

Spatial Partitioning of Predation Risk in a Multiple Predator–Multiple Prey System

TODD C. ATWOOD,¹ *Department of Wildland Resources, Utah State University, Logan, UT 84322, USA*

ERIC M. GESE, *United States Department of Agriculture/Animal and Plant Health Inspection Service/Wildlife Services/National Wildlife Research Center and Department of Wildland Resources, Utah State University, Logan, UT 84322, USA*

KYRAN E. KUNKEL, *Department of Wildland Resources, Utah State University, Logan, UT 84322, USA*

ABSTRACT Minimizing risk of predation from multiple predators can be difficult, particularly when the risk effects of one predator species may influence vulnerability to a second predator species. We decomposed spatial risk of predation in a 2-predator, 2-prey system into relative risk of encounter and, given an encounter, conditional relative risk of being killed. Then, we generated spatially explicit functions of total risk of predation for each prey species (elk [*Cervus elaphus*] and mule deer [*Odocoileus hemionus*]) by combining risks of encounter and kill. For both mule deer and elk, topographic and vegetation type effects, along with resource selection by their primary predator (cougars [*Puma concolor*] and wolves [*Canis lupus*], respectively), strongly influenced risk of encounter. Following an encounter, topographic and vegetation type effects altered the risk of predation for both ungulates. For mule deer, risk of direct predation was largely a function of cougar resource selection. However, for elk, risk of direct predation was not only a function of wolf occurrence, but also of habitat attributes that increased elk vulnerability to predation following an encounter. Our analysis of stage-based (i.e., encounter and kill) predation indicates that the risk effect of elk shifting to structurally complex habitat may ameliorate risk of direct predation by wolves but exacerbate risk of direct predation by cougars. Information on spatiotemporal patterns of predation will become increasingly important as state agencies in the western United States face pressure to integrate predator and prey management. (JOURNAL OF WILDLIFE MANAGEMENT 73(6):876–884; 2009)

DOI: 10.2193/2008-325

KEY WORDS antipredator behavior, functional response, habitat attributes, predation, risk enhancement, spatial modeling.

Theory suggests that predation effects of multiple predators can vary relative to the nature of the predator–predator interaction. Predation risk for shared prey may increase when risk effects (i.e., antipredator behavioral responses; Creel and Christianson 2008) of one predator species facilitates direct (i.e., lethal) predation by another species (Paine 1974, Kerfoot and Sih 1987, Soluk 1993, Losey and Denno 1998). For example, prey may be able to reduce risk of direct predation from a primary predator by shifting patterns of diel microhabitat use, thereby avoiding preferred hunting habitat (Fraser et al. 2004). However, in avoiding habitats preferred by the primary predator (a risk effect), prey may expose themselves to direct predation by a secondary predator (Kotler et al. 1993, Soluk 1993, Fraser et al. 2004). This form of predator facilitation predominantly occurs when a predator induces a phenotypic response from prey that increases its overall vulnerability to direct predation from other species (Soluk and Collins 1988, Kotler et al. 1993). However, it should not be assumed that direct predation by multiple predators is always additive. Indeed, cumulative direct predation can be less than predicted based on direct predation by each species separately (Sih et al. 1998). For example, introduction of an additional predator species can cause competition and interference (antagonism) among predators, resulting in reduced risk of direct predation for shared prey (Rosenheim et al. 1993). Whether multiple predator effects increase or reduce risk of direct predation depends largely on how prey respond behaviorally to potentially simultaneous threats.

Recently, several studies have documented shifts by elk (*Cervus elaphus*) from structurally simple (e.g., grasslands and shrub-steppe) to structurally complex (aspen and mixed conifer) vegetation types, presumably in attempts to lessen predation risk from wolves (*Canis lupus*; Creel and Winnie 2005, Fortin et al. 2005, Atwood et al. 2007). Although these behavioral shifts may have the primary effect of reducing risk of direct predation associated with wolves, they may have the secondary effect of making elk more vulnerable to direct predation by cougars (*Puma concolor*), which prefer to hunt structurally complex habitats (Kunkel et al. 1999, Atwood et al. 2007). In areas where elk are sympatric with mule deer (*Odocoileus hemionus*), wolf-induced habitat shifts may alter risk of direct predation by cougars for both prey species. For example, wolf-induced habitat shifts by elk could result in a decrease in either risk of being encountered or killed by wolves, while increasing either of those risks with respect to cougars. In such a scenario, risk of encounter and (or) death may be reduced for mule deer as elk retreat to structurally complex refugia habitat already occupied by mule deer. Spatial distribution of cumulative risk of direct predation is increased but compensatory for elk if accompanied by a corresponding decline in direct predation by wolves, and is reduced for mule deer (assuming mule deer are not displaced by elk) as elk dilute risk of direct predation by cougars in structurally complex habitat. Detecting these processes is important when population-level consequences are a concern; total risk of direct predation may not be the sum of its constituent parts.

Risk of direct predation, as derived from the functional response of Holling's (1959) disk equation, can be

¹ E-mail: todd.c.atwood@aphis.usda.gov

decomposed into the relative risk of prey being encountered (α) and the relative risk of being killed given an encounter (d ; Lima and Dill 1990). In systems where multiple predator species share prey but partition other resources or employ discrepant hunting strategies (e.g., coursing vs. ambush), α and d can change with habitat for a given predator and influence not only spatial distribution of risk of direct predation, but whether that risk is increased or reduced, because predators place behavioral constraints on prey by forcing trade-offs between predator avoidance and resource acquisition (Sih 1987, Lima and Dill 1990, Preisser et al. 2005). In simple systems (i.e., 1-predator, 1-prey) prey may be able to balance those trade-offs by shifting to a given suite of habitat attributes that reduces α or d (Soluk 1993, Hampton 2004, Fortin et al. 2005). However, in more complex systems (e.g., 2-predator, 2-prey), shifts to habitat attributes that reduce α or d for one predator may actually increase α or d for a second predator. Thus, for us to better understand multiple predator effects, it will be important to predict the conditions under which habitat attribute trade-offs influence α and d and, in turn, how those may mediate spatial distribution of risk of direct predation.

The reintroduction of wolves to Yellowstone National Park (YNP), and their subsequent recolonization of the Greater Yellowstone Ecosystem (GYE), provides a unique opportunity to elucidate effects of multiple predators on shared prey. In this regard, our goals were 3-fold: 1) to develop statistical models for risk of direct predation on elk and mule deer in a multipredator, multiprey system, 2) to explicitly link behavioral risk effects (via predator and prey resource selection) and spatial distribution of direct predation risk, and 3) to determine if sympatric wolves and cougars increased risk of direct predation on elk and mule deer. To those ends, we modeled α and d for each predator-prey pair, and based on these relationships, mapped cumulative risk of direct predation to examine its spatial distribution and to evaluate whether there were overlapping areas where risk may be increased.

STUDY AREA

We conducted our study in the Northern Madison Study Area (NMSA; 680 km²), located in southwest Montana's Madison Range of the Rocky Mountains, USA, during December through April of 2002–2005. The NMSA was approximately 50 km northwest of YNP and was bordered on the east by the Gallatin River, on the west by the Madison River, and on the south by the Spanish Peaks of the Gallatin National Forest. Shrub-steppe habitat (535 km²) dominated the NMSA; coniferous forest (145 km²) comprised approximately 23% of the remaining area. Elevations range from 1,300 m on the Madison River floodplain to 2,500 m in the Spanish Peaks. Vegetation tracked elevation, with xeric grassland-juniper (*Juniperus scopulorum*) savannah at lower elevations and closed-canopy Douglas fir (*Pseudotsuga menziesii*) or lodgepole pine (*Pinus contorta*) forests on mesic sites at higher elevations. High-elevation xeric sites occurred on southern exposures and ridgelines and were predominantly mountain big sage

(*Artemisia tridentata*)-grassland mosaics. Temperatures ranged from highs of 21–32°C in summer to lows of –34°C in winter.

The Bear Trap wolf pack (pack size 2–8 individuals) recolonized the NMSA in winter of 2002, representing the recolonizing front of wolves in the Madison Range. Cougars, grizzly bears (*Ursus arctos*), black bears (*U. americanus*), and coyotes (*Canis latrans*) also were present in the NMSA. Resident ungulates included elk, mule deer, white-tailed deer (*Odocoileus virginianus*), and moose (*Alces alces*). The NMSA was privately owned and elk were managed for trophy hunting, whereas mule deer remained unexploited.

METHODS

Determining Effects of Multiple Predators

We determined ungulate numbers annually by fixed-wing aerial transect surveys. We stratified transect subunits based on ungulate densities observed on previous flights and we applied a sightability model (Singer and Garton 1992) to reduce habitat-related bias in estimates. We located elk and mule deer kills by continuous snow-tracking of wolves and cougars initiated within 24 hours of snowfall. During tracking sessions, we recorded the spatial intersection of wolves, cougars, elk, and mule deer and classified intersections of predator and prey tracks as encounters (α) if evidence indicated a chase ensued. We defined kill sites (d) as locations where chases ended in kills (Hebblewhite et al. 2005). We used a key adapted from Kunkel et al. (1999) to characterize predator-specific injury patterns and behavior such as point of attack, method of killing, and diameter and spacing of puncture wounds. We differentiated kills from scavenging by occurrence of chase trails and presence of subcutaneous hemorrhaging.

We collected spatial data for wolves and cougars during continuous snow-tracking sessions in which we initially searched for tracks by bisecting expected travel routes and continued backtracking from kill sites. To address concerns of autocorrelation, we sampled habitat characteristics of wolf and cougar point locations at 800-m intervals (Bergmann et al. 2006). We located mule deer and elk using systematic (daily) ground-based radiotelemetry (mule deer) and direct observation via 15–45× spotting scopes (mule deer and elk). We backtracked elk and mule deer located via spotting scopes to random distances of 100 m to 1,000 m to minimize potential for bias in sightability relative to habitat type. Collection of data on habitat characteristics at radiotelemetry point and backtracking locations occurred after elk and mule deer left the general area. We considered point locations separated by a 24-hour interval to be spatially independent. Research protocols were approved by Institutional Animal Care and Use Committees at Utah State University (approval no. 1113) and the National Wildlife Research Center (QA-1195).

Resource Selection Modeling

For each independent animal location, we chose 3 random sites to represent resource availability. We selected random

sites from circular buffers centered on individual animal locations (Arthur et al. 1996, Johnson et al. 2006) with radii equal to the mean Euclidean distance ($\bar{x} = 915$ m, SE = 427 m) between consecutive daily locations for ungulates. Resource use and availability were related to 6 categorical vegetation type (i.e., conifer, juniper, riparian, grassland, shrub-steppe, and aspect) and aspect variables, and 5 continuous variables (i.e., distance from road and water features [m], elevation in [m], slope [$^{\circ}$], and snow depth [cm]). We modeled categorical habitat and aspect variables using dummy variable coding, excluding reference categories.

We pooled location data across individuals and used resource selection functions (RSF) to develop population-level models of use versus availability of habitat attributes for prey and predators. We then used RSF and resource selection probability functions (RSPF) to test for differences in effects of topography and vegetation type on predation stages (α and d). We estimated RSF via logistic regression using the following formula:

$$w(\mathbf{x}) = \exp(\beta_1 X_1 + \beta_2 X_2 + \dots + \beta_p X_p) \quad (1)$$

where $w(\mathbf{x})$ is an index of relative probability of use of a given site and β_1 is the selection coefficient of resource variable X_1 (Manly et al. 2002). In designs with used and available units, the true population-sampling fraction is unknown and the resulting RSF is actually a relative probability because the intercept or β_0 coefficient is incorrectly scaled (Boyce and McDonald 1999). Thus, following Manly et al. (2002) and Hebblewhite et al. (2005) we dropped the intercept and denominator from the logistic form for this relative function. Accordingly, the RSF for relative risk of a given predator species encountering a given prey species took the form:

$$\alpha(x) = \exp\left(\sum \beta_i x_i\right) \quad (2)$$

where i refers to landscape variables 1 through n for encounters (obtained through snow-tracking) and available locations. In models of prey and predator resource selection and predator encounter, we compared attributes of used sites to attributes of random available sites.

Because our data set consisted of encounters and, thus, that fraction of encounters resulting in kills, we extended our use of RSF for predator-prey pairs to estimate conditional relative risk of death given an encounter $d(x)$ as a function of habitat attributes. Following Hebblewhite et al. (2005), we coded kill locations as used and encounter locations where no kill occurred as unused. When data consist of known encounters, the used-unused distinction corresponds to a true probability function (RSPF), and conditional relative risk of a kill given an encounter is expressed in the full logistic form:

$$d(x) = \left[\exp\left(\beta_0 + \sum \beta_i x_i\right) / 1 + \exp\left(\beta_0 + \sum \beta_i x_i\right) \right] \quad (3)$$

where i refers to landscape variables 1 through n for kills and encounters. Unlike equation 2, the intercept is included

because the sampling probability is known and a true probability function is estimated (Manly et al. 2002). We estimated individual (predator-prey pair) RSF (eq 2) and RSPF (eq 3) models for kill and encounter stages of wolf and cougar predation on elk and mule deer. We then substituted individual estimates of $\alpha(x)$ and $d(x)$ into a reformulation (Lima and Dill 1990) of Holling's (1959) functional response to generate a spatially explicit estimate of the relative magnitude of variation in direct predation risk, $P(k)$, across habitat types (Hebblewhite et al. 2005):

$$P(k) = 1 - \exp^{-\alpha d T} \quad (4)$$

where α and d are relative risk of encounter and conditional relative risk of kill, respectively, and T is the time interval over which we are integrating variation in predation risk.

We used a constrained model selection approach to select consistent sets of parameters to compare across individual predation risk models. This method resulted in consistent covariance matrices, which allowed us to directly compare coefficients from encounter and predation models (Hosmer and Lemeshow 2000). We first created sets of hypothesized resource selection and encounter-predation candidate models and then fit RSF and RSPF models. We used Akaike's Information Criterion (AIC_c) to rank models based on Akaike weights (w_i) for each model (Burnham and Anderson 1998). Following Burnham and Anderson (1998), we used the sum of all w_i for each variable to rank them in order of importance. For each prey species, we used the same set of landscape attributes from the ranked set of top models to build comparative models for the encounter and kill stages of predation.

For all logistic regression analyses, we checked continuous variables for conformity to linearity using the quartile method (Hosmer and Lemeshow 2000). We ensured final model fit by testing with the Hosmer and Lemeshow goodness-of-fit statistic (Hosmer and Lemeshow 2000). We evaluated predictive performance of models using k -fold cross validation (Boyce et al. 2002), where we partitioned the model data set following a test-to-training ratio of 20% (i.e., 5 subsets). Finally, we assessed predictive capacity using Spearman rank correlations (r_s) between grouped training and test data with a test-to-training ratio of 20% (Fielding and Bell 1997).

RESULTS

Over the 3 winters, we tracked wolves for 518 km ($n = 57$ tracking sessions) and cougars for 272 km ($n = 28$ tracking sessions). We located 211 predator-killed elk ($n = 123$) and mule deer ($n = 88$) during the study. Wolves killed the most (70%) elk, whereas the remaining 30% of elk and 95% of mule deer kills were attributed to cougars. We found 160 spatial encounters (i.e., intersecting tracks) between elk and wolves that resulted in a chase sequence, 86 of which resulted in kills. For cougars, 37 of 60 spatial encounters with elk and 84 of 146 spatial encounters with mule deer resulted in kills. We had sufficient numbers of spatial encounters and kills to partition risk of predation for elk

Table 1. Akaike weights (w_i) for variables evaluated in resource selection function and resource selection probability function models for mule deer and cougar resource selection and encounter and kill stages of predation on the Northern Madison Study Area, Montana, USA, 2002–2005. Shown are the Akaike's Information Criterion (AIC_c) weights for each variable averaged over all selection functions (mule deer, cougar, encounter, and kill), and the average rank of variable importance.

| Variable | Mule deer | Cougar | Encounter | Kill | Mean AIC _c wt (w_i) | Mean rank |
|---------------------|-----------|--------|-----------|-------|------------------------------------|-----------|
| Juniper | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1 |
| S aspect | 0.978 | 1.000 | 1.000 | 1.000 | 0.994 | 2 |
| Distance from water | 1.000 | 0.803 | 0.987 | 1.000 | 0.947 | 3 |
| Distance from road | 0.974 | 0.789 | 0.941 | 1.000 | 0.926 | 4 |
| Slope | 1.000 | 0.802 | 0.671 | 0.998 | 0.867 | 5 |
| Elevation | 1.000 | 0.803 | 1.000 | 0.231 | 0.758 | 6 |
| Shrub-steppe | 0.726 | 0.774 | 0.439 | 0.226 | 0.541 | 7 |
| Riparian | 0.293 | 0.704 | 0.158 | 0.224 | 0.345 | 8 |
| Grassland | 0.296 | 0.902 | 0.108 | 0.023 | 0.332 | 9 |
| W aspect | 0.061 | 0.000 | 0.000 | 0.000 | 0.015 | 10 |
| Conifer | 0.000 | 0.004 | 0.000 | 0.000 | 0.001 | 11 |
| Snow depth | 0.000 | 0.001 | 0.001 | 0.000 | 0.001 | 11 |
| E aspect | 0.001 | 0.001 | 0.000 | 0.000 | 0.001 | 11 |
| N aspect | 0.001 | 0.001 | 0.000 | 0.000 | 0.001 | 11 |

among wolves and cougars. However, because most mule deer kills were attributable to cougars ($n = 84$ out of 88), we were unable to partition mule deer predation among predators, and mule deer risk of predation solely reflects risk of predation by cougars.

Following the arrival of wolves, elk abundance increased 5% in 2003, declined 24% in 2004, and increased 33% in 2005. Declining elk abundance in 2004 was attributed to a large herd (≈ 550 – 650 animals) temporarily leaving the study area (Atwood 2006). Mule deer abundance increased by an average of 16% over the duration of our research (Atwood 2006). Throughout the study, elk were numerically superior ($2,416 \pm 423$; $\bar{x}_{2003-2005} \pm SE$) and, on average, comprised 72% of the total ungulate availability; white-tailed deer (550 ± 119 ; $\bar{x}_{2003-2005} \pm SE$) and mule deer (425 ± 133 ; $\bar{x}_{2003-2005} \pm SE$) comprised 16% and 12%, respectively.

Resource Selection Modeling

Despite some overlap in the variables retained in the best models of elk and mule deer resource selection (Tables 1–2), there were important differences in the use of landscape attributes (Table 3). Probability of elk occurrence on the

NMSA increased in riparian ($\beta = 2.502$), grassland ($\beta = 2.274$), shrub-steppe ($\beta = 2.186$), and juniper savanna ($\beta = 2.313$) habitats and with decreasing distance to water ($\beta = 0.0001$). Elk probability of occurrence decreased on south aspects ($\beta = -0.714$), and with increasing elevation ($\beta = -0.001$), slope ($\beta = -0.026$), and distance from roads ($\beta = -0.0003$). Probability of mule deer occurrence increased on steeper slopes ($\beta = 0.018$), in juniper savanna ($\beta = 3.337$), shrub-steppe ($\beta = 1.105$), and grassland ($\beta = 1.960$) habitats, on south aspects ($\beta = 0.625$), and with distance from water ($\beta = 0.002$). Probability of mule deer occurrence decreased in riparian ($\beta = -2.271$) habitat and with increasing elevation ($\beta = -0.011$) and distance from roads ($\beta = -0.002$).

Similar to prey models, wolves and cougars differed in their use of key landscape attributes (Table 3). Probability of wolf occurrence increased on south aspects ($\beta = 0.956$) and in riparian ($\beta = 1.916$), grassland ($\beta = 0.766$), and shrub-steppe ($\beta = 1.688$) habitats and decreased in juniper savanna habitat ($\beta = -14.724$) and with increasing elevation ($\beta = -0.001$) and distance from roads ($\beta = -0.0003$) and water ($\beta = -0.0002$). Probability of cougar occurrence increased on south aspects ($\beta = 1.139$), steeper slopes ($\beta = 0.076$),

Table 2. Akaike's Information Criterion (AIC_c) weights (w_i) for covariates evaluated in resource selection function and resource selection probability function models for elk, wolf, and cougar resource selection and encounter and kill stages of predation on the Northern Madison Study Area, Montana, USA, 2002–2005. Shown are the Akaike weights for each variable, average weight across all models, and average rank of variable importance.

| Variable | Elk | Wolf | Cougar | Encounter | Kill | Mean AIC _c wt (w_i) | Mean rank |
|---------------------|-------|-------|--------|-----------|-------|------------------------------------|-----------|
| S aspect | 0.991 | 0.866 | 0.994 | 0.911 | 0.996 | 0.952 | 1 |
| Riparian | 1.000 | 1.000 | 0.704 | 1.000 | 0.988 | 0.938 | 2 |
| Elevation | 1.000 | 0.684 | 0.803 | 0.871 | 0.940 | 0.860 | 3 |
| Distance from water | 1.000 | 0.852 | 0.947 | 0.961 | 0.502 | 0.852 | 4 |
| Grassland | 0.999 | 0.981 | 0.902 | 1.000 | 0.371 | 0.851 | 5 |
| Slope | 0.866 | 0.544 | 0.802 | 0.877 | 0.877 | 0.793 | 6 |
| Distance from road | 0.946 | 0.713 | 0.926 | 0.779 | 0.206 | 0.714 | 7 |
| Shrub-steppe | 0.999 | 0.784 | 0.774 | 0.230 | 0.140 | 0.586 | 8 |
| Juniper | 0.865 | 0.216 | 1.000 | 0.079 | 0.033 | 0.439 | 9 |
| Conifer | 0.134 | 0.121 | 0.001 | 0.014 | 0.033 | 0.061 | 10 |
| W aspect | 0.000 | 0.001 | 0.000 | 0.003 | 0.000 | 0.000 | 11 |
| Snow depth | 0.001 | 0.001 | 0.000 | 0.000 | 0.000 | 0.000 | 11 |
| E aspect | 0.000 | 0.001 | 0.000 | 0.001 | 0.000 | 0.000 | 11 |
| N aspect | 0.000 | 0.001 | 0.000 | 0.001 | 0.000 | 0.000 | 11 |

Table 3. Relative odds ratios of parameter estimates, standard errors, and corresponding *P*-values for independent variables in consistent-set resource selection function models for elk, mule deer, wolf, and cougar resource selection on the Northern Madison Study Area, Montana, USA, 2002–2005.

| Model | Riparian | Grassland | Shrub | Juniper | S | Slope | Elevation | Distance road | Distance water |
|-----------------|----------|-----------|--------|---------|--------|--------|-----------|---------------|----------------|
| Elk | 12.205 | 9.719 | 8.902 | 10.104 | 0.490 | 0.974 | 0.998 | 1.000 | 1.000 |
| SE | 0.641 | 0.457 | 0.457 | 0.479 | 0.222 | 0.013 | 0.0005 | 0.0001 | 0.0001 |
| <i>P</i> -value | <0.001 | <0.001 | <0.001 | <0.001 | 0.001 | 0.042 | 0.198 | 0.001 | 0.118 |
| Mule deer | 0.103 | 7.103 | 3.020 | 3.337 | 1.862 | 1.018 | 0.988 | 0.998 | 1.002 |
| SE | 1.039 | 0.692 | 0.704 | 0.685 | 0.220 | 0.014 | 0.001 | 0.0001 | 0.0001 |
| <i>P</i> -value | 0.029 | 0.005 | 0.116 | <0.001 | 0.005 | 0.214 | <0.001 | <0.001 | <0.001 |
| Wolf | 6.791 | 2.151 | 1.688 | 0.771 | 2.601 | 0.982 | 1.001 | 0.999 | 0.999 |
| SE | 0.414 | 0.274 | 0.277 | 0.301 | 0.164 | 0.013 | 0.0005 | 0.0001 | 0.0001 |
| <i>P</i> -value | <0.001 | 0.005 | 0.059 | 0.961 | <0.001 | 0.144 | 0.038 | 0.009 | 0.013 |
| Cougar | 1.387 | 0.251 | 0.360 | 1.529 | 3.122 | 1.079 | 0.995 | 0.999 | 0.999 |
| SE | 0.547 | 0.333 | 0.321 | 0.300 | 0.205 | 0.011 | 0.001 | 0.0001 | 0.0001 |
| <i>P</i> -value | 0.549 | <0.001 | 0.001 | 0.157 | <0.001 | <0.001 | <0.001 | <0.001 | <0.001 |

and in juniper savanna ($\beta = 0.424$) habitats. Probability of cougar occurrence decreased in shrub-steppe habitat ($\beta = -1.021$), at lower elevations ($\beta = -0.004$), and with distance from roads ($\beta = -0.001$) and water ($\beta = 0.0004$).

Determining Effects of Multiple Predators

Substantial differences existed in constrained models (i.e., constant sets of parameters across individual predation risk models) of landscape attributes of prey encounter and kill stages (Table 4). Based on odds ratios from wolf encounter and kill models, elk were approximately 4 times as likely to be killed on south aspects (2.996) and twice as likely to be killed in riparian habitat (5.185) as opposed to encountered (0.706 and 2.427, respectively). Relative odds of elk being killed in grassland (1.455) and shrub-steppe habitats (1.434) were greater than those of an encounter (1.397 and 1.327, respectively). After an encounter in juniper savanna habitat (1.474), elk were 3.3 times less likely to be killed. There were no pronounced differences in the odds of elk being killed after an encounter relative to slope and distance from roads and water (Table 4). For cougar encounters and kills, elk were approximately 8 times as likely to be killed on south aspects (7.769) and nearly 8 times less likely to be killed in riparian habitat (0.202) as opposed to encountered (0.994 and 1.653, respectively). Relative odds of a cougar killing an elk in grassland habitat (0.391) were slightly less than that of an encounter (0.400), whereas odds of an elk being killed (0.385) following an encounter (1.087) in shrub-steppe habitat decreased by 65%. Finally, after a cougar encounter in juniper savanna habitat (2.411), elk were >17 times less likely to be killed (0.137). Similar to wolves and elk, there were no pronounced differences in odds of elk being killed after cougar encounters relative to slope and distances from road and water (Table 4).

For mule deer, relative odds of being killed in shrub-steppe (3.79) were 10.8 times greater than the odds of being encountered (0.351), whereas odds of being killed in juniper savanna (0.198) were several orders of magnitude less likely than the odds of encounter (7.664). Once encountered, mule deer were 72% less likely to be killed on south aspects (encounter odds ratio = 3.202; kill odds ratio = 0.904).

There were no differences in odds of mule deer being encountered and killed relative to elevation, slope, and distances from road and water (Table 4).

Partitioning Total Risk of Direct Predation

Elk used riparian, grassland, shrub-steppe, and juniper savanna vegetation types more than wolves and cougars (Table 3). Both predators used south aspects more than elk, and wolves used riparian, grassland, and shrub-steppe habitat substantially more than cougars. Thus, elk–predator encounters were concentrated on south aspects and in open valley bottoms or shrub-steppe benches. For wolf–elk interactions, strength of vegetation type overwhelmed otherwise significant topographic effects; given an encounter, vegetation type appeared to have the strongest effect on the risk of being killed (Table 4). By contrast, in cougar–elk interactions, the topographic effect of aspect overwhelmed effects of other variables; given a cougar encounter on south aspects, risk of death increased and was 2.5 times greater than risk associated with wolves. For elk, cumulative risk of direct predation was primarily attributed to increased risk of death following encounters with wolves in riparian, grassland, and shrub-steppe. Secondarily, elk experienced increased risk of encountering cougars in juniper savanna and increased risk of death following encounters with wolves and cougars on south aspects (Table 4; Fig. 1). In general, conditional relative risk of an elk kill increased where relative odds of wolf occurrence were substantially greater than those for cougars, but overlap in risk of death likely occurred on south aspects (Table 4).

Mule deer used juniper savanna twice as much as cougars and used south aspects and shrub-steppe less than cougars (Table 3). Mule deer–cougar interactions were concentrated on south aspect–juniper savanna associations (Fig. 1), and the topographic effect of aspect was stronger than that of vegetation type (i.e., juniper savanna). For mule deer, relative odds of risk of death following an encounter were generally lower than those for elk. The exception was for shrub-steppe habitat where, given an encounter, risk of death was 10.8 times greater (Table 4). Thus, for mule deer, total risk of direct predation could be decomposed into the

Table 4. Relative odds ratios of parameter estimates, standard errors, and corresponding *P*-values for independent variables in consistent-set resource selection function and resource selection probability function models for elk and mule deer predation encounter stages on the Northern Madison Study Area, Montana, USA, 2002–2005. Note that mule deer models are for cougar predation only.

| Model | <i>N</i> | Riparian | Grassland | Shrub | Juniper | S | Slope | Elevation | Distance road | Distance water |
|------------------------|----------|----------|-----------|-------|---------|-------|-------|-----------|---------------|----------------|
| Mule deer-encounter | 1,062 | | | 0.351 | 7.664 | 3.202 | 1.028 | 0.986 | 0.998 | 1.002 |
| SE | | | | 0.718 | 0.444 | 0.393 | 0.024 | 0.002 | 0.0003 | 0.0002 |
| <i>P</i> -value | | | | 0.145 | <0.001 | 0.003 | 0.258 | <0.001 | <0.001 | <0.001 |
| Mule deer-predation | 146 | | | 3.799 | 0.198 | 0.904 | 1.077 | 1.004 | 1.002 | 0.999 |
| SE | | | | 0.875 | 0.611 | 0.447 | 0.028 | 0.001 | 0.0003 | 0.0006 |
| <i>P</i> -value | | | | 0.007 | 0.008 | 0.822 | 0.009 | 0.313 | 0.001 | 0.002 |
| Elk-encounter (wolf) | 1,097 | 2.427 | 1.397 | 1.327 | 1.474 | 0.706 | 0.966 | 1.000 | 0.999 | 0.999 |
| SE | | 0.609 | 0.414 | 0.439 | 0.467 | 0.290 | 0.017 | 0.001 | 0.0001 | 0.0001 |
| <i>P</i> -value | | 0.006 | 0.019 | 0.019 | 0.407 | 0.231 | 0.047 | 0.568 | 0.132 | 0.006 |
| Elk-predation (wolf) | 220 | 5.185 | 1.455 | 1.434 | 0.441 | 2.996 | 1.052 | 0.999 | 0.999 | 0.999 |
| SE | | 0.710 | 0.555 | 0.578 | 0.660 | 0.362 | 0.022 | 0.0001 | 0.0002 | 0.0002 |
| <i>P</i> -value | | 0.020 | 0.499 | 0.533 | 0.215 | 0.002 | 0.016 | 0.313 | 0.225 | 0.225 |
| Elk-encounter (cougar) | 1,023 | 1.653 | 0.400 | 1.087 | 2.411 | 0.994 | 1.031 | 0.994 | 0.999 | 0.999 |
| SE | | 1.421 | 1.033 | 0.942 | 0.869 | 0.549 | 0.031 | 0.002 | 0.003 | 0.003 |
| <i>P</i> -value | | 0.723 | 0.375 | 0.929 | 0.312 | 0.926 | 0.326 | 0.001 | 0.005 | 0.239 |
| Elk-predation (cougar) | 58 | 0.202 | 0.391 | 0.385 | 0.137 | 7.769 | 1.185 | 0.999 | 0.999 | 0.999 |
| SE | | 2.184 | 1.517 | 1.484 | 1.449 | 0.898 | 0.056 | 0.003 | 0.006 | 0.005 |
| <i>P</i> -value | | 0.464 | 0.536 | 0.519 | 0.170 | 0.022 | 0.002 | 0.638 | 0.647 | 0.824 |

following: encounter risk in juniper savanna and on south aspects and risk of death in shrub-steppe (Table 4). It is noteworthy that risk of direct predation for mule deer was greater in shrub-steppe, given that all mule deer mortalities were attributable to cougars in our RSPF, which suggests that shrub-steppe can be associated with risk of predation from cougars and represents another vegetation type where risk of predation from wolves and cougars may overlap.

In all models, most predictor variables were selected for, and models containing the top 9 variables were consistently ranked either first or second (Table 5). Based on Hosmer–Lemeshow tests, all final models displayed adequate fit (Table 5). Spearman rank correlations from the *k*-fold cross-validation indicated a strong relationship between the training and test data (Table 5). Given the above, we felt justified in using the consistent-set modeling approach to compare covariates across models.

DISCUSSION

We found that risk of direct predation for mule deer was primarily a function of habitat selection by cougars, and landscape attributes selected by deer following encounters with cougars did not render deer more vulnerable to predation. By contrast, risk of direct predation for elk was not only a function of where wolves were, but also of landscape attributes that increased elk vulnerability to predation following an encounter. Based on our analyses of predation stages, the risk effect of elk shifting to structurally complex habitats (i.e., juniper) may ameliorate risk of direct predation from wolves, but in turn, exacerbate risk of direct predation from cougars. Consistent with findings from other systems (e.g., aquatic communities: Soluk 1993, Peckarsky and McIntosh 1998, Hampton 2004), our results suggest there is potential for predator–prey interactions in large-mammal systems to be modified by presence of >1 predator species.

For elk, risk of direct predation was less of a function of predator resource selection and more related to vegetation type. By contrast, most vegetation types did not increase risk of death for mule deer following a predator encounter, and mule deer and cougar resource selection were closely related. Thus, relative to elk, vegetation types selected by mule deer generally rendered them less vulnerable to direct predation, and predation risk was largely a function of predator resource selection. It is notable that risk of death declined for both elk and mule deer in juniper savanna, presumably for 2 reasons. First, juniper savanna was used intensively by both elk and mule deer, and simultaneous use may have diluted relative risk of direct predation for one prey species. Because elk were more abundant on the NMSA, mule deer would likely benefit the most from this dilution of risk. Second, vegetative cover may have impeded search efficiency of wolves, thereby reducing prey catchability (Kunkel et al. 2004, Hopcraft et al. 2005). For the latter, relative odds of both elk and mule deer being killed in juniper savanna were lower than odds of encounter. With regards to the former, use of juniper savanna by elk, mule deer, and cougars was greater than use by wolves. Thus, risk of direct predation in

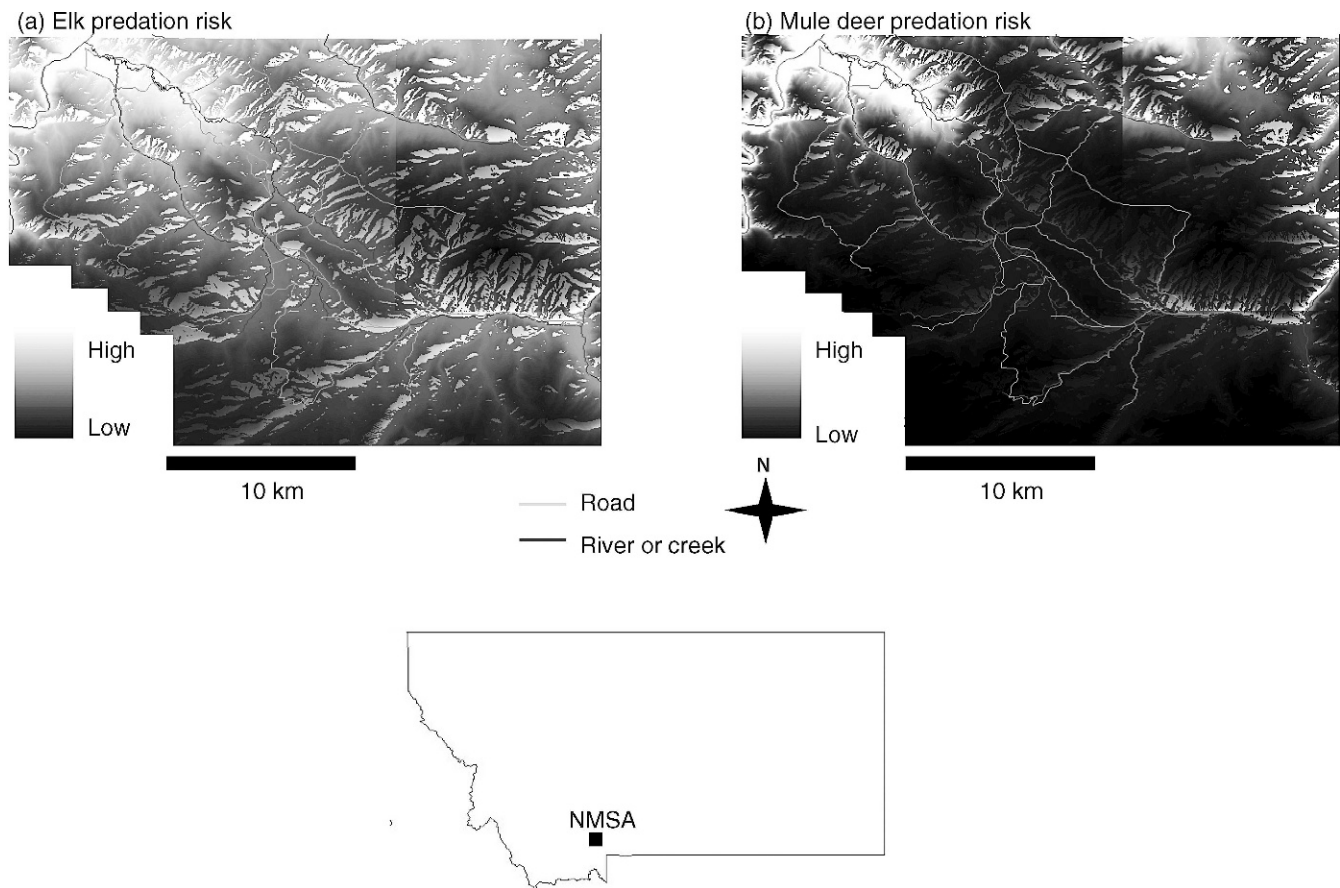


Figure 1. Spatial distribution of total predation risk for (a) elk and (b) mule deer on the Northern Madison Study Area (NMSA), Montana, USA, 2002–2005. Total predation risk for elk is composed of risk of encountering wolves and cougars and risk of death given an encounter. Total predation risk for mule deer is composed of risk of encountering a cougar and risk of death given an encounter.

juniper savanna could be primarily attributed to risk of direct predation from cougars, and this further dilution of predation risk may have made juniper savanna the most effective refugia for prey.

Recent research within the GYE indicates elk may indeed be avoiding areas of intense wolf activity (Creel and Winnie 2005, Fortin et al. 2005), presumably in response to perceived elevation of predation risk. Based on our analyses of predation stages, shifts to structurally complex vegetation types by elk may ameliorate risk of direct predation from

wolves, but in turn, exacerbate risk of direct predation from cougars. For example, elk were more vulnerable to wolf predation in open vegetation types (e.g., grassland, shrub-steppe), and although shifting to juniper savanna decreased odds of encountering wolves, it increased odds of encountering cougars. As a result, use of putative refugia vegetation types merely resulted in a shift of risk of direct predation (Fraser et al. 2004, Hampton 2004) from wolves to cougars. Indeed, during our short study, we saw a steady increase in cougar predation on elk, with the ratio of mule deer:elk

Table 5. Model fit and cross validation with standard error of ability to predict relative probabilities of 1) resource use by mule deer, elk, wolves, and cougars, 2) relative risk of mule deer and elk predator encounters, and 3) conditional relative risk of mule deer and elk being killed by predators, given an encounter, on the Northern Madison Study Area, Montana, USA, 2002–2005.

| Model | k_i | HL χ^2 ^a | HL P -value | Likelihood ratio χ^2 | Likelihood ratio P -value | k -folds cross-validation (r_c) | SE |
|------------------------|-------|--------------------------|---------------|---------------------------|-----------------------------|---------------------------------------|------|
| Mule deer | 7 | 7.36 | 0.518 | 112.30 | <0.001 | 0.92 | 0.02 |
| Elk | 9 | 9.11 | 0.461 | 823.42 | <0.001 | 0.73 | 0.04 |
| Wolf | 9 | 5.46 | 0.707 | 119.49 | <0.001 | 0.82 | 0.04 |
| Cougar | 7/9 | 10.70 | 0.219 | 233.12 | <0.001 | 0.77 | 0.05 |
| Mule deer-encounter | 7 | 4.24 | 0.752 | 264.83 | <0.001 | 0.87 | 0.01 |
| Mule deer-predation | 7 | 6.19 | 0.626 | 70.61 | <0.001 | 0.83 | 0.03 |
| Elk-encounter (wolf) | 9 | 18.09 | 0.020 | 50.91 | <0.001 | 0.66 | 0.07 |
| Elk-predation (wolf) | 9 | 12.22 | 0.142 | 27.85 | 0.001 | 0.79 | 0.04 |
| Elk-encounter (cougar) | 9 | 8.71 | 0.491 | 76.11 | <0.001 | 0.74 | 0.05 |
| Elk-predation (cougar) | 9 | 9.33 | 0.412 | 82.36 | <0.001 | 0.63 | 0.08 |

^a Hosmer–Lemeshow χ^2 statistic.

killed nearly reaching parity in the final year (Atwood et al. 2007). The extent to which potentially increased risk of direct predation for elk modulates population processes will depend on whether they are additive or compensatory and warrants further scrutiny.

Interestingly, we found no evidence of increased direct predation on mule deer. Direct predation of mule deer by wolves was negligible and, as a result, total risk of direct predation for mule deer equated to partitioned risk of direct predation by cougars. Predicted effects of wolf recolonization on mule deer have varied (Boyce 1993, White and Garrott 2005), and little effort has been devoted to quantifying those effects subsequent to recolonization (but see Husseman et al. 2003). Based on our analyses, we could hypothesize that total risk of direct predation for mule deer might actually be reduced where sympatric with wolves, cougars, and elk. From a mechanistic standpoint, wolf-induced adaptive shifts to structurally complex refugia by elk may dilute cougar predation on mule deer. In dense cover, mule deer should be the more vagile prey species and, similar to aquatic systems (Hampton 2004, Warfe and Barmuta 2004), where structural complexity may impede the escape ability of larger prey species, woody obstructions may be more likely to slow escape of larger terrestrial prey (Kunkel and Pletscher 2000). Where elk are more abundant than mule deer, primary predation by wolves and increased predation by cougars on elk may benefit mule deer populations. It has long been recognized that direct predation can reduce the strength of competition between sympatric prey, and interference competition with elk has been posited as a partial explanation for declines in regional mule deer populations.

We made 3 critical assumptions in development of our stage-based models. First, we assumed that embedded within data of prey spatial behavior are attempts to minimize exposure to predators (Lima and Dill 1990). If prey demonstrate predator-sensitive resource selection, then differences should exist in predator and prey RSF. That differences in RSF exist lends credence to this first assumption. Next, we assumed that predator spatial behavior can be viewed as a surrogate for search behavior (Kunkel et al. 2004, Hebblewhite et al. 2005). This assumption may be more tenuous, in that space use by predators is unlikely always associated with a search for prey. However, without information on decision-making processes by predators, we were constrained to assuming that search behavior was subsumed by all space use by predators. Implicit in this assumption is the notion that predators utilize space in a way that should maximize the potential to encounter prey (Sih 1984, 1987). Finally, we assumed that a spatial encounter (intersection of predator and prey tracks and evidence of chase) adequately represents the relative risk of prey being encountered by predators for a given set of habitat attributes. We agree with Hebblewhite et al. (2005) that this is a reasonable assumption and much preferred to the alternative, that predator locations, alone, equal risk to prey. The latter does not permit decomposition of predation

risk (Hebblewhite et al. 2005) and would prohibit us from comparing risk between encounter and predation stages.

MANAGEMENT IMPLICATIONS

When the northern Rocky Mountain distinct population segment of the gray wolf is removed from the federal list of threatened and endangered species, respective state agencies will assume responsibility for management. As a result, information on spatiotemporal patterns of predation will become increasingly important as state agencies face pressure to integrate predator and prey management. Results from our work indicate that there is potential to take a nuanced stage-based approach to managing direct predation based on integrated prey- and habitat-based goals. For example, consider a situation where the goals are to reduce direct predation by wolves on elk and the impact of herbivory on winter range. By reducing structural complexity in cover types such as shrub-steppe or riparian zones, managers may be able to induce greater risk effects and accompanying reductions in foraging intensity (Lima and Dill 1990). Reduction of structural complexity may have the added benefit of increasing potential for interference competition (i.e., antagonism) between cougars and wolves, thus reducing potential for synergistic direct predation. If the goal is to reduce direct predation on mule deer, areas surrounding winter range shared with elk can be managed for contiguous blocks of dense timber. Although dense timber provides stalking cover for cougars, wolf-induced shifts to timbered refugia by elk dilutes risk of cougar predation on mule deer (Atwood et al. 2007). Reduced predation on mule deer, accompanied by short-term synergistic (i.e., additive) predation on elk, may reduce the strength of competition between prey species and spur an increase in mule deer population numbers. We caution that specific courses of action will be location-dependent, and recommend applying habitat manipulations as experiments conducted within an adaptive management framework.

ACKNOWLEDGMENTS

This study was funded by United States Department of Agriculture–Animal Plant Health Inspection Service–Wildlife Services–National Wildlife Research Center, Boone and Crockett Club, Pope and Young Club, Turner Endangered Species Foundation, and Turner Enterprises International. B. Beehler, J. Brown, A. Corcoran, J. Morel, A. Nelson, K. Nittinger, and A. Webber provided valuable assistance in the field. We thank J. Goheen, F. Provenza, M. Wolfe, R. Schmidt, N. T. Hobbs, and J. Fryxell for helpful comments on an earlier version of the manuscript.

LITERATURE CITED

- 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.
- Atwood, T. C. 2006. Coyotes, wolves, elk, and mule deer: predator–prey behavioral responses in southwest Montana. Dissertation, Utah State University, Logan, USA.
- Atwood, T.C., E. M. Gese, and K. E. Kunkel. 2007. Comparative patterns of predation by cougars and recolonizing wolves in Montana's Madison range. *Journal of Wildlife Management* 71:1098–1106.

- Bergmann, E. J., R. A. Garrott, S. Creel, J. J. Borkowski, R. Jaffe, and F. G. R. Watson. 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. *Ecological Applications* 16:273–284.
- Boyce, M. S. 1993. Predicting the consequences of wolf recovery to ungulates in Yellowstone National Park. Pages 234–269 *in* R. S. Cook, editor. *Ecological issues on reintroducing wolves into Yellowstone National Park*. United States Department of Interior, National Park Service, Scientific Monograph, Denver, Colorado, USA.
- Boyce, M. S., and L. L. MacDonald. 1999. Relating populations to habitats using resource selection functions. *Trends in Evolution and Ecology* 14:268–272.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmeigelow. 2002. Evaluating resource selection functions. *Ecological Applications* 15:281–300.
- Burnham, K. P., and D. R. Anderson. 1998. *Model selection and inference: a practical information-theoretic approach*. Springer-Verlag, New York, New York, USA.
- Creel, S., and D. Christianson. 2008. Relationships between predation and risk effects. *Trends in Ecology and Evolution* 23:194–201.
- Creel, S., and J. A. Winnie, Jr. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour* 69:1181–1189.
- Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24:38–49.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330.
- Fraser, D. F., J. F. Gilliam, J. T. Akkara, B. W. Albanese, and S. B. Snider. 2004. Night feeding by guppies under predator release: effects on growth and daytime courtship. *Ecology* 85:312–319.
- Hampton, S. 2004. Habitat overlap of enemies: temporal patterns and the role of spatial complexity. *Oecologia* 138:475–484.
- Hebblewhite, M., E. H. Merrill, and T. L. McDonald. 2005. Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk predator–prey system. *Oikos* 111:101–111.
- Holling, C. S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Canadian Entomologist* 91:293–320.
- Hopcraft, J. G. C., A. R. E. Sinclair, and C. Packer. 2005. Planning for success: Serengeti lions seek prey accessibility rather than abundance. *Journal of Animal Ecology* 74:559–566.
- Hosmer, D. W., and S. Lemeshow. 2000. *Applied logistic regression*. John Wiley & Sons, Hoboken, New Jersey, USA.
- Hussemann, J. S., D. L. Murray, G. Power, C. M. Mack, C. R. Wegner, and H. Quigley. 2003. Assessing differential prey selection patterns between two sympatric large carnivores. *Oikos* 101:591–601.
- Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use–availability data: theoretical motivation and evaluation methods. *Journal of Wildlife Management* 70:347–357.
- Kerfoot, W. C., and A. Sih. 1987. *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, New Hampshire, USA.
- Kotler, B. P., J. S. Brown, R. H. Slotow, W. L. Goodfriend, and M. Strauss. 1993. The influence of snakes on the foraging behavior of gerbils. *Oikos* 67:309–316.
- Kunkel, K. E., and D. H. Pletscher. 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. *Canadian Journal of Zoology* 78:150–157.
- Kunkel, K. E., D. H. Pletscher, D. K. Boyd, R. R. Ream, and M. W. Fairchild. 2004. Factors correlated with foraging behavior of wolves in and near Glacier National Park, Montana. *Journal of Wildlife Management* 68:167–178.
- Kunkel, K. E., T. K. Ruth, D. H. Pletscher, and M. G. Hornocker. 1999. Winter prey selection by wolves and cougars in and near Glacier National Park, Montana. *Journal of Wildlife Management* 63:901–910.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619–640.
- Losey, J. E., and R. F. Denno. 1998. Positive predator–predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology* 79:2143–2152.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. *Resource selection by animals: statistical design and analysis for field studies*. Kluwer Academic, Norwell, Massachusetts, USA.
- Paine, R. T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15:93–120.
- Peckarsky, B. L., and A. R. McIntosh. 1998. Fitness and community consequences of avoiding multiple predators. *Oecologia* 113:565–576.
- Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* 86:501–509.
- Rosenheim, J. A., L. R. Wilhoit, and C. A. Armer. 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia* 96:439–449.
- Sih, A. 1984. The behavioral response race between predator and prey. *The American Naturalist* 123:143–150.
- Sih, A. 1987. Predators and prey lifestyles: an evolutionary and ecological overview. Pages 203–224 *in* W. C. Kerfoot and A. Sih, editors. *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, New Hampshire, USA.
- Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution* 13:350–355.
- Singer, F. J., and E. O. Garton. 1992. Estimating the size of the northern Yellowstone elk herd from fixed-wing aircraft and helicopter surveys—a progress report. *Wolves for Yellowstone? A report to the United States Congress*. Volume IV. Yellowstone National Park, Mammoth, Wyoming, USA.
- Soluk, D. A. 1993. Multiple predator effects: predicting combined functional responses of stream fish and invertebrate predators. *Ecology* 74:219–225.
- Soluk, D. A., and N. C. Collins. 1988. Synergistic interactions between fish and stoneflies: facilitation and interference among stream predators. *Oikos* 52:94–100.
- Warfe, D. M., and L. A. Barmuta. 2004. Habitat structural complexity mediates the foraging success of multiple predator species. *Oecologia* 141:171–178.
- White, P. J., and R. A. Garrott. 2005. Yellowstone's ungulates after wolves—expectations, realizations, and predictions. *Biological Conservation* 125:141–152.

Associate Editor: Conner.