Running headline: Behavior shapes a trophic cascade

WOLVES INFLUENCE ELK MOVEMENTS: BEHAVIOR SHAPES A TROPHIC CASCADE IN YELLOWSTONE NATIONAL PARK

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Abstract. A trophic cascade recently has been reported among wolves, elk and aspen on the northern winter range of Yellowstone National Park, but the mechanisms of indirect interactions within this food chain have yet to be established. We investigated whether the observed trophic cascade might have a behavioral basis by exploring environmental factors influencing the movements of 13 female elk equipped with GPS-radiocollars. We developed a simple statistical approach that can unveil the concurrent influence of several environmental features on animal movements. Paths of elk traveling on their winter range were broken down into steps, which correspond to the straight-line segment between successive locations at 5-hour intervals. Each observed step was paired with 200 random steps having the same starting point, but differing in length and/or direction. Comparison between the characteristics of observed and random steps using conditional logistic regression were used to model environmental features influencing movement patterns. We found that elk movements were influenced by multiple factors, such as the distance from roads, the presence of a steep slope along the step, and the cover type in which they ended. The influence of cover type on elk movements depended on the spatial distribution of wolves across the northern winter range of the park. In low wolf-use areas, the relative preference for step end point locations followed: aspen stands>open areas>conifer forests. As the risks of wolf encounter increased, elk's preference for aspen stands gradually decreased, and selection became strongest for steps ending in conifer forests in high wolf-use areas. Our study clarifies the behavioral mechanisms involved in the trophic cascade of Yellowstone's wolf-elk-aspen system: elk respond to wolves on their winter range by a shift in habitat selection, which leads to local reductions in the use of aspen by elk.

Key words: *Aspen;* Canis lupus; Cervus canadensis*; conditional logistic regression; elk; habitat selection; movement analysis;* Populus tremuloides; *roads; robust variance; trophic cascade*; *wolf.*

INTRODUCTION

Carnivores can have a profound influence on the structure and function of ecological systems. Not only can predators directly regulate populations of their prey (Gasaway et al. 1983, Boertje et al. 1996, Eberhardt 1997), but they also can alter patterns of primary production by influencing plant-herbivore interactions (McIntosh and Townsend 1996, Beckerman et al. 1997, Schmitz et al. 1997). Indirect effects of carnivores on plant populations are referred to as a trophic cascade (Beckerman et al. 1997). While the existence of such top-down forces on food webs have been widely demonstrated (e.g., Marquis and Whelan 1994, McLaren and Peterson 1994, Peacor and Werner 2000, Ripple et al. 2001, Schmitz 2003, Beschta 2003), less research has been devoted to clarifying the processes by which carnivores can influence vegetation. Indeed, most studies attempt to expose trophic cascades statistically without revealing underlying mechanisms (Schmitz et al. 2000). For example, McLaren and Peterson (1994) only provided correlative evidence for trophic cascades between wolves (*Canis lupus*), moose (*Alces alces*) and balsam fir (*Abies balsamea*) (Schmitz et al. 2000), which can lead to faulty conclusions (Boyce and Anderson 1999).

Similar circumstantial evidence of trophic cascade driven by wolves has been reported in Yellowstone National Park (YNP). Recruitment of trembling aspen (*Populus tremuloides*, a deciduous tree) overstory essentially ceased during 1927-1995 when wolves were absent from YNP (Ripple and Larsen 2000). Since wolf reintroduction in 1995-1996, the use of aspen stands by elk (*Cervus canadensis*) on their winter range appears to have been influenced by the spatial distribution of predation risks. Lower counts of elk pellets have been observed in high than low wolf-use areas (Ripple et al. 2001). Also, aspen stands associated with riparian/wet meadow habitats had longer suckers in high wolf-use than in low wolf-use areas. Reports of a trophic

cascade driven by wolves (Ripple et al. 2001) can have important management and conservation implications. Aspen has declined over the past century in YNP (Romme et al. 1995, Huff and Varley 1999, Ripple and Larsen 2000), as in other parts of the Rocky Mountains (Boyce 1989, White et al. 2003). Aspen stands may be at risk of disappearing from many national parks of the Rocky Mountains (see White et al. 2003). The decline of aspen appears to have been the result of multiple factors (Romme et al. 1995), among which elk herbivory played a central role (Huff and Varley 1999, Ripple and Larsen 2000). Clarifying the cascading effect of wolves on aspen stands thus could help maintain the long-term integrity of Rocky Mountain ecosystems.

Although Ripple et al. (2001) provided interesting hypotheses to explain spatial variation in elk-aspen interactions, their study was not designed to unveil the underlying mechanisms of trophic cascades. In three-level food chains, top predators can influence not only net primary production by decreasing the abundance of their herbivore prey (Dyer and Letourneau 1999), but also by altering prey foraging behavior and distribution (McIntosh and Townsend 1996, Beckerman et al. 1997, Schmitz et al. 1997). Trade-offs between gaining access to resources and minimizing predation risks can influence behavioral decisions of prey, such as the timing of their activity, the intensity with which they exploit food patches, as well as their food and habitat selection (Edwards 1983, Brown and Morgan 1995, Beckerman et al. 1997, Schmitz et al. 1997, Grand and Dill 1999). Although non-lethal effects of predators might have even stronger influence on food webs than lethal effects (Beckerman et al. 1997), few studies have tried to untangle the role of behavioral factors in shaping communities (McIntosh and Townsend 1996).

Given that the browsing pressure on YNP's aspen appears linked to elk distribution (Ripple et al. 2001), the mechanisms of this trophic cascade should be related to factors controlling the movements of elk in the park. Animal movements result from trade-offs among multiple components of the environment. Nevertheless, studies of animal movement generally investigate the potential effect a single aspect of landscape heterogeneity on animal displacement (e.g., Harrison 1989, Zollner and Lima 1999, Schultz and Crone 2001). This limited approach might be due in part to the lack of simple analytical tools available to extract empirical movement rules from field observations. Given the potential influence of trade-offs on individual movements, it is important to account for multiple aspects of landscape heterogeneity before drawing conclusions about the specific effects of wolves on the movements and spatial distribution of elk. In this paper, we outline a simple statistical approach that can expose multiple components of complex environments influencing animal movement. We then used the probabilistic movement rules extracted with this method to examine whether the trophic cascade observed in the wolf-elk-aspen food chain of YNP may be structured by the influence of wolves on elk movements in winter. Specifically, we considered two non-exclusive hypotheses that might lead to the spatial patterns of aspen use reported on elk's winter range (Ripple et al. 2001): 1) elk avoid traveling in relatively high wolf-use areas, and 2) elk respond differently to habitat distribution when traveling in high than in low wolf-use areas.

METHODS

Study area and animals

This study took place in Yellowstone National Park (YNP) from 6 February 2001 to 4 February 2002. Elevation in the park ranges from 1500 m to over 3000 m. Annual precipitation at Mammoth (northwest of YNP) averages 41.5 cm, with mean daily temperature is -7.3^{o}C in January and 18.3^{o}C in July (Merrill and Boyce 1991). During winter, elk aggregate in the northern portion of the park, which is referred to as Yellowstone's northern winter range. The northern winter range is characterized by grassland and shrub-grasslands with isolated stands of trees,

including most of the YNP's aspen stands (Romme et al. 1995). A general description of the park can be found in Meagher (1973) and Houston (1982), and a detailed description of YNP's vegetation is provided by Despain (1990).

We followed movements of 13 female elk equipped with global positioning system (GPS) radiocollars (11 GPS-collars from Telonics, Mesa, Arizona, USA, and two from Advanced Telemetry Systems Inc. [ATS], Isanti, Minnesota, USA). Elk were relocated every five hours, a schedule that, over time, spreads relocations throughout the day. Individuals were followed when they occupied the northern winter range, which occurred from 6 February 2001 to 23 May 2001 (n = 13 elk followed during this period) and from 13 October 2001 to 4 February 2002 (n = 11 elk followed due to the malfunctioning of two Telonics radiocollars at the end of the first winter).

Statistical analysis of animal movement: a case-control design

The straight-line segment linking successive animal locations taken at regular time intervals can be defined as steps (Turchin 1998). We investigated whether the locations of elk steps (all of which were segments between locations at 5-hour intervals) the landscape was influenced by environmental heterogeneity. Our analysis of external biases to animal movement was based on a case-control design, an approach especially powerful for studying small-scale habitat selection (Compton et al. 2002). Unlike other ecological studies using a case-control approach (e.g., Compton et al. 2002, Boyce et al. 2003), we considered steps (i.e., segments of landscape) instead of individual locations as sampling unit. Each observed step (n = 7600) was paired with 200 random steps, and landscape characteristics (e.g., average energy costs required to travel the step from beginning to end, see *Characterization of steps from landscape variables* for a complete list of independent variables) of observed and random steps were contrasted using conditional logistic regression. Individual elk and pairs of observed-random steps were considered as two strata in the analyses. The large number of random steps (200 random steps matched with each observed steps) used here would not always be necessary to build SSF models. We needed such a large number of random steps because we were interested in the influence of aspen on elk movement, and because aspen is generally distributed in small discrete stands and makes up <1% of the landscape. Hence, only a large number of random steps could appropriately characterize the local availability of aspen.

Random and observed steps of a given pair shared the same starting point, but differed in their length and/or direction. Based on principles of correlated random walk (Turchin 1998), lengths and turning angles (i.e., the angle between previous and next locations) of random steps were drawn from two distributions established from observations on many individuals. First, observations were tallied for each individual into 20^{o} bins for turning angles, and into 50-m bins for step lengths. Then, the percentage of observations associated with each bin was calculated for a given individual considering all of its observed turning angles or step lengths. To minimize problems of circularity, random steps considered for a given radiocollared animal were drawn from the average distribution (percent step length or percent turning angle) of all *other* elk equipped with GPS-collars (Fig. 1). Also, each average distribution of turning angles was calculated considering only individuals having >45 observations, i.e., 11-12 individuals (with individual distribution based on 158-890 turning angles). Average distribution of step lengths considered for a given animal was determined based on the other 12 elk (individual distribution based on 100-942 step lengths), with this distribution truncated at 3000 m to save processing time. This length encompassed 99% of all observed steps. The length and turning angle of random steps were independently drawn from the two distributions, because circular correlations (Batschelet 1981) revealed these variables related poorly to one another ($r^2 < 0.03$ for any animal). To be able

to assign random steps to each observed step using turning-angle information, we need to know where the animal was coming from (i.e., the bearing direction of the preceding step is an essential parameter). In other words, each unit of data included in our analysis was comprised of two successive steps (hence three successive locations at 5-hour intervals), with the current step corresponding to the observed step and with information from the preceding step being used to generate random steps.

Parameter estimation and robust variances

Step Selection Function (SSF) was estimated from the observed and random steps using conditional logistic regression. Patterned after a Resource Selection Function (Manly et al. 2002), a SSF takes the structure:

$$\hat{w}(\boldsymbol{x}) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \ldots + \beta_p x_p), \quad (1)$$

where β_1 to β_p are coefficients estimated by conditional logistic regression, and associated with the variables x_1 to x_p, respectively. Steps with higher SSF score ($\hat{w}[\boldsymbol{x}]$) have higher odds of being chosen by an animal. SSFs thus can expose the influence of environmental heterogeneity on animal movements, by revealing where animals are most likely to be found after 5 hours (i.e., at the end of a step).

Because animals were relocated every 5 hours, successive steps were not independent from one another. Such autocorrelation does not influence β-values, but it biases their standard errors (Nielson et al. 2002). Robust standard errors of SSF parameters still can be obtained using a robust sandwich estimate of the covariance matrix (Lin and Wei 1989, Wei et al. 1989, see also Appendix for mathematical details). The approach requires dividing observations into independent clusters. A cluster may be comprised of steps that are autocorrelated, as long as steps are independent between clusters (Wei et al. 1989, Hardin and Hible 2003). Our analysis indicates that steps can be considered as independent among the 13 radiocollared elk (see RESULTS). Also, an analysis of autocorrelations and partial autocorrelations of the deviance residuals showed that autocorrelation disappeared beyond lag 14 (~3 days) for all animals, hence steps separated >14-distance lag can be viewed as independent. On this basis, we created a total of 94 independent clusters (which should be sufficient to calculate a valid estimate of the variance matrix of the regression coefficients, Fay and Braubard 2001) by dropping segments of 15 successive steps for each animal. Each cluster consists of a sequence of successive steps performed by a given animal. The 94 clusters were statistically independent from each other, as they were either comprised of information from different animals or, for a given animal, the steps in one cluster were >14 time-lags apart from the steps in any other clusters. The number of clusters per elk was proportional to its radiotracking period; most individuals ended up with 8-9 clusters and a few with 4 clusters. Robust standard errors and associated significance levels were estimated based on these 94 clusters (see Appendix).

Characterization of steps from landscape variables

Given our interest in clarifying wolf-elk-aspen interactions, the landscape was simplified to focus on variables related to wolf or aspen, or believed to potentially have a major influence on elk movements. Random and observed steps were characterized based on their minimum distance (km) to the nearest road (*Drmin*; e.g., 0 km for steps crossing a road), the proportion of their length comprised of conifer forests ($Forest_{prop}$), the average energy (kJ/km) required to travel the step (E), and the wolf index averaged over the step length (W_{avg}). A dummy variable (0 or 1) also accounted for the presence of a steep slope (>20 m vertical for 10 m horizontal displacement) along the steps (*Sslope*), while considering the absence of a steep slope as the reference point. We also determined the habitat cover type in which the step ended (open areas, conifer forests or aspen

stands), and quantified this observation via two dummy variables (one variable associated with aspen, $Aspen_{end}$, and one with conifer, $Forest_{end}$), while considering open areas as the reference habitat type. Finally, we also accounted for interactions between these variables.

Habitat covariates were based on data layers in a geographical information system (GIS) primarily provided by the Spatial Analysis Center at Yellowstone National Park. These included a digital elevation model (10 m grid cell size), the National Wetlands Inventory (USFWS) datasets, roads, and a habitat classification (Dixon 1997). Daily maps of snow water equivalents were generated for the entire study period, using a snow model developed by Farnes et al. (1999). These maps were converted into maps of snow depth and density based on a conversion table (Farnes et al. 1999).

Wolf data

Wolves in each pack were radiocollared and relocated on one of two schedules: (1) daily from mid-November through mid-December, and in March; (2) approximately weekly for the rest of the year. Group size was recorded for each of these relocations. Locations were filtered to remove entries from the same group on the same day. Bivariate normal kernel density estimates with a fixed bandwidth of 3 km and weighted by group size were generated with ArcGIS 8.3 (ArcGIS, Release 8.3, Environmental Systems Research Institute Redlands, California, USA) to derive an index of wolf use for each pack during each of the two winters (19 October 2000 to 11 May 2001 and 25 October 2001 to 12 May 2002). These kernels were standardized by dividing each kernel by the sum of all values in that kernel. For each winter the standardized kernels were averaged to produce a single wolf-activity index. This index was used to identify areas where wolves are more likely to be found on the Northern Range. Our wolf index was averaged over the length each step (observed or random) to create a variable (W_{avg}) that reflects the relative use of the landscape by wolves (e.g., high versus low wolf-use areas).

Energy costs of locomotion

Energy cost of locomotion (E) was used to summarize variation in snow conditions (depth and density) and topography (uphill, downhill and horizontal) into a single variable. Based on Parker et al. (1984), locomotion costs can be estimated for elk of Yellowstone following a few assumptions. First, we assumed that snow depth corresponds to the animal's sinking depth, i.e., the animal sinks down to the ground. Because only adult females were equipped with radiocollars, we also assumed a body mass of 266 kg (M), a brisket height of 80 cm (Parker et al. 1984), and a travel speed of 3 km/h (Gates and Hudson 1978). Finally, we considered that energy costs of locomotion augment linearly with increasing uphill slopes and with decreasing downhill slopes. Under these assumptions, the energy costs of locomotion (kJ/km) can be estimated by:

$$E = 12.43M^{0.66}([T+W+100]/100), \quad (2)$$

where T is the percent change in the energy costs of traveling due to topography, and W is the percent increase in energy costs in presence of snow. T should covary with uphill slopes (S, in degree) according to $T = 0.2015S$, and with downhill slopes following $T = -0.0120S$ (Parker et al. 1984). W changes with snow depth (Y, cm) and density (ρ, g/cm^3) following: $W = (0.71 + 2.6[\rho - 0.2])(Y/0.8)\exp([0.0191 + 0.016(\rho - 0.2)][Y/0.8])$ (Parker et al. 1984).

To calculate energy costs of travel along steps, a program was written in a GIS to segment this path whenever it crossed a cell in the elevation (DEM) grid (horizontal resolution: 10 m). For each segment slope was calculated using the elevation values between consecutive segments. Using snow depth and density values from the center of that segment, the energy cost of movement was calculated and summed across all segments to obtain the total energy cost for that movement. This

value was then divided by the total length of the step to convert it to cost per unit distance (E, kJ/km).

Independence of movements among radiocollared elk

During captures we attempted to distribute radiocollars widely across the northern range to broadly sample the population (Cook et al. 2004 provide details on capture methods). We estimated the distance between concurrent locations of the 13 elk equipped with radiocollars to evaluate the level of independence in individuals' movements. We considered that elk belonged to the same herd when ≤100 m from each other, as assumed by Fortin et al. (2003) for bison.

RESULTS

Evaluation of concurrent locations among all possible pairs of radiocollared female elk (n = 78 pairs) revealed a median distance between individuals of 16.6 km during the winters of 2000-2001 and 2001-2002. Elk #1 and #4 spent 16% of the time in the same herd during the winter of 2000-2001, whereas elk #2 and #9 spent 6% of their time together during that winter. All other pairs of elk spent less than 3% (median = 0%, overall for the 78 pairs of individuals) of their time in the same herd during any of the two winters. Movements of radiocollared elk thus generally were independent among individuals, and were considered as such in our analyses.

The autocorrelation among successive steps had an important impact on standard error estimates of most landscape variables in our SSF; robust variances were up to 2.1 that of associated "naïve" variances (see SE ratio, Table 1). Considering its robust variance, we found that energy costs of locomotion did not significantly influence step selection (P = 0.16). This variable was mostly a function of snow conditions, with 88% (r = 0.94, n = 1218067) of the variation in energy costs along steps directly related to changes in average snow water equivalent (i.e., snow depth × density). Energy costs of locomotion thus were dropped from the final SSF model (Table 1).

Our analyses revealed that elk movements were influenced by multiple components of their environment (Table 1). In fact, SSF provided probabilistic movement rules for elk, where the choice of a given step is contingent on the set of options available at the animal's location. Roads had significant non-linear effects on elk movements. Assuming that other environmental factors remain constant, elk were less likely to move towards rather than parallel or away from the nearest road when that road was ≤6.6 km away, but more likely when the road was >6.6 km away (Fig. 2). The average distance between radiocollared elk and the nearest road ranged from 0.61 to 2.4 km ($\overline{X}$: 1.5 km, n = 13 elk), and only four of the 13 individuals were ever >6.6 km away from a road in winter. Slopes steeper than ~65^{o} (i.e., >20 m vertical for 10 m horizontal displacement) negatively impeded movement (Table 1).

Elk generally avoided steps in areas made up of a large proportion of conifer forest (Table 1). Also, steps ended in certain habitat types disproportionately to random expectations ($Aspen_{end}$ and $Forest_{end}$, Table 1). Compared to W_{avg}, the transformation W_{avg}^3 led to a 25% increase in the χ^2 statistic of the "robust" Wald test for the hypothesis that all wolf-related variables have no effect. This is because W_{avg}^3 accounted for non-linear effects of wolf distribution on elk movements. The final model thus is based on the transformation W_{avg}^3 (Table 1). We observed that selection for cover types varied with the relative risks of encountering a wolf along a step ($Aspen_{end} \times W_{avg}^3$ and $Forest_{end} \times W_{avg}^3$, Table 1). In low-wolf-use areas (i.e., wolf index < 0.72, Fig. 3), steps were more likely to end in open than conifer forest areas, but less likely to end in open areas than in aspen stands (Fig. 3). As W_{avg}^3 increased an elk's affinity for steps ending in aspen stands was gradually

replaced by a preference for steps ending in conifer forest areas. As a consequence, a shift in selection for cover types was observed between wolf index <0.72 and >0.98 (Fig. 3). The variable W_{avg}^3 was not significant on its own, but remained in the final model because it is part of significant interactions (i.e., $Aspen_{end} \times W_{avg}^3$, $Forest_{end} \times W_{avg}^3$). Finally, an increase in W_{avg}^3 did not generally decrease the odds of elk choosing these steps (Table 1), as indicated by the positive association between our wolf index and the probability of elk making steps ending in the two most widely available vegetation cover types (i.e., open areas and conifer forests, Fig. 3).

DISCUSSION

Our results demonstrate that the trophic cascade reported for the wolf-elk-aspen system of YNP (Ripple et al. 2001) has a behavioral basis in the movement patterns of elk as shaped by the distribution of wolves. Multiple biotic and abiotic attributes of landscape heterogeneity influenced the movements of elk in YNP. Movement patterns reflected trade-offs between individual goals, such as the need to occupy certain habitat cover types, and to avoid major obstacles (e.g., steep slopes) or wolf predation.

Analysis of animal movement: Step Selection Functions

Extrinsic biases to elk movements were evaluated through a comparison between observed and random steps. The statistical approach is based on conditional logistic regression, and was inspired by resource selection studies having a case-control design (e.g., Compton et al. 2002, Boyce et al. 2003, see also Manly et al. 2002). Our procedure is novel, however, because landscape segments are compared, instead of locations (Arthur et al. 1996, Boyce et al. 2003) or areas (Johnson et al. 2002). As a consequence, we explicitly considered landscape characteristics that animals would have been likely to encounter along their path. These environmental features could influence the probability that elk are found at given locations, regardless of the specific attributes of those locations. For example, our study indicates that, in low wolf-use areas, elk should select a step ending in an aspen stand, except if they have to negotiate a steep slope to get there (Table 1). Assuming that reaching any aspen stand from the animal's location would require crossing a steep slope, the odds would then be higher that the elk would avoid the steep slope, and terminate its course in an open area. Such differences in selection due to the occurrence of landscape features along animal steps have not been considered in habitat selection studies.

We quantified landscape characteristics along the straight lines comprising each step. This method is not based, however, on the stringent assumption that elk went from the beginning to the end of their steps following straight lines. In fact, SSFs only indicate that step selection is related to the characteristics of certain landscape features located between their starting and ending locations, not that animals necessarily travelled that path. On the other hand, environmental features located directly along the steps are identified as influencing animal movement probably because they well reflect the paths actually used by the animals. This might be due either because animals did indeed follow rather closely the straight-line segments making up the steps, or because the spatial autocorrelation (see Boyce et al. 2003 for autocorrelation of many landscape variables in YNP) of landscape variables is such that the actual paths have similar characteristics to the corresponding steps. Consistently, we can expect that SSF would less likely detect extrinsic biases to animal movement as the time interval between successive relocations increases.

Given that environmental factors causing departure from random expectations of animal movements are identified from a comparison between used and random steps, the rules used to place the random steps in the landscape are crucial to the estimation of SSFs, as they are for other selection studies (Arthur et al. 1996, Boyce et al. 2003). We drew random steps from observed

distributions of lengths and turning angles, as for correlated random walk models (e.g., Turchin 1998, Morales and Ellner 2002, Fortin 2003). This approach differs, however, from resource selection studies where random locations are drawn from uniform distributions (Arthur et al. 1996, Johnson et al. 2002), within a range of distances that may capture, for example, 80% of the observed step length (Boyce et al. 2003). While consideration of uniform distributions of step lengths may be adequate for point-based selection studies, this approach could introduce biases into SSF, especially if the median differs between the observed and random distributions of step lengths. Step lengths often display leptokurtic distributions (cf. Fraser et al. 2001), where some very long steps are observed, but most displacements are rather short (Fig. 1). Consequently, drawing random step length from a uniform distribution ranging from 0 m up to a distance that includes 80% of step length would cause median steps to be much longer for the distribution of random than observed steps. As a consequence, the presence of certain landscape features, such as steep slopes, should be detected more often for random than observed steps simply because random steps would tend to be longer. This difference could lead to significant coefficients for certain landscape features that might not reflect animal selection. Hence, drawing end point locations from observed distributions of step length appears more appropriate.

Departure from a uniform distribution also can be expected for turning angles. Turning angles are generally biased towards 0^o because organisms have a propensity to keep moving in a given direction (directional persistence). Directional persistence is considered as internal to organisms (Bovet and Benhamou 1991), and such intrinsic influence on animal movement may lead to erroneous interpretation of the influence of habitat heterogeneity on movement patterns (Turchin 1998, p. 168). Directional persistence thus needs to be considered in studies of animal movement (Schultz and Crone 2001). We accounted for internal biases by drawing the direction of random steps from distributions of turning angles comprised of all observations on the northern winter range. Because we estimated these turning angle distributions by pooling observations taken in multiple habitat cover types, during all periods of the day, over extensive periods of time (two winters) and for multiple animals occupying different home-range locations, we believe the bias toward 0^o that was still observed for turning angles (e.g., Fig. 1) illustrated the propensity of organisms to keep moving in a given direction. Although there are no perfect ways to account for intrinsic biases (Turchin 1998), our approach should allow the identification of factors influencing animal movement beyond directional persistence. We believe that SSFs constitute a simple, but powerful, statistical approach to identify environmental features attracting or repulsing organisms traveling in heterogeneous landscapes, hence this technique should facilitate empirical investigations of factors controlling animal distribution in complex environments.

Landscape attributes influencing elk movement in Yellowstone National Park

SSF identified multiple features of the environment influencing movements of female elk in YNP. First, the presence of steep slopes decreased the probability of elk making that step. Areas in the vicinity of roads might be safer for elk, because wolves tend to remain away from such infrastructures (Mladenoff et al. 1999). Nonetheless, elk generally were unlikely to make movements heading towards the nearest road. Other studies have also reported elk's tendency to remain away from roads used by motorized vehicles, which shapes their distribution in many landscapes (see Rowland et al. 2000 and references therein). Elk became more likely to head back towards the nearest road as they got >6.6 km away. In YNP, roads follow the valley bottom that runs along the winter northern range. Consequently, to further increase their distance from the nearest road when >6.6 km away, elk would have to climb into the mountains where temperatures are colder, and where deeper snow conditions make travel and foraging more difficult. Elk's

selection of winter range is partly related to a search for favorable snow conditions (Sweeney and Sweeney 1984). Hence, the non-linearity in effects of roads on winter movements of elk appear to reflect a trade-off between avoiding human disturbance, and taking advantage of the climate and conditions associated with the valleys of the northern range. On the other hand, energy costs of locomotion, which largely reflected spatial distribution of snow water equivalent, did not significantly influence elk movements. Given the 5-hour interval between successive radiolocations, this lack of detectable selection should mostly reflect decisions associated with local (i.e., within few hundred meters) rather than regional (e.g., valley bottom vs. the surrounding mountains) differences in snow conditions.

Movement paths of elk were influenced by the spatial distribution of vegetation cover types in the landscape. Aspen was the preferred cover type of elk travelling in low wolf-use areas of their winter range. Resource selection functions based on 93 elk equipped with VHF radiocollars, which were followed concurrently to our movement study, confirmed winter preference by elk in YNP for aspen stands over open areas and conifer forests (Mao et al. 2005). Aspen offers high quality browse (Hobbs et al. 1982, Jelinski and Fisher 1991), and elk consume the tips of aspen sprouts, as well as the bark of mature trees (Romme et al. 1995). Elk studies conducted in the Rocky Mountains generally report a relative habitat preference of grassland>aspen>conifer (reviewed by White et al. 2003), a ranking also expected for elk of YNP, but only when elk were found in intermediate wolf-use areas of their northern winter range (Fig. 3). Indeed, as the risk of encountering wolves increased, affinity for aspen stands was gradually replaced by a preference for conifer forest areas, so that the ranking of habitat preference went from aspen stands>open areas>conifer forest areas for low values of wolf index, to open areas>aspen stands>conifer forest areas for intermediate values of wolf index (~0.78), to conifer forest areas>open areas>aspen stands for high values of wolf index (Fig. 3).

Our findings are consistent with general observations of wolf-elk interactions. Elk commonly respond to an increase in predation risks by intensifying their use of forested areas (Wolff and Van Horn 2003, Mao et al. 2005), as well as by decreasing the time spent in aspen stands (White et al. 2003). Predators can have a significant influence on the use of resources by their prey (Brown 1988, Brown 1999, Lima and Dill 1990), because prey species need not only to find high quality food patches, but also need to minimize the risks of becoming food themselves. Given that predators commonly focus their activity in areas where the resources of their prey are highly available (Kunkel and Pletscher 2001, Lima 2002), habitat selection by herbivores should reflect a balance between the marginal loss of fitness due to predators and the marginal fitness gain due to improved forage resource access (Fryxell and Lundberg 1997). The decrease in the use of aspen stands by elk inhabiting risky areas might indeed reflect a trade-off between the search for food and safety (White et al. 2003). Little is known, however, about how cover types and landscape features influence the security of cervids in the Rocky Mountains (Kunkel and Pletscher 2001). White et al. (2003) hypothesized that elk might have greater ability to escape from predators when in open areas than in aspen stands due to differences in habitat structure and snow depth. Ungulates also should detect predators more easily when foraging in open areas than in aspen stands (White et al. 2003). YNP's aspen are found mostly along the forest edge, hence the hunting success of wolves targeting elk in aspen stands should benefit from the possibility of stalking elk from the nearby forest cover (Kunkel and Pletscher 2001). Wolves tend to travel along riparian areas (Peterson 1977 in Ripple and Larsen 2000), making aspen stands located in these areas even riskier for elk. Conifer forests in high-wolf use areas of the winter northern range of YNP were mostly comprised of Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*). Neither of these forest cover types was selected for travel routes by wolves in and near Glacier

National Park, Montana (Kunkel and Pletscher 2001). In fact, wolves even avoided traveling in lodgepole pine forests. Movement patterns of elk thus also may reflect an avoidance of wolf travel routes (Ripple and Larsen 2000), which ends up reducing elk's use of certain aspen stands and increasing their use of conifer forests when traveling in high wolf-use areas.

Mechanisms of trophic cascade

Our study of elk movement clarifies the behavioral mechanisms involved in the trophic cascade reported for the wolf-elk-aspen system of YNP (Ripple et al. 2001). We considered two hypotheses, both which could explain spatial variation in aspen use by risk-sensitive elk. Our first hypothesis is based on the observation that wolves maintain territories that rarely overlap (Ballard et al. 1987, Okarma et al. 1998). Avoidance among wolf packs creates buffer zones where ungulates may aggregate (Mech 1977, Lewis and Murray 1993). As a general corollary, we predicted that elk would be more likely to make steps in low than high wolf-use areas. Our SSF did not support this hypothesis. An increase in the average wolf index along steps was positively related to the probability of elk using those steps, with the exception of steps ending in aspen stands. Given that aspen stands make up <1% of the landscape, winter Kernel distributions of elk tends to be very similar to those of wolves (Mao et al. 2005). Hence, the indirect influence of wolves on aspen of the northern winter range does not appear to result from elk avoiding general areas. Our second hypothesis specified that elk would display different movement patterns with respect to the distribution of vegetation cover types when traveling in low and high wolf-use areas. Accordingly, selection for aspen stands decreased as the wolf index increases along their steps. Such a decrease in preference can explain the spatial variation in aspen use characterizing the trophic cascade reported in the wolf-elk-aspen system of YNP's winter northern range (Ripple et al. 2001).

Our study reveals that YNP's trophic cascade has a behavioral basis, but other mechanisms also need to be considered. The classic view of trophic cascade is that predators reduce the density of their herbivore prey with repercussion on primary production (Schmitz et al. 1997). McLaren and Peterson (1994) suggest that wolves have indirect effects on balsam fir due to their effect on moose population; hence wolves might be capable of driving top-down trophic cascades by regulating herbivore density. On the other hand, YNP's elk population was artificially maintained at 3000-6000 individuals from 1930-1968 (Romme et al. 1995), without significant effects on aspen recruitment in the park (Ripple and Larsen 2000). During our study and the study of Ripple et al. (2001) that provided some evidence of trophic cascade in the park, the population of elk was 2-3 times higher (Smith et al. 2003) than during the years of artificial control. This trophic cascade thus appears unlikely to be the result of a general decrease in elk density due to predation, but should instead be largely behaviorally mediated.

Revealing the mechanisms of trophic cascade is critical for understanding ecosystem dynamics. For example, when predators reduce the overall density of herbivores, carnivores are expected to produce a global net-positive-indirect effect on plants (Schmitz et al. 2000). The situation differs when spatial variations in the top-down influence on the herbivore-plant interactions result from a behavioral adjustment of herbivores to predation risks. Predators can influence the movements of their herbivore prey, which may lead to either an increase or a decrease in the density of the resources of their prey, depending on the influence of predators on the herbivores' movement rules (Abrams 2000). We found that elk do not avoid travelling in high wolf-use areas, but when travelling in these areas, they switch their habitat preferences. Such behavioral response should produce net-positive-indirect effects on some plants and net-negative-indirect effects on other plants (Schmitz et al. 2000). Specifically, the reduced browsing pressure

in aspen stands should be mirrored by an increase in herbivory in the conifer forests and open areas located in high wolf-use areas. Also, given that the trophic cascade reported in YNP results from a behavioral response of elk to predation risks, the long-term persistence of an increase in aspen biomass would depend on the stability of spatial distribution of wolf activity centers. Unbrowsed aspen would be unlikely to grow to sufficient height during a single year to escape elk herbivory over subsequent years. Consequently, any annual increase in aspen biomass might simply get browsed the next winter if wolves changed their activity patterns over the landscape (i.e., within and among territories). Changes in wolf activity centers among winters were in fact observed during our study. In other words, the increase in aspen biomass reported by Ripple et al. (2001) during their fieldwork of 1999 may not necessarily be the precursor of an increase in aspen in YNP. Further investigations of the ecosystem consequences of wolf reintroduction should clarify this emerging hypothesis.

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LITERATURE CITED

Abrams, P. A. 2000. The impact of habitat selection on the spatial heterogeneity of resources in varying environments. Ecology **81**:2902-2913.

Arthur, S. M., B. F. J. Manly, L. L. McDonald, and G. W. Garner. 1996. Assessing habitat selection when availability changes. Ecology **77**:215–227.

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife Monographs **98**:1–54.

Batschelet, E. 1981. Circular statistics in biology. Academic Press, London, UK.

Beschta, R. L. 2003. Cottonwoods, elk, and wolves in the Lamar Valley of Yellowstone National Park. Ecological Applications **13**:1295–1309.

Beckerman, A. P., M. Uriarte, and O. J. Schmitz. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. Proceedings of the National Academy of Sciences USA **94**:10735-10738.

Boertje, R. D., P. Valkenburg, and M. E. McNay. 1996. Increases in moose, caribou, and wolves following wolf control in Alaska. Journal of Wildlife Management **60**:474-489.

Bovet, P., and S. Benhamou. 1991. Optimal sinuosity in central place foraging movements. Animal Behaviour **42**:57-62.

Boyce, M. S. 1989. The Jackson elk herd: intensive wildlife management in North America. Cambridge University Press, New York, New York, USA.

Boyce, M. S., and E. M. Anderson. 1999. Evaluating the role of carnivores in the Greater Yellowstone Ecosystem. Pages 265-283 *in* T. W. Clark, C. P. Curlee, S. C. Minta, and P. M. Kareiva, editors. Carnivores in ecosystems. Yale Univ. Press, New Haven, Connecticut, USA.

Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. M. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Écoscience **10**:321-332.

Brown, J. S. 1988. Patch use of an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology **22**:37-47.

Brown, J. S. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. Evolutionary Ecology Research **1**:49-71.

Brown, J. S., and R. A. Morgan. 1995. Effects of foraging behavior and spatial scale on diet selectivity: a test with fox squirrels. Oikos **74**:122-136.

Burnham, K., and D. Anderson 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Cook, R. C., J. G. Cook, and L. D. Mech. 2004. Nutritional condition of Northern Yellowstone elk. Journal of Mammalogy, *in press*.

Compton, B. W., J. M. Rhymer, and M. McCollough. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. Ecology **83**:833-843.

Despain, D. G. 1990. Yellowstone vegetation: consequences of environment and history in a natural setting. Robert Rinehart Publishers, Boulder, Colorado, USA.

Dixon, B. G. 1997. Cumulative effects modeling for grizzly bears in the greater Yellowstone ecosystem. Thesis. Montana State University, Bozeman, Montana, USA.

Dyer, L. A., and D. K. Letourneau. 1999. Trophic cascades in a complex terrestrial community. Proceedings of the National Academy of Sciences USA **96**:5072-5076.

Eberhardt, L. L. 1997. Is wolf predation ratio-dependent? Canadian Journal of Zoology **75**:1940-1944.

Edwards, J. 1983. Diet shifts in moose due to predator avoidance. Oecologia **60**:185-189.

Farnes, P., Heydon, C. and Hansen, K. 1999. Snowpack distribution across Yellowstone National Park. Final Report Cooperative Agreement Number CA 1278-1-9017, Department of Earth Sciences, Montana State University, Bozeman, Montana, USA.

Fay, M. P., and B.I. Braubard. 2001. Small-sample adjustments for Wald-type tests using sandwich estimators. Biometrics **57**:1198-1206

Firle, S., R. Bommarco, B. Ekbom, and M. Natiello. 1998. The influence of movement and resting behavior on the range of three carabid beetles. Ecology **79**:2113-2122.

Fortin, D. 2003. Searching behaviour and use of sampling information by free-ranging bison. Behavioral Ecology and Sociobiology **54**:194-203.

Fortin, D., J. M. Fryxell, L. O'Brodovich, and D. Frandsen. 2003. Foraging ecology of bison at the landscape and plant community levels: the applicability of energy maximization principles. Oecologia **134**:219-227.

Fraser, D. F., J. F. Gilliam, M. J. Daley, A. N. Le, and G.T. Skalski. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. American Naturalist **158**:124-135.

Fryxell, J. M., and P. Lundberg. 1997. Individual behavior and community dynamics. Chapman and Hall, New York, New York, USA.

Gasaway, W. C., R. O. Stephenson, J. L. Davis, P. E. K. Shepherd, and O. E. Burris. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildlife Monographs 84.

Grand, T. C., and L. M. Dill. 1999. Predation risk, unequal competitors and the ideal free distribution. Evolutionary Ecology Research **1**:389-409.

Hardin, J. W., and J. M. Hilbe. 2003. Generalized estimating equations. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Harrison, S. 1989. Long-distance dispersal and colonization in the bay checkerspot butterfly, *Euphydryas editha bayensis*. Ecology **70**:1236-1243.

Hobbs, N.T., D.L. Baker, J.F. Ellis, D.M. Swift, and R.A. Green. 1982. Energy- and nitrogen-based estimates of elk winter-range carrying capacity. Journal of Wildllife Management **46**:12-21.

Houston, D. B. 1982. The Northern Yellowstone elk: ecology and management. Macmillan Publishing, New York, New York, USA.

Huff, D. E., and J. D. Varley. 1999. Natural regulation in Yellowstone National Park 's northern range. Ecological Applications **9**:17-29.

Jedrzejewski, W., K. Schmidt, J. Theuerkauf, B. Jedrzejewska, and H. Okarma. 2001. Daily movements and territory use by radio-collared wolves *(Canis lupus*) in Bialowieza Primeval Forest in Poland. Canadian Journal of Zoology **7**9:1993–2004.

Jelinski, D. E., and L. J. Fisher. 1991. Spatial variability in the nutrient composition of *Populus tremuloides*: clone-to-clone differences and implications for cervids. Oecologia **88**:116–124.

Johnson, C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002. A multi-scale behavioral approach to understanding the movements of woodland caribou. Ecological Applications **12**:1840-1860.

Kunkel, K., and D. H. Pletscher. 2001. Winter hunting patterns of wolves in and near Glacier National Park, Montana. Journal of Wildlife Management **65**:520-530

Lewis, M. A., and J. D. Murray. 1993. Modeling territoriality and wolf-deer interactions. Nature **366**:738-740.

Lima, S. L. 2002. Putting predators back into behavioural predator-prey interactions. Trends in Ecology and Evolution **17**:70-75.

Lima, S. L., and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology **68**:619-640.

Lin, D. Y., and Wei, L. J. 1989. The robust inference for the proportional hazards model. Journal of the American Statistical Association **84**:1074 -1078.

Manly, B. F. J., L. L. McDonald, D. A. Thomas, T. L. McDonald, and W. E. Erickson. 2002. Resource selection by animals, statistical design and analysis for field studies. Second edition. Kluwer Academic Publishers, Dordrecht, Netherlands.

Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park, Wyoming. Journal of Wildlife Management (*in press*).

Marquis, R. J., and C. J. Whelan. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. Ecology **75**:2007-2014.

McIntosh, A. R., and C. R. Townsend. 1996. Interactions between fish, grazing invertebrates and algae in a New Zealand stream: a trophic cascade mediated by fish induced changes to grazer behaviour? Oecologia **108**:174-181.

McIntyre, N. E., and J. A. Wiens. 1999. How does habitat patch size affect animal movement? An experiment with darkling beetles. Ecology **80**:2261-2270.

McLaren, B. E., and R. O. Peterson. 1994. Wolves, moose, and tree rings on Isle Royale. Science **266**:1555–1558.

Meagher, M. M. 1973. The bison of Yellowstone National Park. National Park Service Scientific Monograph Series No. 1.

Mech, L. D. 1977. Wolf-pack buffer zones as prey reservoirs. Science **198**:320-321.

Merrill, E. H., and M. S. Boyce. 1991. Summer range and elk population dynamics in Yellowstone National Park. Pages 263-273 *in* R. D. Keiter, and M. S. Boyce, editors. The Greater Yellowstone Ecosystem: redefining America's wilderness heritage. Yale University Press, New Haven, Connecticut, USA.

Mladenoff D. J., T. A. Sickley, and A. P. Wydeven. 1999. Predicting gray wolf landscape recolonization: Logistic regression models vs. new field data. Ecological Application **9**:37-44.
Morales J. M., and S. P. Ellner. 2002. Scaling up movements in heterogeneous landscapes: the importance of behavior. Ecology **83**:2240-2247.
Nielson, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2002. Modeling grizzly bear habitats in the Yellowhead Ecosystem of Alberta: taking autocorrelation seriously. Ursus **13**:45-56.
Okarma, H., W. Jędrzejewski, K. Schmidt, S. Śnieżko, A. N. Bunevich, and B. Jędrzejewska. 1998. Home ranges of wolves in Białowieża Primeval Forest, Poland, compared with other Eurasian populations. Journal of Mammalogy **79**:842–852.
Parker, K. L., C. T. Robbins, and T. A. Hanley. 1984. Energy expenditures for locomotion by mule deer and elk. Journal of Wildlife Management **48**:474-488.
Peacor, S. D., and E. E. Werner. 2000. Predator effects on assemblage of consumers through induced changes in consumer foraging behavior. Ecology **81**:1998-2010.
Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. National Park Service Scientific Monograph series No. 11.
Ripple,W. J., and E. J. Larsen. 2000. Historic aspen recruitment, elk, and wolves in Northern Yellowstone National Park, USA. Biological Conservation **95**:361–370.
Ripple, W. J., E. J. Larsen, R. A. Renkin, and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. Biological Conservation **102**:227-234.
Romme, W. H., M. G. Turner, L. L. Wallace, and J. S. Walker. 1995. Aspen, elk, and fire in Northern Range of Yellowstone National Park. Ecology **76**:2097-2106.
Rowland, M. M., M. J. Wisdom, B. K. Johnson, and J. G. Kie. 2000. Elk distribution and modeling in relation to roads. Journal of Wildlife Management **64**:672-684.
Schmitz, O. J. 2003. Top predator control of plant biodiversity and productivity in an old-field ecosystem. Ecology Letters **6**:156–163
Schmitz, O. J., A. P. Beckerman, and K. M. Obrien. 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. Ecology **78**:1388-1399
Schmitz, O.J., P.A. Hambäck, and A.P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of top carnivore removals on plants. American Naturalist **155**:141–153.
Schultz, C. B., and E. E. Crone. 2001. Edge-mediated dispersal behavior in a prairie butterfly. Ecology **82**:1879-1892
Smith, D. W., T. D. Drummer, K. M. Murphy, D. S. Guernsey, and S. B. Evans. 2004. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995-2000. Journal of Wildlife Management **68**:153-166.
Sweeney, J. M., and J. R. Sweeney. 1984. Snow depths influencing winter movements of elk. Journal of Mammalogy **65**:524-526
Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer, Sunderland, Massachusetts, USA.
Wei, L. J., D. Y. Lin, and L. Weissfeld. 1989. Regression-analysis of multivariate incomplete failure time data by modeling marginal distributions. Journal of the American Statistical Association **84**:1065-1073.
White, C. A., M. C. Feller, and S. Bayley. 2003. Predation risk and the functional response of elk–aspen herbivory. Forest Ecology and Management **181**:77-97.
Wolff, J. O., and T. Van Horn. 2003. Vigilance and foraging patterns of American elk during the rut in habitats with and without predators. Canadian Journal of Zoology **81**:266-271.

Zollner, P. A., and S. L. Lima. 1999. Search strategies for landscape-level interpatch movements. Ecology **80**:1019-1030.

Table 1. Coefficients for the final model of Step Selection Function (SSF) for 13 elk equipped with GPS-radiocollars on winter range in Yellowstone National Park in 2000 and 2001. SE ratio corresponds to the ratio between the "naïve" (i.e., uncorrected for autocorrelation) and robust standard error. Variables included in the SSF model are the minimum distance to the nearest road (*Drmin*), dummy variables representing the cover type in which the step ended (conifer forests $Forest_{end}$ or aspen stands $Aspen_{end}$, with open areas as the reference variable), the proportion of the step comprised of conifer forests $(Forest_{prop})$, a dummy variable having the absence of a steep slope along the step as its reference point (*Sslope*), and the wolf index cubed (with high values indicative of high wolf-use areas) averaged over the step length (W_{avg}^3).

Variable	β-Value	Robust SE	SE ratio	χ^2	$P\leq$
Drmin	0.744	0.110	1.9	45.8	0.001
$Drmin^2$	-0.056	0.020	2.1	7.9	0.005
$Aspen_{end}$	0.338	0.160	1.4	4.4	0.03
$Forest_{end}$	-0.289	0.059	1.3	23.7	0.001
$Forest_{prop}$	-0.770	0.105	1.3	54.1	0.001
Sslope	-2.189	0.443	1.0	24.4	0.001
$Aspen_{end} \times W_{avg}^3$	-0.885	0.406	1.3	4.7	0.03
$Forest_{end} \times W_{avg}^3$	0.313	0.171	1.6	3.4	0.06
W_{avg}^3	0.240	0.214	1.7	1.2	0.26

FIGURE LEGENDS

Fig. 1. Distribution of average step lengths and turning angles for radiocollared elk relocated every 5 hours on their winter range of Yellowstone National Park in 2000-2001. These average distributions were used to assign random steps to radiocollared elk #12, hence averages (+SD) were calculated excluding individual #12 (see METHODS).

Fig. 2. Relative probability (within the range of 0-17 km) of a given step being selected by an elk on its winter range, given its distance from the nearest road, as calculated from the SSF model provided in Table 1. Elk were more likely to select steps directed towards than away or parallel to the nearest road when they were >6.6 km away, but less likely when <6.6 km.

Fig. 3. Relative probability that elk select steps ending in various habitat types when traveling on their winter range, as a function of a wolf index averaged along the individual's step. Relative probabilities reflect the range of wolf indices 0-1.4 (i.e., from absence of wolves to high and low wolf-use areas), and were calculated the SSF model provided in Table 1.

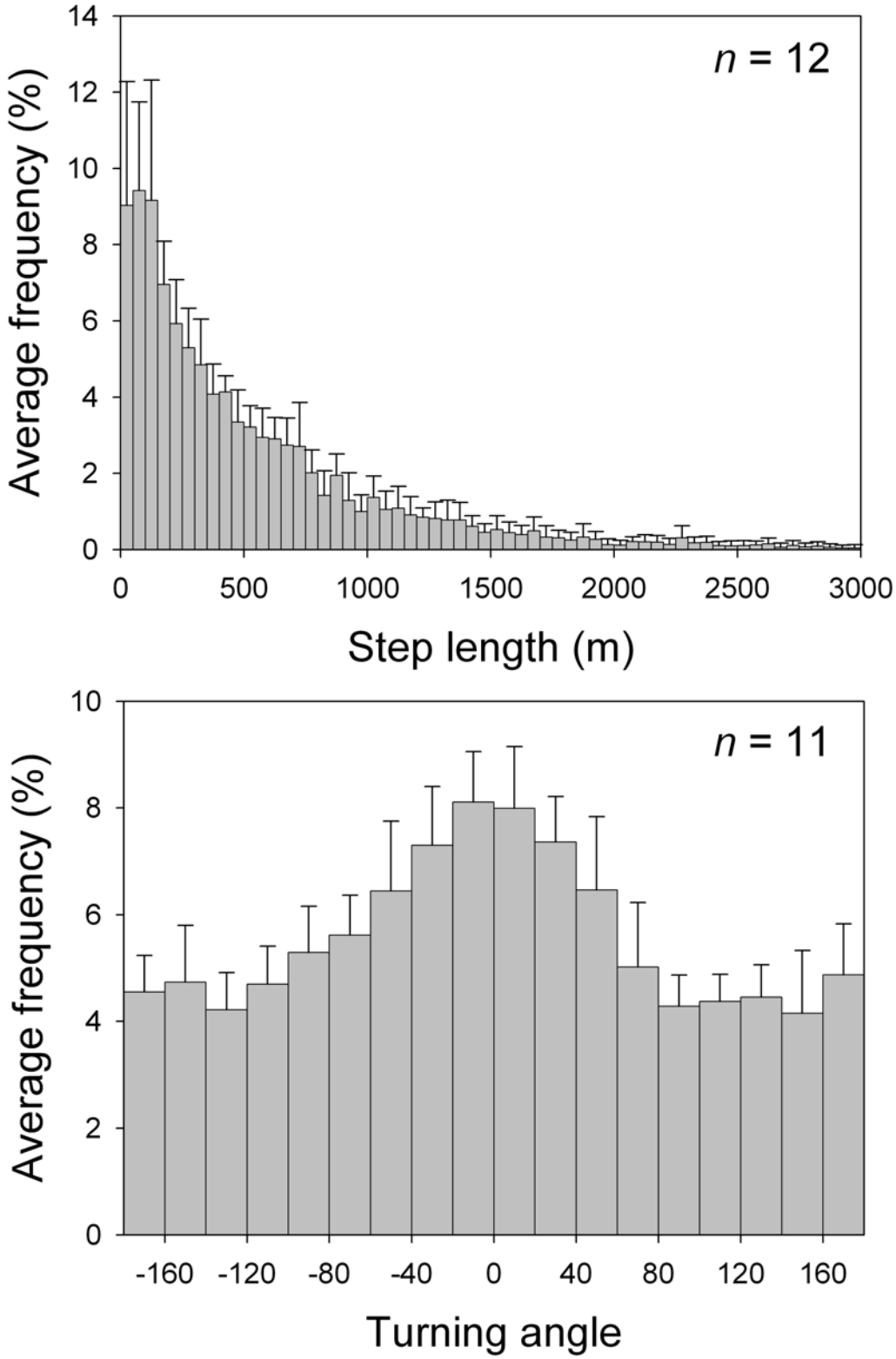
n = 12
Average frequency (%)
Step length (m)
0
2
4
6
8
10
12
14
0
500
1000
1500
2000
2500
3000
n = 11
Average frequency (%)
Turning angle
0
2
4
6
8
10
-160
-120
-80
-40
0
40
80
120
160

Fig. 1

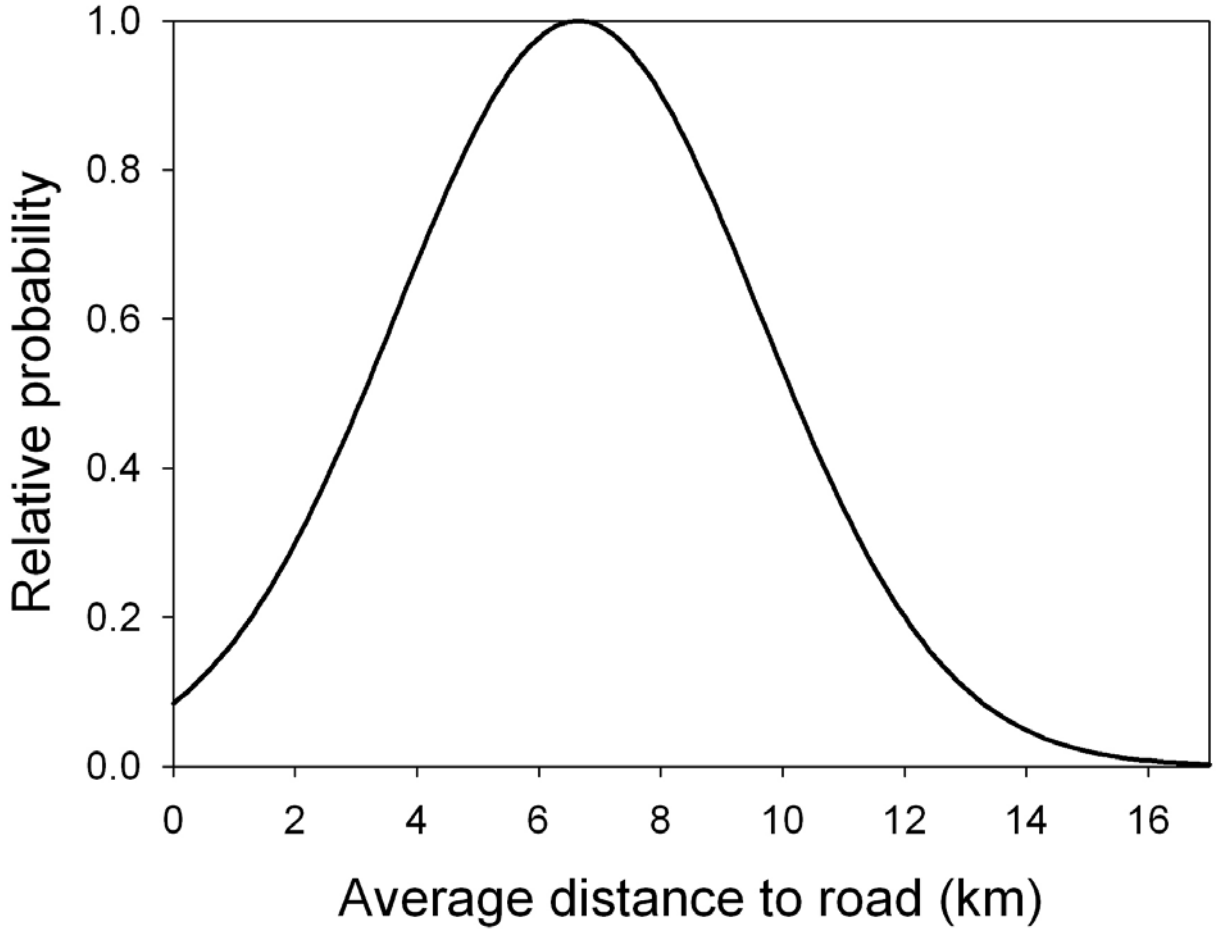
Relative probability
1.0
0.8
0.6
0.4
0.2
0.0
0
2
4
6
8
10
12
14
16
Average distance to road (km)

Fig. 2

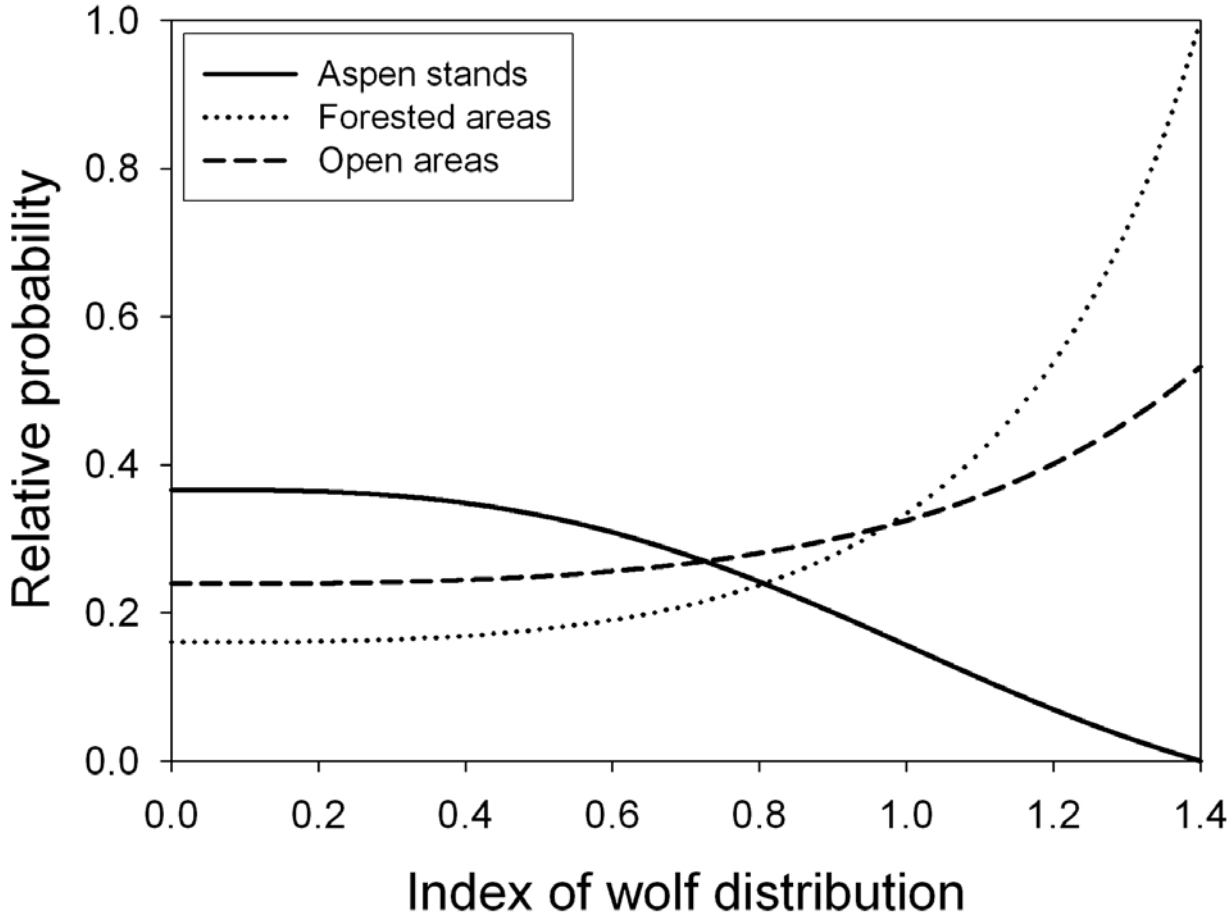
Aspen stands
Forested areas
Open areas
Relative probability
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Index of wolf distribution

Fig. 3

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Daniel Fortin, Hawthorne L. Beyer, Mark S. Boyce, Douglas W. Smith, Thierry Duchesne, Julie S. Mao. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*

Appendix A. Mathematical details on the estimation of valid variance for the regression coefficient estimates of Step Selection Functions

We provide details on the statistical methods used to obtain valid variance estimates for the regression coefficient estimates of Step Selection Functions, considering that our data exhibited within-cluster correlation. Based on Hardin and Hilbe (2003, Section 2.2), we provide a brief overview of the general theory of estimating equations, and we clarify how this theory can be used to derive robust variance estimators when data are autocorrelated within each cluster. Then, we explain how these robust variance estimators can be obtained in the specific case of conditional logistic regression. Finally, we provide a general example of the SAS and S-Plus code that can be used to implement our statistical approach.

Theory of estimating equation

The statistical inference techniques used in our paper (point estimation of, and hypothesis tests on, the value of the regression coefficients in the conditional logistic regression model) are based on the theory of estimating equations. Suppose that we wish to estimate the *p* unknown parameters contained in the vector $\boldsymbol{\beta}$ on the basis of *n* observations. Most estimators, say $\hat{\boldsymbol{\beta}}$, in statistical theory can be viewed as the solution of estimating equations of the form

$$U(\hat{\beta}) = \sum_{i=1}^{n} U_i(\hat{\beta}) = 0 \quad , \qquad \text{(A.1)}$$

where U, U_i and 0 are vectors of dimension *p* by 1. This general equation also applies to conditional logistic regression (we provide specific details in the next section).

Under mild regularity conditions, $U(\hat{\beta})$ in (A.1) will behave approximately like a multivariate normal random vector with mean **0** and variance matrix **B** (see Huber 1967, for the original derivation). If $U(\beta)$ is a function that is continuous and smooth in β, then the approximate normality of $U(\hat{\beta})$ implies the approximate normality of $\hat{\beta}$ (Vaart 1998). More precisely, $\hat{\beta}$ will be approximately normal with mean β and variance **ABA**, where

$$A^{-1} = E\left[-\frac{\partial}{\partial \beta'} U(\beta) \right] .$$

In most situations, the matrix A^{-1} can be estimated by

$$\hat{A}_n^{-1} = -\frac{\partial}{\partial \beta} U(\beta)_{\beta=\hat{\beta}} .$$

When $U_1(\beta), \ldots, U_n(\beta)$ are independent, then $B = Var[U(\beta)]$ can be consistently estimated by the empirical variance matrix based on $U_1(\beta), \ldots, U_n(\beta)$:

$$\hat{B}_n = \sum_{i=1}^{n} U_i\left(\hat{\beta}\right) U'_i\left(\hat{\beta}\right) \quad \text{(A.2)}$$

The variance estimate $\hat{A}_n \hat{B}_n \hat{A}_n$, referred to as sandwich variance estimator, is robust to model misspecification (Huber 1967). However, when the *n* observations are not independent, $\hat{B}_n$ given by (A.2) is not a valid estimator of $B = Var[U(\beta)]$. Since our data exhibit autocorrelation, we must adjust $\hat{B}_n$ to obtain a valid estimator of the variance of $\hat{\beta}$. Fortunately, such an adjustment can be achieved by clustering the data so that observations from different clusters are uncorrelated. Let us suppose that the *n* observations are divided into *K* such clusters, where observations within a cluster may be correlated, but observations from different clusters are uncorrelated. In this case we can rewrite the estimating equation (A.1) as follows:

$$U(\beta) = \sum_{c=1}^{K} \sum_{i=1}^{n_c} U_{c,i}(\beta) = \sum_{c=1}^{K} \widetilde{U}_c(\beta) = 0,$$

where the pair (*c*, *i*) represents the *i*th observation in the *c*th cluster, n_c is the number of observations in the *c*th cluster and $\widetilde{U}_c(\beta)$ is the sum of the estimating functions $U_{c,i}(\beta)$ over all observations in the *c*th cluster. Although the estimating functions $U_{c,i}(\beta)$ are not all uncorrelated, the estimating functions $\widetilde{U}_1(\beta), \ldots, \widetilde{U}_K(\beta)$ are because observations are independent between clusters. This leads to the estimator of $B = Var[U(\beta)]$ given by

$$\hat{B}_n^{Mod} = \sum_{c=1}^{K} \widetilde{U}_c\left(\hat{\beta}\right) \widetilde{U}'_c\left(\hat{\beta}\right) \quad \text{(A.3)}$$

(Hardin and Hilbe 2003, pp. 30-31). Now, by taking $\hat{V}\left(\hat{\beta}\right) = \hat{A}_n \hat{B}_n^{Mod} \hat{A}_n$, we obtain a variance estimator robust to misspecification of the correlation structure within clusters. In other words, the variance estimator $\hat{V}\left(\hat{\beta}\right) = \hat{A}_n \hat{B}_n^{Mod} \hat{A}_n$ remains valid even when the observations within clusters are correlated, as long as there is no correlation between clusters. The estimator (A.3) is the modified robust sandwich estimator (Hardin and Hilbe 2003, p. 31).

Application to SSF parameters estimated with conditional logistic regression

We now apply this general theory to the 1-*M* conditional logistic regression model (Hosmer and Lemeshow 1989, Chapter 7), which is a model where each success (hereafter termed "case") is matched to *M* failures (hereafter termed "controls"). In the case of conditional logistic regression, the estimators of the regression coefficients obtained with the conditional maximum likelihood method are also the solution of an estimating equation. In the 1-*M* case, the estimating function $U_i(\beta)$ is given by

$$U_i(\beta) = \frac{\partial}{\partial \beta} \ln \frac{\exp\left(\beta' x_{i,1}\right)}{\sum_{j \in S_i} \exp\left(\beta' x_{i,j}\right)},$$

where $\boldsymbol{x}_{i,1}$ is the vector of explanatory variables for the case in the *i*th stratum, $\boldsymbol{x}_{i,j}$ is the vector of explanatory variables for the *j*th observation in the *i*th stratum and $j \in S_i$ denotes all observations in the *i*th stratum. This estimating equation corresponds exactly to the partial likelihood score

equation for a stratified proportional hazards model with the case dying and all the controls being censored at a time greater than the case's time of death (Klein and Moeschberger 2003). Lin and Wei (1989) derived the $\hat{A}_n$ and $\hat{B}_n$ matrices for the proportional hazards model. Their results are programmed in the PHREG procedure of SAS as well as in the coxph() function of S-Plus.

In our paper, each stratum corresponds to one observed step matched to 200 random steps. Our analyses revealed that the steps of different animals can be considered as independent. Autocorrelation analyses indicate that the steps of each animal become uncorrelated beyond lag-14. Therefore, we can partition the dataset into clusters such that strata from different clusters are either from a different animal, or if they are from a same animal they are more than 14 lags apart. With such partitioning, we obtain the independence that is required between clusters to calculate a robust variance. If we let *c*, *i*, and *j* respectively denote the clusters, the strata and the observations, with $j = 1$ corresponding to the case and $j > 1$ corresponding to the controls, then we are estimating the regression coefficients β with the estimating equation

$$U(\hat{\beta}) = \sum_{c=1}^{K} \tilde{U}_c(\hat{\beta}) = \sum_{c=1}^{K} \sum_{i=1}^{n_c} \frac{\partial}{\partial \beta} \ln \frac{\exp(\hat{\beta}' x_{c,i,1})}{\sum_{j \in S_i} \exp(\hat{\beta}' x_{c,i,j})} = 0$$

The variance of $\hat{\beta}$ can then be estimated with $\hat{V}(\hat{\beta}) = \hat{A}_n \hat{B}_n^{Mod} \hat{A}_n$. Whereas Lin and Wei (1989) derived the formulas for $\hat{A}_n$ and $\hat{B}_n$, Wei et al. (1989) extended the approach to correlated data by deriving the formula for $\hat{B}_n^{Mod}$. This modified robust sandwich estimator is also available in PHREG (SAS) and coxph (S-Plus or R).

Implementation of the method in SAS and S-Plus

We provide a typical example of how this method can be implemented in SAS (SAS Institute Inc. 1999, Version 8.1, Cary, NC, USA) and S-Plus (S-Plus, Version 6.2, Insightful Corporation, Seattle, Washington, USA). For each observation (observation = step) in the dataset, let `stratum`, `clus`, `faketime` and `case` be the variables containing the stratum and cluster identification numbers, a fake time value (1 for a case, 2 for a control) and the case indicator (1 for a case, 0 for a control), respectively. Again for each observation, let `x1`, `x2`, …, `xp` be the *p* explanatory variables of interest.

In SAS (Version 8.1), if one reads all the variables described above in a dataset called `mydata`, then the PHREG procedure can be used directly to obtain the regression coefficient estimates as well as their robust standard errors:

```
PROC PHREG DATA=mydata COVSANDWICH;
  MODEL faketime*case(0) = x1 x2 … xp;
  STRATA stratum;
  ID clus;
RUN;
```

In S-Plus (Version 6.2) or R, the equivalent code used the coxph() function:

```
> myfit <-coxph(Surv(faketime,case)~x1+
+ x2+…+xp+strata(stratum)+cluster(clus),
+ robust=T,data=mydata)
```

Literature Cited

Hardin, J. W., and J. M. Hilbe. 2003. Generalized estimating equations. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Hosmer, D. M., and S. Lemeshow. 1989. Applied logistic regression. John Wiley and Sons, New York, New York, USA.

Huber, P. J. 1967. The behavior of maximum likelihood estimates under non-standard conditions. Proceedings of the Fifth Berkeley Symposium on Mathematical Statistics and Probability **1**:221-233.

Klein, J. P., and M. L. Moeschberger. 2003. Survival analysis: techniques for censored and truncated data. Second edition. Springer-Verlag, New York, New York, USA.

Lin, D. Y., and L. J. Wei. 1989. The robust inference for the Cox proportional hazards model. Journal of the American Statistical Association **84**:1074-1079.

van der Vaart, A. W. 1998. Asymptotic statistics. Cambridge University Press, Cambridge, UK.

Wei, L. J., D. Y. Lin, and L. Weissfeld. 1989. Regression-analysis of multivariate incomplete failure time data by modeling marginal distributions. Journal of the American Statistical Association **84**:1065-1073.