed for 260 s (SE ± 8). Results from Welch's two-sample t-test revealed no differences (P-value ≥0.1) in observation length, Impediment, Conifer Edge, and Group Size between years or by Social Status. We therefore pooled the summer landscape explanatory variables from both years by social status (Table 2) to examine general observation trends. Female elk with calves spent an average ± SE of 22 ± 5% of their time being vigilant, while females without calves spent an average of 9 ± 2% of their time being vigilant.

Evidence from the AIC_c analysis strongly suggested Impediment was the most important variable measured in explaining summer elk vigilance (Table 3). When ranked by AIC_c score from lowest to highest value, all models with this explanatory variable were selected before any other model. Its importance was further supported by an examination of Akaike weights (Table 3). The combined Akaike weight, or importance value, of all models with the variable Impediment was 0.99 out of a possible total weight of 1.00, indicating 99% of the weight in favor of any of the 21 candidate models was for the six models containing this

Table 2 Summary statistics of explanatory variables (mean ± SE; and range) included in the Aikaike's information criteria (AIC_c) analyses

Observations	n	Impediment (m)	Visibility (m)	Conifer edge (m)	Group size
Summer					
Female with calf	17	32 ± 6; 0.5–79	74 ± 13; 8–187	116 ± 20; 17–260	9 ± 1.5; 1–23
Female without calf	39	45 ± 6; 0.5–169	96 ± 6; 11–182	157 ± 19; 40–763	9 ± 1.0; 1–22
All females	56	41 ± 5; 0.5–169	90 ± 6; 8–187	144 ± 14; 17–763	9 ± 0.8; 1–23
Winter					
All females	22	29 ± 6; 0.5–104	30 ± 8; 12–119	250 ± 50; 6–850	30 ± 3.0; 9–59

Table 3 Results of AIC_c analysis for models explaining summer female elk vigilance. The number of parameters estimated in the model (k), the negative 2 log-likelihood ($-2LogL$), the AIC_c, the difference in AIC_c values between any given model and the model with the lowest AIC_c (Δ_i), the Akaike's weight (ω_i), and evidence ratio are listed for each candidate model

Model	k	-2LogL	AIC_c	Δ_i	ω_i	Evidence ratio
Impediment + social status	4	176.6	187.9	0.00	0.63	–
Impediment × social status + impediment + Social status	5	176.6	190.4	2.51	0.18	3.5
Impediment	3	183.9	192.7	4.81	0.06	10.5
Impediment + group size	4	181.5	192.7	4.82	0.06	10.5
Impediment + conifer edge	4	182.3	193.5	5.68	0.04	15.8
Impediment + visibility	4	183.8	195.0	7.16	0.02	31.5
Impediment × conifer edge + impediment + conifer edge	5	182.2	195.9	8.08	0.01	63.0
Impediment × visibility + impediment + visibility	5	183.8	197.5	9.67	0.00	–
Visibility + social status	4	196.2	205.0	17.15	0.00	–
Social status + group size	4	196.3	205.1	17.22	0.00	–
Social status	4	200.8	207.2	19.36	0.00	-
Social status × visibility + social status + visibility	5	196.2	207.4	19.53	0.00	–
Social status + conifer edge	4	200.7	209.5	21.62	0.00	–
Social status × conifer edge + social status + conifer edge	5	200.6	211.8	23.92	0.00	–
Visibility	3	203.0	211.8	23.98	0.00	–
Visibility + group size	4	200.7	212.0	24.10	0.00	–
Visibility + conifer edge	4	201.2	212.5	24.59	0.00	–
Group size	3	206.9	215.7	27.84	0.00	–
Group size + conifer edge	4	206.0	217.2	29.35	0.00	–
Null model	2	212.0	218.5	30.60	0.00	–
Conifer edge	3	210.6	219.4	31.52	0.00	–

variable. In addition, results from our analysis suggested that of the other explanatory variables measured, Social Status helped explain additional variation in vigilance (importance value = 0.81). The top two candidate models included both the additive and interaction model with Impediment and Social Status. Models including Group Size, Visibility, and Conifer Edge had relatively low ΔAIC_c, Akaike weight, and importance values. The non-hypothesized variable Road Distance had no relationship with summer vigilance levels ($F_{1,53} = 0.00$, $R^2 = 0.00$)

We created a graph of predicted elk vigilance using parameter estimates from the additive model: Impediment + Social Status (Fig. 1). Predicted vigilance levels for females with calves were greater than predicted vigilance levels for females without calves (Fig. 1). Predicted vigilance decreased with log-transformed escape-impediment distance regardless of social status. The relationship between predicted vigilance and Impediment was not linear with predicted vigilance levels initially decreasing rapidly with increasing escape-impediment distances before flattening. Because approximately 95% of our impediments were of the same type (down wood), we were unable to investigate any variation in vigilance levels by impediment type.

Winter elk vigilance

We observed 22 elk during the 2005 winter (Table 2). Mean ± SE winter observation length was 284 ± 7 s. On average, female wintering elk spent 10 ± 3% of their time being vigilant. Results from our comparison between combined summer explanatory variables to winter explanatory variables indicated wintering female elk were not further from impediments ($t_{56,22} = 1.13$, P-value = 0.26) or conifer edges ($t_{56,22} = -0.52$, $P = 0.61$), but had larger group sizes ($t_{56,22} = -6.67$, $P < 0.001$) (Table 2). The non-hypothesized variable Distance to Road had no relationship with winter vigilance levels ($F_{1,17} = 0.04$, $R^2 = 0.00$)

Although the top candidate models were within four ΔAIC_c units of the null model (Table 4), the Akaike weight of the null was small relative to the top three candidate models. The model with the greatest Akaike weight, Impediment + Conifer Edge, was slightly stronger than either explanatory variable by itself. The pattern of the results support that both Impediment (importance value = 0.61) and Conifer Edge (importance value = 0.59) likely influence winter vigilance behavior, but that our overall power was slightly low. Group

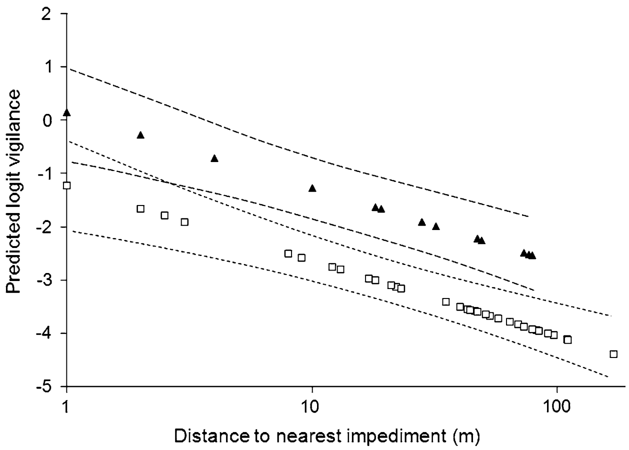

Fig. 1 Predicted summer elk vigilance for females with (*dark filled triangle*) and without (*open square*) calves based on the best approximate model of summer elk vigilance without an interaction, 1.51 (0.68) − 1.38 × Social Status (0.36) − 0.62 × log impediment (0.11), SE *in parentheses*. Logit vigilance is calculated as log[Y/1 − Y] where Y is the proportion of time an elk is vigilant. 95% confidence interval for Social Status is −2.09, −0.66. The back-transformed confidence interval for log distance to nearest impediment is 0.43, 0.38. *Dashed lines* represent 95% confidence bounds. A graph of the interaction between Impediment and Social Status was similar in appearance and interpretation. Note the use of log scale for distance to nearest impediment

Size (importance value = 0.18) was only selected first in models that also contained Impediment or Conifer Edge.

Impediments and predation risk—post hoc analyses

Summering female elk were more vigilant when $\leq$30 m from the nearest escape impediment (P-value $\leq$0.02) (Fig. 2a). However, we found no difference in vigilance levels between summer and winter female elk $\leq$30 m ($t_{27,14} = 0.09$, P-value = 0.93) or for summer and winter female elk >30 m from the nearest structural impediment to escape ($t_{29,8} = -0.52$, P-value = 0.61, Fig. 2b). We then compared vigilance levels between all female elk without consideration of season (Fig. 2c). Regardless of social status and season, female elk were more vigilant $\leq$30 m from the nearest impediment than they were beyond 30 m from it ($t_{41,37} = 4.40$, P-value <0.001) (Fig. 2c).

Discussion

We found that structural escape impediments in the landscape influence summering female elk vigilance at a very fine spatial (1–187 m) and temporal scale (145–300 s). It is therefore possible that measured escape impediments might be fine-scale analogs of broader-scale hard edges such as ravines, riparian areas, ice, and burned forest edges, where greater numbers of wolf-killed ungulates have been found (Bergman et al. 2006; Gula 2004; Kunkel and Pletscher 2001) and where elk maneuverability could be hampered.

Like other vigilance studies conducted in YNP (Laundré et al. 2001; Childress and Lung 2003; Wolff and Van Horn 2003), we also observed greater vigilance by females with calves as compared to females without calves. In fact, our vigilance levels by social status were very similar to those reported by Childress and Lung (2003). While excluded from all analyses, on several occasions ($n = 4$), we opportunistically observed constant vigilance by a mother when a calf was actively suckling. Such observations, along with our observed greater vigilance by females with calves, are consistent with predation risk theory. From a risk perspective, since females with calves must not only assess their

Table 4 Results of AIC$_c$ analysis for models explaining winter female elk vigilance. k, −2LogL, the AIC$_c$, Δ_i, ω_i, and evidence ratio are listed for each candidate model; for abbreviations, see Tables 2 and 3

Model	k	−2LogL	AIC$_c$	Δ_i	ω_i	Evidence ratio
Impediment + conifer edge	4	65.9	76.2	0.00	0.24	–
Conifer edge	3	69.3	76.6	0.41	0.20	1.2
Impediment	3	69.7	77.0	0.78	0.16	1.5
Impediment + group size	4	67.9	78.2	2.00	0.09	2.7
Conifer edge + group size	4	68.7	79.0	2.82	0.06	4.0
Impediment + visibility	4	69.0	79.3	3.10	0.05	4.8
Null model	2	74.9	79.5	3.27	0.05	4.8
Impediment × conifer edge + impediment + conifer edge	5	65.8	79.6	3.34	0.05	4.8
Conifer edge + visibility	4	69.3	79.6	3.40	0.04	6.0
Group size	3	73.9	81.2	4.99	0.02	12.0
Visibility	3	74.6	82.0	5.73	0.01	24.0
Impediment × visibility + Impediment + visibility	5	69.0	82.7	6.50	0.01	24.0
Visibility + group size	4	73.0	83.3	7.31	0.001	24.0

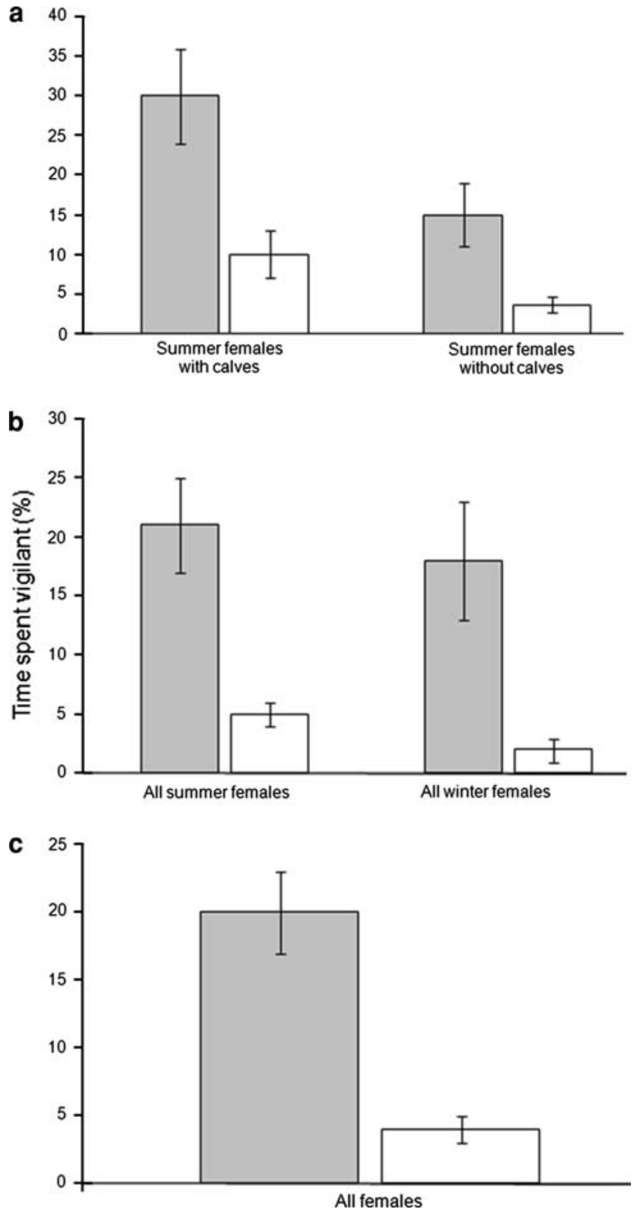

Fig. 2 Variations in the percent of time female elk were vigilant (mean ± SE) within (*gray bars*) and beyond (*white bars*) 30 m from the nearest impediment to escape for **a** summer females with and without calves, **b** all summer vs. winter females and **c** all females. Significance was determined from Welch's two-sample *t*-tests with unequal variances on the logit-vigilance data. Social status data (with/without calves) were unavailable for winter elk

surroundings for themselves, but also for their calves, we would anticipate greater vigilance from mothers. In addition, it is likely a suckling calf underneath the mother increases calf exposure to predators while also causing the mother to be less able to maneuver if surprised by a predator.

Both this study, as well as Laundré et al. (2001), Wolff and Van Horn (2003), and Childress and Lung (2003) found no relationship between group size and vigilance levels for individual females with calves. These mothers may need to be highly vigilant for their neonates, as well as for themselves, resulting in increased vigilance levels irrespective of group size. Of the same studies, only Childress and Lung (2003) documented a decrease in vigilance levels with group size for females without calves.

Consistent with the summer data, distance to nearest impediment helped explain winter female elk vigilance (Table 4). Thus, results from different YNP locations, seasons, and herds suggest a similar mechanism, distance to impediments, influencing elk vigilance. Unlike the summer models, Conifer Edge was also associated with female winter elk vigilance. The data indicated an increase in vigilance levels with closer conifer-edge distances. Greater elk vigilance near conifer edges is consistent with Mao et al. (2005), who found elk winter range use shifted to more open habitat following wolf reintroduction. In a winter study, Bergman et al. (2006) found wolves preferred to move along hard edges, with elk vulnerability to wolf predation greatest along meadow/conifer and riparian hard edges. Frair et al. (2005) found elk in Canada were more likely to relocate when within 50 m of human-created linear clearings; they suggested that elk predation risk was greater near linear features due to either wolf travel preferences or to the association of the clearings with people.

Creel et al. (2005) and Fortin et al. (2005) observed a shift to conifer forest by elk in the presence of wolves. Such findings do no necessarily contradict our results of greater vigilance near conifer edges. Because conifer forests can afford elk protection from some predators while open areas will typically contain more biomass available for consumption (Anderson et al. 2005), the transition zone between ecotypes and the associated wolf movement along hard edges could cause elk to temporarily be more vulnerable to predation and therefore be more vigilant. Levels of vigilance near conifer edges also could vary depending on the structural complexity of the forest, wolf presence, and/or current anti-predator strategy employed by elk.

Because models with the variable Impediment were top candidate models for both summer and winter observations, we further investigated the relationship between vigilance levels and Impediment. We found female elk tended to be more vigilant within 30 m of an impediment despite the differences in location, group size, and potential predation risk between winter and summer data. As suggested by the AIC_c results and post hoc analyses, distance to impediments appears to be biologically important with respect to vigilance and thus to elk predation risk. While elk were responding to impediment distance, due to the high correlation between the variable Impediment and the average distance to the nearest two and three impediments, it is possible elk were responding to a cluster of structural features rather than just to the distance of the nearest single impediment. As noted previously, Ripple and Beschta

(2006) found locations of tall willow growth in northern YNP tended to be ≤30 m from the nearest impediment and tall willows had lower browsing intensities relative to shorter willows. Taken together, their observation of greatest willow heights ≤30 m from an impediment and our study of greatest female vigilance levels ≤30 m from the nearest escape impediment suggest the observed patchy distribution of woody plant release in YNP may be at least partially due to differences in elk browsing behavior mediated by predation risk.

Although our vigilance responses were similar to those reported in other wolf–elk behavior studies in YNP, knowledge of additive or compensatory vigilance behavior by elk in the presence of sympatric predators in this area, such as grizzly bear (*Ursus arctos*), cougars (*Felis concolor*), and coyotes (*Canis latrans*) that feed on calves during the spring and summer (Houston 1978; Gese and Grothe 1995; Mattson 1997), is limited. We were therefore unable to quantify any effects that specific predators may have had on vigilance levels observed in this study. Our study was limited by the type of impediment information we collected. Future studies should consider including additional information on specific impediment length, width, and height. Further relationships might also be elucidated if data are collected on the proportion of surrounding space containing impediments.

Conclusion

In addition to any density-mediated effect, the evidence we present here is consistent with a fine-scale behaviorally mediated trophic cascade between carnivore predators, elk, and woody browse species. Predation risk has also been observed over broad scales whereby elk select habitat based on the frequency of wolf–ungulate encounter and distance to safe habitat in YNP. We propose predation risk be considered as an additional factor by which plant communities are structured across multiple spatio-temporal scales in this landscape of fear.

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