Elk decision-making rules are simplified in the presence of wolves

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Abstract The risk of predation drives many behavioral responses in prey. However, few studies have directly tested whether predation risk alters the way other variables influence prey behavior. Here we use information theory (Akaike's Information Criterion, AICc) in a novel way to test the hypothesis that the decision-making rules governing elk behavior are simplified by the presence of wolves. With elk habitat use as the dependent variable, we test whether the number of independent variables (i.e., the size of the models) that best predict this behavior differ when wolves are present vs absent. Thus, we use AICc scores simply to determine the number of variables to which elk respond when making decisions. We measured habitat use using 2,288 locations from GPS collars on 14 elk, over two winters (14 elk winters), in the Gallatin Canyon portion of the Greater Yellowstone Ecosystem. We found that the use of three major habitat components (grass, conifer, sage) was sensitive to many variables on days that wolves were locally absent, with the best models (ΔAICc≤2) averaging 7.4 parameters. In contrast, habitat use was sensitive to few variables on days when wolves were present: the best models averaged only 2.5 parameters. Because fewer variables affect elk behavior in the presence of wolves, we conclude that elk use simpler decision-making rules in the presence of wolves. This simplification of decision-making rules implies that predation risk imposes selection pressures that do not allow prey to respond to other pressures in ways that they otherwise would. If the affected processes are important, then this indirect effect of predation is likely to be important.

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Introduction

When faced with the threat of predation, most animals engage in behaviors that reduce risk, and selection should favor individuals who best balance the benefits of risk reduction against its costs (Lima and Dill 1990; Illius and Fitzgibbon 1994). Responses to predation risk include increased vigilance (Elgar 1989; Lima and Dill 1990), reduced foraging time (Hughes and Ward 1993; Abramsky et al. 2002), reduced movement (Sih and McCarthy 2002), reduced use of conspicuous behavioral displays (Sih et al. 1990), changes in group size (Lima and Dill 1990; Creel and Winnie 2005), and habitat shifts (e.g., retreat to low risk areas or refuges: Bergerud et al. 1983; Formanowicz and Bobka 1988; Blumstein and Daniel 2002; Heithaus and Dill 2002).

The above studies address direct behavioral responses to the threat of predation. However, prey must do more than simply manage predation risk to survive (Lima and Dill 1990), and shifting habitats in response to predators will interact with other important demands. Regardless of the presence of predators, most prey species must move about the environment frequently and forage to meet their daily

needs, and variables unrelated to risk should also affect foraging behavior and movements.

There is an emerging literature on decision-making that addresses the use of simple heuristics or rules-of-thumb vs complex optimization algorithms (Hutchinson and Gigerenzer 2005; Kemp 2005). This literature suggests that simple rules (algorithms based on little information) produce good, broadly applicable solutions. However, complex optimization strategies (based on more information) produce better solutions to specific problems. In this paper, we use data on habitat use by elk to test whether predation risk affects the complexity of decision-making rules.

When prey are free of predation risk, their foraging decisions might be optimized by using a wide range of information and responding to many variables. Conversely, when facing elevated risk, prey may be forced to forego complex decision-making strategies and resort to simpler algorithms or rules-of-thumb (Kemp 2005). Prey decision-making rules may further be simplified if preferred foraging environments are not the same as escape terrain. When predators are absent, foraging prey may accumulate relatively little information about escape terrain. If this is the case, prey engaging in a spatial shift to escape terrain in response to elevated risk may not have the information necessary to optimize their behavior in a habitat-specific manner, forcing the use of simpler algorithms when making foraging and movement decisions.

In the winter, elk in the Upper Gallatin River drainage respond to short-term changes in the threat of wolf predation at multiple scales: individual, herd, and landscape. When wolves are present in a drainage, some individuals (females) increase vigilance at the expense of foraging (Winnie and Creel 2006), mean herd size decreases and herd composition changes (Creel and Winnie 2005), and elk leave open grassy areas and move into the protective cover of timbered areas (Creel et al. 2005). These responses appear to be limited by body condition, indicating that antipredator behaviors carry foraging costs (Winnie and Creel 2006).

Regardless of the presence of wolves, elk move about the landscape to forage, and we would expect that foraging and movement are affected by variables other than risk. Net energy and protein content differ between woody browse and grasses (Christianson and Creel 2006), and both the availability of plants and foraging costs are affected by interactions between growth form and snow conditions (Jenkins and Wright 1987). Thus, we might expect elk behavior to be affected by differences in snow depth and snow density across local landscapes (Sweeney and Sweeney 1984). Elk of both sexes face a negative energy budget in winter, but males appear to face stronger energetic constraints because they enter winter with depleted energy stores after the fall rut (Geist 2002; Winnie

and Creel 2006). Consequently, we might expect gender to play a role in behavior. Winter weather in the Northern Rockies can be extreme even for cold-adapted species, so we might expect rules for selection of open and closed habitats to be sensitive to temperature and wind speed (Merrill 1991; Jones et al. 2001).

Differences in elk decision-making rules should be reflected in differences in models that best describe their behavior. Here, we test the hypothesis that the rules by which elk select habitats are simplified by the presence of wolves Specifically, when elk are free of predation risk, models describing behavior should contain more parameters; conversely, when risk is high, models should contain fewer parameters.

Materials and methods

Study area

Our study area is a mosaic of the National Forest, National Park, State, and private land, covering 125.8 km^2 in four drainages along the upper Gallatin River (Porcupine, 30.3 km^2; Taylor, 56.0 km^2; Tepee, 13.1 km^2; Daly, 26.4 km^2). South-facing slopes and valley bottoms are generally a mixture of open sage (*Artemesia* spp.) and grassland (dominated by Idaho fescue and bluebunch wheatgrass: *Festuca idahoensis* and *Agropyron spicatum*) with riparian areas bordering creeks. North-facing slopes and higher elevations are primarily coniferous forest (lodgepole pine and Douglas fir: *Pinus contorta* and *Pseudotsuga menziessii*) broken by occasional small meadows. Elevation runs from 1,975 to 2,432 m above sea level.

We surveyed fixed areas (viewsheds) in each of the four drainages, beginning at first light, every 2 weeks from mid-January, 2002 until the end of May, 2002, and during the same period in 2003, and recorded all wolves, elk and elk carcasses located in these surveys. Survey routes were chosen to maximize the area scanned in each drainage while minimizing disturbance caused by our presence. During a survey, we scanned from fixed highpoints and while walking fixed routes between highpoints. Each drainage was divided into six to eight viewsheds. In addition to this formal sampling regimen, we attempted to visit each drainage on every day of the winter–spring study period, in either the morning or evening, usually traversing part of our fixed sampling routes. These ad lib samples provided additional information on wolf presence (see "Wolves" below).

Elk

The elk in the study area are part of a largely migratory population (averaging 1,725 [se 63] and varying from 1,214

to 3,028 animals annually since 1928) that winters along the upper Gallatin River and its tributaries from the northwest corner of Yellowstone National Park, north to Big Sky, Montana (Brazda 1953; Peek et al. 1967; Peek and Lovaas 1968). Both the migration route and winter range encompass state, private, and federal lands, while the summer range for most of the elk lies within western Yellowstone National Park.

We designed and built data-logging GPS units based on SiRFstar I GPS engines (SiRF Technology, San Jose, CA) and riveted them to the tops of conventional VHF radio collars equipped with timed drop-off mechanisms (Advanced Telemetry Systems, Isanti, MN, USA). We collared seven elk each winter (ten adult females, four adult males) for a total of 14 elk winters. Each collar was set to fix every 2 h, and the mean realized fix rate was 61.7% (mean fix interval of 3.24 h), yielding 18,317 fixes. Of these fixes, 2,288 fell in winter periods in study drainages at times for which we have data on wolf presence or absence. We tested for differences in fix rate between forested and open habitat types and found no significant differences ($F_{(1,2287)}=1.67$, $P=0.196$). Wolf presence or absence in a drainage did not detectably alter the fix rate ($F_{(1,2287)}=0.88$, $P=0.35$).

Wolves

Wolves colonized the upper Gallatin drainage in 1997, and during the course of this study, two packs (12–16 wolves) used the study area each year.

We used a combination of direct observations, conventional VHF collars, snow tracking, and detection of scats and wolf kills to determine wolf presence in each of the study drainages on each day. While walking survey routes or collecting ad lib behavioral observations, we continuously checked for signs of wolves. We considered wolves present within a drainage on a given day if we located them via VHF radiotelemetry, found a fresh kill, fresh scat, or fresh tracks in snow, mud or loose soil. We considered wolves absent from a drainage if we surveyed and detected no sign of wolf presence for that day. For days that a drainage was not surveyed, we excluded the GPS data. If wolves denned in a drainage (near April 15th both years), we scored wolves as present in that drainage on all days during the denning period. Because not all wolves in the study area were radio-collared and we undoubtedly missed some physical evidence of their presence, it is likely that we failed to detect wolves on some days. This failure to detect wolf presence might mask responses by elk to wolves (type II errors), but should not create apparent differences where none exist (type I errors), so tests comparing data from wolf-present and wolf-absent conditions are conservative.

Our work in this study system (Creel and Winnie 2005; Creel et al. 2005; Winnie and Creel 2006) has shown that elk respond to the presence and absence of wolves at the scale of our data and analyses, both temporally (days and hours) and spatially (drainages, broad habitat types measured at 30 m pixels). Of course, elk might respond to wolves at other spatial and temporal scales (see "Discussion").

Habitat composition at elk locations

To assess habitat types at elk GPS locations, we applied logistic regression models for the probability of occurrence of dominant plant species, developed for Yellowstone's Northern Range (Rew et al. 2005, 2006). These regressions were selected using Akaike's Information Criterion (AICc) via single term deletions from a full model including slope, elevation, sine (E/W) and cosine (N/S) of aspect, and seven bands of Landsat 7 ETM reflectance data. Model selection via single term additions yielded the same result in all cases. We validated the regression models using 315 sampling locations stratified by drainage and elevation across the Gallatin study site. To simplify the analysis of habitat selection by elk, we combined probabilities of occurrence for all conifer species (lodgepole pine, limber pine, subalpine fir, Douglas fir, and Englemann spruce) into one habitat component (*conifers*), combined the probabilities of occurrence for the two dominant native grasses (bluebunch wheatgrass and Idaho fescue) into a second component (*grass*), and combined sage species (big sage, *Artemesia tridentata* and silver sage *Artemesia cana*) into a third component (*sage*). Using ArcGIS, each elk location was assigned separate probabilities of conifer, grass, and sage occurrence. The use of only three vegetation types is probably an oversimplification of how elk perceive habitats, but our previous work (Creel et al. 2005; Winnie and Creel 2006) has shown that the probabilities of occurrence of these vegetation types at elk locations respond to wolf presence in this system. To test the hypothesis that the complexity of decision-making rules responds to predation risk, all that is required are dependent variables known to be affected by risk.

Each habitat component is modeled independently of the other two components, so the three probabilities of occurrence need not sum to 1. This is appropriate, because many locations have a high likelihood of more than one habitat component being present. This approach incorporates continuous spatial variation in preferred food (grass), protective cover (conifers), and sage, which is associated with food but also may provide limited cover. Incidental properties of this approach are that the probability of occurrence for each habitat component on any pixel (30×30 m) was never 1 or 0 (the model was never absolutely certain that a habitat component did or did not

occur in a given pixel), and probabilities did not share the same scale from model to model, i.e., relative probabilities of occurrence are consistent across locations within a habitat model, but probabilities of occurrence cannot be directly compared across habitat models. This method of mapping habitat components is more descriptive than simply categorizing habitats into three exclusive types because it is unlikely that elk perceive locations categorically, as one habitat type or another. Locations are mixtures of food and cover that vary along continuous scales, and multiple plant components can and do occur in the same patch (in the case of our models, 30×30-m pixels).

Environmental variables

We recorded temperature and wind speed during every trip to a drainage using Kestrel pocket weather stations. During each biweekly survey trip up a drainage, we gathered data on snow depth and density at three fixed monitoring locations (at low, middle, and high elevations in each drainage). Sites at each elevation consisted of a pair of open and timbered measurement areas within 50 m of each other. We measured snow depth by digging down to dirt and using a retractable tape measure. We measured snow density by dropping a 3-kg steel shot attached to a cord from 30 cm above the snow surface and recording the depth of penetration. We express snow density as depth of penetration from a 30-cm drop divided by total depth, yielding numbers ranging from 0 to 1, with numbers near 1 representing the least dense snow. At times and in places where snow depth was 0, we scored snow density as 1, to reflect the fact that snow did not impair access under this condition. We averaged depths and densities for the three elevations within each drainage to get one mean snow depth in the timber and one in the open and one snow density in the timber and one in the open. We made snow depth and density measurements at 2-week intervals in each drainage and used linear interpolation between measurement days to estimate daily values in each drainage. Because we collected these data across the study site using a design stratified by drainage, elevation, and habitat type, we preferred them to daily data on snow–water equivalent accumulation from regional NRCS SNOTEL sites.

Statistical analysis

To test our hypothesis, we compared the complexity of regression models that best fit data on elk behavior in high and low risk conditions. We did this via model selection using AICc, applied in a novel way. Typically, AICc is used to distinguish among competing hypotheses,

each framed as a model fit by maximum likelihood. Here, we used AICc simply to test whether well-supported regression models included a larger set of independent variables when wolves were absent. That is, we used AICc scores to identify models with good support from the data (within two AICc units of the best model), so that the number of parameters in these models could be compared.

Using the set of models identified by AICc, our intention shifted from identifying strong models to determining whether elk decision-making rules were simplified in the presence of wolves. Overall, the logic of our analysis is as follows. We hypothesized that the presence of wolves (high predation risk) would simplify elk habitat selection rules. The models of habitat use selected when wolves are present identify the number of variables to which elk respond when facing immediate risk. Similarly, the models of habitat use selected when wolves are absent identify the number of variables to which elk respond without the threat of immediate predation risk. We hypothesized that models would be larger (more complex) when elk were not facing immediate predation risk and smaller when wolves were present. We used "best subsets" modeling, allowing elk to tell us how many environmental variables were important to them when making habitat use decisions. Because this approach yields a large model list, we limit all subsequent inferences (including model averaging and calculating relative variable importance) to models within two AIC units of the best model. In the normal context of using AICc to compare a set of models, each of which represents a hypothesis of direct interest, best subsets modeling has been criticized as data dredging (Burnham and Anderson 2002; Stephens et al. 2005). But we use AIC only to determine the complexity of the best models under two conditions. Our hypothesis is simply that the model sets that receive support from the data will differ in the number of parameters they contain; thus, the data-dredging criticism does not apply.

To address how predation risk affected habitat selection rules, we divided the elk GPS locations into two data sets based on differences in short-term predation risk: wolves present vs wolves absent from that drainage on that day. For each of the data sets (wolves present, wolves absent), we used model selection based on information theory (using Akaike's Information Criterion with sample size correction, AICc) to identify the models that best predicted the probabilities of occurrence of grass, sage, and conifer at elk locations. Thus, we compared models of habitat selection for three dependent variables (habitat components), each under two conditions (wolves present = high risk, wolves absent = low risk), for a total of six model selection analyses. We applied a log-odds transformation to the dependent data $log\left(y/(1-y)\right)$ that yielded an approx-

imately normal distribution and specified an identity link to the independent variables.

Independent variables

For each of the six dependent variables, our independent variables were:

– *Previous location*. The attributes of an elk's current location are related to the attributes of its location 2 h earlier; therefore, treating all of the GPS fixes as independent data points would cause pseudo-replication. To avoid this, we used autoregression, including the value of the dependent variable for the previous location in the time series as a predictor. We tested whether the inclusion of more than one time lag improved the model, but AICc scores strongly supported the single-lag model (Creel et al. 2005). This procedure accounts for repeated measures and temporal autocorrelation in the data while retaining all of the GPS fixes for maximum valid power.
– *Sex*. Our previous work revealed behavioral differences between bulls (branch antlered males) and cows (females>1 year old) in their responses to wolves (Winnie and Creel 2006).
– Minimum recorded *temperature* in each drainage for that day.
– Maximum *wind speed* in each drainage on that day.
– *Temperature × wind speed* interaction (minimum × maximum, respectively).
– *Depth* of snow in the *open*.
– *Depth* of snow in *timber*.
– *Density* of snow in the *open*.
– *Density* of snow in *timber*.
– *Day of year*, beginning January 1. This variable incorporates three effects that we did not measure directly. Forage quality declines as winter progresses (Demarchi 1968). Forage quantity also declines because this was a winter study, and there was no plant regrowth after grazing and browsing. Finally, body condition declines due to the interaction of the declining forage quantity and quality with high winter

metabolic demands. Declining body condition through winter has been reported in other ungulate studies, and we have presented evidence for elk in this system (Winnie and Creel 2006). This factor is problematic because it is correlated with temperature and snow depth and thus contributes to overdispersion in models that also contain these variables.

Because regression models (and parameter estimates) can be expected to differ from one data set to another, it is important to keep in mind that these analyses use six discrete data sets (predicting three habitat variables under two levels of risk). Thus, differences in parameter estimates between models should be interpreted cautiously, and we limit our inferences to overall differences between sets of model-averaged parameters.

Results

Model selection revealed marked and consistent differences in the number of parameters that influenced elk behavior when wolves were present vs absent. The probability of occurrence of all three habitat components at elk GPS locations was best predicted by models with many environmental parameters when wolves were absent and fewer parameters when wolves were present. The attributes of elk GPS locations when wolves were present and absent are summarized in Table 1. For conifers, the mean number of parameters with wolves present was 2.2 vs 7.2 when wolves were absent. For sage, the mean number of parameters with wolves present was 2.2 vs 6.7 when wolves were absent. For grass, the mean number of parameters with wolves present was 2.0 vs 8.2 when wolves were absent.

When wolves were absent, several models within two AIC units of the best model included eight or more parameters (overall wolves absent: mean=7.42 parameters in the top models: Fig. 1a–c). For conifers, the global model (ten parameters) was in the set of best models. In particular, parameters describing snow conditions significantly affected the occurrence of all three habitat compo-

Table 1 Habitat attributes of elk GPS locations with wolves present and absent

Log odds[a]	N[b]	Mean	Min.	Max.	SD	CV
Wolves absent						
Conifer	1,604	−2.3137	−4.4192	0.1523	1.0261	44.35055
Grass	1,604	−0.3238	−2.2196	1.5293	0.7439	229.7303
Sage	1,604	−0.4022	−3.2369	2.1450	1.1383	282.9774
Wolves present						
Conifer	684	−1.6923	−4.4988	0.5202	1.1860	70.08538
Grass	684	−0.8218	−2.3234	2.4966	0.7832	95.29943
Sage	684	−1.1548	−3.4624	1.9323	1.2375	107.1621

CV Coefficient of variation
[a] Lower log-odds indicate a lower probability of occurrence of a habitat component.
[b] Autocorrelation in these data are accounted for in the analysis; see "Materials and methods."

nents at elk locations and appeared in most of the top models when wolves were absent (Tables 4 and 5 in Appendix).

When wolves were present, the best models describing elk behavior were much simpler. Most of the top models contained two parameters and none had more than four (wolves present: mean=2.46 parameters). For all three

habitat components, previous location alone was the best model, based on AICc scores (Fig. 1a–c and Tables 4 and 5 in the Appendix). Given this, the worst ΔAICc score that any two-parameter model could attain when wolves were present was two AIC units worse than previous location alone. Consequently, for all of the two parameter models with ΔAICc values near 2, the second parameter has

Fig. 1 Summary of the best models of habitat selection by elk, identified via Akaike's Information Criterion. Each *panel* summarizes the set of best models for a given habitat component, for data with wolves absent (*black bars*) and present (*cross hatched bars*). **a** Conifers, **b** sage, **c** grassland. See Table 3 for details of each model
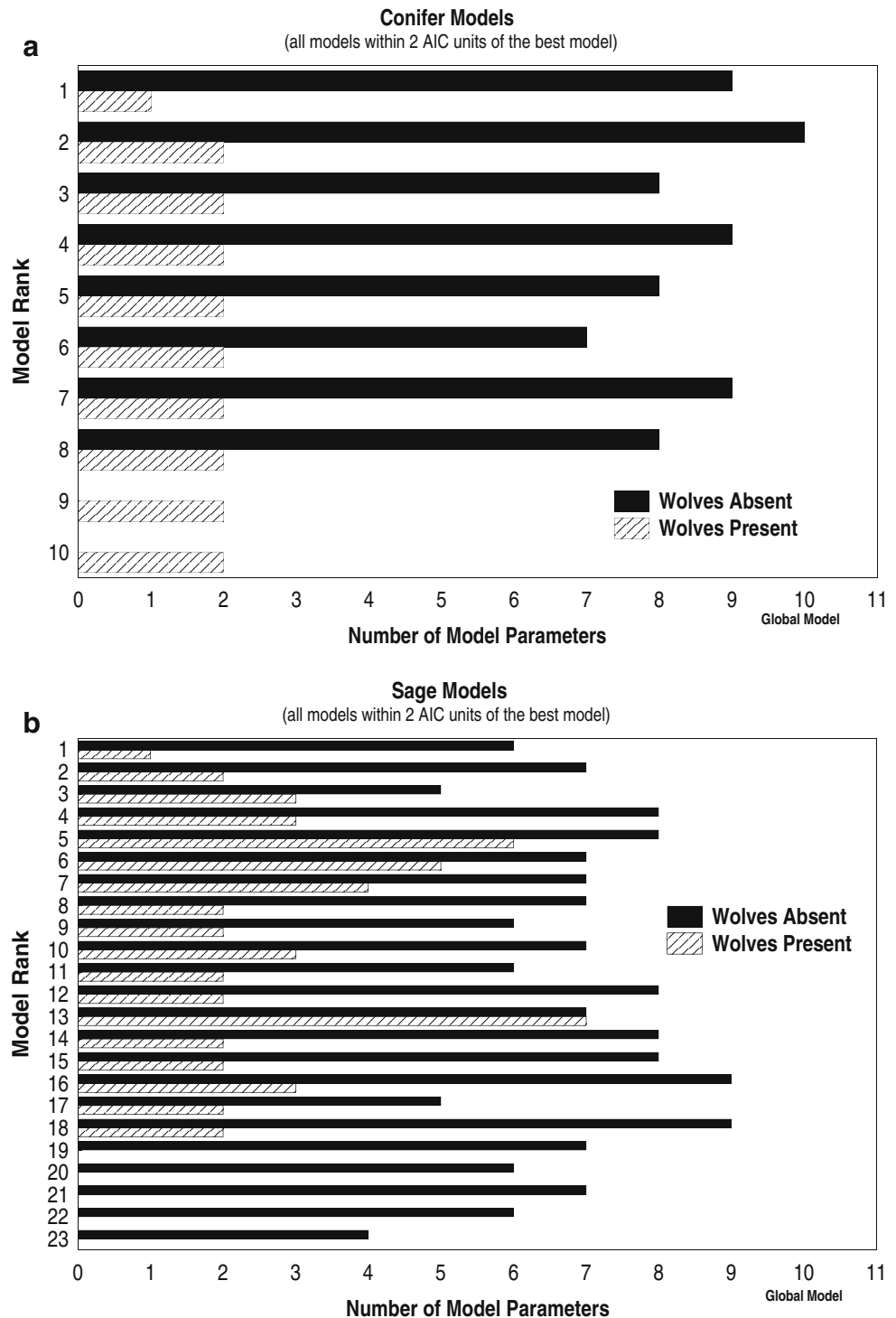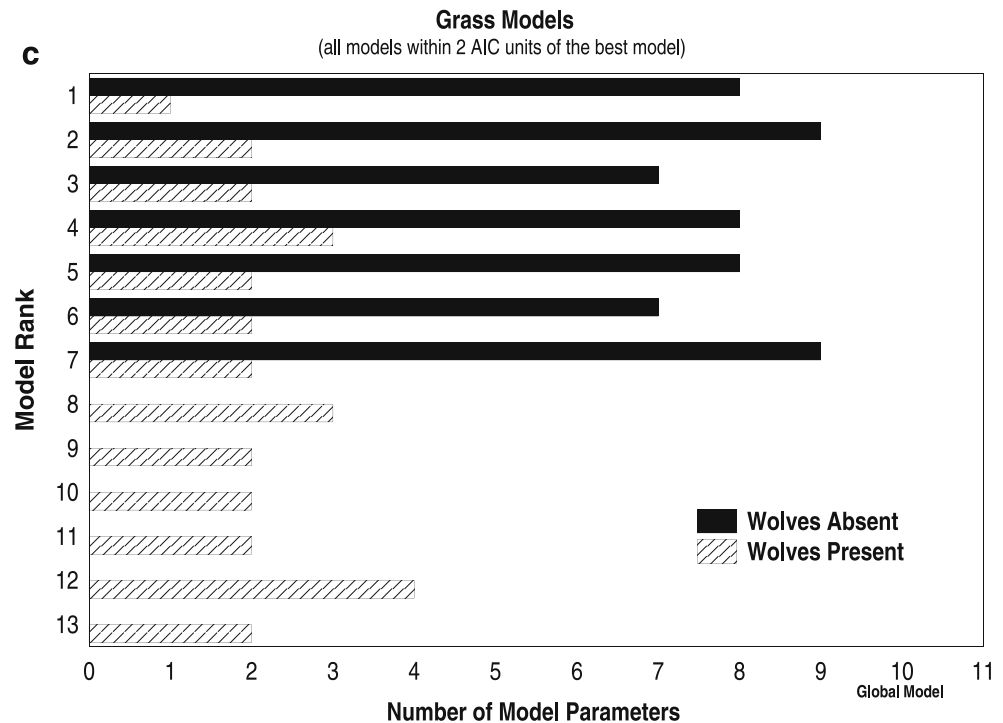
Fig. 1 (continued)

Grass Models
(all models within 2 AIC units of the best model)

Table 2 Coefficients and their standard errors from model averaging using AICc weights (ω_i)

Parameter	Conifer				Grass				Sage			
	Wolves absent (0.96)		Wolves present (1.37)		Wolves absent (0.52)		Wolves present (0.62)		Wolves absent (1.23)		Wolves present (1.5)	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Previous location	**0.2141**	**0.0249**	**0.2496**	**0.0384**	**0.1828**	**0.0249**	0.1183	0.1325	**0.1469**	**0.0252**	**0.2011**	**0.0390**
Sex	−0.1152	0.0418	0.0004	0.0562	0.0597	0.0306	0.0138	0.0376	0.0460	0.0459	−0.0354	0.0593
Day of year	0.0042	0.0025	0.0006	0.0015	**−0.0041**	**0.0019**	−0.0004	0.0010	**−0.0055**	**0.0028**	0.0041	0.0057
Temperature	−0.0080	0.0062	0.0007	0.0078	0.0029	0.0040	−0.0040	0.0056	0.0082	0.0063	−0.0051	0.0099
Wind speed	−0.0115	0.0070	0.0031	0.0123	0.0059	0.0051	0.0069	0.0083	0.0146	0.0078	−0.0002	0.0130
Temp. × wind	**−0.0026**	**0.0011**	0.0011	0.0018	0.0012	0.0007	−0.0015	0.0012	0.0022	0.0012	−0.0010	0.0019
Snow depth open	**0.0115**	**0.0043**	−0.0005	0.0020	**−0.0104**	**0.0030**	0.0594	0.0754	**−0.0099**	**0.0043**	0.0245	0.0168
Snow depth timber	**−0.0119**	**0.0044**	−0.0002	0.0031	**0.0067**	**0.0032**	−0.0034	0.3386	0.0059	0.0048	−0.0371	0.0244
Snow density open	**0.2719**	**0.1105**	−0.2063	0.2260	**−0.2135**	**0.0811**	0.0973	0.1526	−0.1993	0.1230	0.5737	0.3832
Snow density timber	**−0.4052**	**0.1583**	−0.1494	0.3373	**0.2767**	**0.1155**	0.1645	0.2257	0.3029	0.1768	−0.8440	0.7566

Parameter estimates from model averaging (bold indicates 95% CI does not contain 0)
Coefficients reported separately for each habitat component under each predation risk condition. Bold entries indicate parameters that differ from zero at $\alpha=0.05$. Deviance/DF (c) for each global model is reported in parentheses under wolf presence headings.

Table 3 Relative importance values from AICc

Parameter	Conifer		Grass		Sage	
	Wolves absent	Wolves present	Wolves absent	Wolves present	Wolves absent	Wolves present
Previous location	1	1	1	1	1	1
Sex	1	0.0805	0.9007	0.0620	0.2324	0.0433
Day of year	0.6769	0.0806	1	0.0586	0.9004	0.1513
Temperature	0.4270	0.0809	0.2159	0.1316	0.3667	0.1175
Wind speed	0.5808	0.0828	0.2867	0.0817	0.9307	0.0381
Temp. × wind	0.9232	0.0935	0.5998	0.1166	0.7743	0.0819
Snow depth open	1	0.0832	1	0.1935	1	0.3604
Snow depth timber	1	0.0807	1	0.1913	0.2776	0.3676
Snow density open	1	0.1133	1	0.1946	0.5565	0.4243
Snow density timber	1	0.0856	1	0.0671	0.8039	0.3440

Relative importance values are the sum of the scaled Akaike weights for models in which a parameter appears. Low values indicate that the parameter is in fewer models with less support from the data, while high values indicate that the parameter is in more and better supported models.

relatively little effect on habitat use (Tables 2, and 3, and in Tables 4 and 5 within the Appendix). This is reflected in the parameter estimates and their standard errors (Table 2) and in relative importance values (Burnham and Anderson 2002) for each variable (Table 3). No factors other than previous location had significant effects on habitat use at $\alpha=0.05$ (Table 2), and no factors other than previous location had relative importance approaching 1 when wolves were present (Table 3).

Discussion

Differences in the complexity of the models suggest differences in the rules that elk use to make decisions about habitat use. In the absence of wolves, elk respond to many environmental factors, particularly snow conditions, when making habitat use decisions. On days that wolves were absent, the probability of both conifer and grass occurrence at elk locations is sensitive to snow depth and density in both open and forested areas (Tables 2 and 3). Sensitivity to environmental conditions is probably a response to the combination of poor winter food quality and the energetic costs of moving and foraging in snow. Frequent adjustments to movements and foraging locations based on fine temporal and spatial scale information about snow conditions may be necessary to optimize trade-offs between energy expenditure and intake. For elk facing a long-term negative energy budget throughout winter (Cook 2002; Hudson et al. 2002), selection pressures on this optimization are likely to be strong.

On days that wolves were present, the same elk, in the same drainages, showed substantially less complexity in their decisions about habitat use. The lack of sensitivity to snow conditions when wolves are present implies that elk are not attempting to gain tactical antipredator advantages (or reduce tactical disadvantages) by avoiding or favoring areas with particular snow conditions. When combined with our previous research showing that elk retreat to the cover of timbered areas when wolves are present (Creel and Winnie 2005; Winnie and Creel 2006), this result suggests (but does not prove) that elk spatial responses are weighted toward avoiding encounters with wolves, rather than manipulating the outcome of encounters. Alternatively, it is possible that the temporal (biweekly) and spatial (open vs timbered) scales at which we measured snow conditions were only able to detect conditions that mattered to elk when they are not facing immediate predation risk. When wolves are present, elk may be sensitive to snow conditions (and possibly other unmeasured variables) at finer scales than we measured, i.e., fine enough scales to avoid terrain traps created by deep and crusty snow if they are pursued by wolves.

The results of model selection for sage are not as clear as the results for conifers and grass (Fig. 1b). This is not due to sage being uniformly distributed among elk locations, because sage probability of occurrence has a higher coefficient of variation than either grass or conifer (Table 1). At the risk of telling *Just So Stories* (Kipling 1902), we believe this is because sage offers neither preferred foraging habitat when wolves are absent, nor preferred cover when wolves are present. When unhindered by snow and not facing immediate predation risk, elk strongly prefer grazing to browsing (Christianson and Creel 2006), and when faced with elevated predation risk they move to timber (Creel et al. 2005; Winnie and Creel 2006). Anecdotally, from substantial experience walking on this study site, moving through sage is particularly difficult. The complex plant structure collects snow and creates suspended surfaces that collapse

when weighted. When walking surveys, the most difficult stretches to traverse were consistently patches with sage.

For grass and sage, coefficients of variation were smaller in the data with wolves present (Table 1). This creates the possibility that simpler models are supported for data with wolves present simply because there is less variation to be explained. However, the coefficient of variation for conifer probability of occurrence was greater when wolves were present than when they were absent. Despite this, the data with wolves absent supported a set of very complex models, suggesting that the differences in complexity are real.

The overall differences between the wolf-present and wolf-absent models sets indicate that predator avoidance may carry costs beyond forced diet changes due to habitat shifts (Morgantini and Hudson 1985; Christianson and Creel 2006). Because elk are more sensitive to environmental factors when wolves are not present, this implies that there are benefits to environmental sensitivity, such as increased foraging or movement efficiency. Conversely, a lack of response to environmental factors that decreases foraging and movement efficiency could add to, or compound, the negative effects of a diet shift. However, it is possible that environmental sensitivity is only beneficial when elk are free of predation risk, because the dietary shift that accompanies a habitat shift in response to elevated risk might negate the need for environmental sensitivity (to the parameters we measured). For example, moving from the open into timber may reduce the snow's influence on movement efficiency, and the corresponding diet shift from grass to woody browse may reduce the influence of snow pack on foraging efficiency. If this is the case, then diet shifts are likely to be the primary cost of habitat shifts, and the loss of environmental sensitivity in response to wolves would carry little cost.

The higher sensitivity of elk to environmental factors in the absence of wolves may lend some insight into current discussion surrounding trophic cascades in the Greater Yellowstone Ecosystem. Our data on elk locations with "wolves absent" were gathered after wolf reintroduction, so it is reasonable to believe that our analysis underestimates elk sensitivity to environmental conditions before wolf reintroduction (because the risk of wolf predation probably never truly drops to zero as it was before wolf reintroduction). If habitat use and foraging decisions are based on a complex suite of environmental parameters when wolves are absent, then changes in these environmental parameters would result in changes in elk habitat use and foraging patterns. Consequently, it would be prudent to consider patterns of snow depth and density when evaluating the drivers of trophic cascades from wolves to elk to plants.

Appendix

Table 4 Specific parameters in each of the models in Fig. 1, with ΔAICc scores

Wolves present

Rank	1	2	3	4	5	6	7	Delta AIC
Sage								
1	Previous location							0.000
2	Previous location	Snow density open						0.140
3	Previous location	Snow depth open	Snow depth timber					0.332
4	Previous location	Snow density open	Snow density timber					0.732
5	Day of winter	Previous location	Snow depth open	Snow depth timber	Snow density open			0.764
6	Previous location	Snow depth timber	Snow depth open	Snow depth timber	Snow density open	Snow density timber	Snow density timber	0.943
7	Previous location	Snow depth open	Snow depth open	Snow density timber	Snow density timber			1.185
8	Previous location	Snow depth timber	Snow depth timber					1.563
9	Previous location	Sex	Snow density open					1.740
10	Temp × wind	Previous location	Snow density open					1.822
11	Day of winter	Previous location						1.877
12	Temp × wind	Previous location						1.883
13	Day of winter	Temp c	Previous location	Snow depth open	Snow depth timber	Snow depth open	Snow density open	1.885
14	Previous location	Snow depth open						1.889
15	Previous location	Snow density timber						1.919

Table 4 (continued)

Wolves present

Rank	1	2	3	4	5	6	7	Delta AIC
16	Temp c	Previous location	Snow density open					1.944
17	Temp c	Previous location						1.998
18	Wind sp	Previous location						2.000
Grass								
1	Previous location							0.000
2	Temp × wind	Previous location						0.606
3	Wind sp	Previous location						1.318
4	Previous location	Snow depth open	Snow depth timber					1.492
5	Previous location	Snow density open						1.539
6	Temp c	Previous location						1.669
7	Previous location	Snow density timber						1.709
8	Temp × wind	Previous location	Snow density open					1.835
9	Previous location	Sex						1.869
10	Previous location	Snow depth open						1.928
11	Day of winter	Previous location						1.983
12	Temp × wind	Previous location	Snow depth open	Snow depth timber				1.987
13	Previous location	Snow depth timber						2
Conifer								
1	Previous location							0.000
2	Previous location	Snow density open						1.317
3	Temp × wind	Previous location						1.701
4	Previous location	Snow density timber						1.879
5	Previous location	Snow depth open						1.936
6	Wind sp	Previous location						1.945
7	Temp c	Previous location						1.991
8	Previous location	Snow depth timber						1.996
9	Day of winter	Previous location						1.997
10	Previous location	Sex						2.000

Table 5 Specific parameters in each of the models in Fig. 1, with ΔAICc scores

Wolves absent

Rank	1	2	3	4	5	6	7	8	9	10	Delta AIC
Sage											
1	Day of winter	Wind sp	Temp × wind	Previous location	Snow depth open	Snow depth open	Snow density timber	Snow density timber			0.000
2	Day of winter	Wind sp	Temp × wind	Previous location	Snow depth open	Snow density open	Snow density open	Snow density timber			0.120
3	Day of winter	Wind sp	Temp × wind	Previous location	Snow depth open	Snow depth open					0.275
4	Day of winter	Wind sp	Temp × wind	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density open	Snow density timber		0.450
5	Day of winter	Wind sp	Temp × wind	Previous location	Snow depth open	Snow density open	Snow density timber	Sex			0.683
6	Day of winter	Temp c	Wind sp	Previous location	Snow depth open	Snow density open	Snow density timber				0.997
7	Day of winter	Wind sp	Temp × wind	Previous location	Snow depth open	Snow density timber	Sex				1.195
8	Day of winter	Wind sp	Temp × wind	Previous location	Snow depth open	Snow depth timber	Snow density timber				1.242
9	Day of winter	Temp c	Wind sp	Previous location	Snow depth open	Snow density timber					1.277
10	Day of winter	Temp c	Wind sp	Temp × wind	Previous location	Snow depth open	Snow density timber				1.435
11	Wind sp	Temp × wind	Previous location	Snow depth open	Snow density open	Snow density open	Snow density timber				1.488
12	Day of winter	Temp c	Wind sp	Temp × wind	Previous location	Snow depth open	Snow density open	Snow density timber			1.512
13	Day of winter	Temp × wind	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density timber				1.540
14	Day of winter	Temp c	Wind sp	Previous location	Snow depth open	Snow depth open	Snow density open	Snow density open	Snow density timber		1.628
15	Day of winter	Temp c	Wind sp	Previous location	Snow depth open	Snow density open	Snow density timber	Sex			1.683
16	Day of winter	Wind sp	Temp × wind	Previous location	Snow depth open	Snow depth open	Snow density open	Snow density timber	Sex		1.707
17	Day of winter	Temp c	Wind sp	Previous location	Snow depth open	Snow depth open					1.759
18	Day of winter	Temp c	Wind sp	Temp × wind	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density open		1.793
19	Day of winter	Temp c	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density timber	Snow density timber	Snow density timber		1.799
20	Day of winter	Temp c	Wind sp	Temp × wind	Previous location	Snow depth open	Snow depth open				1.817
21	Wind sp	Temp × wind	Previous location	Snow depth open	Snow density open	Snow density timber	Sex				1.827
22	Day of winter	Wind sp	Temp × wind	Previous location	Snow depth open	Sex					1.848
23	Wind sp	Temp × wind	Previous location	Snow depth open	Snow depth open						1.968

Table 5 (continued)

Wolves absent

Rank	1	2	3	4	5	6	7	8	9	10	Delta AIC
Grass											
1	Day of winter	Temp × wind	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density timber	Sex			0.000
2	Day of winter	Wind sp	Temp × wind	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density timber	Sex		0.618
3	Day of winter	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density timber	Sex				0.752
4	Day of winter	Temp c	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density timber	Sex			1.274
5	Day of winter	Wind sp	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density timber	Sex			1.466
6	Day of winter	Temp × wind	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density timber				1.730
7	Day of winter	Temp c	Temp × wind	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density timber	Sex		1.904
Conifer											
1	Day of winter	Wind sp	Temp × wind	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density timber	Sex		0.000
2	Day of winter	Temp c	Wind sp	Temp × wind	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density timber	Sex	0.644
3	Wind sp	Temp × wind	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density timber	Sex			0.672
4	Day of winter	Temp c	Temp × wind	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density timber	Sex		1.040
5	Day of winter	Temp × wind	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density timber	Sex			1.042
6	Temp × wind	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density timber	Sex				1.492
7	Temp c	Wind sp	Temp × wind	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density timber	Sex		1.933
8	Day of winter	Temp c	Previous location	Snow depth open	Snow depth timber	Snow density open	Snow density timber	Sex			1.971

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