WOLVES, COYOTES, ELK, AND MULE DEER: PREDATOR-PREY BEHAVIORAL INTERACTIONS IN SOUTHWESTERN MONTANA

by

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Predator recolonization can have profound effects on prey communities, particularly when a predator recolonizes an already complex predator-prey community. In the following chapters, I investigated direct and indirect effects of wolf (*Canis lupus*) recolonization on prey and competitor behavior. In Chapter II, I examined comparative patterns of cougar (*Puma concolor*) and wolf predation on elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*Odocoileus virginianus*). I found that increases in the proportion of elk killed by cougars were mediated by wolves inducing elk to shift to more structurally complex refugia habitat to mitigate predation risk from wolves which, in turn, made elk more vulnerable to predation by cougars. In Chapter III, I examined the interaction between landscape attributes and predator and prey resource selection in influencing the spatial distribution of predation risk. Using the functional response theoretic to model total predation risk for elk and mule deer, I found that landscape covariates could exert a strong influence in mediating the conditional probability of death following a predator encounter. In Chapters IV and V, I investigated the effects of wolf recolonization on coyote (*Canis latrans*) space use and scavenging behavior. I found that coyotes routinely exploit space used by wolves putatively in the hopes of encountering scavenge subsidies in the form of wolf-killed prey. Upon encountering wolf-killed prey, coyotes rely on a gradient of risk-sensitive behaviors, ranging from increased vigilance to aggressively confronting wolves, to guide scavenging behavior. Coyote social rank strongly influences risk sensitivity as socially dominant coyotes spend more time vigilant at carcasses, but also are exposed to greater risk as they tend to feed at carcasses in the earliest stages of consumption by wolves. As a result, there is greater potential for agonistic interactions between socially dominant coyotes and wolves.

(165 pages)

DEDICATION

To my wife Laura, we've done it! For the wonderful canine companions that sparked and maintain my interest in canid behavior- thank you Sid, Joker, Beverly, Orson, Carmilla, Ike, Midge, Monkey, and Blue. I've had a joyful time studying your canid cousins.

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CHAPTER I

INTRODUCTION TO RESEARCH

In ecology a paradigm shift is occurring, in which emphasis is being placed on multi-species and ecosystem management, rather than traditional single-species assessments. Recently, holistic approaches have been employed in various endeavors ranging from explaining community assemblage (Conroy et al. 1999) to investigating effects of fragmentation on vertebrate population dynamics (Schweiger et al. 2000). Data exist elucidating predator dynamics in communities with diverse assemblages of large predators and prey species (Huggard 1993; Boyd et al. 1994; Weaver 1994; Kunkel and Pletscher 1999); however, there is a paucity of information relative to the underpinnings of behavioral interactions between sympatric predators and their prey. The next logical step in elevating our understanding of predator-prey relationships should be an examination of the interaction between direct and indirect effects of predation in multi-predator/multi-prey systems.

Predation effects of multiple predators are inherently difficult to disentangle; commonalities and contradictions exist and inference regarding factors influencing interactions with prey is often system-specific. Despite this, overwhelming evidence exists demonstrating that predators can exert a tremendous influence on community structure and dynamics. This evidence comes in the form of two rarely integrated, yet complementary, lines of research: direct and indirect predation effects. Lethal direct effects are manifest as a loss in prey numbers or biomass (Schmitz 1998) and constitute a preponderance of large mammal predator-prey studies. Indirect effects examine how predators cause adaptive shifts in prey behavior or life history allocation (Schmitz et al.

1997). These indirect risk effects can be either lethal or nonlethal depending on the extent to which trade-offs between mitigating predation hazard and satisfying energetic demands compromise survival. For example, lethal indirect effects might occur when predation hazard constrains foraging time and starvation results (Abrams 1984; McNamara and Houston 1987; Hik 1995), whereas nonlethal indirect effects might include shifts out of predator-specific hunting habitat to refugia (Stapley 2004). There is now increasing acknowledgment of the value of integrating these two lines of research, particularly when evaluating the impact of large carnivores recolonizing already complex predator-prey systems (Berger et al. 2001) and nonlethal and lethal predation effects are expected to be interactive.

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 be enhanced when the nonlethal predation effects one predator species facilitates (synergism) lethal predation by another species (Kerfoot and Sih 1987; Soluk 1993; Losey and Denno 1998). Facilitation predominantly occurs when a predator induces a phenotypic response from prey that increases its overall vulnerability to predation from other species (Soluk and Collins 1988; Kotler et al. 1993). Typically, these phenotypic responses involve a change in behavior or habitat use by prey species that positively benefit a second predator species (Kerfoot and Sih 1987; Korpimaki et al. 1996; Losey and Denno 1998). For example, prey may be able to reduce predation risk 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, prey expose themselves to predation by a secondary predator (Kotler et al.

1993; Soluk 1993; Fraser et al. 2004). Thus, it should not be assumed that multiple predator effects are always additive. Indeed, predation effects of multiple predators can be less than predicted based on 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 risk reduction for shared prey (Rosenheim et al. 1993). Whether multiple predator effects are risk-enhancing or risk-reducing depend largely on how prey respond behaviorally to potentially simultaneous threats.

Just as prey must develop adaptive behaviors to manage dynamic predation risk, competing predators must also demonstrate phenotypic plasticity in the wake of recolonization by a competitively dominant predator. In many cases, antagonistic predator-predator interactions can result in the competitively subordinate predator partitioning space and resources to mitigate the likelihood of encountering the dominant predator (Creel et al. 2001). In extreme cases, interspecific strife can lead to the death of the subordinate competitor (Palomares and Caro 1999). Indeed, the direct negative effects of predator-predator interactions is relatively well documented in reviews by Creel et al. (2001) and Palomares and Caro (1999), which has led to a tacit generalization that all predator-predator interactions are founded in obligate hostility. However, there is evidence pointing to the contrary, particularly with respect to indirect effects. For example, Paquet (1991) and Wilmers et al. (2003) noted that coyotes might receive substantial energetic benefit through scavenging wolf-killed prey. For coyotes to benefit from wolf presence, they must trade-off the energetic benefit of kleptoparasitizing wolf kills with the risk of injury or death associated with directly encountering wolves.

Balancing a direct risk with an indirect benefit should require a fairly advanced repertoire of risk-sensitive behaviors: on one hand, coyotes have strong motivation to avoid space used by wolves; on the other hand, access to scavenge subsidies provides strong incentive to exploit space used intensively by wolves. Investigating risk sensitivity of prey and a putative competitor in response to predator recolonization may provide useful insights into the similarities and disparities of the ontogeny of risk-sensitive behaviors.

How do prey and competitors cope with predator recolonization? This general question forms the basis for the following chapters. From January 2003 through August 2005, I investigated the behavioral responses of elk, mule deer, and coyotes in response to wolf recolonization of Montana's northern Madison range. I approached this broad question from a perspective that acknowledges many factors are likely to interact in determining responses to predator recolonization. Processes considered in this work run the gamut from adaptive learning to interactions between landscapes attributes and animal behavior. Two chapters are devoted to direct and indirect predation effects and two chapters are devoted to direct and indirect effects of predator-predator interactions. I chose this approach, integrating direct and indirect effects, because I believe it to be superior to viewing predation or interspecific competition through a reductionist lens.

In Chapter II, I investigate comparative patterns of wolf and cougar (*Puma concolor*) predation in elk, mule deer, and white-tailed deer. In Chapter III, I explore the interaction between landscape characteristics and predator and prey behavior in determining the spatial distribution of predation risk. In Chapter IV, I examine coyote resource selection in relation to wolf spatial ecology to determine whether coyotes partition space relative to wolf activity. In Chapter V, I investigate risk-sensitive scavenging behavior by coyotes and role wolf activity and perceived wolf presence may play in mediating risk-conditional foraging by coyotes. Finally, In Chapter VI, I summarize my findings and present my synthesis of the greater research.

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CHAPTER II

COMPARATIVE PATTERNS OF PREDATION BY COUGARS AND RECOLONIZING WOLVES IN MONTANA'S MADISON RANGE

Abstract Numerous studies have documented how prey may use antipredator strategies to reduce the risk of predation from a single predator. However, when a recolonizing predator enters an already complex predator-prey system, specific antipredator behaviors may conflict and avoidance of one predator may enhance vulnerability to another. I studied the patterns of prey selection by recolonizing wolves (*Canis lupus*) and cougars (*Puma concolor*) in response to prey resource selection in the northern Madison Range, Montana. Elk (*Cervus elaphus*) were the primary prey for wolves, and mule deer (*Odocoileus hemionus*) were the primary prey for cougars, but elk made up an increasingly greater proportion of cougar kills annually. While both predators preyed disproportionately on bull elk, wolves were most likely to prey on bulls in poor physical condition. Although I found that the predators partitioned hunting habitats, structural complexity at wolf kill sites increased over time, whereas complexity of cougar kill sites decreased. I concluded that shifts by prey to structurally complex refugia were attempts by formerly naïve prey to lessen predation risk from wolves; nevertheless, shifting to more structurally complex refugia might have made prey more vulnerable to cougars. Following a change in predator exposure, use of refugia may represent a compromise to minimize overall risk.

Introduction

When a recolonizing predator expands into a formerly depopulated ecosystem, complexities may quickly accrue making it difficult to infer the relative importance of various ecological agents in mediating interactions with prey. This may be particularly true when the recolonizing predator must integrate into an already complex predator-prey system. It is generally accepted that prey should behave in a manner which is optimal in deterring predators (Illius and FitzGibbon 1994). Prey can employ an array of behaviors to manage predation risk including spending time vigilant while foraging or resting (Elgar 1989), aggregating in groups (Messier and Barrette 1985; FitzGibbon 1990), spatially dispersing (Bergerud and Page 1987), or seeking refugia habitat (Bergerud et al. 1983; Formanowicz and Bobka 1988). Likewise, predators may employ various tactics to keep pace in the behavioral arms race, including modifying space use relative to changes in prey abundance (Kunkel et al. 2004) or by differential assessment of prey vulnerability (FitzGibbon and Fanshawe 1989). The former is strongly influenced by prey spatial ecology and habitat attributes. The latter is likely a function of predator perceptual ability and hunting style. What remains unknown is how quickly and to what extent a recolonizing predator forces prey to modify antipredator behaviors to accommodate a new predation risk.

Effects of habitat attributes on predation risk from a single predator species have been well documented (e.g., Bergerud et al. 1983; Kunkel et al. 2004) and predominantly support *a priori* expectations that coursing predators (e.g., canids) require open habitats (Kruuk 1972; Schaller 1972), whereas ambush predators (e.g., felids) rely on structurally complex habitats (Rosenzweig 1966; Caro and Fitzgibbon 1992). However when coursing and ambush predators are considered simultaneously, the role of habitat attributes in mediating prey selection becomes less clear (Kunkel et al. 1999; Husseman et al. 2003; Warfe and Barmuta 2004). For example, in the case of predator recolonization, habitat shifts by prey in response to an additional predation risk may not be immediate. Indeed, if habitat shifts reflect a fear response (Brown et al. 1999), there may be a time lag where formerly naïve prey (Berger et al. 2001) must become cognizant of the threat posed by the recolonizing predator and seek habitats that may mitigate the new predation risk. This scenario can be tested by contrasting key habitat attributes of predator kill sites over time. As prey process information regarding the threat posed by a new predator, behavioral modifications regarding habitat use might arise in subsequent years that lessen predation risk (Berger et al. 2001; Testa et al. 2000).

Physical disadvantages are believed to interact with predator-specific hunting behaviors to determine patterns of prey selection (Estes and Goddard 1967; Murtaugh 1981; Sih and Moore 1990). For example, group-hunting by coursing predators can facilitate the capture of larger prey (Rosenzweig 1966; Gittleman 1989), particularly when prey are experiencing the direct effects of poor physical condition (FitzGibbon and Fanshawe 1989; Sinclair and Arcese 1995). In contrast, solitary hunting, common among ambush predators, can impose limits on the size of prey captured (Sunquist and Sunquist 1989; Murphy 1998). It remains unknown to what extent a recolonizing coursing predator may alter prey selection of an ambush predator. The most plausible scenario is that risk enhancement may result when nonlethal predation by one predator facilitates lethal predation by another (Kerfoot and Sih 1987; Losey and Denno 1998). If this scenario occurs consistently, disadvantaged prey may, over time, make up greater proportions of prey killed by ambush predators.

I investigated the influence of habitat characteristics and prey physical attributes in mediating predation on elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and white-tailed deer (*Odocoileus virginianus*) by cougars and recolonizing wolves. Specifically, I was interested in whether prey altered their habitat use over time to lessen predation risk and whether wolves and cougars displayed different patterns of prey selection in response. First, I examined whether kill site habitat attributes changed as prey were forced to accommodate a new predation risk (wolves). I predicted that (i) over consecutive years, habitat attributes of wolf kill sites would be dynamic and shift to more structurally complex habitat types (e.g., greater hiding cover, steeper slope), whereas attributes of cougar kill sites would remain static. Next, I characterized predator-specific patterns of prey selection relative to prey relative abundances, demographics, and physical condition. In particular, I was interested in whether prey selected by cougars and wolves over consecutive years differed with respect to physical condition and sex and age classes. I predicted that relative to cougars, (ii) wolves would prey disproportionately on physically disadvantaged prey (i.e., young, old, or in poor physical condition); (iii) cougars would display no clear pattern of selection based on age or infirmity; and (iv) both predators would select prey proportional to their occurrence.

Methods

I conducted the study in the Northern Madison Study Area (NMSA; 680 km^2), located in southwest Montana's Madison Range of the Rocky Mountains, during January-May of 2003-2005. The NMSA is approximately 50 km northwest of Yellowstone National Park and is 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 (Fig. 1). Shrub/steppe habitat (535 km^2) dominates the NMSA; coniferous forest (145 km^2) comprises approximately 23% of the remaining area. Elevations range from 2500 m in the Spanish Peaks to 1300 m on the Madison River floodplain. Elevation changes mediate an ecological gradient varying from dry grassland/juniper (*Juniperus scopulorum*) savannah at lower elevations to closed canopy Douglas fir (*Pseudotsuga menziesii*) or lodgepole pine (*Pinus contorta*) forests on moist sites at higher elevations. High elevation dry sites occur on southern exposures and ridgelines and are predominantly mountain big sage (*Artemesia tridentada tridentata*)/grassland mosaics. Temperatures range from highs of 21-32°C in the summer months to lows of -34°C in the winter months. A suite of predators are present on the NMSA including grizzly bears (*Ursus arctos horribilis*), black bears (*Ursus americanus*), cougars, coyotes (*Canis latrans*) and gray wolves. Wolves recolonized the NMSA in the winter of 2002, and represented the recolonizing front of wolves in the Madison Range. Ungulates present on the NMSA included elk, mule deer, white-tailed deer, and moose (*Alces alces*). The NMSA is privately-owned, and bull elk are managed for trophy hunting with a maximum annual hunter take of ≈7.5%/yr; cows are managed through late-season public hunts in which hunter take can reach 20% (R. Arnaud, Montana Outfitters, personal communication).

I estimated population sizes for elk, white-tailed deer, and mule deer and age/sex structure for elk from aerial surveys conducted yearly in March. I conducted additional ground surveys after aerial surveys to estimate white-tailed and mule deer age/sex structures. I used 4 fixed transects, ranging from 11-19 km in length and located within deer winter ranges, for our ground surveys. I drove each transect over 4 consecutive evenings and, for each transect, I averaged age (fawn and adult) and sex structure before combining them to provide an estimate for the entire study area. I monitored a single wolf pack (Bear Trap pack) on the study site via visual observation and snow-tracking. Wolf pack size ranged from 2-8 animals, one of which was radiocollared and subsequently dispersed. Over the duration of the study, the Bear Trap pack averaged 5 individuals. An unknown number of cougars resided in the study area and were monitored via snow-tracking.

Ungulate carcass location and examination

I located predator-killed ungulates by backtracking wolves and cougars to kill sites, investigating areas where scavenging birds had aggregated, homing in on mortality signals from radiocollared mule deer, and searching along 25 transects on a 3 wk rotation within wolf and cougar territories. Transect length was dictated by proximity to study area boundaries and each transect was searched by 2-4 individuals walking parallel to the origin line and spaced at 50 m intervals. Prior to each rotation, I randomized transect starting points and directions. This method should have ensured that, over time, I searched all habitat types available to wolves and cougars, thus minimizing possible habitat-specific search bias. When a carcass was located, I first determined the cause of death (e.g., starvation, predation, human-caused, etc.) and, in case of predation, identified the predator species responsible for the mortality. I used a key adapted from Kunkel et al. (1999) to characterize predator-specific injury patterns and behaviour such as point of attack, method of killing, diameter and spacing of puncture wounds, and carcass location.

I differentiated kills from scavenging by the occurrence of chase trails and the presence of subcutaneous hemorrhaging.

I examined kills for physical abnormalities and collected femur and (or) mandible bones for marrow fat analysis. Marrow fat analysis provides a measurement of pre-starvation absolute physical condition (condition at the time of death) (Mech and DelGuidice 1985) and can be used to qualitatively classify prey condition at the time of death. I removed and weighed a 5-7 cm sample of marrow from the central portion of the bone. I then oven-dried the sample at 60° for 48 hr and reweighed to calculate the dry-to-wet mass of fat (Neiland 1970). For kills in which only mandibles were available, I followed the procedure outlined in Husseman et al. (2004) to adjust mandible fat values to femur fat equivalents. I estimated prey age based on patterns of tooth eruption and wear (Robinette et al. 1957); animals were then classified as juveniles or adults.

Characterization of kill site attributes and ungulate habitat selection

In order to determine the relationships between prey resource selection (elk and mule deer) and habitat at kill sites, I measured percent hiding cover, percent canopy coverage, physiography (percent slope, aspect), snow depth, and determined the dominant vegetation class at wolf and cougar kill sites and point locations obtained from observing mule deer and elk. I determined percent hiding cover, expressed as the mean of 4 measurements taken from the cardinal directions (Kunkel 1997), by visually estimating the percentage of an elk or deer obscured at 30 m. I estimated percent canopy coverage, expressed as a continuous percentage (Kunkel 1997), by counting the number of points under canopy at 2 m intervals along 2 (1 north-south, 1 east-west) 30 m perpendicular transects centered on the carcass. I located mule deer using radiotelemetry and direct observation via 15-45× spotting scopes. I located elk opportunistically while observing mule deer or while searching transects for predator kills. I collected data on habitat attributes after mule deer and elk left the general area. I considered point locations separated by a 24 hr interval to be spatially independent.

I used forward stepwise ($\alpha = 0.05$ to enter and remain) logistic regression to evaluate whether vegetative and physiographic characteristics of cougar and wolf kill sites differed from resources selected by prey. I controlled for multicollinearity by eliminating any 1 of a pair of variables with $r^2 \geq 0.50$. For models of kill site attributes, predator species was the dependent variable, with "wolf" used as the reference, and independent variables were percent hiding cover, canopy cover, percent slope, aspect, snow depth, and vegetation classes of riparian, forest, juniper/canyon, shrub/steppe, and grassland. I included categorical vegetation class and aspect variables in models using dummy variable coding, excluding the reference categories (shrub/steppe and north). I evaluated the same group of covariates for models of prey resource selection, comparing "used" locations to paired random "available" locations separated by a distance of 500 m. For all logistic regression analyses, I checked continuous variables for conformity to linearity using the quartile method (Hosmer and Lemeshow 2000). I ensured final model fit by testing with the Hosmer and Lemeshow goodness-of-fit statistic (Hosmer and Lemeshow 2000). I used Akaike Information Criteria with a small sample size correction factor (AIC_c) to determine which parameters were to be retained in regression models; AIC_c values that exceeded 2.0 were considered to be significant (Burnham and Anderson 1998).

Assessment of habitat complexity

I assessed the potential for interactive effects of time and predator species on kill site vegetation complexity by calculating a cover complexity index (CCI) for each wolf and cougar kill site. I calculated the CCI using percent slope and hiding cover, physiographic characteristics most influential in identifying disparate habitat types (i.e., simple as opposed to structurally complex; Attrill et al. 2000) on the NMSA. Because I was interested in whether kill site cover complexity remained static over consecutive years, I calculated the index where $\mathrm{CCI} = (\mathrm{x}_{\%\mathrm{slope}}/\bar{x}_{i}) \times (\mathrm{x}_{\%\mathrm{hidecover}}/\bar{x}_{\%\mathrm{hidecover}\ i})$, and i = focal year. Based on *a priori* expectations of wolves inducing prey to shift to more structurally complex refugia, I anticipated increases in yearly mean CCI values (prediction i). I tested for the interactive effects of time and predator species on the CCI by performing an unbalanced 2-way factorial ANOVA (Zar 1999) with predator species and year as main effects.

Patterns of prey selection

I used Poisson distributed 2-factor log-linear analyses (Agresti 1990) to examine the interaction between year and prey species selected by the 2 predators. I used Pearson chi-square analysis (Zar 1999) to assess associations between age and sex of prey selected. I used a forward stepwise logistic regression to identify factors characterizing prey selected by wolves versus cougars (Hosmer and Lemeshow 2000). Independent variables evaluated included prey species, sex, age, percent femur fat, year, and month of kill. The conservative management of hunter-killed bull elk relative to cows resulted in a near even sex ratio ($\bar{x}_{2003\text{-}2005}$ = 1.1 bull:1.0 cow). Because of this, I felt it prudent to perform a second regression analysis after removing adult male elk from the data set to eliminate the potential effect of percent femur fat bias on parameter estimation (Husseman et al. 2003). Male elk expend considerable energy during the rut and probably enter winter in poorer physical condition than females. I further tested for differences in the percent femur fat in adult elk using an unbalanced factorial ANOVA, with month of kill as a blocking factor and predator species and year as main effects. Femur fat percentage distributions were normalized with an arcsine of the square root transformation (Krebs 1999).

Results

I documented 96 wolf- and 110 cougar-killed ungulates over the duration of the study. Elk comprised the majority (70%) of wolf kills, followed by white-tailed deer (26%), and mule deer (4%). Mule deer were the primary prey (55%) of cougars, followed by elk (35%), and white-tailed deer (10%). Ungulate numbers varied slightly during the study (Arnaud 2005). 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 (R. Arnaud, personal communication). Mule deer abundance increased by an average of 16% over the duration of our research (Arnaud 2005). Throughout the study, elk were numerically superior and, on average, comprised 72% ($\bar{x}$ = 2211 animals, SE = 269) of the total ungulate availability; white-tailed deer and mule deer comprised 16% ($\bar{x}$ = 553 animals, SE = 78) and 12% ($\bar{x}$ = 314 animals, SE = 45), respectively.

Characteristics of kill sites and resource selection

My comparison of wolf versus cougar kill site habitat attributes provided evidence that the two predators partitioned hunting habitat over the duration of the study. Percent slope was the first variable to be retained in the model, followed by percent hiding cover, and riparian habitat (Table 1). Based on the respective odds-ratios, wolf kills were 0.75 (95% CI = 0.66-0.85) times as likely to be located on steep slopes (>15%), 0.72 (95% CI = 0.69- 0.85) times as likely to be located in areas characterized by substantial hiding cover, and 45 (95% CI = 24- 62) times more likely to occur in riparian habitats compared to cougar kills (Table 1). Substantial differences existed in resource selection between elk and mule deer. The probability of elk occurrence decreased on south aspects ($\beta = -0.77$), and was greatest in grasslands ($\beta = 2.3$) and on shallower slopes ($\beta = -0.09$). The probability of mule deer occurrence increased on south aspects ($\beta = 1.5$), in shrub/steppe habitats ($\beta = 2.1$), and with increasing slope ($\beta = 0.15$), and decreased in riparian ($\beta = -3.9$) and grassland habitats ($\beta = -5.1$). All models performed well under additional fit testing and met assumptions of linearity.

Although the habitat characteristics of wolf and cougar kill sites were clearly disparate, evidence also suggested that over consecutive years, wolves were killing prey in habitats characterized by increasingly greater structural complexity (Fig. 1). There was a strong interaction between predator species and year ($F_{2,204} = 10.42$, $P < 0.001$) relative to incremental change in the mean kill site CCI. Least squares means testing revealed a significant difference in CCI values, when mean values at wolf kill sites rose sharply in year 2 ($\bar{x}_{2003}$ = 0.24, 95% CI = 0.22 – 0.26; $\bar{x}_{2004}$ = 0.55, 95% CI = 0.47 – 0.63) and increased slightly in year 3 ($\bar{x}_{2005}$ = 0.59, 95% CI = 0.47 – 0.71) (Fig. 1). Contrary to the yearly increases in wolf kill site CCI values, cougar kill site values declined from year 2 to year 3 (Fig. 1). Thus in years 2 and 3, wolf kill site structural complexity increased concurrent with declines in vegetation structure at cougar kill sites.

Patterns of prey selection

I restricted log-linear and chi-squared analyses of wolf kills to elk and white-tailed deer and cougar kills to elk and mule deer because small sample sizes of wolf-killed mule deer (n = 4) and cougar-killed white-tailed deer (n = 10) precluded meaningful analyses. The proportions of elk and white-tailed deer killed by wolves remained consistent over consecutive years (78% elk in 2003, 65% in 2004, and 77% in 2005; Fig. 2), and based on log-linear analyses, proportions of wolf-killed prey did not differ relative to yearly availability (year: χ^2 = 0.04, d.f. = 2, P = 0.830; species χ^2 = 1.53, d.f. = 1, P = 0.2160). Contrary to wolves, the proportion of elk and mule deer killed by cougars differed between years (year: χ^2 = 6.83, d.f. = 2, P = <0.0001; species χ^2 = 8.27, d.f. = 1, P = 0.0090), as elk comprised an increasingly greater proportion of yearly kills (16% in 2003, 36% in 2004, and 41% in 2005; Fig. 3). There were no between year differences in the proportions of bull, cow, and juvenile elk killed by wolves (χ^2 = 7.82, d.f. = 4, P = 0.098), nor were there differences in the age/sex class proportions of elk (χ^2 = 0.925, d.f. = 4, P = 0.921) or mule deer (χ^2 = 2.814, d.f. = 4, P = 0.589) selected by cougars. Because no annual differences were found in age/sex class selection of elk and mule deer by cougars and wolves, I pooled kill samples from different years for each predator species. The aggregate proportion of elk age/sex classes killed by wolves differed from their availability on the NMSA ($\chi^2 = 16.79$, d.f. = 2, P = 0.0002). Relative to availability, wolves selected more bulls (64%) and fewer cows (18%) than expected. Similarly, cougars killed more bull elk (61%) and fewer cows (28%) than expected ($\chi^2 = 6.81$, d.f. = 2, P = 0.033). Cougars selected from mule deer age/sex classes in proportion to availability ($\chi^2 = 2.03$, d.f. = 2, P = 0.361), and both predators killed calves (wolves: 18%; cougars: 11%) in proportion to their availability.

Logistic regression revealed that prey species, sex, and physical condition influenced patterns of prey selection between wolves and cougars. Prey species, sex, and percent femur fat content (absolute physical condition) were the variables retained in the full model (adult male elk included), and wolves were 1.6 (95% CI = 0.59- 4.1) times more likely to kill elk, 2.3 (95% CI = 1.0-5.3) times more likely to kill males, and 7.1 (95% CI = 3.3-16.7) times more likely to kill prey in relatively poor physical condition than cougars (Table 2). When adult males (reduced model) were removed from the data set, prey species and percent femur fat were the most significant variables in predicting predator species (DelGiudice 1998; Mech et al. 1995), indicating that differential predation for males between wolves and cougars occurred primarily among adult elk, and to a lesser degree white-tailed deer. Femur fat coefficients were similar in the model without adult males. Further analysis of percent femur marrow fat confirmed a robust relationship between prey condition and predator species; after blocking for month of kill, percent femur marrow fat was significantly less in wolf-killed than cougar-killed adult elk (wolf: $\bar{x} = 44.1 \pm 2.8\%$; cougar: $\bar{x} = 65.6 \pm 2.3\%$; $F_{1,87} = 75.43$, P <0.0001). There was no significant predator × year interaction ($F_{2,86} = 0.16$, P = 0.85). Both logistic regression models performed well under additional model fit tests (full model H-L stat = 6.57, d.f. = 7, P = 0.47; reduced model H-L stat = 2.24, d.f. = 4, P = 0.69) and met assumptions of linearity.

Discussion

Results of my study indicate that predator recolonization has the potential to impact aspects of antipredator behavior relating to space use, increasing the likelihood of enhanced predation risk for some shared prey. Because we initiated the study at the onset of wolf recolonization, we were able to document patterns of prey selection and predator avoidance when prey were putatively naïve (Berger et al. 2001) to the threat posed by wolves. The response of prey to a recolonizing predator might depend on the extent of prior interaction: prey with little or no experience with a predator may fail to display the appropriate avoidance behaviors. However, threat information can be acquired quickly (Berger et al. 2001; Blumstein et al. 2002), particularly among prey that aggregate (Houston et al. 1993), allowing implementation of avoidance behaviors, such as habitat shifts, to mitigate the new predation risk. My data support the notion that prey might process threat information rapidly (i.e., within a year), as evidenced by the sharp increase in CCI values at wolf kill sites in year 2 (2004).

Simple grassland habitats, characterized by shallow slopes with little hiding cover, were the preferred foraging areas for elk and, similar to other studies, offered the additional benefit of carrying a diminished risk of predation by cougars (Hornocker 1970; Murphy 1998; Kunkel et al. 1999). Mule deer were most likely to occur in juniper/canyon habitats characterized by steeper slopes, greater hiding cover, and little risk of wolf predation, consistent with the attributes of sites where they were killed by cougars. However, unlike mule deer, elk resource selection differed modestly from where they were killed by wolves and substantially from where they were killed by cougars. Decomposition of the CCI at kill sites indicated that percent hiding cover, and to a lesser degree slope, increased over consecutive years at wolf kills while remaining static at cougar kills. Thus, over time, elk kills were distributed in areas of greater structural complexity. This finding is consistent with those of Creel and Winnie (2005) and Fortin et al. (2005), that elk in and around Yellowstone National Park shifted to more structurally complex habitats in response to predation from wolves. These observations suggest a behavioral response in large mammals that is common among prey of various taxa faced with threats from multiple predators: movement to interstitial space where predation risk might be diminished for a primary predator but slightly heightened for a secondary predator (e.g., Losey and Denno 1998; Novotny et al. 1999; Hampton 2004). These results also indicate there may be a threshold of vegetation structure, above which wolves are mostly unsuccessful in capturing prey. I did not calculate CCI values for point locations of elk and mule deer used in resource selection modeling. However such an approach, coupled with information on group size, would be valuable in further exploring the nexus between refugia habitat and antipredator behavior.

On the NMSA, structurally complex sites are often associated with canyons and gullies dominated by Rocky Mountain juniper and Douglas fir, which offer substantial stalking cover for an ambush predator. Accordingly, prey retreating to complex refugia habitat may be reducing their risk to predation by wolves only to become more vulnerable to cougars. Indeed, my data indicate that the occurrence of elk kills in increasingly more complex habitats coincided with a rise in the proportion of elk killed by cougars. Perhaps more importantly, the increase in the proportion of elk killed by cougars was not accompanied by a decrease in the proportion of elk killed by wolves. That raises the obvious question: are wolf-induced shifts to refugia by elk enhancing cumulative predation risk from both predators? Wolves selected prey species in proportion to their availability; cougars, in the aggregate, preyed disproportionately on mule deer and underutilized elk. However, beginning in year 2, the proportion of elk killed by cougars increased by >100%; by year 3, the proportion of elk to mule deer killed by cougars approached unity. The age/sex class proportions of prey selected by both predators remained consistent over consecutive years with the pooled analysis revealing that adult male elk were disproportionately preyed upon by both wolves and cougars. It appears that predation risk among elk was enhanced, and bull elk were most vulnerable.

It is unlikely that habitat shifts alone were responsible for the enhanced predation risk for bull elk. Logistic regression results of prey selection (full model) indicated that bull elk in poor physical condition were most likely to be killed by wolves. When bull elk were dropped from the data set (reduced model), wolves were most likely to kill cow elk in poor physical condition. This suggests wolf selection of prey in poor physical condition was not biased by disproportionate selection of bull elk and confirms that selection of disadvantaged prey is a particularly important divergent behavior between the two predators (Husseman et al. 2003; Kunkel et al. 1999). Indeed, femur fat analysis revealed that wolves generally killed older infirmed elk; however, cougars killed mainly prime age elk in relatively good condition. Prey in declining physical condition may face a trade-off between retreating to structurally complex habitat, which on the NMSA is forage poor, or remaining in open habitats that are generally forage rich (Lima and Dill 1990; McNamara and Houston 1992). It is likely that some bull elk, in extremely poor physical condition from the cumulative effects of the rut and a harsh winter, are not able to trade-off foraging for a diminished predation risk. Contrary to my predictions, patterns of prey selection based on physical condition were consistent between years which support theoretical expectations (Rosenzweig 1966; Estes and Goddard 1967; Caro and Fitzgibbon 1992) regardless of whether prey were naïve or savvy.

An interesting, and certainly not ancillary, finding of my research has been the effect of recolonizing wolves on mule deer. It can be argued, despite the systematic use of search transects, that my study design had a methodological bias towards the recovery of predator-killed mule deer: mule deer were radiocollared whereas elk were not. This putative bias should have led to sampling a greater proportion of mule deer mortalities and underestimating predation effects on elk. Yet, my results indicate wolf predation on mule deer was negligible whereas cougar predation on mule deer declined as predation on elk increased. It would appear that wolf recolonization, in the short term, had little direct effect on mule deer survival. Indirect effects may be harder to quantify, and I can envision two likely scenarios in which wolf recolonization, via wolf-mediated antipredator behavior in elk, may indirectly influence predation risk to mule deer in areas where elk are numerically superior. First, on the NMSA, elk have been observed to displace mule deer from prime foraging habitat while on winter range (Atwood, unpubl data). Elk typically move around winter range in groups of 100-200 cows; mule deer groups may range from 10-15 individuals. Large groups of elk easily displace mule deer from open savannah habitats; mule deer retreat to structurally complex habitats in response. As a result, elk may be buffering mule deer from wolf predation by evicting mule deer from prime wolf hunting habitats. This scenario may also help explain why cougars preyed disproportionately on mule deer on the NMSA. Second, as mentioned earlier, results from our study and others (Creel and Winnie 2005; Fortin et al. 2005) suggest that wolf activity can induce habitat shifts in elk, presumably to ameliorate predation risk from wolves. Temporary shifts to structurally complex habitats by elk may expose them to greater predation risk from cougars but dilute the risk of predation for mule deer. Since our data provide some support for both scenarios, further research in this area is warranted.

Management Implications

It has become increasingly important to understand the effects of multiple predators on prey, particularly when a recolonizing predator must integrate into an already complex predator-prey system. Recent studies of established multiple predators on shared prey have quantified theorized effects including risk enhancement (Chang 1996; Losey and Denno 1998; Sih et al. 1998) and modulation of hunting success via vegetation complexity (Clark and Messina 1998; Rypstra et al. 1999) in fish and invertebrates. My study documents these effects in a large mammal system and suggests that the potential exists where switching habitat locations will have no net effect on mortality risk. Conceptually, I show that predation risk is dynamic as predators and prey interact across heterogeneous landscapes. This dynamism appears to have increased predation effects on elk, while diluting predation risk for mule deer. If sustained, reduced predation on mule deer may help spur an increase in population numbers and create momentum to overcome downward population trends in some areas. Likewise, short-term enhanced predation on elk may aid in reducing the strength of competitive interactions between elk and mule deer. The next logical step would be to develop spatially explicit functions of predation risk to partition cumulative multiple predator effects by species and relative to landscape attributes. This would facilitate the identification of areas where risk enhancement is likely to occur and help focus efforts to further explicate predator-prey interactions in complex systems. More work will be needed to determine whether enhanced predation risk for elk results in additive predation.

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Table 1. Top logistic regression models of variables found significant in predicting habitat characteristics at wolf and cougar kill sites. Model structure is accompanied by odds ratios, corresponding 95% confidence intervals, and AIC_c values and weights.

Model	$O.R._1$(C.I.)	$O.R._2$(C.I.)	$O.R._3$(C.I.)	$O.R._4$(C.I.)	$O.R._5$(C.I.)	$O.R._6$(C.I.)	AIC_C	w_i	P-value
Kill site attributes									
$g(x) = 6.5 - 0.28_{slope} - 0.08_{hidcov} + 3.8_{veg}{}^{a}$	0.75(0.66-0.85)	0.72(0.69-0.85)	45.1(24.1-61.6)	—	—	—	66.7	0.99	<0.001
Elk resource selection									
$g(x) = 0.87 - 0.09_{slope} - 0.77_{aspect}{}^{e} + 2.3_{grass}{}^{a}$	0.61(0.55-0.86)	0.46(0.22-0.86)	9.9(2.2-15.9)	—	—	—	234.8	0.93	<0.001
Mule deer resource selection									
$g(x) = -2.1 + 0.15_{slope} + 1.5_{aspect}{}^{e} - 3.9_{veg}{}^{a} - 5.1_{veg}{}^{b} - 0.88_{veg}{}^{c} + 2.1_{veg}{}^{d}$	1.2(1.1-1.3)	4.7(2.4-9.1)	0.01(0.001-0.04)	0.02(0.01-0.03)	0.42(0.07-2.5)	7.7(1.7-16.3)	271.1	0.99	<0.001

[a-d] Vegetation class coded with "shrub/steppe" habitat as the reference category (variables included riparian[a], grassland[b], forest[c], juniper/canyon[d], and shrub/steppe).

[e] Aspect coded with "north" aspect as the reference category (south[e]).

Table 2. Logistic regression models of variables significant in predicting the likelihood of ungulate kills being made by wolves versus cougars. Model structure is accompanied by odds ratios with associated 95% confidence intervals and AIC$_c$ values.

Model	O.R.$_1$ (C.I.)	O.R.$_2$ (C.I.)	O.R.$_3$ (C.I.)	O.R.4 (C.I.)	O.R.5 (C.I.)	AIC$_C$	ΔAIC$_c$	P-value
Full (all prey)								
$g(x) = -0.356$	—	—	—	—	—	268.4	90.5	0.094
$g(x) = -0.453 + 0.997_{spp}$[f]	1.28[f] (0.84-2.99)	[g]0.03 (0.01-0.11)	[h]0.78 (0.33-1.84)	—	—	204.7	26.7	<0.001
$g(x) = -0.451 + 1.116_{spp} + 0.314_{sex}$[i]	1.13 (0.47-2.70)	0.03 (0.09-0.10)	0.89 (0.37-2.12)	1.87 (0.89-3.94)	—	180.2	2.3	<0.001
$g(x) = -0.380 + 1.019_{spp} + 0.423_{sex} - 0.992_{femur\ fat}$	1.56 (0.59-4.13)	0.019 (0.01-0.08)	0.64 (0.24-1.70)	2.33 (1.02-5.32)	7.14 (3.29-16.67)	177.9	—	<0.001
Reduced (bull elk removed)								
$g(x) = 0.053$	—	—	—	—	—	151.2	56.6	0.914
$g(x) = -0.116 + 0.586_{spp}$	2.97 (0.84-10.42)	0.02 (0.01-0.09)	0.34 (0.09-1.18)	—	—	106.8	12.2	<0.001
$g(x) = 0.007 + 0.617_{spp} - 1.006_{femur\ fat}$	3.08 (0.79-12.05)	0.02 (0.01-0.08)	0.32 (0.08-1.26)	7.14 (3.29-16.67)	—	94.6	—	<0.001

[f-h]Design coded with elk as reference ([f]O.R.$_1$ = elk, [g]O.R.$_2$ = mule deer, [h]O.R.$_3$ = white-tailed deer).

[i]Design coded with male as reference.

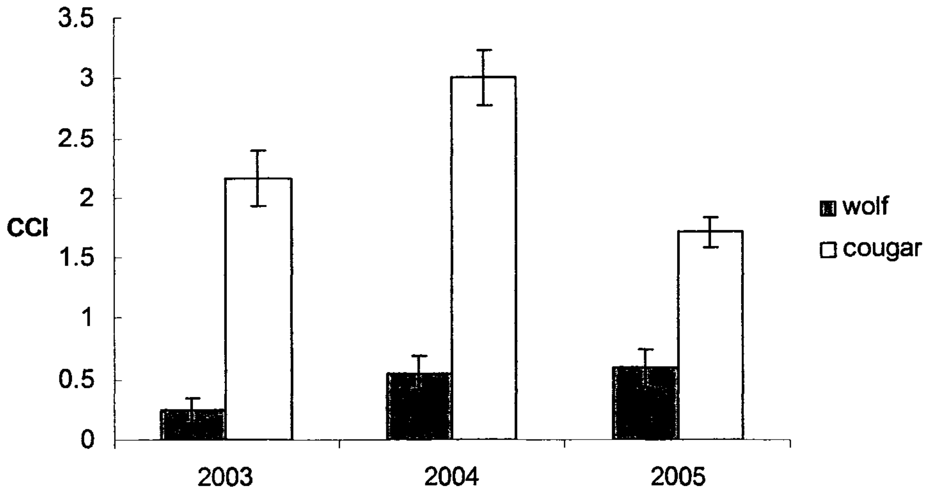

Figure 1. Yearly mean cover complexity index (CCI) values for wolf and cougar kill site locations on the NMSA, southwest Montana, 2003-2005. Bars represent the standard error of the estimate.

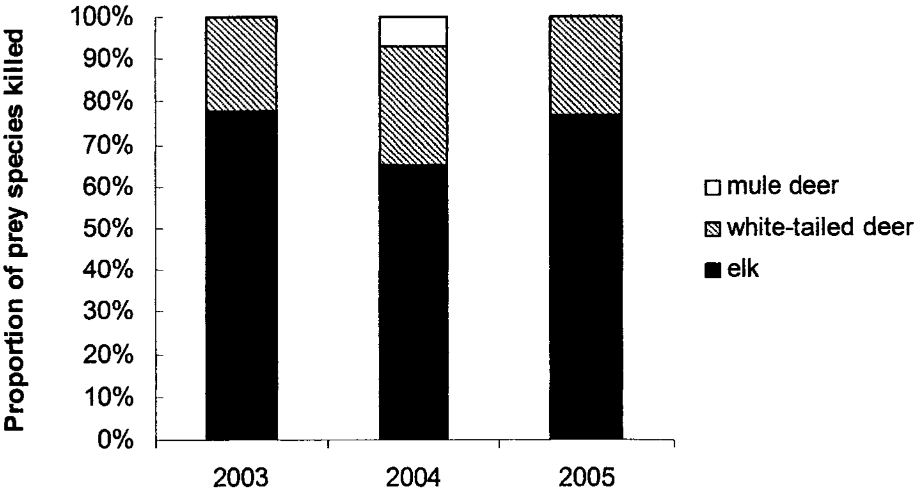

Figure 2. Yearly proportions of elk, white-tailed deer, and mule deer killed by wolves on the NMSA, southwestern Montana, 2003-2005.

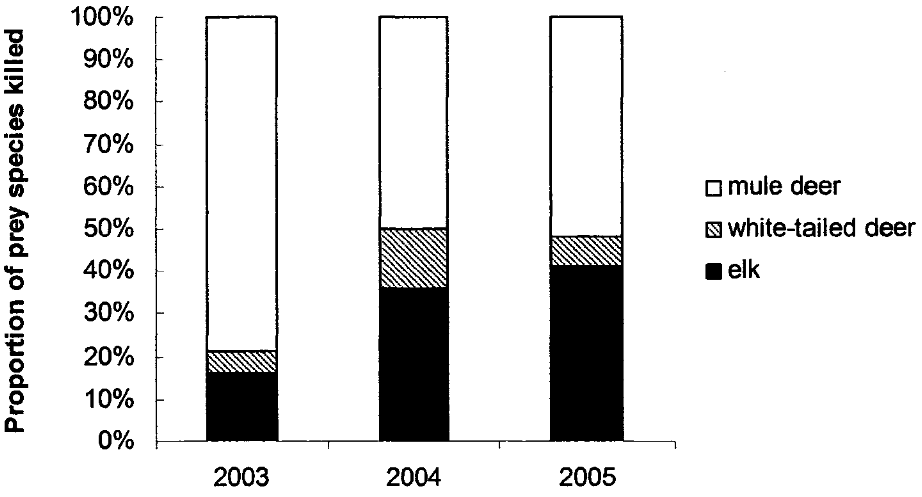

Figure 3. Yearly proportions of elk, white-tailed deer, and mule deer killed by cougars on the NMSA, southwestern Montana, 2003-2005.

CHAPTER III

SPATIAL PARTITIONING OF TOTAL PREDATION RISK IN A MULTIPLE PREDATOR-MULTIPLE PREY SYSTEM

Abstract Partitioning predation risk among multiple predators can be exceptionally difficult, particularly when the indirect effects of one predator enhance the direct effects of another. Because habitat that serves as refugia from one predator may enhance predation by another, it is necessary to understand how predation risk varies over space and between prey species. In this paper, I decomposed spatial predation risk in a wolf-cougar-elk-mule deer predator-prey system into the probabilities of prey being encountered and the conditional probabilities of being killed given an encounter. I then generated spatially explicit functions of total predation risk for each prey species by combining the encounter and conditional kill probabilities. For both mule deer and elk, topographic and habitat effects, along with resource selection by their respective primary predator, strongly influenced encounter probabilities. However, once a predator was encountered, habitat effects increased the risk of death for elk and decreased the risk of death for mule deer. For example, the odds of mule deer encountering a predator were greatest in juniper savanna (7.664) and on south aspects (3.202), where the odds of cougar occurrence (1.529 and 3.081) were elevated. However, given an encounter, the risk of death for mule deer declined for those landscape covariates. This would suggest that landscape attributes did not render mule deer more vulnerable to predation by cougars. By contrast, elk were substantially more likely to be killed on south aspects and in riparian, grassland, and shrub/steppe habitats after encountering a predator, and the conditional probability of an elk kill generally increased in habitats where the relative

odds of wolf occurrence was greatest. Thus, predation risk 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. I endorse a spatial modeling approach as a crucial step in helping to increase our understanding of predator-prey interactions in complex systems.

Introduction

Predation effects of multiple predators are inherently difficult to disentangle; commonalities and contradictions exist and inference regarding factors influencing interactions with prey is often system-specific. Despite this, overwhelming evidence exists demonstrating that predators can exert a tremendous influence on community structure and dynamics (Abrams et al. 1996; Schmitz 1998). This evidence comes in the form of two rarely integrated, yet complementary, lines of research: direct and indirect predation effects. Lethal direct effects are manifest as a loss in prey numbers or biomass (Schmitz 1998) and constitute a preponderance of large mammal predator-prey studies (e.g., Mech 1970; Fuller 1989; Jedrzejewski et al. 2002). Indirect effects examine how predators cause adaptive shifts in prey behavior or life history allocation (Schmitz et al. 1997). These indirect risk effects can be either lethal or nonlethal depending on the extent to which trade-offs between mitigating predation hazard and satisfying energetic demands compromise survival. For example, lethal indirect effects might occur when predation hazard constrains foraging time and starvation results (Abrams 1984; McNamara and Houston 1987; Hik 1995), whereas nonlethal indirect effects might include shifts out of predator-specific hunting habitat to refugia (Stapley 2004). There is now increasing acknowledgment of the value of integrating these two lines of research, particularly when evaluating the impact of large carnivores recolonizing already complex predator-prey systems where nonlethal and lethal predation effects are expected to be interactive (Berger et al. 2001).

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 be enhanced when the nonlethal predation effects of one predator species facilitates (synergism) lethal predation by another species (Paine 1974; Kerfoot and Sih 1987; Soluk 1993; Losey and Denno 1998). Facilitation predominantly occurs when a predator induces a phenotypic response from prey that increases its overall vulnerability to predation from other species (Soluk and Collins 1988; Kotler et al. 1993). Typically, these responses involve a change in behavior or habitat use by prey that positively benefits a second predator species (Kerfoot and Sih 1987; Korpimaki et al. 1996; Losey and Denno 1998). For example, prey may be able to reduce predation risk 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, prey may expose themselves to predation by a secondary predator (Kotler et al. 1993; Soluk 1993; Fraser et al. 2004). Despite this, it should not be assumed that multiple predator effects are always additive. Indeed, predation effects of multiple predators can be less than predicted based on 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 risk reduction for shared prey (Rosenheim et al. 1993). Whether multiple predator effects are risk-enhancing or risk-reducing depend largely on how prey respond behaviorally to potentially simultaneous threats.

Within the Greater Yellowstone Ecosystem (GYE), several studies have documented shifts to more structurally complex habitat by elk (*Cervus elaphus*), presumably in response to predation from wolves (*Canis lupus*) (Fortin et al. 2005; Creel and Winnie 2005). Wolf-mediated habitat shifts by elk may facilitate cougar (*Puma concolor*) predation while buffering mule deer (*Odocoileus hemionus*) from predation by both wolves and cougars. Prior to wolf recolonization of the GYE, cougars were the primary predator of adult mule deer and there was no consensus on the putative impact wolves might have on mule deer populations. For example, Boyce (1993) predicted direct predation effects would result in a decrease in abundance of at least 10-15% for mule deer in YNP following wolf restoration. However, Mack and Singer (1992, 1993) predicted that the abundance of mule deer on the northern range of Yellowstone could increase up to 36% as wolf predation on elk indirectly released mule deer from resource limitation. Ten years after wolf reintroduction to YNP, wolf predation on mule deer appears negligible; to date, elk have comprised ≈92% of wolf diets (White and Garrott 2005). Unfortunately, data are unavailable regarding changes in direct effects of cougars on elk and mule deer over this time. In general, mule deer would not be expected to be highly vulnerable to predation by wolves, particularly where sympatric with numerically superior elk herds. Although mule deer and elk habitat selection tend to be similar at a coarse grain, microhabitat selection can vary substantially (Collins and Urness 1983; Stewart et al. 2002); mule deer select microhabitats with greater slope and vegetative cover; both of which create greater structural complexity which also may serve as refugia habitat for elk avoiding wolves.

In order to determine whether risk enhancement or reduction is plausible in the system described above, it is necessary to understand how predation risk varies over space between prey species (Lima and Dill 1990; Lima 2002). Predation risk, as derived from the functional response of Holling's (1959) disk equation, can be decomposed into 2 fundamental components: probability of prey being encountered (α) and the conditional probability of being killed given an encounter (*d*) (Hebblewhite et al. 2005). In systems where 2 predators with diverse hunting styles (e.g., coursing versus ambush) prey on different species, probabilities of encounter and kill should differ for a given suite of landscape covariates and the potential for risk enhancement should be low. In systems where predators share prey, probabilities of encounter and kill may differ over some, but not all, suites of landscape covariates, thereby increasing the potential for risk enhancement. Wolf-induced shifts to refugia habitat by elk set the stage for a scenario where predation risk may be enhanced. If elk use of a habitat complex increases vulnerability to predation by cougars, with no concomitant decline in predation from wolves, then total predation risk is enhanced and may be additive. Conversely, if use of a habitat complex increases vulnerability to predation by cougars, with a corresponding decline in predation from wolves, then total spatial predation risk is enhanced but likely compensatory. This is an important distinction to make if prey population-level consequences are a concern: total predation risk may not be the sum of its constituent parts.

The reintroduction of wolves to Yellowstone National Park (YNP), and their subsequent recolonization of the GYE provide a unique opportunity to elucidate the effects of multiple predators on shared prey. In this regard, my goals were three-fold: first, I wanted to develop models of predation risk for prey in a multiple predator system; second, I wanted to link predation ecology to landscape attributes to explore the nexus between behavior and the spatial distribution of predation risk; finally, using predation risk models, I wanted to determine if prey risk enhancement was a plausible scenario where wolves and cougars are sympatric. To those ends, I modeled characteristics of resource selection and the encounter and kill stages of predation to (i) predict spatial predation risk for elk and mule deer, (ii) determine whether landscape attributes mediated changes in predation risk relative to encounter and kill stages, and (iii) identify areas where predation risk is likely to be enhanced for shared prey. Based on these relationships, I mapped predation risk to examine its spatial variation and to evaluate whether there are areas of low predation risk that could act as refugia from predators.

Methods

The study was conducted in the Northern Madison Study Area (NMSA; 680 km^2), located in southwest Montana's Madison Range of the Rocky Mountains, during December through April of 2002-2005. The NMSA is approximately 50 km northwest of YNP, and is 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 (fig. 4). Shrub/steppe habitat (535 km^2) dominates the NMSA; coniferous forest (145 km^2) comprises approximately 23% of the remaining area. Elevations range from 2500 m in the Spanish Peaks to 1300 m on the Madison River floodplain. Elevational changes mediate an ecological gradient varying from dry grassland/juniper (*Juniperus scopulorum*) savannah at lower elevations to closed canopy Douglas fir (*Pseudotsuga menziesii*) or lodgepole pine (*Pinus contorta*) forests on moist sites at higher elevations. High elevation dry sites occur on southern exposures and ridgelines, and are predominantly mountain big sage (*Artemesia tridentada vaseyana*)/grassland mosaics. Temperatures range from highs of 21-32°C in the summer months to lows of -34°C in the winter months.

The Bear Trap wolf pack (pack size 2-8 individuals) recolonized the NMSA in the winter of 2002, representing the recolonizing front of wolves in the Madison Range. An unknown number of cougars resided on the NMSA. Grizzly bears (*Ursus arctos horribilis*), black bears (*Ursus americanus*), and coyotes (*Canis latrans*) also were present. Resident ungulates included elk, mule deer, white-tailed deer, and moose (*Alces alces*). The NMSA is privately owned and elk are managed for trophy hunting, whereas mule deer remain unexploited. Ungulate numbers varied slightly during the study. Elk were numerically superior and, on average, comprised 72% of the total ungulate availability; white-tailed deer and mule deer comprised 16% and 12%, respectively (see abundance estimates in Chapter II; Arnaud 2005). Over the duration of the study, elk sex ratios averaged 1.15 bull:1.00 cow (Arnaud 2005), whereas mule deer sex ratios averaged 0.74 buck:1.00 doe (Atwood, unpubl data).

Determination of multiple predator effects

I located predator-killed ungulates by backtracking wolves and cougars to kill sites, investigating areas where scavenging birds had aggregated, homing in on mortality signals from radiocollared mule deer, and searching along 25 transects on a 3 wk rotation within wolf and cougar territories. Transect length was dictated by proximity to study area boundaries and each transect was searched by 2-4 individuals walking parallel to the origin line and spaced at 50 m intervals. Prior to each rotation, I randomized transect starting points and directions. This method should have ensured that, over time, I searched all habitat types available to wolves and cougars, thus minimizing possible habitat-specific search bias. When a carcass was located, I first determined the cause of death (e.g., starvation, predation, human-caused, etc.) and, in case of predation, identified the predator species responsible for the mortality. I 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, diameter and spacing of puncture wounds, and carcass location. I differentiated kills from scavenging by the occurrence of chase trails and the presence of subcutaneous hemorrhaging. I determined habitat cover type (riparian, shrub/steppe, grassland, juniper savanna, conifer forest), elevation, slope, and aspect at kill site and encounter locations.

Resource selection modeling

I assessed availability of landscape attributes by placing 1000 random geo-referenced locations on a 10 m^2 resolution digital elevation model in ArcGis 9.0 (ESRI, Inc.). Attributes of interest included the above-mentioned variables assessed at kill and encounter locations, as well as distance from water and road features. This method was also used to determine the distances from water and road features for kill and encounter sites, and point locations used for models of predator and prey resource selection.

Categorical habitat and aspect variables were modeled using dummy variable coding, excluding reference categories.

Resource selection functions (RSF) were used to determine use versus availability of landscape attributes for prey and predators, and to test for differences in the effects of landscape attributes on predation stages. Resource selection functions were estimated via logistic regression using the following formula:

$$W^* = \exp(\beta_1 X_1 + \beta_2 X_2 \ldots + \beta_p X_p) \qquad (1)$$

where W* is an index of the probability of use of a given site (RSF) and β_1 is the selection coefficient of resource variable X_1 (Manly et al. 2002). Following Manly et al. (2002) and Hebblewhite et al. (2005) I dropped the intercept and denominator of the logistic form for the probability of encounter $\alpha(x)$ function. Accordingly, the RSF for the probability of a predator encountering prey took the form:

$$\alpha(x) = \exp(\sum \beta_i x_i) \qquad (2)$$

where i = refers to landscape covariates 1 through n for encounters and available locations. In models of prey and predator resource selection and predator encounter, I compared attributes of "used" sites to the attributes of the 1000 random sites.

Because our data set consisted of both kill and encounter locations, I extended my use of RSF's to estimate the conditional probability of death given an encounter d(x) as a function of landscape attributes. Following Hebblewhite et al. (2005), kill locations were coded as "used" and encounter locations where no kill occurred were coded as "unused." When data consists of known encounters, the used-unused design corresponds to a true probability function (RSPF), and the conditional probability of a kill given an encounter is expressed as:

$$d(\mathrm{x}) = [\exp(\beta_0 + \sum\beta_i x_i)/1 + \exp(\beta_0 + \sum\beta_i x_i)] \qquad (3)$$

where i = refers to landscape covariates 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). I estimated individual RSF (eq. 2) and RSPF (eq. 3) models for kill and encounter stages of predation on elk and mule deer. Individual estimates of $\alpha(\mathrm{x})$ and $d(\mathrm{x})$ were then substituted into a reformulation (Lima and Dill 1990) of Holling's (1959) functional response to generate a spatially-explicit estimate of prey-specific predation risk (Hebblewhite et al. 2005):

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

where α and d are the probability of encounter and the conditional probability of kill, respectively, and T is the time interval over which predation risk is being integrated.

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

Model performance and assessment

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

Results

I located 211 predator killed elk (n = 123) and mule deer (n = 88) over the duration of the study. Wolves killed the majority (70%) of elk, whereas 98% of mule deer kills were attributed to cougars; I documented 4 instances in which wolves killed mule deer. Because of sample size constraints, I was unable to partition mule deer predation among predators. Thus, models of mule deer predation risk solely reflected risk from predation by cougars. According to aerial and ground surveys, ungulate numbers varied slightly during the study (Arnaud 2005). Elk were numerically superior and, on average, comprised 72% of the total ungulate availability; white-tailed deer and mule deer comprised 16% and 12%, respectively. Over the 3 winters, I tracked wolves for 518 km and cougars for 272 km.

Resource selection models

Despite some consistency in covariates retained in the best models of elk and mule deer resource selection (Tables 3-4), there were important differences in the use of landscape attributes (Table 5). 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 on shallower slopes ($\beta = -0.026$) and with distance from water ($\beta = 0.0001$). Elk probability of occurrence decreased on south aspects ($\beta = -0.714$), with increasing elevation ($\beta = -0.001$), and with distance from roads ($\beta = -0.0003$). Probability of mule deer occurrence increased at lower elevations ($\beta = -0.011$), 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 distance from roads ($\beta = -0.002$).

Similar to prey models, wolf and cougar resource selection differed with respect to the use of key landscape attributes (Table 5). 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 ($\beta = 0.076$), and in juniper savanna ($\beta = 0.424$) habitats. Probability of cougar occurrence decreased in shrub/steppe habitat (β = -1.021), at lower elevations (β = -0.004) and with distance from roads (β = -0.001) and water (β = 0.0004).

Landscape predictors of encounters and kills

Substantial statistical differences existed in the constrained models of landscape attributes of prey encounter and kill stages (Table 6). Elk were approximately four 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). The relative odds of elk being killed in grassland (1.455) and shrub/steppe habitats (1.434) were slightly greater than that of an encounter (1.397 and 1.327, respectively). After an encounter in juniper savanna habitat (1.474), elk were over a third less likely to be killed (0.441). There were no pronounced differences in the odds of elk being killed after an encounter relative to slope and distances from road and water (Table 6). For mule deer, the relative odds of being killed in shrub/steppe (3.79) was over ten times greater than the odds of being encountered (0.351), whereas the odds of being killed in juniper savanna (0.198) was several orders of magnitude less likely than the odds encounter (7.664). Once encountered, mule deer were a fourth less likely to be killed on south aspects (encounter odds ratio = 3.202; kill odds ratio = 0.904). There were no differences in the odds of mule deer being encountered and killed relative to elevation, slope, and distances from road and water (Table 6).

Partitioning total predation risk

Elk used riparian, grassland, shrub/steppe, and juniper savanna habitats more than wolves and cougars (Table 6). 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 relatively open valley bottoms or shrub/steppe benches (figure 5); areas used more intensively by wolves than cougars. For those interactions, the strength of habitat effects overwhelmed topographic effects; given an encounter, habitat appeared to have the strongest effect on the risk of being killed (Table 6). Cougar use of south aspects and juniper savanna habitat was greater than wolves and cougar-elk interactions were most likely concentrated in that habitat association (figure 6). For those comparisons, the topographic effect of aspect overwhelmed the effects of other variables; given an encounter on south aspects, risk of death increased. Thus, for elk, total predation can be decomposed into the following: encounter risk in juniper savanna habitat and risk of death in riparian, grassland, and shrub/steppe habitats, and on south aspects (Table 6). In general, the conditional probability of an elk kill increased where the relative odds of wolf occurrence was substantially greater than those for cougars, but overlap in risk of death likely occurred on south aspects (Table 6).

Mule deer used juniper savanna habitat more than cougars and used south aspects and shrub/steppe habitat less than cougars (Table 5). Mule deer-predator interactions were concentrated on south aspect/juniper savanna habitat associations (figure 6), and the topographic effect of aspect was stronger than the habitat effect. Unlike elk, the risk of death for mule deer following an encounter generally declined. The exception was for shrub/steppe habitat where, given an encounter, the risk of death increased substantially (Table 6). Thus, for mule deer, total predation risk could be parsed into the following: encounter risk in juniper savanna habitat and south aspects, and risk of death in shrub/steppe habitat (Table 6). It is noteworthy that predation risk for mule deer was greater in shrub/steppe habitat, given that all mule deer mortalities were attributed to cougars. This finding suggests that shrub/steppe habitat can be associated with cougar predation risk and represents another habitat association where wolf and cougar predation risk may overlap.

Model assessment and predictive performance

In all models, a strong majority of predictor variables were selected for and models containing the top nine covariates were consistently ranked either first or second (Table 7). Based on Hosmer-Lemeshow tests, all final models displayed adequate fit (Table 7). Spearman rank correlations from the k-fold cross-validation indicated a strong relationship between the training and test data (Table 7). Given the above, I felt justified in using the consistent-set modeling approach to compare covariates across models.

Discussion

Whether introduction of an additional predator suppresses or enhances predation risk for shared prey is important to consider, particularly where large mammalian predators are reintroduced and effects on economically important prey species are unknown. However, unlike research conducted with other taxa (e.g. Schmitz 1998; Losey and Denno 1998; Sih et al. 1998), manipulative experiments of large mammal predator-prey interactions are often logistically or socially prohibitive. As a result, our understanding of multi-species interactions in complex predator-prey systems is incomplete. The crucial gap in knowledge is the putative link between predator and prey behavior with landscape physiography. Hebblewhite et al. (2005) provide an elegant framework for identifying the behavior-landscape nexus in a simple predator-prey system, and I build upon their foundation by extending similar concepts to a complex predator-prey system. In so doing, I illustrate the importance of partitioning predation risk among landscape covariates and between prey species and reveal several important observations of how the behavior-landscape nexus may mediate the potential for predation risk enhancement and predator facilitation. I show that although species-specific differences exist in resource selection and the encounter and kill stages of predation, attributes of resource selection and predation stages also converge in some areas. When predator-specific predation stages converge, evidence suggests that the effect of landscape features in facilitating predation may be predator-specific.

In order to adequately demonstrate the potential for risk enhancement, I first decomposed predation into discrete stages of (i) prey spatial behavior, (ii) predator search behavior, (iii) predator encounter of prey, and (iv) predator killing of prey. I made 3 critical assumptions in the development of stage-based models. First, I 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 manifest differences should exist in predator and prey resource selection functions. Next, I 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 a little more tenuous in that all predator space use is likely not associated with a search for prey. However, in the absence of information on predator satiety and cognitive processes that inform the decision to hunt prey, I was constrained to assuming that predator search behavior was subsumed by all space use by predators. Implicit in this assumption is the notion that predators utilize space in a way which should maximize the potential to encounter prey. Finally, I assumed that a spatial encounter (intersection of predator and prey tracks) adequately represented the probability of predators encountering prey for a given set of landscape covariates. I agree with Hebblewhite et al. (2005) that this is a perfectly 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.

Prey spatial behavior and predator search behavior

It is critically important that prey spatial behavior be considered in concert with predator space use. As pointed out by Lima (2002), predators are not unresponsive "black boxes," but effectual participants in the predator-prey behavioral dynamic. Consideration of prey space use relative to predator search behavior allows us to move beyond the ubiquitous fixed-risk (i.e., predator locations equal risk) and patch-specific risk (i.e., risk for a given habitat patch is static through time and space) assumptions of predation (Lima 1985, 2002). My work clearly illustrates the importance of carefully parsing total predation risk into constituents of encounter and predation. Landscape attributes did not increase the likelihood of elk encountering a predator but, given an encounter, they did render elk more vulnerable to predation. For elk, predation risk was less of a function of predator resource selection, and more related to landscape attributes that increased the risk of death. By contrast, the majority of landscape attributes did not increase the risk of death for mule deer following a predator encounter, and mule deer and cougar resource selection were closely related. Thus, landscape attributes generally rendered mule deer less vulnerable to predation, and predation risk was largely a function of predator resource selection. My observations lend evidence in support of the notion that wolf search behavior may be primarily influenced by their ability to catch prey (Kunkel et al. 2004; Hebblewhite et al. 2005), whereas cougar search behavior may be primarily influenced by prey resource selection (Hopcraft et al. 2005).

How do landscape attributes limit avoidance/hunting options?

The role of habitat attributes in influencing catchability of prey has been well explicated for aquatic systems (e.g., Hugie and Dill 1994; Bouskila 2001; Fraser et al. 2004), but is often overlooked in studies of terrestrial predator-prey interactions. It has been established that coursing predators generally are more successful in catching prey in open, physiographically simple habitats, whereas ambush predators are more successful catching prey in structurally complex habitats (Rosenzweig 1966; FitzGibbon and Fanshawe 1989; Kunkel et al. 1999). However, until recently (Hebblewhite et al. 2005) there has been no discussion of how landscape attributes interact with hunting style to influence the capture of prey. My analyses provide novel insight into the interaction of landscape characteristics with predator hunting styles in a complex predator-prey system. Based on conditional probabilities, risk of death declined for elk and mule deer in juniper savanna habitat. Presumably, this occurred for two reasons. First, juniper savanna habitat was used intensively by both elk and mule deer; simultaneous use may have diluted predation risk for a single prey species. Second, vegetative cover may have impeded the search efficiency of wolves, thereby reducing prey catchability. Indeed, for the latter, the relative odds of both elk and mule deer being killed in juniper savanna were lower than the 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, predation risk in juniper savanna habitat could be primarily attributed to risk of predation from cougars, and this further dilution of predation risk may have made juniper savanna the most effective refugia habitat for prey.

It is important to note that although we did not include measures of snow depth as a covariate (see Chapter II, where snow depth was not retained in kill site attribute models), others (e.g., Mech 1970; DelGuidice 1998; Kunkel and Pletscher 2000) have found snow depth important in mediating predation effects. My study took place in the midst of a 7 yr drought and the lack of substantial snowfall likely played a role in how predators and prey responded to landscape attributes. Most notably, the use of south aspects by prey may have reflected attempts to exploit space where little snow was present. South aspects were retained in encounter and kill models for both elk and mule deer: mule deer were less likely to be killed following an encounter, whereas elk were more likely to be killed after an encounter. Thus, even though my study took place over a period of less than average snowfall, prey might have behaved in a manner that could be inferred as being sensitive to the presence of snow by exploiting habitat associations on south aspects.

Predation risk in a complex predator-prey system

At first glance, these data would suggest that little potential for risk enhancement or predator facilitation exists. However, when total predation risk is decomposed, it becomes clear that refugia from a primary predator may increase predation risk from a secondary predator. For example, elk were more vulnerable to predation in open habitats, and while shifting to juniper savanna refugia increased the odds of encountering a predator it reduced the relative odds of death. In other words, total predation risk was enhanced from the risk of encountering a predator in putative refugia habitat. Because that risk can be attributed primarily to cougars, it is possible that wolf-induced shifts to refugia habitat can facilitate predation by cougars. My work was not explicitly designed to determine whether adaptive shifts in habitat use were mediating risk enhancement in prey, but rather to identify areas where risk enhancement may occur. However, recent research within the Greater Yellowstone Ecosystem 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 habitats by elk may ameliorate risk of predation from wolves, but in turn, exacerbate predation risk from cougars. Over the relatively short duration of my study, I saw a steady increase in cougar predation on elk, with the ratio of mule deer:elk killed nearly reaching unity in the final year (Atwood, unpubl data). The extent to which this potentially enhanced predation on elk modulates population processes will depend on whether said predation effects are additive or compensatory, and warrants further scrutiny.

Interestingly, I found no evidence of enhanced predation effects on mule deer. Direct effects of wolves on mule deer were negligible and, as a result, total predation risk for mule deer equated to partitioned predation risk from cougars. The predicted effects of wolf recolonization on mule deer has 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 my analyses, it can by hypothesized that total predation risk 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 habitat 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 the escape of larger terrestrial prey (Kunkel and Pletscher 2000). Where elk are numerically superior to mule deer, primary predation by wolves and enhanced predation by cougars on elk may benefit mule deer populations. It has long been recognized that predation can reduce the strength of competition between sympatric prey, and scramble competition with elk has been posited as a partial explanation for declines in regional mule deer populations. My modeling approach provides a useful platform to generate and test hypotheses relating to resource competition and sympatric prey.

I built a case of the potentiality of risk enhancement by first explicating predation stage isolates and then coalescing them into a risk enhancement composite. In so doing, I elucidated the behavior- landscape- predation nexus for a multiple predator- multiple prey terrestrial system. Conceptually, I show that predation risk is not a fixed property of a particular location, but rather is dynamic as predators and prey interact across heterogeneous landscapes. Dynamism in interactions increases the potential for multiple predator effects such as risk enhancement and/or synergism (Sih et al. 1998; Schmitz et al. 1997), thereby increasing total predation risk for some shared prey. If risk enhancement (or reduction) can be identified, the next step would be to determine the strength of the effect. A risk enhancement effect that is not trivial may be sufficient to have important population-level consequences for the prey and predators. Investigations of multiple predator effects in large mammals systems remain a difficult endeavor to undertake. I, along with Hebblewhite et al. (2005), endorse a spatial modeling approach as a crucial step in helping to increase our understanding of predator-prey interactions and landscape ecology in complex systems.

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Table 3. Akaike weights (w_i) for covariates evaluated in RSF and RSPF models for mule deer and cougar resource selection and encounter and kill stages of predation. Shown are the Akaike weights for each covariate, the average weight across all models, and the average rank of covariate importance.

Covariate	Mule deer	Cougar	Encounter	Kill	Average AIC_c weight, w_i	Average rank
Juniper	1.000	1.000	1.000	1.000	1.000	1
South aspect	0.978	1.000	1.000	1.000	0.994	2
Dist. from water	1.000	0.803	0.987	1.000	0.947	3
Dist. 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
West aspect	0.061	0.000	0.000	0.000	0.015	10
Conifer	0.000	0.004	0.000	0.000	0.001	11

Table 4. Akaike weights (w_i) for covariates evaluated in RSF and RSPF models for elk, wolf, and cougar resource selection and encounter and kill stages of predation. Shown are the Akaike weights for each covariate, the average weight across all models, and the average rank of covariate importance.

Covariate	Elk	Wolf	Cougar	Encounter	Kill	Average AIC$_c$ weight, w_i	Average rank
South 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
West aspect	0.000	0.001	0.000	0.003	0.000	0.000	11

Table 5. Relative odds ratios of parameter estimates, standard errors (SE), and corresponding p-values for independent variables in consistent-set RSF models for elk, mule deer, wolf, and cougar resource selection on the NMSA, 2002- 2005.

Model	riparian	grassland	shrub	juniper	south	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
P-value	<0.0001	<0.0001	<0.0001	<0.0001	0.0013	0.0425	0.1981	0.0008	0.1179
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
P-value	0.0289	0.0046	0.1164	<0.0001	0.0047	0.2145	<0.0001	<0.0001	<0.0001
Wolf	6.791	2.151	1.688	0.771	2.601	0.982	1.001	1.000	1.000
SE	0.414	0.274	0.277	0.301	0.164	0.013	0.0005	0.0001	0.0001
P-value	<0.0001	0.0052	0.0589	0.9609	<0.0001	0.1439	0.0382	0.0093	0.0128
Cougar	1.387	0.251	0.360	1.529	3.122	1.079	0.995	0.999	1.000
SE	0.547	0.333	0.321	0.300	0.205	0.011	0.001	0.0001	0.0001
P-value	0.5492	<0.0001	0.0015	0.1572	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

Table 6. Relative odds ratios of parameter estimates, standard errors (SE), and corresponding p-values for independent variables in consistent-set RSF and RSPF models for elk and mule deer predation encounter stages on the NMSA, 2002- 2005.

Model	riparian	grassland	shrub	juniper	south	slope	elevation	distance road	distance water
Mule deer- encounter	—	—	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
P-value	—	—	0.1450	<0.0001	0.0031	0.2584	<0.0001	<0.0001	<0.0001
Mule deer- predation	—	—	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
P-value	—	—	0.0071	0.0080	0.8221	0.0088	0.3129	0.0005	0.0002
Elk- encounter	2.427	1.397	1.327	1.474	0.706	0.966	1.000	1.000	1.000
SE	0.609	0.414	0.439	0.467	0.290	0.017	0.001	0.0001	0.0001
P-value	0.0060	0.0197	0.0189	0.4066	0.2313	0.0470	0.5682	0.1329	0.0056
Elk- predation	5.185	1.455	1.434	0.441	2.996	1.052	0.999	1.000	1.000
SE	0.710	0.555	0.578	0.660	0.362	0.022	0.0001	0.0002	0.0002
P-value	0.0204	0.4994	0.5327	0.2151	0.0024	0.0160	0.3129	0.2250	0.2253

Table 7. Model fit and assessment of ability to predict the relative probabilities of (a) resource use by mule deer, elk, wolves, and cougars, (b) mule deer and elk predator encounters, and (c) the true conditional probabilities of mule deer and elk being killed by predators, given an encounter.

Model	k_i	HL X^2	HL P-value	Likelihood ratio X^2	Likelihood ratio P-value	k-folds cross validation, r_s
Mule deer	7	7.36	0.5181	112.30	<0.0001	0.92 ± 0.02
Elk	9	9.11	0.4615	823.42	<0.0001	0.73 ± 0.04
Wolf	9	5.46	0.7066	119.49	<0.0001	0.82 ± 0.04
Cougar	7/9	10.70	0.2192	233.12	<0.0001	0.77 ± 0.05
Mule deer- encounter	7	4.24	0.7519	264.83	<0.0001	0.87 ± 0.01
Mule deer- predation	7	6.19	0.6257	70.61	<0.0001	0.83 ± 0.03
Elk- encounter	9	18.09	0.0205	50.91	<0.0001	0.66 ± 0.07
Elk- predation	9	12.22	0.1416	27.85	0.0010	0.79 ± 0.04

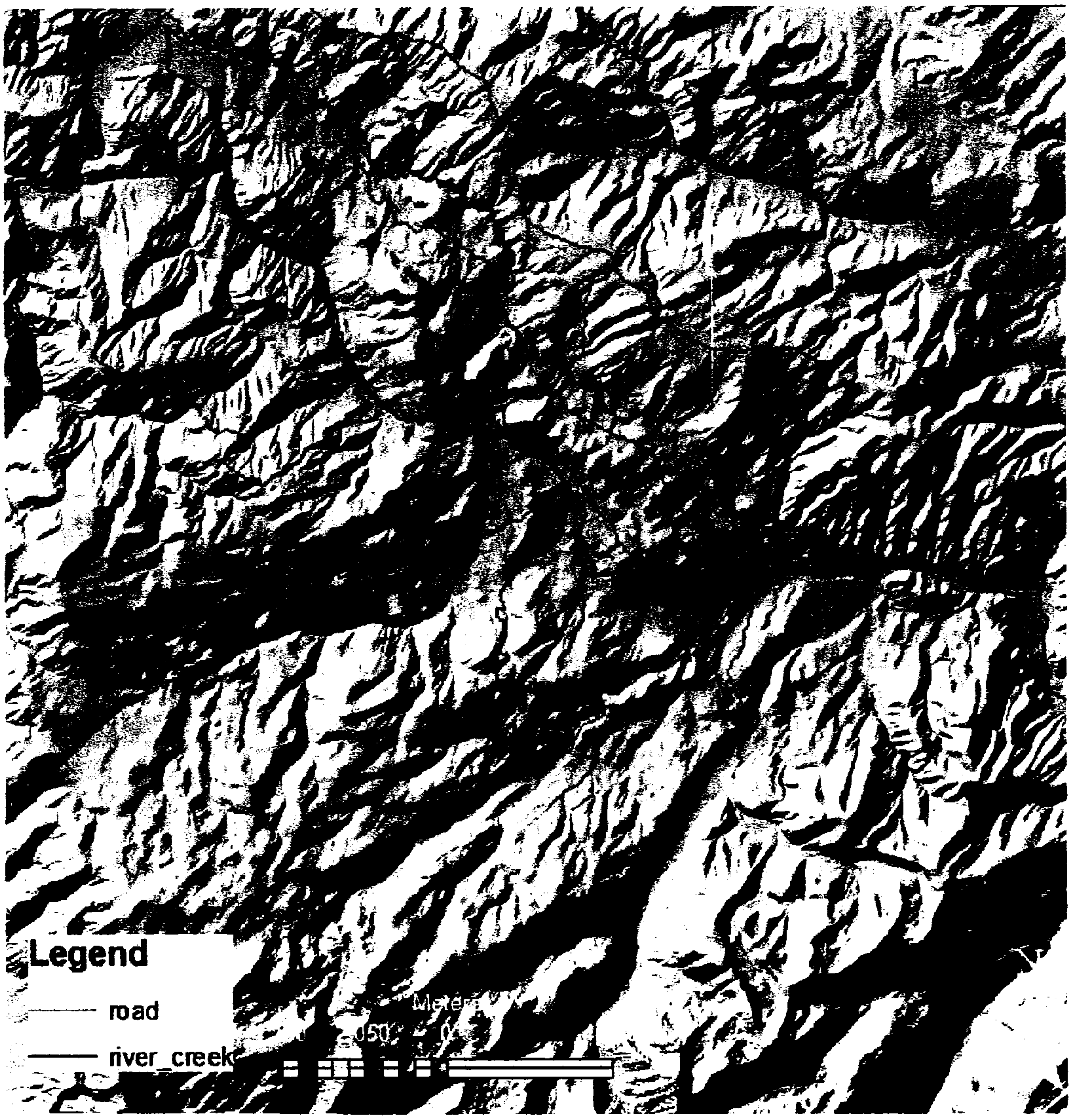

Figure 4. The Northern Madison Study Area (NMSA), located in Madison and Gallatin counties in southwest Montana's Madison Range.

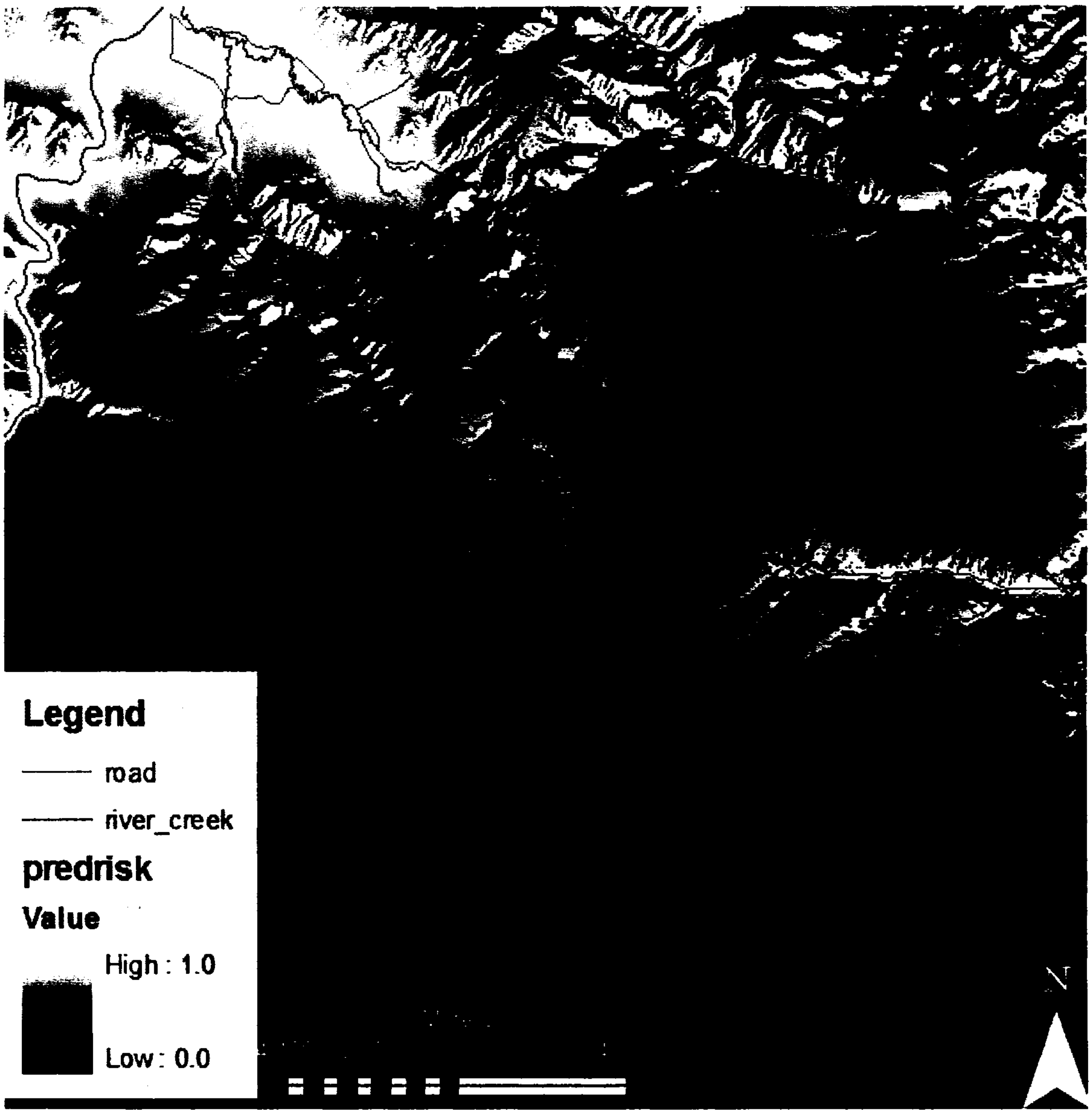

Figure 5. Spatial distribution of total predation risk for elk on the NMSA, 2002- 2005. Total predation risk is composed of the risk of encountering a predator and the risk of death given an encounter.

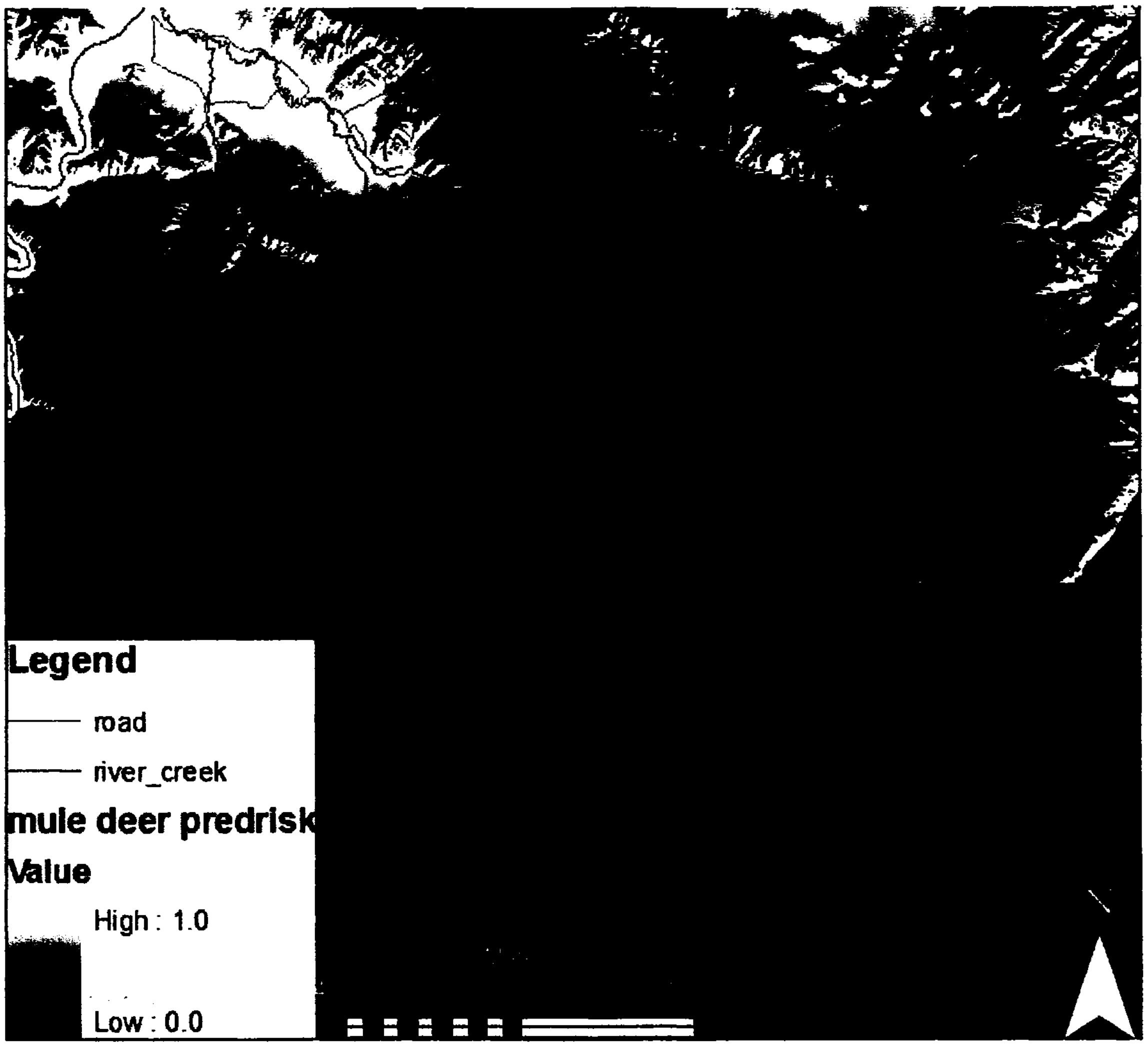

Figure 6. Spatial distribution of total predation risk for mule deer on the NMSA, 2002- 2005. Total predation risk is composed of the risk of encountering a predator and the risk of death given an encounter.

CHAPTER IV

RESOURCE SELECTION AND SOCIAL BEHAVIOR MODULATES THE PARTITIONING OF HOSTILE SPACE BY SYMPATRIC CANIDS

Abstract Investigations into mechanisms of competition are particularly suited to systems where interactive behaviors are emergent. Wolf (*Canis lupus*) recolonization of the Greater Yellowstone Ecosystem (GYE) provided such a system and I was able to identify developing behaviors influencing the outcome of competitive interactions between coyotes (*Canis latrans*) and wolves. I was able to observe coyote-wolf interactions immediately after wolf recolonization, when emergent behaviors mediating the outcome of competitive interaction were detectable and mechanisms of spatial avoidance were identifiable. Coyotes minimized the risk of encountering wolves by making adaptive changes in resource selection that reduced the likelihood of encountering wolves. However, spatially predictable carrion resources, foci of intense competition, provided inducement for coyotes to traverse areas of intense wolf activity. I concluded coyotes do not perceive wolves as a threat requiring generalized spatial avoidance. Rather, the threat of aggressive interactions with wolves is spatially discrete and primarily contained to areas immediate to carrion resources. In most cases, wolves excluded coyotes from carcasses and monopolized access until they decided to forego further feeding. However, occasionally, numerically superior aggressive coyotes were successful in supplanting wolves from carcasses. Thus despite the disadvantage of smaller body size, numerically superior coyotes demonstrated resource holding potential. Coyotes relied on subtle behaviors to avoid spatial interactions with wolves, and

conspicuous behaviors to mitigate the outcome of temporal interactions. By adapting behaviors to fluctuating risk, coyotes might reduce the amplitude of asymmetries.

Introduction

It has become axiomatic that coexisting species with an apparent potential to compete should exhibit differences in behavior that insure they compete little or not at all (e.g., Pianka 1969; Menge and Menge 1974; Robinson and Terborgh 1995). These manifest behavioral differences often are the basis for resource partitioning; perhaps the most commonly cited explanation of sympatry (e.g., Johnson and Franklin 1994; Kitchen et al. 1999). However, investigations of competitive interactions rarely delve deeper to identify behavioral mechanisms that may mediate when or how resources are partitioned. In part, this may reflect that few emergent behaviors are evident when potentially competing species have co-occurred over long periods of time. In such a case, perhaps the only way to uncover mechanisms of coexistence would be to observe interspecific interactions while nascent behaviors developed. Wolf (*Canis lupus*) recolonization of northern Montana and the Greater Yellowstone Ecosystem (GYE) has provided such an opportunity: presumably naïve (Berger et al. 2001) coyotes (*Canis latrans*) must alter behaviors to promote coexistence with a competitively dominant canid.

Given similarities in niche breadth and social behaviors, the potential for coyote-wolf interactions should be great. Likewise, subtle behaviors may be responsible for mediating the outcomes of these interactions, which at times may appear ambiguous. For example, while wolves may kill coyotes, they also provide significant food subsidies in the form of scavenging opportunities (Paquet 1991; Wilmers et al. 2003). As a result, coyotes have strong motivation to exploit the hostile space where wolf-provisioned carcasses are located. However, to realize a net benefit from scavenge subsidies, coyotes need to manage the potential threat posed by wolves. Where coyotes are habituated to wolf presence, they apparently have become adept at partitioning space (Fuller and Keith 1981; Paquet 1991; Switalski 2003), while increasing dietary overlap (Paquet 1992; Arjo and Pletscher 1999). Presumably spatial partitioning is avoidance behavior (Mills and Gorman 1997) in response to the risk of interspecific killing (Palomares and Caro 1999), whereas increased dietary overlap most likely results from coyotes scavenging wolf-killed prey (Paquet 1992; Wilmers et al. 2003). Although seemingly incongruous, these results suggest coyotes may perceive the risk associated with wolves as spatio-temporally dynamic. In fact, it is conceivable that putatively irreconcilable results such as partitioned space use relative to increased dietary overlap reflect a gradient of risk-sensitive responses by coyotes. This would suggest that perception of risk, and attendant behaviors mechanistically drive a dynamic partitioning of space.

How do coyotes manage the risk associated with wolf sympatry? Answers to this question may largely depend on the extent to which coyotes perceive wolves as a spatial and/or temporal threat. This can best be assessed by viewing coyote-wolf interactions as potentially occurring at 3 scales characterized by discrepant levels of risk. First, coyotes have the option to locate all or portions of their home ranges along interstitial spaces between adjacent wolf territories (e.g., Switalski 2003), where the risk of encountering wolves is low. This coarse grain of avoidance would suggest that coyotes view all space used by wolves as hostile; wolves pose a substantial spatial threat and coyotes must employ extreme avoidance behaviors to mitigate risk. Next, within home ranges, coyotes have the option to locate core areas so as to avoid space used intensively by wolves (e.g., Paquet 1991; Arjo and Pletscher 1999). In this case, the risk of negative interactions with wolves is moderate because of spatial overlap, but inconsistent in that risk is allocated differently over space. That is, coyotes perceive that risk is commensurate with intensity of wolf use (e.g., kill, den, and rendezvous sites carry relatively high risk), and manage risk by avoiding space used intensively by wolves. Finally, coyotes may temporally partition attendance at prey kill sites (e.g., Fuller and Keith 1981; Wilmers et al. 2003), indicating the threat posed by wolves is perceived as ephemeral and spatially discrete, and mediated by contest competition for food resources. In such close quarters, risk of negative interactions with wolves is high and behaviors ancillary to spatial avoidance may be necessary to mitigate risk.

In order for coyotes to successfully exploit space used by wolves, they must assimilate cues indicating wolf presence and intensity of activity, and respond appropriately to manage the risk of encounter. Holling's (1959) seminal work on the formulation of the functional response in predator-prey interactions provides a foundation for estimating the probability of a predator encountering prey. Recently, Hebblewhite et al. (2005) provided a framework for decomposing predation risk into constituents of encounter and kill probabilities. I adopted the general concept of this approach to determine how coyotes partitioned space relative to perceived risk of encountering wolves. Among coyote home ranges, wolf activity is spatially inconsistent; portions of some home ranges will be used intensively by wolves while others, despite spatial overlap, may not be used at all. Coyotes residing in home ranges coinciding with areas of intense wolf activity, exposed to a modicum of risk, can most effectively manage risk of encounter by predominantly exploiting resources outside of wolf activity centers. From a behavioral perspective, this would be analogous to prey moving to refugia habitat in an attempt to lessen predation risk (Bergerud and Page 1987; Formanowicz and Bobka 1988). Logically, coyotes are more likely to encounter wolf tracks in areas of intense wolf activity. The extent to which a spatial encounter of wolf tracks is perceived as a threat should be reflected in the aggregate of post-encounter resource selection. That is, if after encountering wolf tracks coyotes shift to less risky habitat associations (risk-averse behavior), differences in landscape attributes characteristic of spatial encounter and general habitat selection should be apparent. Conversely, coyotes may view spatial encounters with wolf tracks as a cue indicating a probability of encountering wolf-killed prey. If the latter is true, then coyote resource selection should reflect the characteristics of wolf kill sites.

Prey kill sites are potential foci for intense contest competition between wolves and coyotes (Atwood 2006). Because of the palpable risk of injury or death, coyotes must become adept at assessing and managing risk when exploiting wolf-killed prey. Many factors may be evaluated when estimating the immediate risk of and response to interspecific strife with wolves, and the level of risk perceived should influence the decision of whether to flee (Ydenberg and Dill 1986; Lima and Dill 1990) or retaliate (Geist et al. 2005). Divergent flee or retaliate strategies reflect disparate levels of fearfulness, which can be influenced through an interaction between prior experience with an aggressor (i.e., knowledge of the attack behavior) and characteristics of interacting agents (e.g. differences in group size or social status). The latter may be a particularly important factor informing the response of coyotes to close-quarter threats from wolves. Indeed, it is acknowledged that numerical superiority partially mediates kleptoparasitism in cooperative African carnivores (Cooper 1991; Carbone et al. 1997). It also has been established that numerical superiority is a primary determinant in the outcome of territorial transgressions between adjacent coyote packs (Gese 2001) and, as a result, indirectly influences access to space within territories. By logical extension, differences in relative group sizes may be an important determinant in when and how coyotes decide to share space with wolves. The extent to which differences in group size may diminish or intensify fine-scale risk perception remains unknown, but may prove critical to reconciling space-sharing by sympatric canids.

I investigated coyote spatial ecology in response to recolonizing wolves in Montana's Madison range. Broadly, my aim was to determine if, when, and where coyotes partitioned space relative to wolf activity and identify mediating behaviors. Accordingly, I started by addressing three specific questions: (i) do coyotes avoid space used by wolves; (ii) do landscape features associated with coyote resource selection differ from where they are likely to encounter wolves; and (iii) does resource selection by coyotes change in response to increasing risk of encountering wolves? I predicted coyotes would be insensitive to wolf activity within home ranges, but would partition space use by locating core activity centers in areas of low-intensity wolf use. Because wolf-killed prey represented a highly valued resource subsidy, I predicted coyotes would be compelled to exploit these sites of intense wolf activity, but partition space use temporally so as to avoid strife with wolves. Finally, I identified behavioral and environmental correlates facilitating coyote exploitation of prey kill sites. I suggest that elucidating mechanisms of sympatry between coyotes and wolves will be extremely important in learning how competition might influence canid community structure.

Methods

I conducted the study in the Northern Madison Study Area (NMSA; 680 km^2), located in southwest Montana's Madison Range of the Rocky Mountains, during the winters (December-April) of 2003-2005. The NMSA is approximately 50 km northwest of Yellowstone National Park, and is 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 km^2) dominates valleys and benches on the NMSA; coniferous forest (145 km^2) comprises approximately 23% of the remaining area. Elevations range from 2500 m in the Spanish Peaks to 1300 m on the Madison River floodplain, and mediate an ecological gradient varying from dry grassland/juniper (*Juniperus scopulorum*) savannah at lower elevations to closed canopy Douglas fir (*Pseudotsuga menziesii*) or lodgepole pine (*Pinus contorta*) forests on moist sites at higher elevations. High elevation dry sites occur on southern exposures and ridgelines, and are predominantly mountain big sage (*Artemesia tridentada vaseyana*)/grassland mosaics. Temperatures range from highs of 21-32°C in the summer months to lows of -34°C in the winter months.

A single wolf pack (Bear Trap pack) recolonized the NMSA in the winter of 2002, representing the recolonizing front of wolves in the Madison Range. Bear Trap pack size ranged from 2-8 individuals, one of which (yearling female) was radiocollared and subsequently dispersed. Over the duration of the study, the Bear Trap pack averaged 5 individuals. Coyotes were distributed over the entire NMSA, and resided in multi-generational packs. Pre-whelping pack size was 4 adults, and average litter size was 6 pups. Coyotes were subjected to hunting and it is estimated that approximately 20% of the population was killed annually (Arnaud 2005).

I captured and radiocollared coyotes in fall and winter 2003-2004 using foothold trapping and helicopter netgunning. I located focal coyotes using ground-based radiotelemetry and then collected spatial data from continuous snow tracking bouts. I obtained sequential point locations at 400 m intervals using handheld global positioning systems (GPS). At each point, I recorded percent slope, elevation, aspect (classified as 4 cardinal directions), cover type, coyote group size, wolf tracks encountered, and wolf group size. I defined an encounter as the spatial intersection of coyote and wolf tracks. In all likelihood, the spatial intersection of coyote and wolf snow tracks does not represent a true spatio-temporal encounter. However, I was only interested in spatial encounters. I estimated wolf space use using the same methods described for coyotes, with the exception that I collected point locations at 1 km intervals. I examined differentially corrected point locations for spatial autocorrelation (Neilson et al. 2002) and censored correlated points from the data set.

I located prey kill sites by backtracking wolves and coyotes, and investigating areas where scavenging birds had aggregated. Once a kill was located, I confirmed predation as the cause of death, and recorded data on habitat and physiographic attributes and canid tracks present. If coyotes and wolves were actively feeding at kill sites, I collected observational data on interactive behavior. I observed activity via 15-45× spotting scopes, recording canid group sizes, social status of individuals present, time spent feeding (carcass access time), and stage of carcass consumption (described by Wilmers et al. 2003). I entered kill site locations into a GIS to quantify the number of wolf-killed prey located within coyote pack home range and core areas, and for subsequent analyses to identify factors influencing space-sharing between coyotes and wolves.

Spatial response of coyotes to wolves

I characterized the static spatial response of coyotes to wolf activity at the home range and core area scales. I weighted spatially independent wolf locations (separated by distances of 1 km) by group size (Fortin et al. 2005) and used the weighted locations to estimate fixed kernel (FK) winter home range (95% FK) and core areas (60% FK; Shivik et al. 1996) using the animal movement extension in ArcView (Hooge et al. 1999; Environmental Systems Research Institute 2000). I used fixed kernel estimators because they are better able to differentiate discrete centers of activity than are adaptive kernel estimators (Kernohan et al. 2001). The weighting procedure was necessary in order to accurately characterize intensity of use. Wolves are cooperative hunters that usually travel in groups and there is often a high degree of dependence in the spatial locations of pack members. This dependence is biologically meaningful because differences in group size have been found to mediate the outcome of competitive interactions between sympatric cooperative carnivores (Cooper 1991; Carbone et al. 1997). I used an overlay routine in ArcView to estimate percent overlap of coyote home range and core areas by the wolf territory. However, in isolation, spatial overlap can be a poor indicator of interaction because kernel contours only represent the outline of an accumulated areal distribution. That is, important information regarding avoidance or attraction of shared space may be lost unless the distributions of point locations within overlapping contours are considered. Thus I superimposed weighted wolf point locations on coyote home range and core contours to quantify the intensity of wolf activity. For each coyote pack, I then indexed wolf intensity (W_{int}) for both contours by calculating the ratio of observed to expected weighted wolf locations using the following formula:

$W_{int} = locations_i / (locations_j \times area_k)$

where i is the observed number of kernel-specific locations, j is the total number of observed wolf locations from both kernels, and k is kernel area (km^2).

I compared the number of weighted wolf locations in coyote home ranges and core areas to expected values (based on the proportion of their respective areas) to determine if coyote spatial response to wolf presence was scale-dependent. If coyotes regard wolves as a general threat, they should avoid centers of wolf activity. That is, coyote activity centers (core areas) should be situated in areas of low intensity wolf occurrence. However, it is also reasonable to consider that coyotes may be attracted to areas used by wolves, particularly if wolves kill prey in a spatially predictable manner. In this case, coyotes may configure core areas to contain prime wolf hunting habitat in order to benefit from scavenge subsidies. I used Pearson chi-square analysis to determine if the relationships between coyote space use, spatial scale, and wolf intensity were independent by comparing observed to expected wolf occurrences between home range and core areas within winters. If differential scale-dependent space use was evident, I tested for homogeneity between odds ratios using the Breslow-Day test (Agresti 1996). When heterogeneity was confirmed, I examined the adjusted cell residuals (Agresti 1996) to determine when avoidance or attraction was taking place.

Resource selection and interaction models

I used logistic regression to model resource selection by coyotes at 3 scales (all within the home range) of potential interaction with wolves characterized by increasing likelihood of physical encounter and risk: encounter of tracks (low risk spatial); visitation of areas used intensively by wolves (high risk spatial); and visitation of prey kill sites (high risk temporal). I compared regression models of resource selection (i) by coyotes and wolves, and for (ii) coyote-wolf track encounter sites, (iii) coyote use of wolf activity centers, and (iv) prey kill sites visited by coyotes to determine if resource selection by coyotes differed relative to wolves and with respect to potentially escalating risk of encountering wolves. I estimated coyote and wolf resource selection by comparing attributes at snowtrack point locations to attributes from 1000 randomly placed point locations distributed throughout the entire NMSA. I estimated selection at encounter sites by comparing wolf encounters obtained from coyote snow tracking with all non-encounter coyote locations. For coyote habitat selection relative to wolf intensity, I compared coyote locations in wolf activity centers (60% FK contours) with locations outside of wolf activity centers. I compared all kill sites visited by coyotes to the remaining coyote locations. Finally, I used general linear models (GLM) to model coyote access time (T_{acc}) at carcasses as a function of year, coyote social status, prey type, cover distance, stage of carcass consumption, snow depth at kill site, and the difference between coyote and wolf group sizes. Year was included as a covariate because I suspected that, over time, coyotes may have learned to better manage the risk of scavenging wolf-killed prey, resulting in greater carcass access time. For all logistic regression analyses, I checked continuous variables for conformity to linearity using the quartile method (Hosmer and Lemeshow 2000), and final model fit was ensured by testing with the Hosmer and Lemeshow goodness-of-fit statistic (Hosmer and Lemeshow 2000). I used Akaike Information Criteria with a small sample size correction factor (AIC_c) to determine which parameters were to be retained in all regression models; I considered AIC_c values that exceeded 4.0 to be significant (Burnham and Anderson 1998). I used Akaike weights (w_i) to gauge relative importance of factors influencing carcass access time, and used the evidence ratio of the ΔAIC_c weights for model i and model j as the likelihood that model i was better than model j.

Results

I captured and radiocollared 29 coyotes, 21 of which were residents belonging to 11 packs (Fig. 7-8). I monitored the same 11 packs (pre-whelping group size: $\bar{x} = 4$ adults, SE = 0.22) over both winters, although within pack composition changed slightly. Over the 2 winters, I tracked coyotes for 1603 km (Table 8) and wolves for 518 km. Backtracked coyotes encountered 97 sets of wolf tracks (Table 8; excluding encounters at kill sites) and followed those tracks in a forward direction for an average of 4.2 km. I located 93 prey kill sites, 77 (83%) of which were visited by coyotes. On 22 occasions, coyotes forward-tracked wolves to prey kill sites. One collared adult coyote (beta female; Little Lamar pack) and 2 uncollared pups (6-11 months old) were found killed by wolves; by comparison, 3 collared adults were killed by cougars (*Puma concolor*). All coyote mortalities attributed to interspecific killing occurred near ($\leq$ 200 m from carcass) prey kill sites.

Percent overlap of coyote home ranges by the Bear Trap pack was extensive in both winters (95% FK: $\bar{x}$ = 78% SE = 5.54%; 60% FK: $\bar{x}$ = 82% SE = 6.69%). In 2003-04, portions of 8 coyote home ranges and 5 core areas fell within 3 wolf activity centers (Fig. 9); in 2004-05, portions of 7 coyote home ranges and 6 core areas fell within 5 wolf activity centers (60% FK; Fig. 10). Because the percent overlap of home ranges (t_{10} = 0.11, P = 0.89) and core areas (t_{10} = 0.40, P = 0.69) did not vary between years, I pooled samples for subsequent analyses. Coyote attraction to wolf activity centers was further corroborated by results from the Pearson chi-square analysis, which indicated a strong association between wolf activity and coyote space use (χ^2 = 29.54, d.f. = 1, P <0.0001). Generally, wolf activity within coyote core areas was proportionally greater than within coyote home ranges; however, this association was heterogeneous (Breslow-Day χ^2 = 4.29, d.f. = 1, P = 0.03). Proportionally, more wolf kill sites were located within coyote core areas than within home ranges (χ^2 = 23.46, d.f. = 1, P <0.0001).

Model assessment and predictive performance

The covariates of elevation, slope, south aspect, and shrub/steppe habitat were consistently retained in top-ranked models of wolf encounter probability and coyote habitat selection in response to wolf activity. For the latter, ΔAIC_c scores suggested a tie (<4 ΔAIC_c) between the lower ranked model containing the above 4 covariates and a higher ranked model in which distance from water was included (Table 9). However, inspection of Akaike weights indicated that the top-ranked model (elevation, slope, south aspect, shrub/steppe, and distance from water) was ≈ four times (w_i/w_j = 4.20) as likely to be the K-L best model. There was little consistency with the covariates retained in the model of kill sites visited by coyotes; only slope and south aspect were retained (Table

9). Hosmer and Lemeshow (2000) tests indicated good model fit for all stage-based models.

Landscape predictors of encounter

The probability of coyotes encountering wolves was greatest in shrub/steppe habitat ($\beta = 1.55$), and increased at lower elevations ($\beta = -0.005$) and on south-facing ($\beta = 0.88$), shallower slopes ($\beta = -0.09$). Within wolf activity centers, probability of coyotes using shrub/steppe habitat ($\beta = -1.35$) declined, use of south-facing ($\beta = 0.613$), shallow slopes ($\beta = -0.056$) remained high, and use increased with increasing elevation ($\beta = 0.005$). The probability of a prey kill site being visited by coyotes was high in riparian zones ($\beta = 0.34$), low in grassland ($\beta = -0.81$) habitats, and increased on shallower slopes ($\beta = -0.08$) and with distance from water ($\beta = 0.001$). The probability of wolf kill sites occurring in riparian zones ($\beta = 3.29$) and on shallower slopes ($\beta = 3.29$) was high, whereas the probability of occurrence on south aspects ($\beta = -0.86$) was low.

Coyote access to wolf-killed prey

I observed 52 individual coyotes (11 packs; 21 collared, 31 uncollared) scavenging in the presence of 6 individual adult wolves (all of known social status) for 681 hr at the 77 ungulate carcasses (Table 10). Forty-three percent (n = 42) of all wolf kill sites were located within wolf activity centers which comprised, on average, 20% of the total area used by the Bear Trap pack. Likewise, 43% (n = 33) of wolf kill sites visited by coyotes were located within coyote core areas, which comprised 23% of the total area occupied by the monitored coyote packs. By contrast, 45% (n = 35) of kill sites visited were within coyote home ranges (core area excluded), and 12% fell outside monitored coyote pack boundaries. I witnessed 36 discrete bouts of agonistic interactions at 23 carcasses involving 6 different coyote packs and the Bear Trap wolf pack. Seventeen bouts ended with coyotes supplanting wolves from carcasses, all of which occurred when the carcass was nearly depleted. The effects of group size and stage of carcass consumption on mediating coyote access to carcasses was further evidenced by modeling results. The top-ranked model, T_{acc} = year + carcass stage + group difference, was ≈ 14 times more likely to be the best candidate model as the second model, T_{acc} = carcass stage + group difference + snow depth (Table 11). Access time at carcasses increased with increasing coyote group size ($\beta = 2.06$; Fig. 11), stage of carcass consumption ($\beta = 1.19$), and between years ($\beta = 4.75$).

Discussion

Ostensibly, heterogeneity in the association between coyote space use and wolf activity was a function of the dispersion of scavenge subsidies in the form of wolf-killed prey. Spatially predictable carrion resources should provide strong motivation to coyotes to routinely traverse these potentially hostile areas with the intent of finding scavenging opportunities. However, the spatial distribution of carcasses interacts with territorial behavior by coyotes (Gese 2001) to limit how many packs are able to configure core area borders to exploit wolf activity centers. The preponderant distribution of wolf kills within core areas, along with the disproportionate spatial overlap, suggests that coyotes are actively traversing areas used intensively by wolves. Given that core areas are relatively small, the concentration of scavenge resources and wolf activity create a situation where the likelihood of encounter is great. Coyotes, then, must decide when and how to exploit these areas while minimizing the risk of aggressive interaction. If coyotes regarded wolves as a spatial threat, they would not, when presented with the opportunity, overwhelmingly locate core areas in wolf activity centers. Rather, they would avoid areas used intensively by wolves in order to reduce the threat associated with encounter. The fact coyotes do exploit these areas indicates that threat perception and avoidance behaviors are more subtle.

My data indicate that, when afforded the opportunity to exploit wolf-killed prey, coyotes made modest changes in key aspects of resource selection that increased the potential of encountering wolves. For example, resource selection within home ranges differed from selection within wolf activity centers only with respect to distance from water: coyotes tended to remain closer to water features (primarily streams and creeks) as they moved through wolf activity centers. Interestingly, although coyotes traveled close to water features, they were not close enough to shift from shrub/steppe to riparian habitat. There are two possible explanations, neither of which is mutually exclusive. First, coyotes may have been reluctant to shift habitats because the dense protective cover characteristic of alder (*Alnus spp*)/willow (*Salix spp*) riparian associations interfered with their ability to visually detect wolves. Second, wolf activity may have been greater in riparian habitats than in shrub/steppe. I believe both scenarios are supported by our models describing the distribution of wolf kills and kill sites visited by coyotes. Consistent with other research, wolf kills were most likely to be located in or near riparian habitats (Mech 1970; Smith et al. 2004), and coyotes showed a proclivity for riparian habitats only when exploiting kills. I believe increased visual occlusion and risk of encountering wolves accounted for coyotes avoiding riparian habitats while traveling through wolf activity centers. However, once a kill was detected, coyotes were compelled to move into the putatively more risky riparian habitat in order to take advantage of scavenging opportunities.

Relationships between sympatric species of canids have been portrayed in the context of obligate hostility, where body size mediates asymmetry and the larger species dominates (Carbyn 1982; Rudzinski et al. 1982; Major and Sherburne 1987; Hersteinsson and Macdonald 1992). While in the aggregate these manifest outcomes of interaction may be the norm, tacit acceptance of this general view may overlook important behavioral adaptations that facilitate sympatry. The potential for coexistence is not an "all or nothing" enterprise; ample research on niche partitioning in terrestrial mammals has confirmed that while interspecific competition frequently occurs, there is a dearth of evidence in support of competitive exclusion (Connell 1983; Schoener 1983). Evidence from my research indicates that, in most cases, wolves are able to exclude coyotes from carcasses and monopolize access until they decide to forego further feeding. However, evidence also suggests that coyotes, on occasion, can be successful in supplanting wolves from carcasses. Several factors play a critical role in determining whether coyotes are successful, chief among them is numeric superiority. Based on my observations, when numerically superior, coyotes were more likely to aggressively engage wolves, using harassment behaviors (e.g., barking, biting), at carcasses.

Condition-dependent superior vigor by a smaller species is not without precedent. For example, smaller-sized black-backed jackals (*Canis mesomelas*) were observed to rely on aggression to routinely displace larger side-striped jackals (*Canis adustus*) from prime foraging habitat (Loveridge and Macdonald 2002). Black-backed jackals also are more likely to risk feeding among lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta*) than are other species of jackals (Mills 1990; Estes 1991), and spotted hyenas are more successful in kleptoparasitizing lions when they can recruit sufficient clan members to appropriate a carcass (Honer et al. 2002). Vigorous displays of aggression can allow a smaller species to gain access to a resource that might otherwise be monopolized by a larger competitor. Maynard-Smith and Parker (1976) termed this successful aggressive behavior by asymmetrically subordinate competitors "resource holding potential." For coyotes, numeric superiority has been identified as a factor critical to the aggressive defense of carcasses and territorial boundaries against incursions by conspecifics (Gese 2001). My study supports the notion coyotes may rely on a similar strategy when exploiting wolf-killed carcasses, namely that, when numerically superior, they may forego temporal partitioning and attempt to supplant wolves from carcasses. Thus despite the disadvantage of smaller body size, coyotes can demonstrate resource holding potential, as measured by carcass access time (T_{acc}), when numerically superior to wolves. However, I caution that for coyotes, resource holding potential is not solely a function of numeric superiority, but rather is dependent on several factors as discussed below.

Numerically superior coyote groups were able to feed at carcasses for a greater duration as the stage of consumption progressed. Foraging theory provides a contextual framework for understanding why access increased concomitant with the diminishing resource. If a prey kill site is analogous to a resource patch, then a forager should feed at that kill until the marginal value (Charnov 1976) of remaining falls below the expected value of realizing future caloric gains. Over time, handling time at a carcass increases as the ease of removing tissue decreases. Wilmers et al. (2003) characterized the stages of carcass consumption by wolves and found that, as wolves progressed from feeding on organs to minor muscles, feeding rate increased while estimated biomass consumed decreased. This increase in carcass handling time, commensurate with a decrease in consumption, may make carcasses less valuable to wolves. As a result, wolves may be less inclined to mount a vigorous defense against kleptoparasitism by coyotes and more likely to leave the resource "patch." The tipping point may occur when coyotes are numerically superior, and the energetic cost of defense by wolves is no longer balanced through carcass biomass ingestion. Access time at carcasses also increased over successive years and may represent adaptive behavioral strategies by coyotes. In other words, formerly naïve (Berger et al. 2001) coyotes may have learned, through previous experience, to exploit carcasses in the latter stages of consumption, when wolf defensive vigor (and attendant risks to coyotes) wanes. With this last point, I want to emphasize that it is not my intention to extend behavioral observation to cognitive inference. Rather, I merely point out that it is plausible that coyotes might have learned, through both positive and negative reinforcement, to identify optimal conditions for exploiting wolf-killed prey. I welcome further investigation into the cognitive processes that may inform adaptive risk-sensitive behaviors.

Investigations into mechanisms of competition are particularly suited to systems where interactive behaviors are emergent, and wolf recolonization of the GYE provided a system where I was able to identify developing behaviors mediating competitive interactions between coyotes and wolves. Previous research has provided a solid foundation for characterizing sympatry between these canids by describing where and when space is partitioned (e.g., Paquet 1991; Arjo and Pletscher 1999; Switalski 2003). I built upon this foundation to elucidate a key behavioral mechanism mediating spatial partitioning: the risk perception- spatial avoidance nexus. My work indicated the following: (i) coyotes displayed adaptive habitat selection in response to escalating risk of encountering wolves; (ii) when wolf-killed prey were available, coyotes traded-off increased risk for scavenge benefits; and (iii) numeric superiority increased resource holding potential for coyotes and may have functioned to lessen the potential for negative outcomes in interactions with wolves. In sum, coyotes relied on subtle behaviors to avoid spatial interaction with wolves, and conspicuous behaviors to mitigate the outcome of temporal interactions. This would suggest that coyotes changed their behavior to reflect the ebb and flow of the wolf risk dynamic; by adapting behaviors to fluctuating risk, coyotes might be successfully dampening the amplitude of asymmetry. Integrating behavior with spatial ecology is a worthwhile endeavor and can prove effective in linking causal mechanisms to observed phenomena.

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Table 8. Total distance snowtracked, number of wolf tracks encountered, and number of wolf kills visited by coyotes on the NMSA, southwest Montana, 2003-2005

Year	Pack Name	Distance Tracked (km)	Wolf Tracks Encountered[a]	Wolf Kills Visited[b]
2003-04	Carpenter Creek	68	11	5
	Cow Camp	57	8	3
	Cowboy Canyon	49	—	2
	Green Hollow	61	—	4
	Little Lamar	93	14	7
	Mill Creek	40	3	2
	Pole Creek	74	7	6
	Reef	46	4	3
	Spanish Creek	67	2	2
	Ted's	53	—	1
	West Fork	61	6	4
2004-05	Carpenter Creek	94	13	5
	Cow Camp	113	7	4
	Cowboy Canyon	83	1	2
	Green Hollow	56	—	—
	Little Lamar	126	11	6
	Mill Creek	77	—	—
	Pole Creek	94	9	4
	Reef	76	1	1
	Spanish Creek	91	2	—
	Ted's	69	1	1
	West Fork	55	1	—

Table 9. Top logistic regression models of variables found significant in predicting habitat characteristics at coyote-wolf track intersections (encounter), areas of intense wolf activity, kill sites visited by coyotes, and all wolf kill sites. Model structure is accompanied by odds ratios, corresponding 95% confidence intervals, and AIC_c values and weights.

Model	$O.R._1$(C.I.)	$O.R._2$(C.I.)	$O.R._3$(C.I.)	$O.R._4$(C.I.)	$O.R._5$(C.I.)	$O.R._6$(C.I.)	AIC_C	w_i	P-value
Coyote selection									
$g(x) = -.093 + 1.97_{veg}^{d} + 1.97_{veg}^{e} + 1.36_{veg}^{g} -0.36_{aspect}^{i}$	7.2(3.8-13.5)	6.7(4.0-11.2)	3.9(2.2-6.8)	0.70(0.52-0.94)	—	—	1213.2	0.86	<0.001
Wolf selection									
$g(x) = 2.3 - 1.42_{veg}^{e} - 0.07_{slope} + 0.78_{aspect}^{j}$	0.24(0.14-0.42)	0.93(0.89-0.97)	2.19(1.13-4.24)	—	—	—	376.7	0.93	<0.001
Spatial track encounter									
$g(x) = 5.4 + 1.55_{veg}^{g} - 0.005_{elev} - 0.09_{slope} + 0.88_{aspect}^{i}$	4.7(2.2-10.1)	0.99(0.99-1.00)	0.91(0.85-0.97)	2.4(1.2-4.8)	—	—	304.4	0.97	<0.001
Wolf activity centers									
$g(x) = -10.1 – 1.35_{veg} + 0.005_{elev} - 0.06_{slope} + 0.61_{aspect}^{i} - 0.001_{water}$	0.26(0.11-0.69)	1.00(1.00-1.01)	0.95(0.91-0.99)	1.85(1.16-2.95)	0.99(0.99-1.00)	—	551.0	0.80	<0.001

Table 9. Continued.

Model	$O.R._1$(C.I.)	$O.R._2$(C.I.)	$O.R._3$(C.I.)	$O.R._4$(C.I.)	$O.R._5$(C.I.)	$O.R._6$(C.I.)	AIC_C	w_i	P-value
Kill sites visited by coyotes									
$g(x) = -2.24 + 0.34_{veg}^{d} - 0.81_{veg}^{e} - 0.08_{slope} + 0.001_{water}$	1.2(1.1-1.3)	4.7(2.4-9.1)	0.01(0.001-0.04)	0.02(0.01-0.03)	0.42(0.07-2.5)	7.7(1.7-16.3)	585.2	0.95	<0.001
Wolf kill sites									
$g(x) = 0.56 + 3.29_{veg}^{d} - 0.11_{slope} - 0.86_{aspect}^{i} + 0.001_{road}$	26.8(3.3-29.3)	0.89(0.84-0.96)	0.43(0.18-0.97)	1.00(0.99-1.01)	—	—	205.9	0.94	<0.001

[c-g]Design coded with “forest” habitat (variables included forest[c], riparian[d], grassland[e], canyon/juniper[f], and shrub/steppe[g]).

[h-k]Design coded with “north” aspect (variables included north[h] , south[i], east[j], west[k]) as the reference categories.

Table 10. Top multiple regression models of factors influencing access time (T_{acc}) for coyotes feeding on wolf-killed prey. Model structure is followed by estimates of regression coefficients and AIC_c values and weights of evidence.

Model	β_0	β_1	β_2	β_3	β_4	β_5	β_6	AIC_c	wi	P-value
1. β_0 + group difference + carcass stage + year	-6.69	2.06	1.19	4.75	—	—	—	313.1	0.85	<0.001
2. β_0 + group difference + carcass stage + snow	0.54	2.01	1.29	0.10	—	—	—	318.4	0.06	<0.001
3. β_0 + group difference + carcass stage + social status + prey type + year – cover distance	-7.09	2.04	1.17	0.03	0.37	4.63	-0.002	319.6	0.04	<0.001

Table 11. Summation of coyote packs observed, numbers of canids present, total hours observed, and mean carcass access time for coyotes scavenging wolf-killed prey in the NMSA, southwestern Montana 2003-2005.

Pack Observed	Coyotes Present	Wolves Present	Hours Observed	Carcass Access Time (hr^{-1})
West Fork	3[i]	2[j]	74	0.63
West Fork	3[i]	1[j]	63	1.08
Little Lamar	2	3[j]	41	0.55
Little Lamar	5	3[j]	32	1.23
Little Lamar	6[i]	1	80	1.47
Little Lamar	5[i]	1	11	1.15
Little Lamar	1	1	7	0.41
Cow Camp	2[i]	1[j]	31	1.41
Cow Camp	5[i]	1[j]	46	1.61
Cow Camp	4[i]	1	37	1.27
Carpenter Creek	2[i]	1[j]	101	0.66
Carpenter Creek	1	1[j]	16	0.32
Carpenter Creek	5[i]	1	43	1.63
Carpenter Creek	2	1	26	1.32
Pole Creek	5[i]	3[j]	18	1.35
Pole Creek	2	3[j]	25	0.41
Pole Creek	1	3[j]	13	0.16
Cowboy Canyon	4[i]	3[j]	6	1.01

Table 11. Continued.

Pack Observed	Coyotes Present	Wolves Present	Hours Observed	Carcass Access Time (hr^{-1})
Cowboy Canyon	2[i]	3[j]	11	0.14

[i] One or both alpha coyotes present; [j] one or both alpha wolves present.

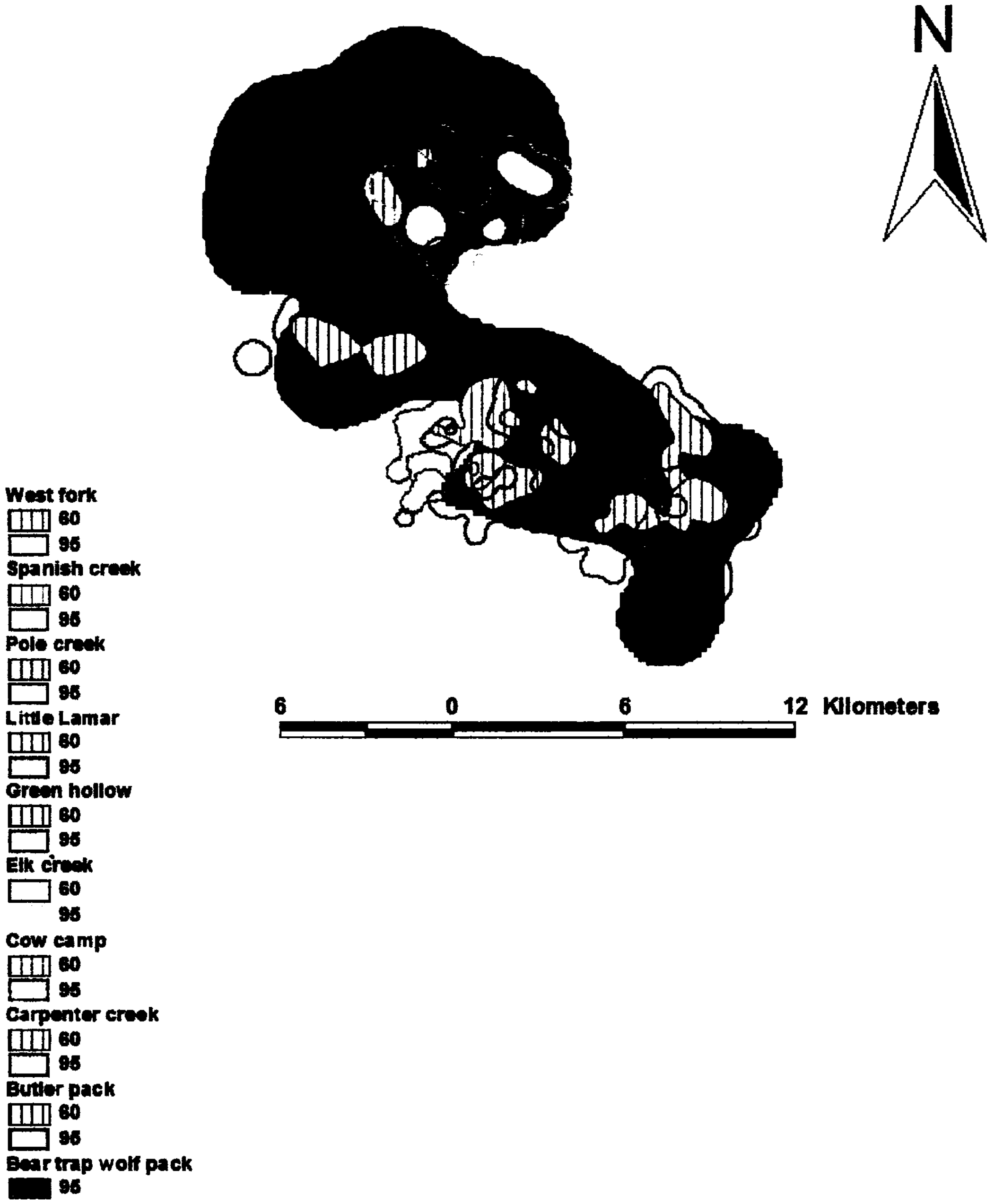

Figure 7. Extent of coyote home range overlap by the Bear Trap wolf pack in the NMSA, southwest Montana, winter 2003-2004.

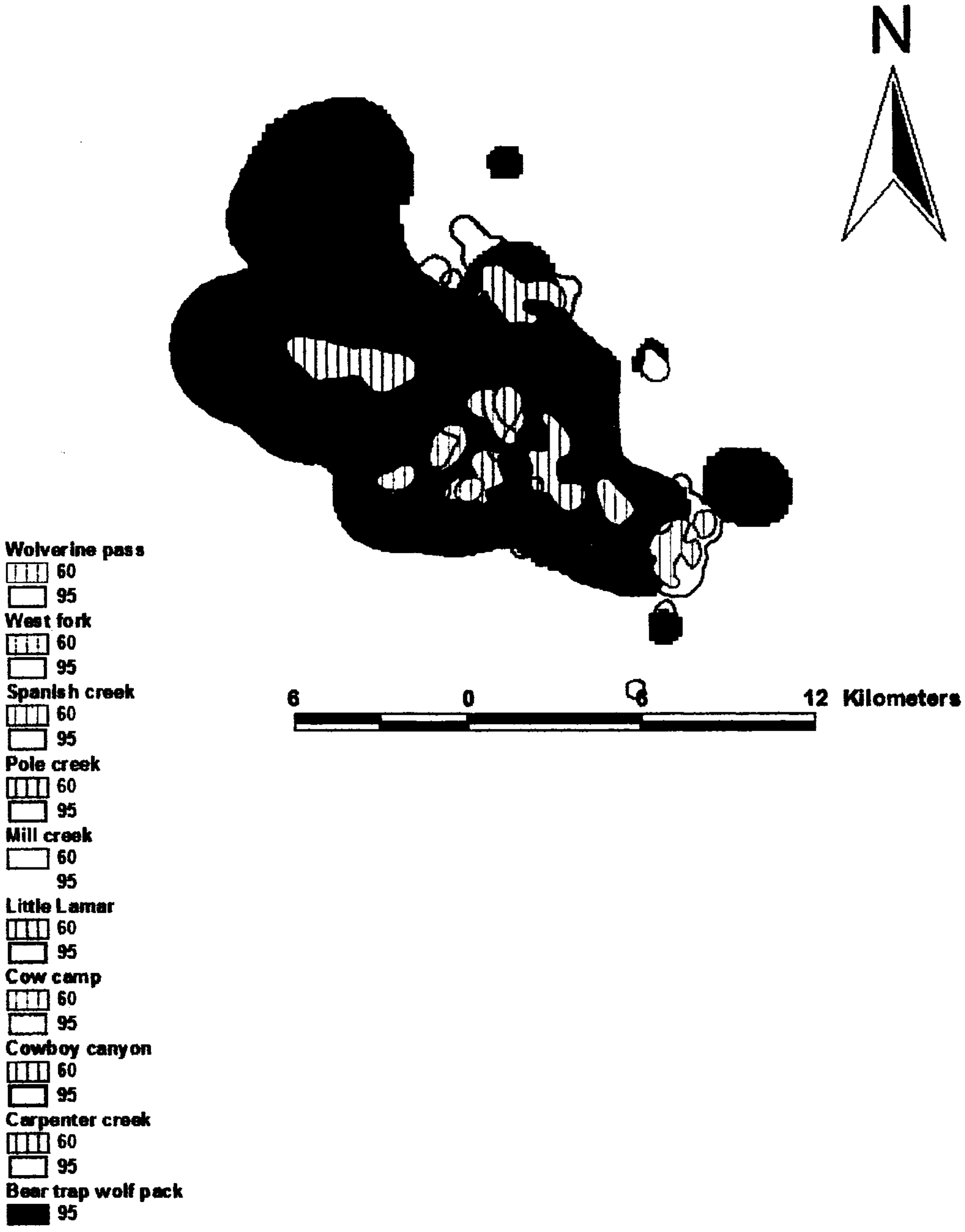

Figure 8. Extent of coyote home range overlap by the Bear Trap wolf pack in the NMSA, southwest Montana, winter 2004-2005.

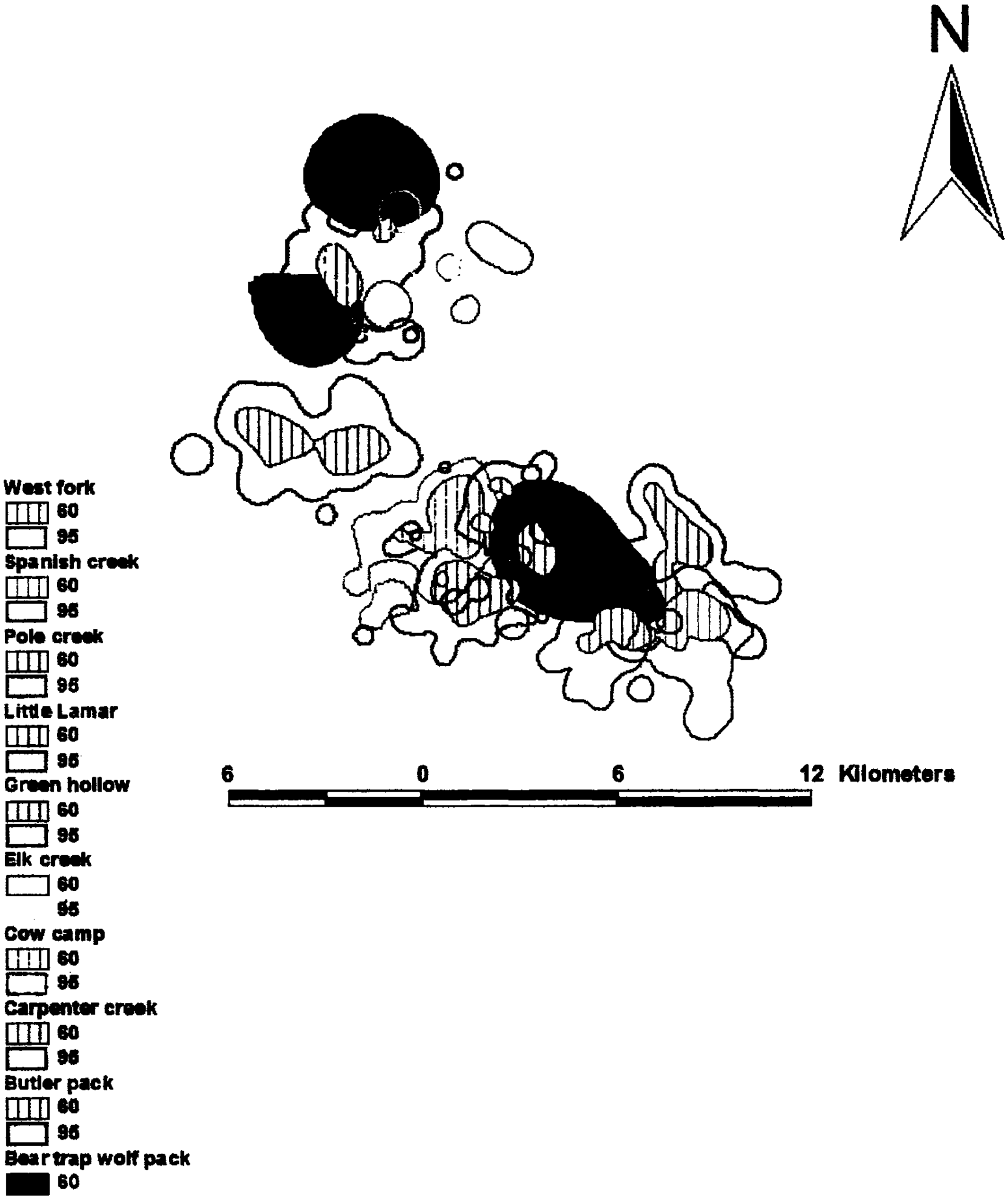

Figure 9. Extent of coyote pack core area overlap with Bear Trap wolf pack core areas on the NMSA, southwest Montana, 2003-2004.

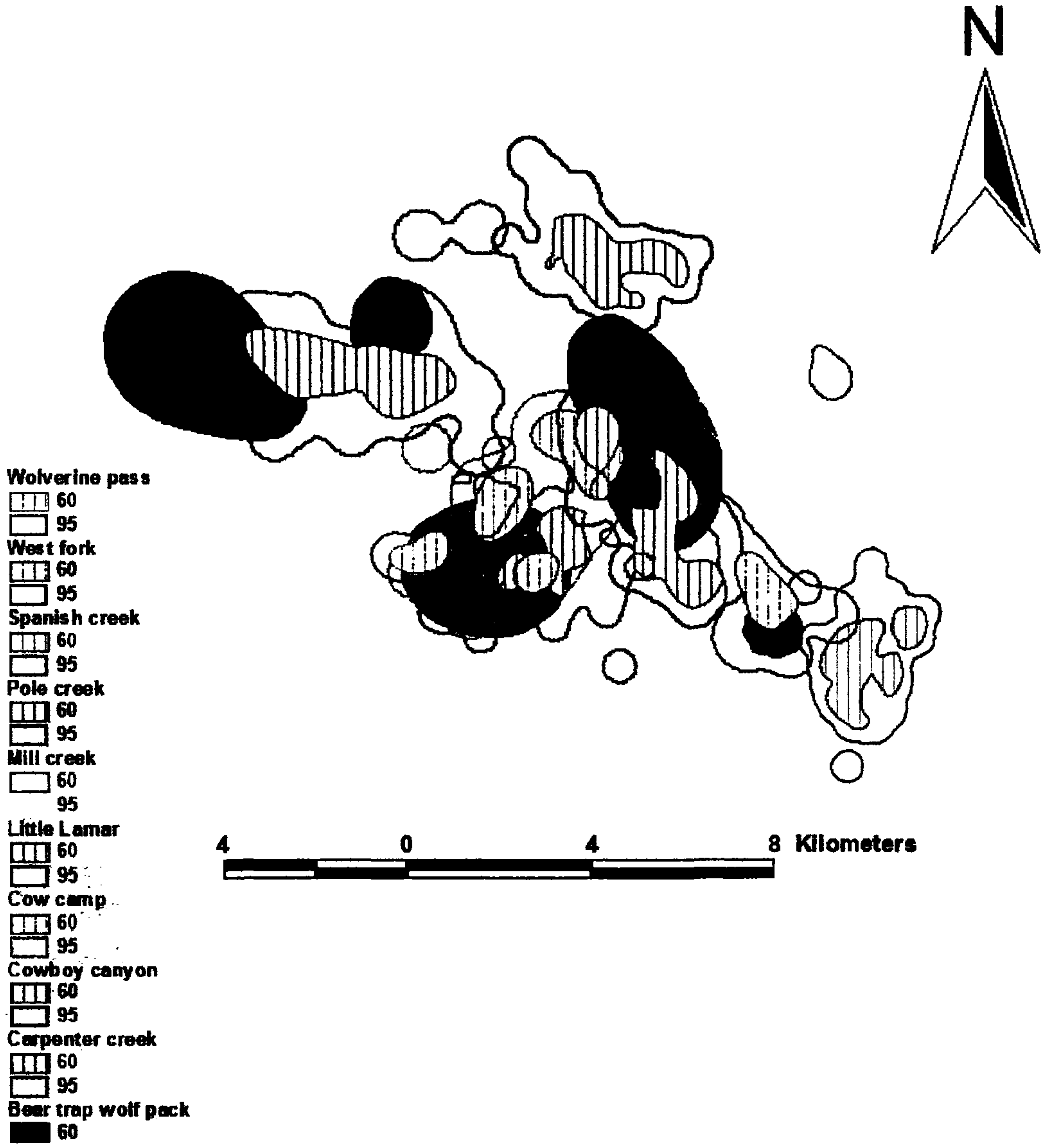

Figure 10. Extent of coyote pack core area overlap with Bear Trap wolf pack core areas on the NMSA, southwest Montana, 2004-2005.

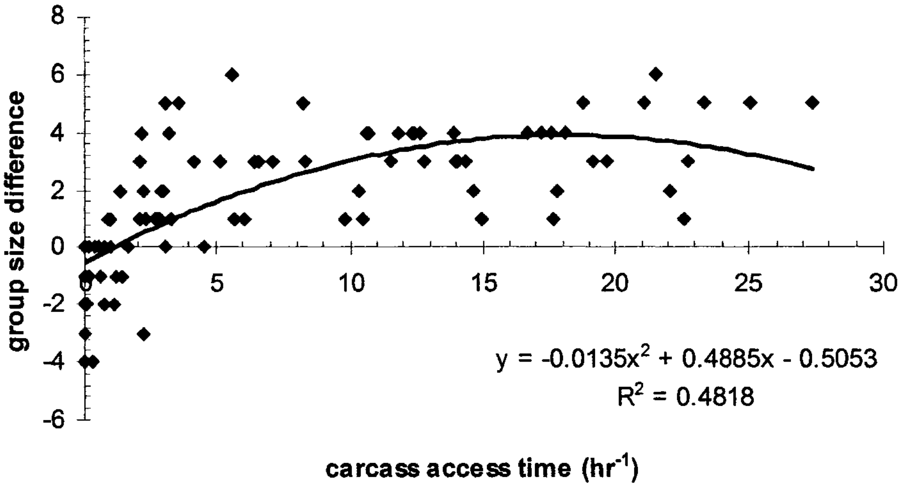

Figure 11. Relationship between group size difference (no. coyotes- no. wolves) and carcass access time (T_{acc}) for coyotes scavenging wolf-killed prey in the NMSA, southwest Montana, 2003-2005.

CHAPTER V

COYOTE SCAVENGING ECOLOGY AND RECOLONIZING WOLVES: FEAR AND LOATHING IN MONTANA'S MADISON RANGE?

Abstract Inference from studies of interspecific competition can be constrained where competitors have remained sympatric for long periods of time and little emergent behaviour is evident. Fortunately, wolf (*Canis lupus*) recolonization of the Greater Yellowstone Ecosystem provides a rare opportunity to identify nascent behaviours facilitating coexistence between sympatric canids. Accordingly, I investigated behavioral interactions between putatively naïve coyotes (*Canis latrans*) and recolonizing wolves at ungulate carcasses in Montana's Madison range. I employed a quasi-experimental study design consisting of a 3-level carcass treatment (actual wolf presence, simulated wolf presence, wolf absence) to assess factors influencing coyote risk assessment, carrion consumption, and aggressive encounters with wolves. Socially dominant coyotes (alphas and betas) responded to actual and simulated wolf presence by increasing the proportion of time spent vigilant while scavenging. Vigilance behavior was more pronounced when scavenging closer to protective cover, where lateral occlusion inhibited the ability of coyotes to scan for, and possibly escape from, returning wolves. Despite greater time spent vigilant, alpha coyotes consumed the greatest amount of carrion biomass. This was accomplished by feeding on carcasses in earlier stages of consumption when organs and large muscle tissues were still present. This suggests that alpha coyotes might trade-off greater risk for higher quality food items. Coyotes would aggressively confront wolves. Numeric superiority of coyotes and the stage of carcass consumption were influential in determining whether coyotes were able to displace wolves from carcasses. Coyotes relied

on a gradient of risk-sensitive behaviors, ranging from elevated vigilance to aggressive confrontation, to manage risk associated with wolf presence. Identification of these behaviors, and their sensitivity to numeric and social factors, is an important step in elucidating mechanisms of sympatry in social canids.

Introduction

Interspecific competition, defined as reciprocal negative effects of one species on another (Hairston et al. 1960), is usually asymmetric in that interactions do not have an equal impact on each competitor (Schoener 1983; Connell 1983; Gurevitch et al. 1992). In carnivores, asymmetric competition can impact the subordinate competitor by limiting spatial distributions (Fuller and Keith 1981), constraining habitat selection (Mills and Gorman 1997), reducing prey encounter rates (Palomares et al. 1996), reducing food intake or requiring increased hunting effort (Gorman et al. 1998), and increasing mortality rates (Palomares and Caro 1999). The direct effects of asymmetry on subordinate competitors are mostly well understood and articulated, however there is a paucity of data describing the mechanistic details. Indeed, it remains difficult to identify behaviors that mediate asymmetry in interactions because when competitors have been sympatric over long periods of time, mechanisms may be subtle (Abramsky et al. 1986) and facilitating behaviors might be undetectable. Ideally then, investigations into mechanisms of competition are particularly suited to systems where interactive behaviors between putative competitors are emergent. Fortunately, wolf (*Canis lupus*) recolonization of the Greater Yellowstone Ecosystem (GYE) has provided a rare opportunity to identify nascent mechanisms of competition with presumably naïve coyotes (*Canis latrans*).

In most cases, coyotes and wolves do not engage in contest competition for live prey (Paquet 1992; Arjo and Pletscher 1999), but rather compete for access to carcasses (Fuller and Keith 1981; Paquet 1992; Wilmers et al. 2003). Accordingly, prey kill sites should be focal areas of intense competition, and the energetic costs and benefits of maintaining or gaining access should impel mechanistic behaviors that mediate the outcome of competitive interactions. For example, free-ranging canids can expend considerable energy while hunting (e.g., ≥ 25 times the BMR; Gorman et al. 1998), and should be highly motivated to maintain primacy in carcass access until the energetic deficit incurred from catching and killing prey has been overcome. In other words, for wolves to realize a net benefit they must monopolize a carcass until the marginal benefit of remaining decreases with respect to future caloric gains. Logically then carcasses should have a temporally declining value to wolves; as value declines, wolves should be less likely to mount a vigorous defense against kleptoparasitism. For coyotes, scavenging wolf-killed prey carries substantial risk of injury or death (Paquet 1992) and the net benefit realized largely depends on energy expended in managing risk. Thus, it seems logical that coyotes should, over time, perceive gradations of less vigorous carcass defense by wolves and become more aggressive in attempts at usurpation when defense begins to wane. Clearly, if coyotes are able to perceive and take advantage of temporal declines in risk it would represent a behavior crucial in facilitating coexistence with wolves, and illustrate the importance of risk assessment in mediating asymmetric interactions between these canids.

Ecological investigations of risk-taking and risk assessment predominantly focus on interactions between predators and their prey (for a review see Elgar 1989). Prey seem to be equipped with an array of potential threat-alleviating behaviors including increased vigilance (Lima 1987a), reduced foraging time (Hughes and Ward 1993; Abramsky et al. 2002), changes in group size or configuration (Creel and Winnie 2005), preemptive aggression (Bertram 1978; Gese 1999), and retreat to refugia habitats (Formanowicz and Bobka 1988; Blumstein and Daniel 2002). Evidence suggests that similar behaviors, either independently or interactively, may prove crucial in mediating interspecific interactions in social carnivores. For example, in asymmetrically subordinate canids, numeric superiority apparently facilitates detection of encroaching competitors (Eaton 1979), mediates the duration over which a kill is retained under threat of kleptoparasitism (Fanshawe and Fitzgibbon 1993; Creel and Creel 1996), and influences the willingness to aggregate and mob intruding interspecifics (Cooper 1991; Creel et al. 2001). Furthermore, because the social status of competitors can significantly influence the outcome of intraspecific interactions (Gese 2001), social status may interact with other behaviors to influence the outcome of interspecific interactions. To my knowledge, mechanisms of risk-conditional behavior between competitively subordinate and dominant predators remain an unexplored facet of carnivore sympatry.

I investigated behavioral interactions between coyotes and wolves to determine the mechanisms and costs of risk assessment and mitigation by coyotes while scavenging wolf-killed prey. Because dominant coyotes typically are the social class that aggressively responds to intruding conspecifics (Gese 2001), I believed they also would be most likely to employ risk-sensitive behavior when scavenging carrion. Accordingly, I predicted that coyote social status and wolf presence would interact to elevate vigilance rates; socially dominant coyotes should be more vigilant than subordinates when scavenging carcasses visited by wolves. Second, I sought to determine whether risk-sensitive behavior in coyotes varied relative to their perception of wolf activity. Specifically, I predicted that coyote scavenging rates would be greater at carcasses actually visited by wolves as opposed to those where wolf visitation was simulated. Third, I sought to determine if there was an energetic cost for risk-sensitive coyotes. I predicted that increased vigilance would result in diminished carrion consumption. Finally, I predicted that numerical superiority would be a critical factor in determining whether coyotes were able to gain access to carcasses by displacing wolves. I believe that directly observing interacting coyotes and wolves provides a rare opportunity to elucidate mechanisms of risk assessment, which may prove important in understanding how canid communities are structured.

Methods

The study took place in the Northern Madison Study Area (NMSA; 680 km^2), located in southwest Montana's Madison Range of the Rocky Mountains, from December through May of 2003-2005. The NMSA is approximately 50 km northwest of Yellowstone National Park, and is 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 km^2) dominates valleys and benches on the NMSA; coniferous forest (145 km^2) comprises approximately 23% of the remaining area. Elevations range from 2500 m in the Spanish Peaks to 1300 m on the Madison River floodplain, and mediate an ecological gradient varying from dry grassland/juniper (*Juniperus scopulorum*) savannah at lower elevations to closed canopy Douglas fir (*Pseudotsuga menziesii*) or lodgepole pine (*Pinus contorta*) forests on moist sites at higher elevations. High elevation dry sites occur on southern exposures and ridgelines, and are predominantly mountain big sage (*Artemesia tridentada vaseyana*)/grassland mosaics. Temperatures range from highs of 21-32°C in summer to lows of -34°C in winter.

A single wolf pack (Bear Trap pack) recolonized the NMSA in the winter of 2002; these wolves represented the recolonizing front for wolves in the Madison Range. Annual wolf pack size ranged from 2-8 individuals, one of which (yearling female) was radiocollared and subsequently dispersed. Over the duration of the study, the Bear Trap pack averaged 5 individuals. Coyotes were captured and radiocollared using foothold traps and aerial netgunning. Coyotes were distributed over the entire NMSA, and resided in multi-generational packs. Pre-whelping pack size was 4 adults, and average litter size was 6 pups. Coyotes were subjected to hunting and it is estimated that approximately 20% of the population was killed annually.

Procedures

I used a quasi-experimental design consisting of 3 treatment levels: (i) wolf presence- wolves fed on wolf-killed or manually-placed carcasses; (ii) simulated wolf presence- wolf visitation was simulated via scat and urine at manually-placed carcasses; and (iii) wolf absence (control)- no evidence was detected that wolves visited manually-placed carcasses. When simulating wolf presence, I placed individual paired samples of scat and 3 ml of urine 5 m from the center of the carcass. Scat and urine samples were collected from captive wolves fed a natural diet (i.e., ungulate carcasses). The number of individual paired samples placed at carcasses varied concomitant with Bear Trap pack size. Although I was not able to randomize the "wolf presence" treatment, I was able to randomize the control and simulation treatments; all coyote packs observed were exposed to all 3 treatment levels at least once. Wolves were considered not to have visited manually-placed carcasses when inspection of carcass sites revealed no evidence (e.g., scat, tracks, and broken long bones) of their presence. All carcasses were exposed to the same intensity of human visitation.

I used all-occurrence sampling (sensu Lehner 1996) to gather behavioral data on coyotes and wolves at carcasses using 15-45× spotting scopes. Each observation session included associated measures of the proportion of time coyotes spent vigilant while scavenging, feeding bout duration, stage of carcass consumption, scavenger social status, coyote and wolf group sizes, and distance to protective cover. Coyote social status was determined by generating dominance matrices (Gese et al. 1996) based on intraspecific interactions; only data from coyotes of known social status were used in subsequent analyses. Protective cover was defined as vegetation tall and dense enough to conceal an animal from view (Molvar and Bowyer 1994). Scavenging was defined as biting, tearing, or chewing food with a lowered head. A coyote was considered vigilant when its head was raised, was in an alert position, or was actively scanning the environment. Periods in which the scavenging behavior of focal coyotes was interrupted by social interactions with packmates, elimination behavior, or resting were omitted. The proportion of time spent vigilant by individual coyotes was summed over the period a carcass was observed to determine a mean proportion.

To determine if there was a cost associated with elevated vigilance, I first needed to estimate the amount of carrion biomass coyotes consumed while scavenging. Wilmers and Stahler (2002) estimated active consumption rates (ACR; ACR = g min^{-1} ingested × feeding bout duration) for captive coyotes feeding on ungulate carcasses, and found that rates differed based on the stage of consumption. On average, coyotes ingested carrion at a rate of 230g min^{-1} when feeding on organs, entrails, and major muscles; consumption rates dropped to 60g min^{-1} when feeding on minor muscles, hide, and stripping bones (Wilmers and Stahler 2002; Wilmers et al. 2003). At the beginning and end of each daily observation period, I approached carcasses close enough to estimate the stage of consumption. I then used stage-based consumption ACR estimates provided in Wilmers and Stahler (2002) to determine the daily amount of carrion biomass ingested by coyotes. Individual consumption amounts were summed over the period a carcass was observed to determine a mean for each coyote. Mean biomass consumption was then used as a metric to estimate the energetic cost of vigilance behavior.

Statistical methods

I used unbalanced factorial analysis of variance with least squares means testing (ANOVA; Zar 1999) to characterize risk assessment and the energetic costs of vigilance by scavenging coyotes. For both analyses, I used a 3-level treatment consisting of wolf absence (control; i.e., wolves never visited), wolf presence (i.e., wolves visited and fed), or simulated wolf presence (i.e., visitation simulated by the deposition of wolf scat and urine) at a carcass. Because data were collected over 3 yr, I first conducted a 2-way ANOVA, with social status and year as main effects, to determine whether vigilance and biomass consumption differed between years as initially wolf-naïve (sensu Berger et al.

2001) coyotes became wolf-savvy. Subsequent analyses included treatment type, coyote social status, and distance from protective cover as main effects. To induce homoscedasticity, vigilance data (proportion of time spent vigilant while foraging) were arcsine square-root transformed and rate data were logarithmically transformed (Neter et al. 1996). Due to dispersal and mortalities, I was unable to collect serial observations on all individuals. Thus, a repeated measures analysis would have been inappropriate (Zar 1999). Because a modest degree of pseudoreplication has been shown not to influence the results of studies like these (Runyan and Blumstein 2004), I treated coyotes as independent sample units.

In order to determine whether numeric superiority and/or stage of carcass consumption mediated the duration over which a kill was retained, I first needed to quantify the outcome of agonistic interactions. I defined a discrete agonistic interaction as the duration over which aggressive behaviors (e.g., bluff attack, biting, chasing, vocal harassment; Schenkel 1967) were employed by coyotes and wolves with the intent of maintaining or usurping carcass access. Eviction of the competing species was equated with success. Success in agonistic interactions (S) of coyotes with group size j was then calculated using a modification of the equation proposed by Henderson and Hart (1995), where S = (N interactions won by $j_{coyotes}$/N interactions lost by $j_{coyotes}$) × (N wolves supplanted/$j_{coyotes}$). This equation takes both the proportion of interactions won and the proportion of individuals supplanted by a coyote group into account. Based on the group size success score (S_j), a rank number, from least to most successful was assigned to each coyote group size (j). I analyzed whether consumption stage (stages I and II- organs, entrails, and major muscles or stages III and IV- minor muscles, hide, bone stripping;

Wilmers et al. 2003) influenced the vigor of carcass defense by wolves using a Wilcoxon rank sum test (Zar 1999).

Results

I observed 54 individual coyotes (12 packs; 23 collared, 31 uncollared) and 6 individual adult wolves (Bear Trap pack) of known social status for 1429 hr at 93 ungulate carcasses. Sixty-one carcasses were observed throughout the duration of their availability, beginning either before (in the case of manually-placed carcasses) or shortly after wolves or coyotes began feeding. Fifty-five percent of the carcasses were white-tailed deer, 35% were elk, 7% were bison, and 3% were mule deer. Forty-seven percent of the carcasses were wolf kills and the rest were manually-placed roadkill carcasses. Carcasses also were fed on by black bears, grizzly bears, golden eagles (*Aquila chryseatos*), bald eagles (*Haliaeetus luecocephalus*), ravens (*Corvus corvax*), and magpies (*Pica pica*).

The proportion of time coyotes spent vigilant (treatment × social status interaction × year: $F_{10,111} = 0.92$, $P = 0.51$) and the amount of carrion biomass consumed (treatment × social status interaction × year: $F_{10,90} = 1.72$, $P = 0.11$) did not differ between years, so data were pooled for subsequent analyses. As predicted, coyote vigilance rates varied based on experimental treatment (wolf presence, wolf absence, simulated wolf presence) at carcasses ($F_{2,119} = 8.61$, $P = 0.0003$) and coyote social status ($F_{2,119} = 9.19$, $P = 0.0002$; treatment × social status interaction $F_{4,117} = 0.35$, $P = 0.84$). The mean proportion of time spent vigilant by coyotes was greatest for alphas, but betas also responded to wolf visitation by increasing vigilance. Compared to control treatments, alphas increased vigilance by 32% when scavenging carcasses visited by wolves and 38% when scavenging carcasses where wolf presence was simulated (visited by wolves: $\bar{x} = 0.49$, SE = 0.03; simulated wolf presence: $\bar{x} = 0.51$, SE = 0.03; wolf absence: $\bar{x} = 0.37$, SE = 0.02). For betas, vigilance increased by 48% when carcasses were visited by wolves and 55% when wolf presence was simulated relative to control treatments (wolves present: $\bar{x} = 0.40$, SE = 0.03; simulated wolf presence: $\bar{x} = 0.42$, SE = 0.03; wolves absent: $\bar{x} =$ 0.27, SE = 0.04). Subordinate coyotes showed little response to wolf presence (wolves present: $\bar{x} = 0.25$, SE = 0.03; simulated wolf presence: $\bar{x} = 0.28$, SE = 0.03; wolves absent: $\bar{x} = 0.25$, SE = 0.01). The social status × cover distance interaction was significant ($F_{2,119} = 6.24$, $P = 0.003$), and simple linear regression indicated that vigilance correlates differed with respect to social status. For dominant coyotes (alphas and betas), the mean proportion of time spent vigilant declined with increasing distance from protective cover when wolves were present and increased when wolves were absent (Figs. 12-13). Conversely, there was no apparent relationship between time spent vigilant and distance from protective cover for subordinate coyotes (Figs. 14-15).

Although socially dominant coyotes spent more time vigilant, they did not incur a cost in terms of diminished carrion consumption. Mean biomass consumed by coyotes did not differ based on treatment type ($F_{2,100} = 0.37$, $P = 0.69$), but did vary relative to social status ($F_{2,100} = 7.66$, $P = 0.0009$; Fig. 16). The feeding bouts of alphas were similar in duration to betas and subordinates (Table 12), yet they ingested substantially more carrion biomass (Fig. 16). Consumption was greater for alphas because they more frequently fed on carcasses during the initial stages of consumption (stages I and II-organs, entrails, and major muscles: ACR = 230 g min^{-1}; Wilmers et al. 2003). For alphas, 64% of observations involved ingestion of organs, entrails, and major muscles, compared to 27% for both betas and subordinates.

I observed 36 bouts of agonistic interactions involving 6 different coyote packs and the Bear Trap wolf pack (Table 13). Seventeen bouts (47%) ended with coyotes supplanting wolves from carcasses, all of which occurred during the last stages of carcass consumption ($Z = 3.57$, $P = 0.0002$; stages III and IV- ingestion of minor muscles, hide, bone stripping; Wilmers et al. 2003). Coyote group size (range 2-6 adults) was numerically superior to wolf group size (range 1-3 adults) in 16 (94%) of the 17 bouts in which coyotes supplanted wolves. At least one alpha coyote was present during 27 (75%) of the bouts; both alpha coyotes were present in the 16 bouts where wolves were supplanted. Thirteen bouts involved groups of 2-6 coyotes supplanting the alpha male wolf (Table 13).

Discussion

My study revealed five novel observations of how coyote scavenging ecology responded to wolf recolonization. I first showed that coyotes assessed risk when scavenging carcasses. Coyotes displayed risk-sensitive foraging behavior by increasing the proportion of time spent vigilant when wolf presence (actual and simulated) was detected. Second, olfactory cues alone elicited vigilance responses similar to actual wolf presence. In other words, wolves did not have to be physically present in order for coyotes to employ risk-sensitive foraging behaviors. Third, responsibility for risk assessment and carcass defense fell most heavily on socially dominant coyotes. Although dominant coyotes (alphas and betas) were always more vigilant than subordinates, they were the only social class found to substantially elevate vigilance when wolf presence was detectable. Fourth, heightened vigilance in dominant coyotes did not adversely affect the amount of carrion biomass consumed. Alpha coyotes consumed more carrion biomass than betas and subordinates regardless of treatment level. Finally, coyotes would aggressively confront wolves to gain or maintain carcass access.

Vigilance of scavenging coyotes was sensitive to effects of social status, treatment level, and distance from protective cover. Socially dominant coyotes (alphas and betas) responded to actual and simulated wolf presence by increasing the proportion of time spent vigilant; alphas were substantially more vigilant (22% higher, on average) than betas. There are two plausible scenarios for hierarchical-dependent vigilance in coyotes: (i) within a pack, vigilance may mediate social competition, and/or (ii) vigilance may ameliorate negative interactions between adjacent packs and with congeners. In the former, heightened vigilance in dominants may reflect intimidation behavior associated with intra-pack dynamics. That is alphas, and to a lesser degree betas, may spend a greater proportion of time vigilant in order to monitor the behaviors and constrain feeding attempts of subordinate pack members. Indeed, Gese et al. (1996) found that alphas and betas in Yellowstone National Park (pre-wolf reintroduction) had the greatest access to carcasses and, similar to our study, fed first while subordinates waited. Once dominant individuals were sated, subordinates then fed. Under this intrapack hierarchy construct, subordinates would not be expected to elevate vigilance unless trying to cheat by feeding at carcasses when dominant individuals were absent. In the latter scenario, it would seem logical that if hierarchical-dependent vigilance is effective in ameliorating intrapack competition then it might also be a potent behavior for mitigating conflict with other competitors. In this case, vigilance would not be used to intimidate, but to gather nuanced information essential to assessing risk such as postures, speed of approach, and competitor group size.

Coyote social status interacted with distance from protective cover to influence the proportion of time spent vigilant. Several studies have documented changes in the allocation of time to vigilance under varying amounts of cover. Evidence generally supports the notion that animals spend more time alert when foraging away from shrub or tree cover (Barnard 1980; Leger et al. 1983; Cassini 1991; Otter 1994; Tchabovsky et al. 2001). However, the nexus between vegetative cover and vigilance is likely far from simple; cover that provides concealment can also obstruct vision and hinder escape (Lima 1987b; 1990, Schooley et al. 1996; Sharpe and Van Horne 1998; Blumstein et al. 2004). Additionally, differences in forager behavior may further complicate the relationship between protective cover and vigilance. For example, the dispersion of data points in figures 12-13 and 14-15 reflected differences in feeding behaviors between dominant and subordinate coyotes. Dominant coyotes fed more frequently on carcasses during the initial stages of consumption and would often tear off large food items, then move short distances away from the carcass prior to consumption. Subordinates, on the other hand, fed more frequently on carcasses during the final stages of consumption, and were often relegated to stripping flesh from bones. As a result, they usually consumed these small food items without leaving the carcass. Indeed, I found evidence that scavenging near shrub cover caused dominant coyotes to spend more time vigilant than when foraging away from cover. Presumably, this occurs because lateral occlusion by shrub cover interferes with the ability of coyotes to scan the environment, which is necessary when scavenging prey recently killed by wolves. After a kill was made, wolves generally fed until pack members were sated then moved off a short distance to rest while keeping the carcass in view. Coyotes were often aware of where wolves were resting and attempted to scavenge in between wolf feeding bouts. However, when cover obstructed the ability of surveillant coyotes to monitor wolf activity, they would have to substantially increase vigilance in order to avoid being ambushed when wolves decided to feed again.

The level of risk perceived has been found to influence the decision of whether animals should flee (Ydenberg and Dill 1986; Lima and Dill 1990) or retaliate (Geist et al. 2005). Because of this, I suspected that our experimental treatment of simulated wolf presence, putatively a less risky environment than actual wolf presence, would result in vigilance intermediate to actual wolf presence and wolf absence. However, the vigilance response of dominant coyotes was indistinguishable for treatments of actual and simulated wolf presence. If my ability to extend inference to observations was restricted to vigilance behavior, then I might have arrived at the specious conclusion that elevated vigilance was a generalized strategy employed by coyotes regardless of threat level perceived. In fact, when vigilance behavior is viewed in concert with observations of agonistic interactions with wolves, it becomes apparent that heightened vigilance is simply a first-order response to the perception of a threat. In other words, increased vigilance represents an initial response to a relatively low-level threat: olfactory stimuli indicating wolf visitation. As coyotes perceive escalations in wolf threat-level (e.g., auditory and visual stimuli), they employ commensurate mitigating behaviors. In this sense, vigilance is properly placed at one end of a continuum of behaviors coyotes rely on when managing a gradient of risk associated with wolves. At the opposite end of this continuum is aggressive confrontation (Geist et al. 2005). These divergent risk-sensitive behaviors might reflect discrepant levels of fearfulness (Stankowich and Blumstein 2005) influenced by experience with an aggressor (i.e., knowledge of the attack behavior), and/or by characteristics of interacting agents (e.g., differences in group size or social status).

Perhaps the most unexpected finding of my study was that coyotes would, on occasion, aggressively confront wolves in attempts to gain or maintain access to carcasses (see Table 13 for details on coyote and wolf group sizes while scavenging). Coyotes confronting wolves as a response to escalating risk would seem paradoxical. Rather than fleeing, preemptively engaging a putative aggressor would seem to further escalate the likelihood of injury. However after deconstructing interactions with wolves, it becomes apparent that decisions by coyotes to confront are partially informed by knowledge that differences in social status and/or group size can exacerbate or ameliorate risk. Indeed, in the confrontation bouts where coyotes successfully displaced wolves from carcasses, both alpha coyotes were present, coyotes were numerically superior to wolves, and no injuries were sustained. Numeric superiority has been found to be a primary determinant in the outcome of interspecific interactions for African social carnivores (Cooper 1991; Fanshawe and FitzGibbon 1993; Creel et al. 2001), and Gese (2001) found that competitor social status significantly affected the outcome of intraspecific interactions in coyotes. Thus it is not surprising to find coyotes relying on both factors to assess risk and guide decision-making when interacting with wolves. The extent to which numeric superiority and the presence of dominant individuals is influential in coyotes displacing wolves from carcasses is likely dependent on how invested wolves are in maintaining primacy.

The stage of carcass consumption likely mediates the vigor with which wolves defend against kleptoparasitism (Wilmers et al. 2003; Vucetich et al. 2004), and may also influence the level of risk coyotes will tolerate. My prediction that elevated vigilance in dominant coyotes would depress carrion consumption rates was incorrect. In fact, alpha coyotes consumed substantially more carrion biomass than other social classes, despite similar feeding bout durations. This occurred because alpha coyotes engaged in riskier behavior by more frequently scavenging carcasses in the early stages of consumption (stages I and II), whereas betas and subordinates primarily fed on carcasses in the latter stages of consumption (stages III and IV). Carcasses in the early stages of consumption should be vigorously defended by wolves; as the carrion resource depreciates, wolves invest less energy in defense, and risk to scavenging coyotes should decline concomitantly. By exploiting carcasses in the early stages of wolf consumption, alpha coyotes appear to trade greater risk for greater biomass consumption. However, by consuming greater biomass over feeding bouts similar in duration to betas and subordinates, alpha coyotes are minimizing time spent foraging and may actually be reducing exposure to risk (Charnov 1976; Pyke et al. 1977). Whether betas and subordinates are minimizing time or maximizing energy is ambiguous and confounded by differences in vigilance behavior; both spend more time feeding on carcasses in the later stages of consumption, and betas are substantially more vigilant than subordinates.

It can be argued that wolf recolonization of the GYE has most profoundly impacted how coyotes behave when exploiting carrion resources. Prior to wolf recolonization of the NMSA, ungulate carrion availability was limited to either cougar-killed prey, which can be hard to detect due to caching, or winter-kill. Because winter kill generally occurs at the end of severe winters, prior carrion availability primarily depended on stochastic, climatic factors. Where wolves have recolonized, formerly benign, ephemeral carrion resources have become spatio-temporally constant (Wilmers et al. 2003) foci of substantial risk. In response to this change, coyotes appear to have developed trenchant behaviors of risk assessment when exploiting wolf-provisioned carrion. The mechanisms of these behaviors, stimuli indicating wolf presence (e.g., urine, scat, and actual presence), coyote social status, and numeric superiority, mediate behaviors coyotes employ in attempts to maintain or usurp carcass access. My study is the first to consider and confirm the interactive effect of group size and social status as influential in the outcome of competitive interactions in social canids.

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Table 12. Feeding time of scavenging alpha, beta, and subordinate coyotes relative to treatment level

		Feeding Time (min)	
Treatment	Social Status	$\bar{x}$ (SE)	(95% Confidence Interval)
wolf presence	alpha	4.12 (0.70)	(2.75- 5.49)
	beta	2.50 (1.10)	(0.34- 4.66)
	subordinate	5.02 (1.71)	(1.67- 8.37)
simulated wolf presence	alpha	4.97 (0.91)	(3.19- 6.75)
	beta	4.41 (1.46)	(1.55- 7.27)
	subordinate	4.73 (0.95)	(2.87- 6.59)
wolf absence (control)	alpha	4.16 (0.50)	(3.18- 5.14)
	beta	5.01 (2.39)	(0.33- 9.69)
	subordinate	4.73 (0.95)	(2.87- 6.59)

Table 13. Characteristics of interacting coyote and wolf group sizes and carcass condition, and their relevance to carcass primacy

Coyote pack	Coyote group size	Wolf group size	No. of confrontations[a]	Stage of carcass consumption[b]	Pre-confrontation carcass primacy[c]	Post-confrontation carcass primacy
West Fork	3[d]	2	1	I and II	wolves	wolves
West Fork	3[d]	1	2	III and IV	wolves	coyotes
Little Lamar	2	3	1	I and II	wolves	wolves
Little Lamar	5	3	1	III and IV	wolves	coyotes
Little Lamar	6[d]	1	2	III and IV	wolf	coyotes
Little Lamar	5[d]	1	2	III and IV	wolf	coyotes
Little Lamar	1	1	1	III and IV	wolf	wolf
Cow Camp	2[d]	1	4	III and IV	coyotes	coyotes
Cow Camp	5[d]	1	1	III and IV	coyotes	coyotes
Cow Camp	4[d]	1	1	III and IV	wolf	coyotes
Carpenter Creek	2	1	2	I and II	wolf	wolf
Carpenter Creek	2[d]	1	3	III and IV	wolf	coyotes

Table 13. Continued

Coyote pack	Coyote group size	Wolf group size	No. of confrontations[a]	Stage of carcass consumption[b]	Initial carcass primacy[c]	Post-confrontation carcass primacy
Carpenter Creek	1	1	1	III and IV	wolf	wolf
Carpenter Creek	5[d]	1	1	I and II	wolf	wolf
Carpenter Creek	5[d]	1	2	III and IV	wolf	coyotes
Carpenter Creek	2	1	1	III and IV	wolf	coyotes
Pole Creek	5[d]	3	1	I and II	wolves	wolves
Pole Creek	2	3	3	I and II	wolves	wolves
Pole Creek	1	3	4	I and II	wolves	wolves
Cowboy Canyon	4[d]	3	1	I and II	wolves	wolves
Cowboy Canyon	2[d]	3	1	III and IV	coyotes	wolves

[a] Confrontations were defined as discrete aggressive interactions between coyotes and wolves ending when access to a carcass was either retained by a defender or ceded to a challenger

[b] Stages I and II include consumption of organs, entrails, and major muscles; stages III and IV include consumption of minor muscles and hide

[c] Carcass primacy refers to the species that had singular access to the carcass

[d] Alpha coyote(s) present

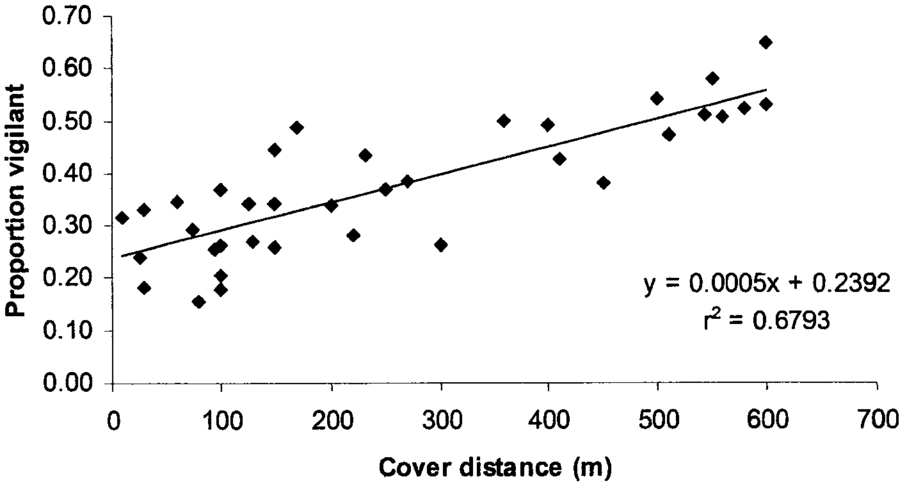


Fig. 12. Proportion of time spent vigilant relative to distance from protective cover for socially dominant (alphas and betas) coyotes scavenging control (wolves absent) carcasses

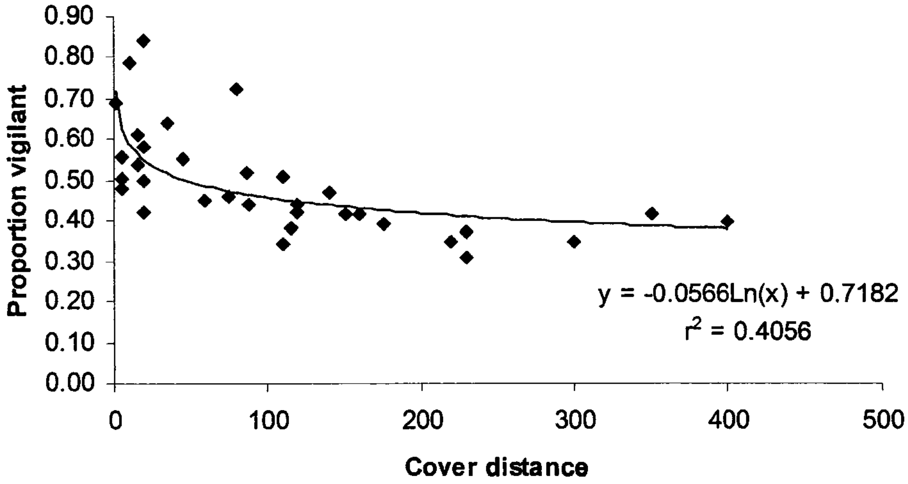


Fig. 13. Proportion of time spent vigilant relative to distance from protective cover for socially dominant (alphas and betas) coyotes scavenging wolf treatment (actual and simulated wolf presence) carcasses

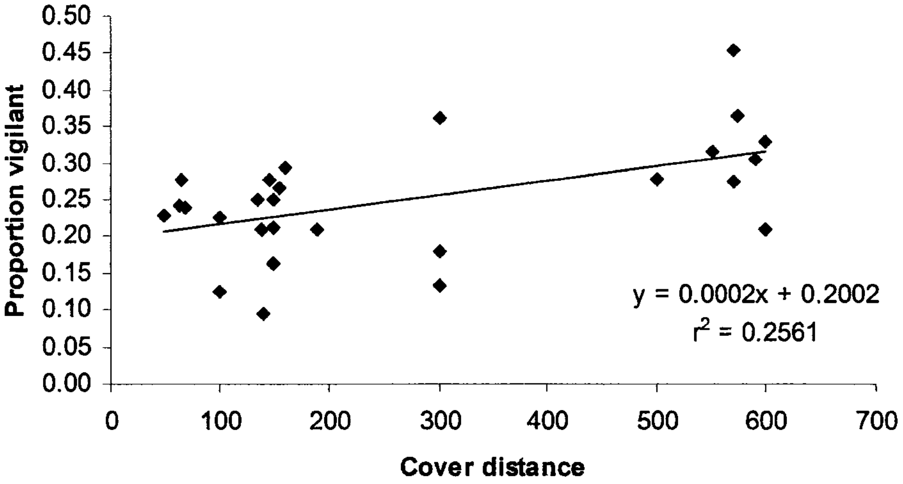


Fig. 14. Proportion of time spent vigilant relative to distance from protective cover for socially subordinate coyotes scavenging control carcasses

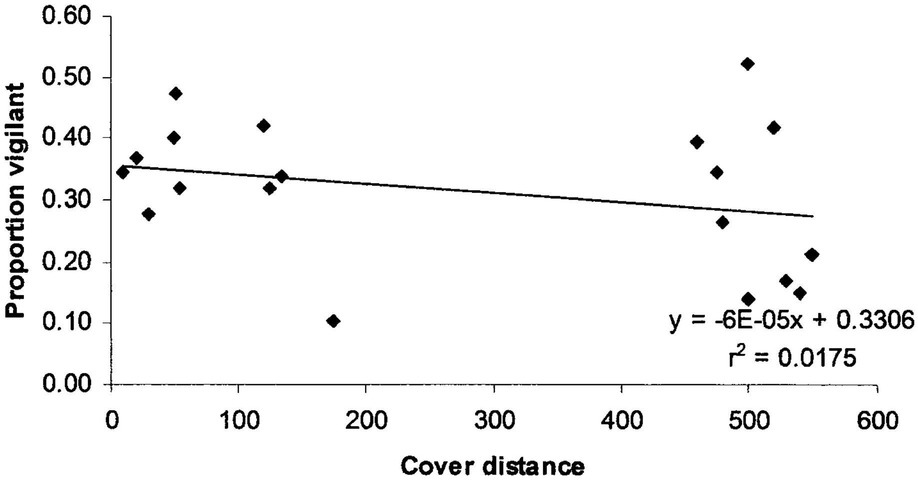
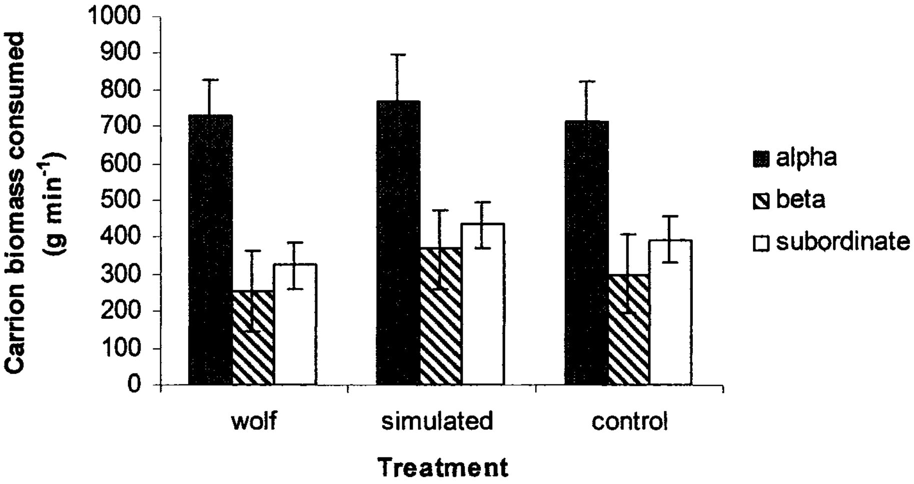


Fig. 15. Proportion of time spent vigilant relative to distance from protective cover for socially subordinate coyotes scavenging wolf treatment carcasses

Fig. 16. Carrion biomass consumed by alpha, beta, and subordinate coyotes relative to carcass treatment level



CHAPTER VI

SUMMARY AND SYNTHESIS OF RESEARCH

The reintroduction of wolves to Yellowstone National Park (YNP), and their subsequent recolonization of the Greater Yellowstone Ecosystem (GYE) have provided a unique opportunity to elucidate the effects of predator recolonization on competitors and prey. To that end, the preceding work identified 4 novel effects of wolf (*Canis lupus*) recolonization on ungulate and coyote (*Canis latrans*) behavior. First, the addition of a new predator (wolves) to an already complex predator-prey system (i.e., cougars [*Puma concolor*], elk [*Cervus elaphus*], and mule deer [*Odocoileus hemionus*]) represented a significant perturbation to the pre-existing predator-prey dynamic (Chapter II, Atwood et al. in press). Cover complexity at wolf kill sites (primarily sites of wolf-killed elk) increased over successive years as prey retreated to structurally complex refugia habitat putatively to ameliorate predation risk from wolves. However, by retreating to structurally complex habitat, in response to wolf predation risk, prey became more vulnerable to predation by cougars. Because wolves preyed primarily on elk (72% of all wolf kills), elk were most likely to trade risk of wolf predation for risk of cougar predation.

Several studies have documented shifts to more structurally complex habitat by elk, presumably in response to predation pressure from wolves (Fortin et al. 2005; Creel and Winnie 2005). However, this prior work did not relate habitat shifts to changes in prey selection or entertain the likelihood that a secondary predator might have benefited from prey seeking to avoid a primary predator. Our investigation was the first to consider (i) whether wolf-mediated habitat shifts by elk may facilitate cougar predation, (ii) examine changes in prey selection relative to habitat shifts, and (iii) whether predator-induced habitat shifts indirectly buffered mule deer predation from predation by cougars. Our findings, although lacking experimental rigor, provide strong inference that predator recolonization can result in non-linear (i.e., non-additive) multi-predator effects for some prey, and linear effects for other prey. For example, as elk shifted to more complex habitats, the proportion of elk killed by cougars increased as the proportion of mule deer killed declined. Over this same time, wolves preyed proportionately on elk and underutilized mule deer. These observations suggest that net predation effects for elk may have been additive, whereas net effects for mule deer may have been reduced. From a basic perspective, our findings of facilitative predation effects for a large mammal system corroborate similar findings in other systems (aquatic: e.g., Saviano and Stein 1989; Hampton 2004; Warfe and Barmuta 2004; terrestrial-insect: e.g., Korpimaki et al. 1996; Losey and Denno 1998; Schmitz et al. 1997; Stapley 2004), and support the notion that theorized predation effects can be generalized across taxa and systems.

From an applied perspective, our findings provide no evidence that wolf recolonization has adversely impacted mule deer populations. Prior to wolf recolonization of the GYE, cougars were the primary predator of adult mule deer and there was no consensus on the putative impact wolves might have on mule deer populations. For example, Boyce (1993) predicted direct predation effects would result in a decrease in abundance of at least 10-15% for mule deer in YNP following wolf restoration. However, Mack and Singer (1992, 1993) predicted that the abundance of mule deer on the northern range of Yellowstone could increase up to 36% as wolf predation on elk indirectly released mule deer from resource limitation. Ten years after wolf reintroduction to YNP, wolf predation on mule deer appears negligible; to date, elk have comprised ≈92% of wolf diets (White and Garrott 2005). Our findings are qualitatively similar to those of White and Garrott (2005); wolves on our study site had no measurable impact on mule deer (we documented 3 wolf-killed mule deer over 3 years). Indeed, wolf presence may indirectly benefit mule deer if wolves reduce elk density, thereby lessening the intensity of competitive interactions between elk and mule deer.

In Chapter III, we further integrate basic and applied ecological principles by adapting Holling's (1959) functional response for use in an applied spatial modeling construct (Hebblewhite et al. 2005). In this chapter, we concluded that predation risk was informed by the interaction of (i) prey behavior, (ii) predator behavior, and (iii) landscape attributes. The above three factors determined the probabilities of prey encountering predators and, for a given suite of habitat attributes, mediated the conditional probabilities of death given an encounter. Using this modeling approach, we were able to determine the spatial distribution of total predation risk (risk of predator encounter and risk of death given an encounter) for elk and mule deer and identify effective refugia habitat for both prey species. The methodology we employed clearly illustrated the importance of carefully defining predation risk for prey, and demonstrated the utility of our approach to spatially decompose predation risk for revealing the behavioral aspects of predation risk in real landscapes. For example, for elk, grassland and juniper savanna habitats reduced risk as predation escalated from encounter to kill. For mule deer, risk reduction was driven both by habitat and topographic variables, as juniper savanna and south aspects reduced risk as predation escalated from encounter to kill. The preceding findings highlight an important aspect of our approach: studies that assume predation risk is equivalent to predator habitat use may be misleading. More specifically, studies that do not distinguish between encounter and kill may not truly identify habitat attributes that mediate predation because the components negate each other at the subsequent stage. By distinguishing between components of predation, mechanisms driving the observed statistical patterns may be hypothesized and tested using field experiments or further analyses.

In Chapters IV and V, we switched our emphasis from predation effects on prey to competitive interactions between wolves and coyotes. Our intent with these chapters was to investigate spatial and socio-behavioral effects of wolf recolonization on coyotes. Since wolf reintroduction to Yellowstone National Park, this work has needed to be addressed. However, because research from YNP is not forthcoming, we felt compelled to investigate these effects at our study site in GYE. Our results reveal a very complex process by which coyotes reconcile the hostile implications of wolf presence with an attendant benefit in the form of scavenge subsidies from wolf-killed prey. In some aspects, our work corroborates the findings of others in that coyotes do not partition space with wolves (Paquet 1991; but see Arjo and Pletscher 1999), but rather are attracted to areas used by wolves. We believe that opportunities for kleptoparasitism largely drive this spatial attraction; similar findings have been reported for predator-predator interactions in African savanna systems (Cooper 1991; Fanshawe and FitzGibbon 1993; Gorman et al. 1998; Creel et al. 2001). However, because of the risks inherent in exploiting space used by wolves and attempting to scavenge wolf-killed prey, coyotes have developed a gradient of risk sensitive behaviors to mitigate the potential for adverse interactions with wolves. These behaviors are largely mediated by coyote group size and individual social rank, and lend evidence to the notion that canids possess the cognitive capacity necessary to adapt risk-sensitive behaviors in highly dynamic settings.

If coyotes regarded wolves as a spatial threat, they would not, when presented with the opportunity, overwhelmingly locate core areas in wolf activity centers. Rather, they would avoid areas used intensively by wolves in order to reduce the threat associated with encounter. The fact coyotes do exploit these areas indicates that threat perception and avoidance behaviors are more subtle. My data indicate that, when afforded the opportunity to exploit wolf-killed prey, coyotes made modest changes in key aspects of resource selection that increased the potential of encountering wolves. For example, resource selection within home ranges differed from selection within wolf activity centers only with respect to distance from water: coyotes tended to remain closer to water features (primarily streams and creeks) as they moved through wolf activity centers. However, although coyotes traveled close to water features, they still preferred to remain in shrub/steppe rather than shifting to riparian habitat. There are two possible explanations: coyotes may have been reluctant to shift habitats because the dense protective cover of riparian associations interfered with their ability to visually detect wolves, and/or wolf activity may have been greater in riparian habitats than in shrub/steppe. Both scenarios are supported by our models describing the distribution of wolf kills (Chapters II and III) and kill sites visited by coyotes.

Once coyotes located wolf-killed prey, they relied on conspicuous behaviors to mitigate the outcome of temporal interactions with wolves, and these behaviors were largely mediated by social rank. For example, socially dominant coyotes, at first glance, appeared to take greater risks by scavenging wolf-kills in the earliest stages of consumption (i.e., when organs and major muscle groups were still available). They managed risk by elevating the proportion of time spent vigilant. However, dominant coyotes may have been minimizing the total amount of time they spent foraging, thus minimizing potential exposure to wolves, by feeding on higher quality food items. Indeed, although time spent feeding by dominants was less than time spent by subordinates, dominant individuals consumed a greater amount of total carrion biomass. Coyotes responded to the physical presence of wolves either by fleeing the immediate area or aggressively challenging wolves for primary access to a carcass. Similar to vigilance/foraging behavior, willingness to engage in aggressive behavior at carcasses was driven by the social status of participating coyotes as well as the ratio of coyotes to wolves. When coyotes were numerically superior, and socially dominant individuals were present, coyotes were more likely to challenge wolves for carcass primacy. Numeric superiority has been found to be a primary determinant in the outcome of interspecific interactions for African social carnivores (Cooper 1991; Fanshawe and FitzGibbon 1993; Creel et al. 2001), and our work is the first to identify this phenomenon as important in interactions between canids in North America. Our work with coyotes and wolves suggests that coyotes changed their behavior to reflect the ebb and flow of the wolf risk dynamic; by adapting behaviors to fluctuating risk, coyotes might be successfully dampening the amplitude of asymmetry. These findings highlight the importance of integrating behavior with spatial ecology when linking causal mechanisms to observed phenomena.

In closing, my research has indicated that (i) elk and coyotes displayed adaptive habitat selection in response to escalating risk of encountering wolves. As a result, (ii) adaptive habitat selection by elk facilitated predation by cougars and reduced predation in mule deer. Thus (iii) net predation risk for elk was a function of predation risk from both wolves and cougars and spatially dispersed across the landscape. By contrast, (iv) net predation risk for mule deer remained a function of cougar predation and was spatially aggregated within the landscape. Coyotes relied on (v) subtle behaviors to avoid spatial interaction with wolves, and (vi) conspicuous behaviors to mitigate the outcome of temporal interactions. Of course, these findings reflect a snapshot in time. That is, the specific behavioral responses of coyotes and prey to wolf recolonization may be informed by climatic factors, predator and prey densities, and landscape physiography that were unique to the study site at the time of the research. However, by studying the responses of predator and prey species to wolf recolonization, I was able to observe principles and processes that also transcend time. Predator-prey interactions need to be viewed as dynamic, where prey make fine adjustments in behavior to mitigate predation risk, while predators make similar adjustments to facilitate prey acquisition. This evolutionary behavioral arms transcends the events I describe from my research to indicate that adaptive learning, manifest by changes in risk-sensitive behaviors can occur relatively quickly (i.e., within a single generation) following predator recolonization. Moreover, these behavioral cascades may significantly reorder the nature of predator-prey and predator-predator interactions.

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Stapley J (2004) Do mountain log skinks (*Pseudemoia entrecasteauxii*) modify their behaviour in the presence of two predators? Behav Ecol Sociobiol 56:185-189

Warfe DM, Barmuta LA (2004) Habitat structural complexity mediates the foraging success of multiple predator species. Oecologia 141:171-178

White PJ, Garrott RA (2005) Yellowstone's ungulates after wolves- expectations, realizations, and predictions. Biol Conserv 125:141-152

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Education

Utah State University, Logan, UT. Ph.D. student in Wildlife Biology. 8/02- 10/06.
Dissertation: Coyotes, wolves, and mule deer: predator-prey behavioral and physiological responses in southwest Montana.
Advisor: Dr. Eric Gese

Purdue University, West Lafayette, IN. M.S. in Wildlife Ecology, 2002.
Thesis: Ecology of coyotes as influenced by landscape fragmentation.

Purdue University, West Lafayette, IN. B.S. in Wildlife with Highest Distinction, 1999.

Manuscripts published/in press

10. **Atwood, T.C.**, K.C. VerCauteren. 2007. Coyotes as a potential sentinel species to detect bovine tuberculosis (*Mycobacterium bovis*) infection in white-tailed deer in Michigan. Journal of Wildlife Management. In Press.

9. **Atwood, T.C.**, E.M. Gese, and K.E. Kunkel. 2007. Comparative patterns of predation by cougars and recolonizing wolves. Journal of Wildlife Management. In Press.

8. **Atwood, T. C.** 2006. Behavioral interactions between wolves, *Canis lupus*, and coyotes, *Canis latrans*, at ungulate carcasses in southwest Montana. Western North American Naturalist 66:390-394.

7. **Atwood, T.C.** 2006. The influence of habitat patch attributes on coyote group size and interaction in a fragmented landscape. Canadian Journal of Zoology 84:80-87.

6. **Atwood, T. C.**, H. P. Weeks, Jr., and T.M. Gehring. 2004. Spatial ecology of coyotes along a suburban-to-rural gradient. Journal of Wildlife Management 85:1000-1009.

5. **Atwood, T. C.** and H. P. Weeks, Jr. 2003. Sex-specific patterns of mineral lick preference in white-tailed deer. Northeastern Naturalist 10:409-414.

4. **Atwood, T. C.** and H. P. Weeks, Jr. 2003. Spatial home-range overlap and temporal interaction in eastern coyotes: the influence of pair types and fragmentation. Canadian Journal of Zoology 81:1589-1598.

3. Swihart, R. K., **T. C. Atwood**, J. R. Goheen, D. A. Scheiman, K. E. Munroe, and T. M. Gehring. 2003. Patch occupancy in North American mammals: is patchiness in the eye of the beholder? Journal of Biogeography 30:1259-1279.

2. **Atwood, T. C.** and H. P. Weeks, Jr. 2002. Facultative dyad formation in adult male coyotes. Northeastern Naturalist 9:353-358.

1. **Atwood, T. C.** and H. P. Weeks, Jr. 2002. Sex- and age-specific patterns of mineral lick use by white-tailed deer. American Midland Naturalist 148:289-296.

<u>Technical reports</u>

Atwood, T.C., E.M. Gese, and K.E. Kunkel. 2006. "2003-05 summary report: patterns of prey selection by wolves and cougars in southwest Montana's Madison range." Summary Report on Findings to Turner Endangered Species Fund, Bozeman, MT.

Atwood, T.C. 2006. "2005 summary report: predation effects and interspecific interactions of the Bear Trap wolf pack in Montana's northern Madison range." Report on findings to USFWS wolf recovery team, Helena, MT.

Atwood, T.C., E.M. Gese, and K.E. Kunkel. 2005. "2003-05 summary report: hunting habitat and prey selection by wolves and cougars in the Northern Madison Study Area." Report on Findings to Turner Endangered Species Fund, Bozeman, MT.

Atwood, T.C., E.M. Gese, and K.E. Kunkel. 2004. "2003-04 summary report: wolf/coyote/mule deer interactions in southwest Montana." Preliminary Report on Findings to Turner Endangered Species Fund, Bozeman, MT.

Atwood, T.C. and E.M. Gese. 2003. “Survival and cause-specific mortality of coyotes and mule deer on and around the Flying D Ranch, southwest Montana.” Preliminary Report on Findings to Turner Endangered Species Fund, Bozeman, MT.

Atwood, T.C. and E.M. Gese. 2003. “Survival and cause-specific mortality of mule deer does in southwest Montana.” Preliminary Report on Findings to Pope and Young Club, Chatfield, MN.

Atwood, T.C. and E.M. Gese. 2003. “Wolf, coyote, and mule deer behavioral interactions and physiological responses in southwest Montana.” Yearly Report on Findings to Montana Fish, Wildlife, and Parks, Region 3 Headquarters, Bozeman, MT.

Atwood, T. C. and H. P. Weeks. 2001. “Impact of coyotes on white-tailed deer population processes in a fragmented landscape.” Preliminary Report on Findings to Pope and Young Club, Chatfield, MN.

Popular articles

Atwood, T.C. Elk, mule deer, cougars, and wolves: life and death in Montana’s Madison range. *Invited article* for Boone and Crockett Club’s Fair Chase magazine. Fall 2006.

Presentations

Atwood, T.C. Direct and indirect effects of predator recolonization (*Invited seminar*). Arizona Game and Fish Department. September 18, 2006, Phoenix, Arizona.

Atwood, T. C., E. M. Gese, and K. E. Kunkel. Coyotes in Montana’s Madison Range: who’s afraid of the big bad wolf? The Wildlife Society, National Conference. September 25-29, 2005, Madison, WI.

Atwood, T. C., E. M. Gese, and K. E. Kunkel. Wolves, cougars, elk, and mule deer: interference competition and predator facilitation in Montana’s Madison Range. The Wildlife Society, State Conference. February 28- March 3, 2005, Helena, MT.

Atwood, T. C., E. M. Gese, and K. E. Kunkel. Relative contributions of prey physical condition and habitat to predation by wolves and cougars. Carnivores 2004, Defenders of Wildlife. November 14-18, 2004, Santa Fe, NM.

Atwood, T. C. and H. P. Weeks. Landscape-level correlates of spatio-temporal home range overlap in eastern coyotes. Carnivores 2002, Defenders of Wildlife. November 17-20, 2002, Monterey, CA.

Swihart, R. K., T. C. Atwood, J. R. Goheen, and D. A. Scheiman. Multi-scale determinants of patch occupancy in North American mammals. 82nd Annual Meeting of American Society of Mammalogists. June 15-19, 2002, Lake Charles, LA.

Atwood, T.C. Effects of urbanization on coyote behavior and space use. Invited speaker, Wolf Park 30th Anniversary, Canid Biology and Behavior Seminar, April 23-24, 2002, Battle Ground, IN.

Atwood, T. C. and H. P. Weeks. Coyote spatial dynamics in fragmented landscapes. The Wildlife Society, Indiana Chapter Annual Meeting. March 7-8, 2002, Bloomington, IN.

Atwood, T. C. Fragmentation ecology of eastern coyotes. The Wildlife Society, Purdue Student Chapter. November 28, 2001. West Lafayette, IN.

Atwood, T. C. and H. P. Weeks. Facultative territoriality in adult male coyotes. 81st Annual Meeting of American Society of Mammalogists. June 16-20, 2001, Missoula, MT.

Atwood, T. C. and H. P. Weeks. Modeling coyote space use in a fragmented landscape (poster). Purdue University Graduate Student Research Symposium. April 12, 2001, West Lafayette, IN.

Atwood, T. C. and H. P. Weeks. Sex- and age-specific patterns of mineral lick preference by white-tailed deer. Midwest Fish and Wildlife Conference Annual Meeting. December 5-8, 2000, Minneapolis, MN.

Atwood, T. C. and H. P. Weeks. Sex- and age-specific patterns of mineral lick use by white-tailed deer. Midwest Fish and Wildlife Conference Annual Meeting. December 3-6, 1999, Chicago, IL.

Atwood, T. C. and H. P. Weeks. Phenology of mineral lick use by white-tailed deer. The Wildlife Society, Indiana Chapter Annual Meeting. February 15-16, 1999, Nashville, IN.

Research grants

Pope and Young Club, Chatfield, MN. "Wolves, cougars, elk, and mule deer: direct and indirect predation effects in southwest Montana. 2006. $1,700.

Boone and Crockett Club, Missoula, MT. "The relative contributions of forage quality and predation to mule deer recruitment in southwestern Montana." 2005. $8,600. (With K.E. Kunkel and E.M. Gese).

Boone and Crockett Club, Missoula, MT. “The relative contributions of forage quality and predation to mule deer recruitment in southwestern Montana.” 2004. $4,933. (With K.E. Kunkel and E.M. Gese).

Pope and Young Club, Chatfield, MN. “Mule deer demography and survival in southwest Montana.” 2004. $2,000.

Pope and Young Club, Chatfield, MN. “Mule deer hormonal profiles as predictors of population vital rates.” 2003. $1,500.

Pope and Young Club, Chatfield, MN. “Impact of coyotes on white-tailed deer population processes in a fragmented landscape.” 2000. $2,000.

FurBearers Unlimited, Charleston, IL. "Behavioral ecology of coyotes in a fragmented landscape." 2000. $2,000.

Research experience

Research Wildlife Biologist (Wildlife Specialist III), Research Branch, Arizona Game and Fish Department, Phoenix, AZ. I conduct Federal Aid research on carnivores and ungulates. I am currently leading investigations into black bear spatial ecology and population genetics in the White Mountains and the Sonoran and Chihuahuan deserts, and the foraging ecology of mule deer on the Kaibab plateau. I prepare grant proposals, technical reports, and manuscripts for peer-reviewed publication. I supervise Wildlife Specialists I and II and Wildlife Technicians. 11/01/06-present.

Consulting Biologist, USDA/National Wildlife Research Center, Mammal Disease Program, Fort Collins, CO. I am conducting the analyses and write-up of research involving the spatial epidemiology of bovine tuberculosis in meso-carnivores. The goal of the project is to identify appropriate sentinel species to monitor bovine tuberculosis prevalence and model disease dynamics among trophic levels. I also assist on various chronic wasting disease research projects. 5/01/06- present.

Ph.D. Candidate, Wolf/Coyote/Mule Deer Trophic Interaction Project, Department of Forest, Range, and Wildlife Sciences, Utah State University, 8/2002-10/2006. I was a doctoral student leading a research effort to determine the effects of recolonizing gray wolves on coyote and mule deer behavioral and physiological ecology. The project required coordinating activities with private foundation and state agency biologists. I supervised 8 full-time seasonal employees over the course of data collection (1/2003- 8/2005). I also prepared research grant proposals and reports to granting organizations.

Mammalogist, ECASE, Department of Forestry and Natural Resources, Purdue University, May 2002 to August 2002. The project was a multidisciplinary research initiative investigating land uses and impacts on floral and faunal communities in west-central Indiana. I used a variety of survey techniques, including grid and web trapping and remote-triggered camera stations to collect data on the abundance of small mammals and mesocarnivores. I also collected tissue samples for genetic analyses. The position was full-time (40 hr/wk) from 5/1/2002 to 8/10/2002.

Graduate Research Assistant, Coyote Project, Department of Forestry and Natural Resources, Purdue University, January 2000 to May 2002. The project entailed determining whether variability in landscape context altered the dynamics of coyote habitat use and social organization. The project required coordinating research activities with state natural resource agency personnel. I supervised 2 part-time technicians. I also prepared research grant proposals. To date, the research has resulted in 4 peer-reviewed publications. The position was full-time (40 hr/wk) and I received an annual salary via a graduate assistantship from 1/7/2000 to 5/1/2002.

Research Assistant (volunteer), Sex- and Age-Specific Phenology of Mineral Lick Use in White-tailed Deer, Department of Forestry and Natural Resources, Purdue University, April 1998 to October 1999. Collected and analyzed data on sex- and age-specific patterns of mineral lick use by white-tailed deer. A secondary aspect of the project investigated patterns of mineral preference in deer visiting mineral, salt, and natural licks. The project was conducted on an active military base and required coordinating activities with military personnel. Additionally, I supervised 1 volunteer technician. The research has resulted in 2 peer-reviewed publications.

Research Assistant (volunteer), White-tailed deer hunter check stations, Department of Forestry and Natural Resources, Purdue University. November and December of 1997, 1998, and 1999. Supervised groups of 10-15 student volunteers at white-tailed deer hunter check stations.

Technician, Vertebrate Collection, Department of Forestry and Natural Resources, Purdue University, August 1998 to January 1999. Assisted in the maintenance of the mammal, herpetological, and ornithological collection. The position was part-time (8 hr/wk).

Research Technician, Grassland Bird Abundance, Department of Forestry and Natural Resources, Purdue University, May 1998 to August 1998. Spot mapped breeding birds ranging from neo-tropical migrants to game birds. Conducted total and brood counts, and nest searches at IDNR game bird management areas. The position was full-time (35 hr/wk).

Technician (volunteer), Wild Turkey Project, Department of Forestry and Natural Resources, Purdue University, April 1998. Manned wild turkey hunter check stations. Obtained blood samples for DNA analysis.

Teaching experience

Guest Lecturer, Purdue University, FNR 241, Ecology and Systematics of Fish and Mammals, fall 2001. I presented a lecture on mammalian nutritional ecology and physiological adaptations in food processing systems.

Teaching Assistant, Purdue University, FNR 341, Wildlife Management, spring 2000 and 2001. I taught the lab sections of the course to undergraduate students in Wildlife. I prepared laboratory lectures and led field exercises in habitat analysis techniques. I prepared and graded lab practicals and maintained course grades.

Teaching Assistant, Purdue University, FNR 547, Vertebrate Population Dynamics, fall 2000. I prepared and presented lectures on stage-structured population models and survivorship analysis of radiotelemetry data. I assisted with the instruction of computer labs, graded assignments, and maintained course grades.

Teaching Assistant, Purdue University, FNR 215, Dendrology, fall 1998 and 1999. I led field labs and introduced students to 220 species of woody and herbaceous plants common to west-central Indiana. I gave field quizzes and lab practicals, and maintained course grades.

Academic awards

American Association for the Advancement of Science- membership award
Presidential Fellowship, Utah State University, 2002-2003.
Graduate Assistantship, Purdue University, 2000-2002.
Outstanding Senior in Forestry and Natural Resources, Purdue University, April 1999.
Senior Academic Merit Award, Purdue University, April 1999.
William A. Rafferty Award, Purdue University, April 1999.

Professional membership and activities

American Association for the Advancement of Science
Animal Behavior Society
The Wildlife Society
Society for Conservation Biology (1996-2000)
American Society of Mammalogists (1998-2000)
Phi Kappa Phi
Guest Editor- Northeastern Naturalist (2002)
Manuscript Referee- Wildlife Society Bulletin