ELK (*Cervus elaphus*) VIGILANCE LEVELS IN RESPONSE TO PREDATION RISK FROM WOLVES (*Canis lupus*)

by

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A thesis submitted in partial fulfillment
of the requirements for the degree

of

Masters of Science

in

Fish and Wildlife Management

MONTANA STATE UNIVERSITY
Bozeman, Montana

April 2007

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of a thesis submitted by

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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the Division of Graduate Education.

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April 2007

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CHAPTER 1

INTRODUCTION

Ecologists study predator prey interactions in an effort to quantify impacts of predators on prey and vice versa. Historically, studies have focused on the direct offtake of prey using models similar to the Lotka-Volterra model, (Volterra 1926; Lotka 1932) in which prey numbers are dependent upon the number of predators in the system, and the killing efficiency of the predator. Such models can correctly account for direct offtake of prey animals, but they overlook the potential effects of antipredator responses exhibited by prey. Studies have shown that most animals alter their behavior in response to predation risk (Lima and Dill 1990; Lima 1998b). Behavioral responses may minimize exposure to risk, but it has been argued that they are likely to also have a negative impact on fitness, either through survival or reproduction (Brown et al. 1999; Nelson et al. 2004; Preisser et al. 2005). Knowing not only the magnitude of the risk, but also the proportion of time an animal spends in each risk level, will give a better understanding of how prey respond to predators, and how these behavioral responses may ultimately affect demography and dynamics (Lima and Bednekoff 1999).

Behavioral responses used to minimize exposure to risk include changes in group size, increased vigilance levels, and habitat shifts. Potential benefits of forming larger groups include increased predator detection through increased group vigilance (Pulliam 1973) and dilution effects where each individual is less likely to be killed by a predator as group size increases (Hamilton 1971). Increasing the time that at least one group member is vigilant increases the probability of a prey individual detecting a predator before it attacks, and therefore gives the prey individual the opportunity to move away, hide, or alert others before the predator becomes too close (Caro 2005). Potentially offsetting these benefits of grouping, larger groups may be more easily detected by predators, more likely to provoke an attack when detected, or more vulnerable once attacked (Creel & Creel 2002). Habitat shifts are adopted to avoid areas of high risk or minimize the probability of encounter between predators and prey (Bergerud et al. 1990; Heithaus and Dill 2002). These behavioral responses could reduce the probability of being killed by a predator, but may come with associated fitness costs: it is likely that habitat selection, foraging, grouping and other aspects of behavior more closely approach the optimum when they are not constrained by predation risk.

Antipredator behavior can affect prey demography in many ways, through impacts on energy intake, survival, and conversion of energy to offspring (Preisser el at. 2005). Habitat shifts in response to predation risk involve prey trading security for a reduction in forage quantity, quality, or both (Heithaus and Dill 2002; Hernandez and Laundre 2005). Increasing vigilance levels to increase the probability of detecting a predator is often negatively correlated with time spent foraging (Underwood 1982; Lima 1998a). Formation of large groups to increase predator detection, or dilution of individual risk can decrease an individuals chance of being preyed upon. However, large groups may be more easily detected, and predators may prefer to attack larger groups (Hebblewhite and Pletscher 2002). Studies in insects and mammals have shown that the presence of the predator alone may be great enough to reduce reproduction and/or survival (Creel et al. 2007; Nelson et al. 2004; Schmitz 1998).

My research addresses elk (*Cervus elaphus*) behavioral responses to the risk of predation from wolves (*Canis lupus*) in the northern range of Yellowstone National Park (YNP). The main section of this thesis is currently in review and is an extension of work already published (Creel and Winnie 2005; Creel et al. 2005; Creel et al. 2007; Winnie and Creel 2007; Winnie et al. 2006). Since the reintroduction of wolves into Greater Yellowstone Ecosystem (GYE) in 1995 a great deal of focus has been placed on the effects of wolves on their prey base. Adult elk are the primary prey for wolves, accounting for approximately 90% of their winter diet (Smith et al. 2004; Creel and Winnie 2005; Winnie et al. 2007). Because elk are the primary prey source for wolves, several studies have focused on elk antipredator behavior. Laundre et al. (2001) compared vigilance levels of elk in areas that overlapped wolf territories to areas that were considered wolf-free. They found no effect of group size on vigilance rates for any of the social classes they looked at (males, females without calves, and females with calves). In terms of vigilance rates they found that males in wolf-areas and males in wolf-free areas had the same vigilance levels, females without calves had higher vigilance levels in wolf-areas compared to wolf-free areas, and females with calves had the highest vigilance levels, and had higher vigilance rates in wolf-areas.

Childress and Lung (2003) reported patterns of vigilance similar to those of Laundre et al. (2001); they compared vigilance levels of elk to different levels of encounter risk based upon wolf, grizzly bear, and coyote density. They combined these densities to identify three areas with different levels of risk (high, intermediate, and low).

Like Laundre et al. 2001 they found that the order of vigilance from highest to lowest was: females with calves > females without calves > yearling (males and females) and adult males. Females with calves and females without calves increased vigilance levels as the level of risk increased, whereas yearlings and adult males did not increase vigilance levels as the level of risk increased. Unlike Laundre they found significant effects of group size on vigilance in some sex-age classes. Only females without calves and yearlings significantly reduced scanning rates with increasing group size. When examining other factors that could potentially effect vigilance levels they found no significant relationship between distance to protective cover (forest) or position within the herd (peripheral or central). Both of these studies considered only spatial variation in risk at a rather large spatial scale (greater than 100km^2). Variation on smaller spatial and temporal scales (for example, within the daily or seasonal range of movements of individual elk) was not examined directly. These studies also did not consider temporal variation in risk within sites: essentially, they treated risk as a constant property of large areas. Their results clearly showed that responses of elk to spatial variation at this scale can be detected, but do not address the question of whether these broad patterns are simply an emergent pattern from more complex responses at smaller spatial scales, or through time.

The effects of wolves on habitat selection by elk has also been examined in YNP, aggregating data over broad spatial and temporal scales. Mao et al. (2005) compared habitat selection of elk before and after wolf reintroduction, and found that in summer elk selected habitats that were in higher elevation, less open habitat, more burned forests, and steeper slopes, than before wolf reintroduction. In winter, the only difference they found between the pre and post wolf periods was that elk selected habitats that were more open. They suggested that elk in the winter did not select habitats to avoid wolves but rely on other antipredator behavior such as grouping to avoid wolves. If wintering elk avoid wolves at small spatial scales or over short time periods (as they do elsewhere in YNP: Creel et al 2005), these effects could have gone undetected. Fortin et al. (2005) compared movement patterns of elk in low wolf-use areas and high wolf-use areas, using step selection functions to test for changes in turning angles and segment lengths for GPS collar locations. From these, they made inferences about likely effects of wolves on habitat use, concluding that elk in low wolf-use areas would be predicted to have the following habitat preferences: aspen stands > open areas > conifer forests. In high wolf-use areas they found different predicted patterns: conifer forests > open areas > aspen stands.

Four other studies examining patterns of aggregation, decision-making, habitat selection, and behavior of elk in response to wolf predation risk came from a different location within the GYE, the Gallatin Canyon, Montana (Creel and Winnie 2005; Creel et al. 2005; Winnie and Creel 2007; Winnie et al. 2006). These studies examined variation in predation risk on a much finer spatial scale and explicitly incorporated temporal variation in risk. They compared the behavior of elk on days when wolves were present in a given drainage to days when wolves were absent from the drainage – although this is a finer spatial scale, risk was still considered uniform over fairly large areas (roughly 30 km^2). When examining patterns of aggregation Creel and Winnie (2005) found that on days when wolves were present within a given drainage, herd sizes were less than half of those when wolves were absent. They found that herd size significantly increased as distance to forest increased (and risk increased), but only on days that wolves were absent. When wolves were present, herd sizes did not increase with distance to forest, suggesting that aggregation was not an antipredator response. Therefore they suggest that formation of large groups far from cover is a foraging response, and suggest that the antipredator response of splitting into smaller herds when wolves are present probably serves to reduce the likelihood of being detected by wolves. Winnie et al. (2006) examined habitat decision-rules of elk when wolves were present in a drainage compared to when wolves were absent. They accomplished this by examining the attributes of GPS radio collar locations of elk on days that wolves were present and absent. Their results showed that in the absence of wolves, elk responded to many environmental variables, particularly snow conditions, when making decisions on habitat use. In contrast on days when wolves were present, the same elk, in the same drainage, showed significantly less complexity in their decisions about habitat use (that is, habitat selection patterns were related to fewer environmental variables, in the presence of wolves). This result and results from previous work (Creel and Winnie 2005) suggests that elk spatial responses are a strategy of avoiding encounters with wolves, instead of influencing the outcome of encounters.

Habitat selection in response to wolves was also of interest. Creel et al. (2005) found that the presence of wolves within a giving drainage on a given day had little effect on the elevation, slope, or aspect at which elk were found. However, they found significantly more elk locations in areas where conifers were common and native grasses (preferred vegetation of elk: Christianson and Creel in press) were uncommon, when wolves were present in the drainage. They also found that cows showed a stronger tendency than bulls to move into conifers when wolves were present. Their results suggest that elk assess open grasslands to be more dangerous than conifers when wolves are present (paralleling prior results on herd size responses).

Finally, Winnie and Creel (2007) examined how wolves affect the vigilance patterns of elk. They examined elk vigilance levels at finer spatial scale than prior work, and assessed the impacts of temporal variation in risk, within a location. Instead of comparing vigilance levels of elk that reside in different locales and different rates of background risk, the authors examined the vigilance levels of elk that occupied the same areas, where risk varied from day to day. Like Childress and Lung (2003) and Laundre et al. (2001), they found that cow elk were more vigilant than bulls. They also found that the same cow elk significantly increased their vigilance levels when wolves were present in the drainage on a given day. In contrast to cows, bulls did not significantly increase their vigilance levels when wolves were present. This research also identified a potential reason why bull elk are less vigilant than cow elk. They found that bulls enter the winter in significantly worse body condition than cows (by comparing marrow fat of wolf killed bulls and cows), and they suggest that these energetic constraints do not allow bulls to allocate as much time to vigilance. Two other factors that were examined: distance to protective cover and herd size had no effect on vigilance levels. While these studies have clearly demonstrated that elk respond to predation risk from wolves, I wanted to examine the relative importance of various factors that influence vigilance and also test whether variables associated with wolves also predict the strength of antipredator responses by elk.

A tremendous amount of information is known about ways that attributes of prey, such as group size, gender or position in a group, influence vigilance levels in mammals (Lima and Dill 1990; Elgar 1989; Caro 2005). Substantially less is known about the variables that describe the predation risk itself, and how they affect vigilance rates. This study is also unusual because it treats predation risk a continuous variable, rather than dichotomizing ‘risk’ and ‘safety’. Finally, I have been unable to locate any field studies that simultaneously consider how characteristics of prey, predators and the environment combine to determine vigilance levels.

CHAPTER 2

WHAT BEST EXPLAINS VIGILANCE IN ELK: CHARACTERISTICS OF PREY, PREDATORS, OR THE ENVIRONMENT?

Abstract

Many studies have shown that levels of antipredator vigilance are sensitive to variation in prey attributes, such as age, sex and group size. It is also well established that vigilance is sensitive to environmental effects, such as the presence of cover. In contrast, little is known about the sensitivity of vigilance to variation in factors associated with the predator itself, such as proximity, the size of the threatening group, and cues about motivation to hunt. Finally, little is known about the relative importance of these three classes of variables (predator, prey, and environment), or about the information content of simple versus complex models of vigilance. We quantified the vigilance levels of elk (*Cervus elaphus*) preyed upon by wolves (*Canis lupus*) in Yellowstone National Park, between January and May in 2005 and 2006, and compared a set of 38 regression models for vigilance levels, using Akaike's Information Criterion. Complex models incorporating the characteristics of the wolf pack, the structure of the elk herd, and the environmental conditions performed better than simple models. While univariate models of vigilance detect significant relationships, they have low information content relative to multivariate models. These results show that elk assess factors of several types when assessing risk and deciding how much time to allocate to vigilance. In particular, we found that all well-supported models of vigilance included several 'prey' variables and

several ‘predator’ variables. This result highlights the need to consider information about predators when trying to explain vigilance levels in prey.

Introduction

To reduce the risk of predation, animals engage in a range of behavioral responses, including habitat shifts, changes in group size, reduced activity, and increased scanning rates for predator detection. Antipredator vigilance has been studied in great detail over the past quarter century (Elgar 1989; Lima & Dill 1990; Caro 2005). By increasing the effort put into scanning the environment, animals are more likely to detect a predator at a distance, and consequently prevent or avoid a direct attack (Caro 2005). Vigilance has been studied in a wide variety of mammals and birds, and these studies have identified many factors that influence scanning rates, including group size (Underwood 1982; Elgar 1989; Roberts 1996), age and sex (Hunter and Skinner 1998; Childress and Lung 2003; Winnie and Creel 2007), body condition (Winnie and Creel 2007), position within the group (Underwood 1982; Keys and Dugatkin 1990; Hunter and Skinner 1998), habitat type (Lima 1987; Scheel 1993; White and Berger 2001), time of day (Scheel 1993; Elgar 1989), and local environmental conditions(Lima and Dill 1990; Elgar 1989).

These studies clearly demonstrate that animals adjust their scanning rates in response to their own condition, the size or type of group they occupy, or in response to the local environment. We know substantially less about the ways animals respond to variation in the type of threat that they face. In most studies, behavioral responses are recorded in response to simulated risk, or in response to the immediate presence or absence of a natural predator. This has been a productive approach, but it gives little scope to ask whether the strength of antipredator responses varies in response to aspects of risk such as the distance to predators, the size of the attacking group, or cues about the predators state of satiation (as indicated by the presence or absence of a kill). It is likely that prey assess risk as a continuous variable, rather than dichotomizing risk into periods of safety and danger, as is assumed by some models (Lima and Bednekoff 1999), experiments (Sih and McCarthy 2002) and observational studies (Creel and Winnie 2005). To address this broad hypothesis, one must test whether variables associated with the predator predict the strength of antipredator responses by the prey.

For example, consider the question "Are prey more or less vigilant when a kill has been made recently?" A priori, it is difficult to know whether prey should regard a fresh carcass as an indication of safety or of risk, because the answer depends on the time scale over which prey assess risks. The fact that an elk (*Cervus elaphus*) has been killed clearly indicates that a lethal risk exists. On the other hand, wolf (*Canis lupus*) packs in Yellowstone National Park (YNP) kill at intervals that average 2-3 days (Stahler et al. 2006). The presence of a fresh kill is a reliable indicator that a hunt is nonrandomly unlikely in the immediate future. Wolves, like other carnivores, sometimes make multiple kills and sometimes hunt opportunistically at kill sites, but this does not appear to be the norm. Do elk perceive a kill as a cue of danger because it reveals that wolves were not only in the area, but hunting actively, or do they recognize a brief period of safety (a period when wolves are satiated and not likely to hunt) and reduce their vigilance levels accordingly?

More broadly, despite the depth and breadth of information on factors that affect antipredator vigilance, we know relatively little about the relative importance of various factors that stimulate vigilance. These factors can be placed in three broad categories: (1) Those related to the prey, including age, sex, condition, or group size. (2) Those related to the environment, including habitat type, light conditions, and other factors that might impede escape or defense, such as snow depth or cover. (3) Factors related to characteristics of the predator, such as: distance to predators, predator group size, presence of a kill, and time since the kill was made. We know of no field study that has simultaneously considered the roles of environmental, predator, and prey effects on vigilance. Here, we use model selection with Akaike's Information Criterion (AICc) to compare regression models of vigilance in elk, models were selected *a priori* to span a range of complexity, and to vary in the degree to which the focus is put on environmental, predator, and prey effects, or combinations of these effects. We find that complex models are better supported than simple ones, and that factors of all three types simultaneously have strong effects on vigilance. We made observations of elk on the northern range of Yellowstone National Park (YNP), where the primary predator of adult elk is the wolf.

Methods

Study Area and Populations

Elk, numbering 12,000 to 14,000 animals are the most numerous ungulate on the site (Smith et al. 2004), followed by bison (*Bison bison*) which are less than a 10th as numerous (600-700 individuals) (Smith et al. 2003). Moose (*Alces alces*), mule deer, (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianous*), and bighorn sheep, (*Ovis canadensis*) also occupy the northern range, but at much lower densities than elk or bison (Smith et al. 2003). Elk are the primary prey of wolves throughout YNP, compromising 88% of the 2347 documented wolf kills from 1995-2003 (Stahler et al. 2006), and wolves are the primary predator of adult elk, accounting for more than 90% of the predation on adults (Smith et al. 2004, Creel & Winnie 2005; Winnie et al. 2007). The spatial structure of wolf territories and the daily movements of wolves within territories cause predation risk for elk to vary spatially on a scale of meters to kilometers, and temporally on a scale of hours to days (Creel et al. 2005; Winnie & Creel 2007). In the northern range wolves and elk are easily observed, without disturbance, at distances of a kilometer or more (Smith et al. 2004). Consequently, this system and site provide an excellent opportunity to record variation in antipredator vigilance in response to variation in predator, prey and environmental characteristics.

We studied the factors that affect vigilance levels in elk during the winter months (January to May) of 2005 and 2006. Our 830 km^2 study site was located in the north-east portion of Yellowstone National Park, Wyoming, USA centered on the ‘northern range’ (Huston 1982), which is defined by the seasonal migration of the elk herd (12,000 – 14,000 individuals) that occupies the area. Wolves were reintroduced into the northern range in the winters of 1995 and 1996 (Bangs and Fritts 1996). During our study, wolf numbers on the site varied from 84 wolves in seven packs in 2005, to 54 wolves in six packs in 2006. The study area is dominated by large open valleys comprised of sage (*Artemesia* spp.) and grassland (*Festuca* and *Agropyron* spp.) with riparian areas bordering the small creeks and the Yellowstone, Lamar, and Gardner rivers. The upper elevations and north facing slopes are primarily coniferous forests (*Pinus* and *Pseudostuga* spp.) with small intertwined meadows. Elevation varies from 1500 m to 3400 m above sea level with 87% of the area falling between 1500 m and 2400 m above sea level. The climate is described by long, cold and snowy winters and short, cool summers. For a more detailed description of the study site see Houston (1982).

Prey (Elk) Variables

We observed elk 3-5 days a week from early January to May in two years, from sunrise to sunset. Observations followed a stratified sampling design. We stratified the northern range by location (Blacktail Deer Creek Plateau, Hellroaring, Tower Junction, Slough Creek, and Lamar/Soda Butte). Each stratum was approximately the same size and received approximately equal observational effort. We made behavioral observations at distances of 0.5 to 2 km using a tripod-mounted 20-56x Nikon ED spotting scope. These distances were usually sufficient to avoid affecting elk behavior. If it became apparent that the elk were focusing on the observer or other humans (any vigilance directed toward humans) or if the elk retreated from any people, we ceased observations and omitted all data from that elk herd.

We observed elk after first recording their distance from the nearest known wolves (see *Predator (Wolf) Variables*, below). Upon sighting an elk or elk herd, we recorded the following preliminary data with respect to the prey (also see Predator Variables and Environmental Variables, below):

(1) *Herd size*: For many species, vigilance declines with group size.

(2) *Herd composition:* (calves [young of the year], cows [female > 1 year old], bulls [adult male with at least one brow tine], and spikes [one year old antlered male with no brow tines]). Our past research and work by others shows that for elk elsewhere in the ecosystem, females with calves exhibit the highest vigilance levels followed by females without calves and then males (Winnie and Creel 2007; Childress and Lung 2003);

(3) *Day of year (Julian date)*: As winter progresses, forage quantity and quality decreases, and elk body condition declines (Winnie and Creel 2007). Thus, elk face stronger constraints on time and energy as winter progresses.

(4) *Position within the herd*: It has been argued that peripheral animals tend to be more vigilant than interior animals because they are at a greater risk of being attacked first by a predator (Hamilton 1971; Underwood 1982; Keys and Dugatkin 1990; Hunter and Skinner 1998).

We used instantaneous scan sampling to collect behavioral data. Instantaneous scan sampling provides unbiased data appropriate to estimate the percent of time an animal spends engaged in various activities, and allows more groups to be sampled in a day than other sampling designs (Altmann 1974; Martin and Bateson 1986). We scanned through elk herds (N =202 herds) at five minute intervals, for a minimum of 3 and a maximum of 8 scans, recording (with a hand held voice recorder) the following information for each individual in the herd: sex and age (cow, calf, bull, or spike); position within the herd (peripheral or interior); and behavior (grazing, moving, vigilant, bedded, bedded vigilant, or other). We defined interior animals as those that a predator could not approach without encountering another animal in the herd. Conversely, peripheral animals were those that could be encountered by a predator before any other animals in the herd. We used behavioral categories established by prior studies of elk responses to wolves (Winnie & Creel 2007) , classifying behavior as follows: (1) Grazing: animals that were standing with their head down collecting forage or with their heads up chewing forage; (2) Moving: animals that were walking or running without feeding; (3) Vigilant: animals that were standing, head erect, with ears cocked forward in the direction of gaze (the position of the head and ears is critical for this category); (4) Bedded: animals that were lying down on their sternum or side, head not erect (often ruminating or apparently sleeping); (5) Bedded vigilant: animals that were lying on their sternum with head erect, with ears cocked forward in the direction of gaze; (6) Other: all other less common activities such as grooming or sparring. We obtained a total of 12,748 individual behaviors from 202 herds.

To avoid pseudoreplication, we combined all of the scans from a herd into a single vigilance rate. Because separate individuals and scans are not fully dependent, this is a conservative approach, relative to a repeated-measures model with random effects.

Predator (Wolf) Variables

As mentioned above, many studies of antipredator behavior (including our own: Creel and Winnie 2005; Winnie and Creel 2007) consider only whether the predator is present or absent, which is likely to oversimplify the information perceived and used by prey in making antipredator responses. In this study we recorded several variables about the predator, to test how they related to vigilance levels in elk. Because at least one (and up to seven) wolf in every pack in the northern range wore a radio collar during this study (Doug Smith pers. comm. [Yellowstone Wolf Project Leader]) we located wolves via VHF radiotelemetry. We then located the pack visually by skiing or hiking to high ground, and using a tripod-mounted 20-56x Nikon ED spotting scope and watching the wolves for as long as was needed to determine the following variables: 1) The number of wolves in the pack. For some coursing predators, as pack size increases the probability of capturing and killing prey individual increases, therefore increasing the risk to a prey group (Creel and Creel 1995). However, we unaware of any studies that have tested how predator group size might affect antipredator behavior in prey, specifically vigilance levels. 2) Whether the wolves were at or near a recent kill (<24hrs old). Fresh blood, carcasses or portions of them, and scavengers helped us to determine if a kill had been made recently. 3) The location of the pack (determined by GPS, range-finding binoculars, compass and USGS 1:50,000 maps). We used this location in combination with a subsequent location of elk herds to determine the straight line distance between elk and the nearest known wolves. By comparing vigilance levels across a wide range of distances from wolves (min 0.2km, max 5.0km), we essentially allowed elk to tell us when they perceived predators to be ‘present’. Five km was the greatest distance we considered, because as the wolf-elk distance increased, there was increased potential for failing to detect wolves within the radius, due to the exponential increase in area.

Environmental Variables

We measured three environmental variables that we hypothesized or knew to affect vigilance levels in elk. First, we recorded the distance from the herd to forest. Numerous studies have shown that habitat type and distance to protective cover affect vigilance levels in prey (Lima 1987; Scheel 1993; White and Berger 2001). Depending on the prey and predator species of concern results have varied. Distance to forest captures two important aspects of the environment, habitat type (open vs. closed) and how far an animal was from protective cover. We measured distance to forest by visually estimating the distance and classifying observations into one of five categories: 0m (herd was in the forest), 1-30m (away from forest), 31-100m, 101-300m, and 301+m. This categorization was previously useful when measuring effects of risk on patterns of aggregation (Creel & Winnie 2005), decision-making (Winnie et al. 2006), habitat selection (Creel et al. 2005) and behavior (Winnie & Creel 2007) for elk elsewhere in the Yellowstone ecosystem. Because distance to forest and habitat type are strongly collinear (we used the covariance matrix to examine collinearity for all pairs of variables considered), we could not include both variables in our analyses. We preferred distance to forest because of its important role in prior studies. The second variable of concern was percent snow cover. We visually estimated how much of the landscape (0-100% by 10%'s) was covered in snow within the viewshied of herd. As snow cover increases it also increases the difficulty of moving and foraging. Snow cover was often less than 100%, and elk tended to congregate on snow free areas. Finally, we obtained daily data on snow-water-equivalent (SWE) from the regional NRCS SNOTEL site at Canyon, YNP, Wyoming, USA (within the study area). SWE provided information on the depth and density of the snow. We quantified snow cover and density (SWE) because the depth, density, and more widespread snow are constraints on time and energy might trade off against vigilance.

Statistical methods

To test the relative importance of predator, prey and environmental variables in their effects on vigilance, we used Akaike's information criterion (with sample size correction, AICc) to compare 38 *a priori* regression models. We used AICc for model selection because it identifies models on the basis of both fit and parsimony (complex models must explain more variance to obtain AICc scores equal to simpler models). Models varied from simple (1 parameter models) to complex (maximum of 9 parameters). Conceptually, our models fell into three subsets. The first subset included the simplest models, which contained independent variables from one of the three types of variables (predator, prey or environment) (total of 15 models). In the second subset we developed models of intermediate complexity that included parameters about the predator and the prey herd (total of 15 models). The last subset contained the most complex models, which contained parameters about the predator, the elk herd, and the environment (total of 8 models) (A list of the dependent variable and independent variables used to create the regression models can be viewed in Appendix B). The possible list of models was extensive (2047 models, without considering interactions), but we restricted our *a priori* model list to 38 (Appendix A), that addressed hypotheses developed through field observations, our past research, and other studies.

We assessed normality for all parameters by observing their distributions, and further tested for deviations from model assumptions by observing residual plots. We arcsin-transformed parameters that were proportions prior to analysis, and back transformed in plots of results (Zar 1999). We used the Generalized Linear Models module of STATISTICA 6.0 (Statsoft Inc, Tulsa, Oklahoma, USA) to fit models and made comparisons using Akaike's Information Criterion corrected for sample size (AIC_c) (Burnham and Anderson 2002). We assessed goodness of fit using the most complex model in the *a priori* set, ($K = 9$) and found no evidence for lack of fit ($\chi^2 = 202.000$, df = 189, $\hat{c} = 1.069$).

Results

Complex models predicted vigilance levels better than simple models (Appendix A). The best model (AICc weight = 0.199) included two parameters related to predators and three related to prey. The second best model, which had information content comparable to the best model (AICc weight = 0.153) was the second most complex model in the *a priori* set, with three parameters related to predators, three related to prey, and two related to the environment. Six models were within two AIC units of the top model. All of these included parameters related to both predators and prey. Out of these six models, two included predator, prey and environmental parameters. Models with the simplest structure preformed much worse; the best simple model (with parameters of only one type – predator, prey or environment) was more than16 AICc units worse than the top model (Appendix A). Models with a single independent variable were all more than 29 AICc units worse than the best model. Overall, Appendix A reveals that decisions about vigilance are simultaneously affected by information about the predator, the prey, and the situation in which the encounter occurs. Predator and prey variables were particularly important (Table 1).

Table 1. Relative importance values from AIC$_c$. Relative importance is the sum of the Akaike weights across all models in which a parameter appears. Low values indicate the parameter is in fewer models with less support from the data, high values indicate the parameter is in more and better supported models (Burnham and Anderson 2002)

Wolf			Elk			Environment		
Parameter	Value	# Models	Parameter	Value	#Models	Parameter	Value	#Models
Distance To Wolves	1	22	Proportion Cow	1	19	Distance To Forest	0.332	6
# Wolves	0.626	11	Proportion Calf	1	19	SWE	0.311	10
Kill Present/Absent	0.483	13	Herd Size	0.650	18	% Snow Cover	0.168	7
			Day of Year	0.063	4			
			Proportion Peripheral	0.063	4			

Predator (Wolf) Variables

Characteristics of the predator were important in determining vigilance levels. In all models within two AICc units of the best model there was at least one wolf parameter and most of these models contained more than one (average of 2.167; Appendix A). Comparing relative importance (RI) scores (Burnham and Anderson 2002) for the wolf variables, distance from the elk herd to the wolves was the most important, with an RI score of 1 (the maximum) (Table 1). Vigilance levels were greatest when wolves were within 1km of the elk herd (Figure 1and Table 2). Elk also showed elevated vigilance levels when wolves were between 1 and 3km away. At distances of greater than 3km, vigilance returned to apparently baseline levels. The number of wolves in the pack also played an important role in determining vigilance levels, with stronger responses to packs larger than 10 wolves (Table 1 and Table 2). The greatest effect occurred when pack sizes were greater than10 wolves (Figure 2). At pack sizes less than 10 wolves, vigilance levels were lower and approximately constant. The presence (N=72) or absence (N=130) of a kill had the lowest relative importance score, in comparison to the other wolf variables (Table 1). Overall, the presence of a kill had only weak effects on vigilance (Table 2). However, we found an unanticipated but strong difference between all-bull groups and cow groups (cows, calves, and spikes) in their reactions to the presence of a kill (Figure 3 and Table 2). Cow groups significantly reduced vigilance levels when a kill was present ($df = 123$ $P < 0.001$) whereas all-bull group significantly increased vigilance levels when a kill was present ($df = 79$ $P = 0.003$).

Table 2. Regression coefficients and their standard errors, from model averaging using AIC_c weights (ω_i). Distance to forest and Kill present/absent were categorical predictors. Kill absent was compared to kill present and distance to forest was compared to distances of greater than 300m. Bold entries identify regression coefficients that differ from zero at $\alpha = 0.05$.

Parameter Estimates From Model Averaging

Wolf			Elk			Environment		
Parameter	Estimate	SE	Parameter	Estimate	SE	Parameter	Estimate	SE
Distance To Wolves	**-0.0931**	**0.0182**	**Proportion Cow**	**0.1000**	**0.0210**	Distance To Forest (0m)	-0.0818	0.0518
# Wolves	0.0057	0.0036	**Proportion Calf**	**0.1986**	**0.0775**	Distance To Forest (1-30m)	-0.0286	0.0235
Kill Absent	0.0085	0.0128	Herd Size	-0.0021	0.0012	Distance To Forest (31-100m)	0.0339	0.0228
						Distance To Forest (101-300m)	**0.0552**	**0.0274**
						SWE	**-0.0130**	**0.0056**
						% Snow Cover	0.0001	0.0004

Figure 1. The response of elk vigilance levels to distance between the herd and the nearest known wolf pack. Proportion vigilant was arcsin-transformed prior to analysis (Zar 1999). Values on the right y-axis show the back-transformation, for which errors are not symmetric.

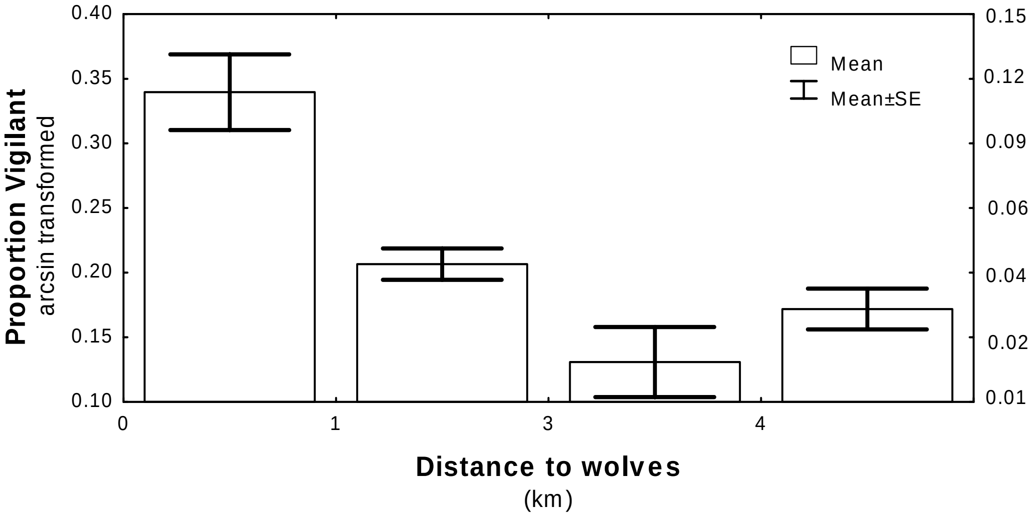


Figure 2. The response of elk vigilance levels to the number of wolves in the pack. Proportion vigilant was arcsin-transformed prior to analysis (Zar 1999). Values on the right y-axis show the back-transformation, for which errors are not symmetric.

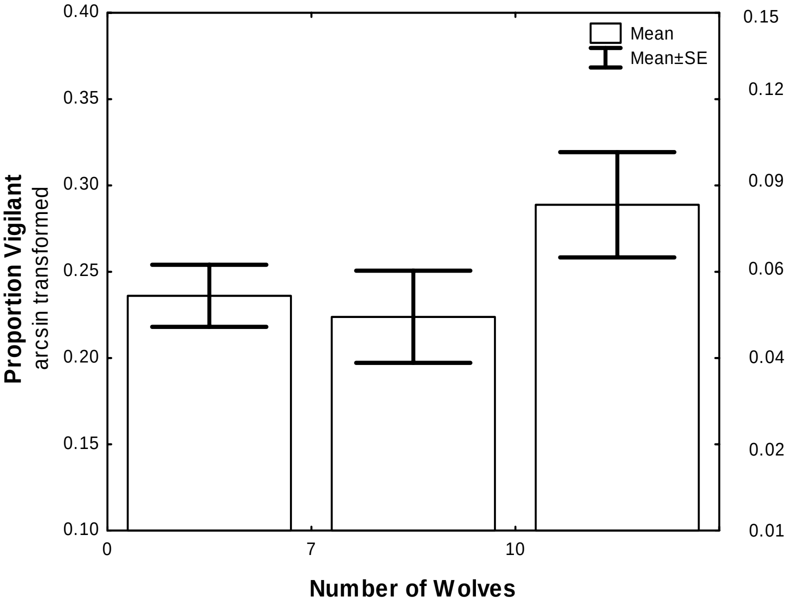
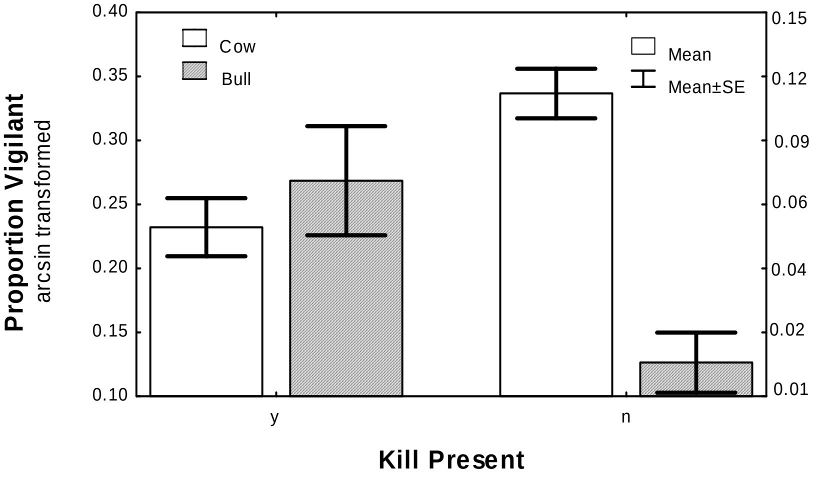


Figure 3. The response of elk vigilance levels to the presence or absence of a kill. Shaded bars represent bull groups and un-shaded bars represent cow groups. Proportion vigilant was arcsin-transformed prior to analysis (Zar 1999). Values on the right y-axis show the back-transformation, for which errors are not symmetric.



Prey (Elk) Variables

Parameters describing characteristics about the elk herd also played an important role in determining vigilance levels. Herd composition had the highest relative importance (RI = 1) (Table 1). Groups including cows (composed of cows, calves, and spikes) had higher vigilance levels than all-bull groups (Figure 4 and Table 2). Vigilance levels also increased when the proportion of calves to cows in the herd increased (Figure 5 and Table 2). The proportions of cows and calves are not fully independent, so these two effects cannot be fully disentangled (Figs. 4 & 5, see percentages within bars). Herd size had a relative importance score of 0.65. Group sizes between 10 and 20 were more vigilant than smaller or larger groups. Once group size exceeded 20 individuals, vigilance levels decreased in a linear fashion (Figure 6 and Tables 1 and 2). Here again, the effect of herd size cannot be fully disentangled from the effect of herd composition. Small groups are often all bulls (Fig. 6, see percentages within bars), and bulls are substantially less vigilant than cows (Winnie and Creel 2007). The other two elk parameters (proportion peripheral and day of year) were less important in determining vigilance levels: both of these variables had low relative importance scores of 0.062 (Appendix A).

Figure 4. The response of elk vigilance levels to the proportion of cows in the group. Percentages within the bars represent the average proportion of the group that was made up of calves. Proportion vigilant was arcsin-transformed prior to analysis (Zar 1999). Values on the right y-axis show the back-transformation, for which errors are not symmetric.

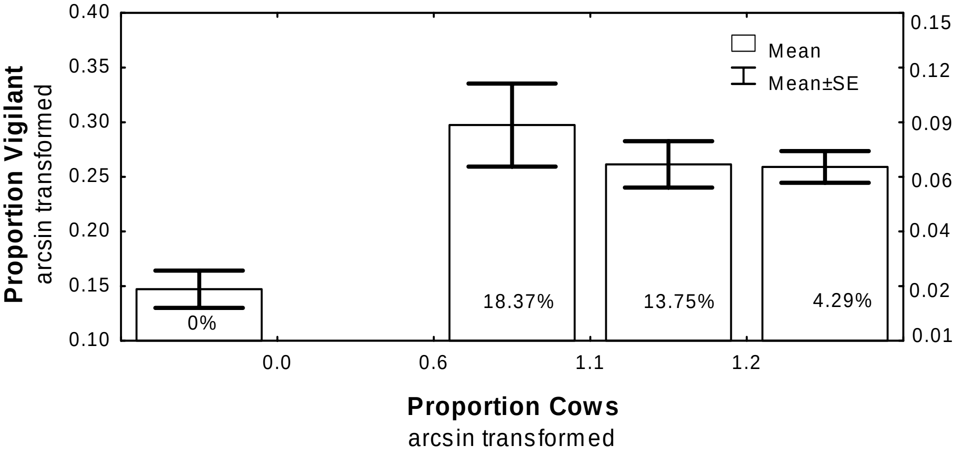


Figure 5. The response of elk vigilance levels to the proportion of the group that was made up of calves. Proportion vigilant was arcsin-transformed prior to analysis (Zar 1999). Values on the right y-axis show the back-transformation, for which errors are not symmetric.

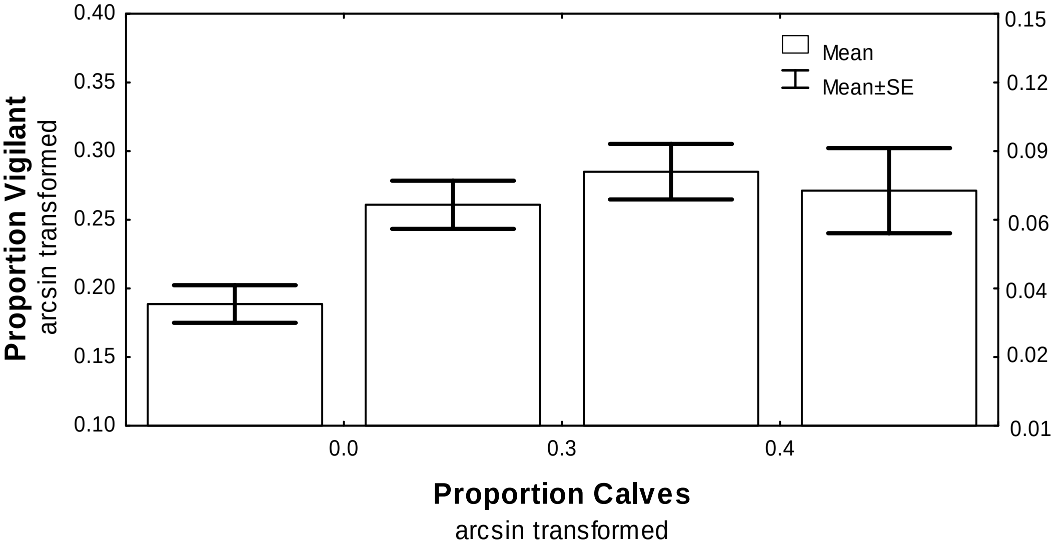
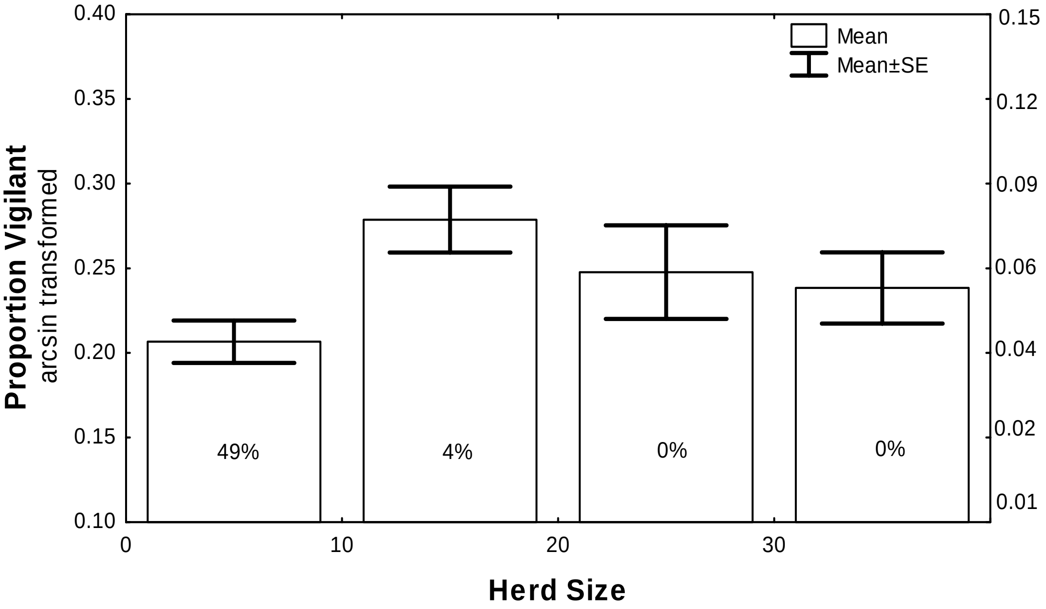


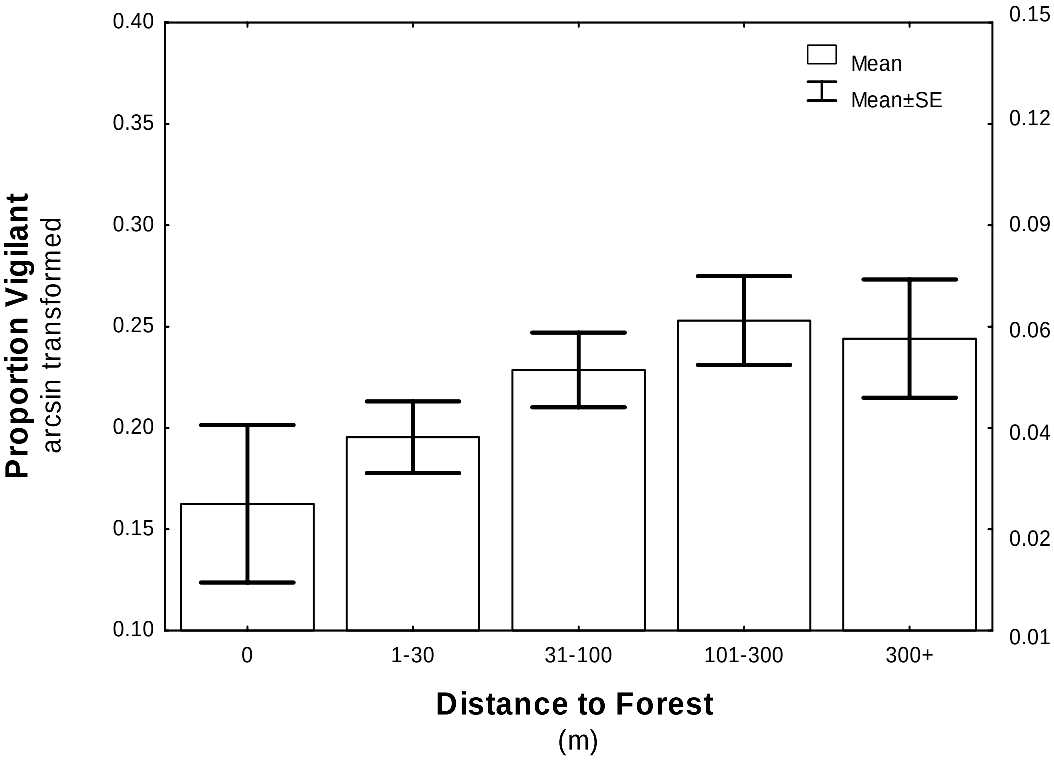
Figure 6. The response of elk vigilance levels to elk herd size. Percentages in the bars represent what proportion of the bars was all bull groups. Proportion vigilant was arcsin-transformed prior to analysis (Zar 1999). Values on the right y-axis show the back-transformation, for which errors are not symmetric.



Environmental Variables

Environmental parameters had a weaker effect, and none of the top models were dominated by environmental variables. However; environmental parameters did appear in some of the best models (Appendix A), and two environmental variables had significant partial regressions on vigilance (Table 2). Distance to forest had the highest relative importance (RI = 0.332, compared to RI = 1 for the top predator and prey variables). The farther elk herds were from protective cover the more vigilant they became. This increase was linear until groups were about 100m from forest, and then appeared to approach and asymptote (Figure 7 and Table 2). Snow depth and density (SWE) had a relative importance value of 0.311 and appeared in two of six models within two AIC units of the best model (Appendix A and Table 1). Vigilance levels decreased as SWE increased (Table 2). Snow cover had the lowest relative importance score (0.168) of all of the environmental parameters, and appeared once in the models within two AIC units of the best model (Appendix A and Table 2). Unlike SWE, as the percent of the landscape that was covered in snow increased, elk vigilance levels tended to increase, though the effect was weak and not significant (Table 2).

Figure 7. The response of elk vigilance levels to how far the elk herd was from forest. Proportion vigilant was arcsin-transformed prior to analysis (Zar 1999). Values on the right y-axis show the back-transformation, for which errors are not symmetric.



Comparison of the Three Subsets of Models

When comparing the performance of the models from each of the three subsets, models from subset one (simple models with independent variables from one of the three categories of variables: predator, prey, or environment) performed the worst (Appendix A: bold table entries indicate the best model in each category). Significant effects on vigilance can be detected with these univariate models (Table 2), but their information content was low in comparison to more complex models. Models from subset two (more complex models containing parameters about predator and prey) performed the best, appearing in two-thirds of the top models (Appendix A). Models from subset three (the most complex models containing parameters about predator, prey, and environment) did not perform as well as models from subset two, but they did represent one-third of the best models (Appendix A).

Discussion

Our results show that elk are sensitive to a suite of variables when allocating time to antipredator vigilance. Vigilance levels are sensitive to characteristics of predators, the structure of the group that is threatened, and the conditions under which the threat arises. Complex models that incorporate all of these features perform better than simpler models. No models that failed to incorporate aspects of both predator and prey had high information content. Including environmental effects improved the models, but environmental effects were less important than predator and prey variables.

The importance of predator variables in determining vigilance levels is one of our most interesting results. If we had simply categorized predators as present or absent, we would have failed to explain substantial variability in vigilance levels that could be predicted by a more complete description of the predators. In our study, elk vigilance levels negatively correlated with distance to wolves at distances up to three kilometers (Figure 1). These data show that elk in the northern range detect and respond to predators within a large area, as they do in the Gallatin Canyon, also in the Greater Yellowstone Ecosystem (Creel et al. 2005; Winnie & Creel 2007). The sensory capabilities of elk are not well-studied (Toweill and Thomas 2002), but our results indicate that they are capable of hearing, seeing or smelling wolves that are not an immediate threat. Whereas most studies of antipredator behavior focus on short-term reactions to real or simulated attacks by predators (Lima 1998), this result suggests that we must also consider the importance of less dramatic but more frequent responses to subtle spatiotemporal variation in risk. Given elk can detect and respond to predators that are several kilometers away, and given the high density of wolves in the Yellowstone ecosystem, it is perhaps not surprising that the demographic costs of behavioral responses to risk are substantial (Creel et al 2007).

Several studies of hunting success have found that as the number of individuals in the predator group increases so does the probability of making a kill (Creel and Creel 1995; Funston et al. 2001 but see Thurber and Peterson 1993; Schmidt and Mech 1997). Despite the apparent importance of predator group size from the perspective of the predator, we have been unable to find any studies that measured how prey respond to this increased threat. It appears that elk in the northern range identify larger pack sizes as a greater risk (Figure 2).

Of all the predator variables, kill presence/absence had the most surprising effects. A priori, we did not have a strong expectation of whether vigilance would increase or decrease in the presence of a fresh kills, and whether a kill indicates safety or danger probably depends on the time scale of the decision. Cow groups appear to treat a recent kill as indicating a period of safety and significantly reduced their vigilance levels, whereas bull groups responded to recent kills by significantly increasing their vigilance levels. We do not have data to explain this difference, although differences in individual condition and vulnerability may be involved (Winnie and Creel 2007).

Cows were more vigilant than bulls in the northern range, as has been shown for elk elsewhere in the Yellowstone ecosystem (Laundre et al. 2001; Childress and Lung 2003; Winnie and Creel 2007). In the Gallatin Canyon portion of the ecosystem, we have shown that bulls enter the winter in significantly worse body condition than cows, so energetic constraints do not allow bulls to allocate as much time to vigilance (Winnie and Creel 2007). Childress and Lung (2003) found that cows with calves were more vigilant than cows without calves, and bulls. Calves are killed more often than expected by chance in YNP (Smith et al. 2004; Creel et al 2007), creating an obvious selection pressure in favor of high vigilance in nursery herds. However, it is worth noting that this logic would also predict higher levels of vigilance for bulls than cows (opposite to our data, as just discussed), because bulls are also killed more often than expected by chance in YNP (Smith et al. 2004; Winnie and Creel 2007).

Elk, like many ungulates, are less vigilant as herd size increases (Underwood 1982; Elgar 1989; Roberts 1996). This decrease in individual vigilance aligns well with Pulliam's (1973) model of 'corporate vigilance'. Herd size is collinear with the proportion of the herd that occupies peripheral positions within a herd. (As herd size increases, more animals can occupy central positions). Because of this collinearity, and because herd size effects are well established in theory (Elgar 1989; Lima 1990), for other species (Roberts 1996), and for elk (Creel and Winnie 2005; Winnie and Creel 2007), we included herd position in only four models.

Vigilance might be more tightly constrained as winter progresses, because body condition declines through the winter (Winnie and Creel 2007). Despite this logic, models that included the day of winter fared relatively poorly, the best being 3.33 AIC_c units worse than the best model. As Winnie and Creel (2007) noted, "[day of winter] is problematic because it is correlated with temperature and snow depth and thus contributes to overdispersion in the models that also contain these variables". Because we considered snow depth (SWE) important and included it in many a priori models, we included day of winter in only three models. *Post hoc* analysis of the correlation matrix showed that day of year and SWE were highly correlated.

The top models, within two AICc units of the best model, always included parameters related to predators and to prey, but included an environmental effect in only a third of the cases. This suggests that vigilance is not well-predicted simply by knowing whether the environmental circumstances are generally risky or safe. Elk adjust vigilance more clearly in response to the group they are in, and the type of immediate threat they are facing from wolves. Environmental variables acted more as modifiers rather than drivers of elk vigilance. Distance to forest, which is closely related to habitat type (open versus closed: see Creel et al. 2005; Winnie et al 2007) appeared in one third of the top models (Appendix A). Based on variation in vigilance, elk in this study system identified forest as a location of safety and open areas as places of danger. This result aligns well with previous results showing that elk adjust herd sizes in response to distance from forest (Creel & Winnie 2005), and that elk move into forested locations when wolves are present (Creel et al. 2005).

As snow water equivalents (SWE) increased, vigilance levels decreased whereas as percent snow cover increased vigilance levels increased (Table 2). SWE and snow cover initially seem likely to be correlated but were not strongly related in our data. SWE was greatest from late March to mid April, and during this period the landscape was rarely covered in 100% snow (approximately 12% of the time). We cannot fully explain the difference between SWE and snow cover in their effects on vigilance. *Post hoc*, it seems possible that high snow cover increases risk and thus promotes vigilance, and deep and/or dense snow conditions make foraging and travel sufficiently difficult and high SWE acts as a constraint on vigilance.

In summary, complex models explain patterns of vigilance in elk better than simple models. While many individual variables play a significant role, univariate models had low information content in comparison to more complex models. From this pattern, we conclude that elk use information of several types when assessing risk and allocating time to vigilance. In particular, predator characteristics were as important as prey characteristics in determining vigilance levels. These results highlight the need to consider information about predators when testing hypotheses about vigilance levels in prey.

CHAPTER 3

CONCLUSION

Summary

When allocating time towards vigilance, elk are sensitive to a suite of variables and no variable by itself will fully explain the patterns seen. The results of this study suggests that field studies examining prey vigilance in response to predators will benefit from treating the predator variable as continuous and not dichotomizing it as predators "present" or "absent". If we had dichotomized the predator variable we would have obtained significant results, however we would have missed a substantial amount of variability in vigilance. As stated by Caro (2005) "treating predation risk as a dichotomous variable (either the predator is in the immediate environment or it is not) raises many problems". How do we define the immediate environment (our perception of immediate environment may be different than that of the prey), and the full span of predation risk lies on a continuum from the predator being completely absent to a predator currently attacking and killing the prey. The results of this study also suggest that investigators should consider a variety of variables (those describing the prey, environment, and predator) and how all these variables interact to determine vigilance levels.

Vigilance historically has been thought of as mutually exclusive with foraging (Underwood 1982; Lima 1998a), and thus likely to carry a cost to the individual who allocates a great deal of time towards vigilance. While this seems plausible our results do not directly rule out the possibility that elk are compensating for lost foraging time. Animals may be able to compensate for reduced intake rate by increasing foraging time, however this conflicts with time allocated towards other activities and may extend the period of time exposed to predators (Illius and Fitzgibbon 1994). We measured time spent vigilant and foraging as a proportion of time observed, and not as a measure of total time spent engaged in each activity. Elk might be compensating for reduced foraging time by increasing foraging bouts or increasing the amount of foraging bouts per day, or both. However, given the low quality and quantity of forage, and the high energetic requirements to obtain forage (elk must paw through the snow) during the winter months, it seems unlikely that elk can completely compensate for the lost foraging time, therefore there are likely to be costs associated with vigilance.

Also we have no data comparing vigilance levels in forest versus open habitats. However, we do know that the closer elk are to forest, vigilance levels fall in a linear fashion. If elk completely forgo vigilance in forest they might use forest as an area to compensate for lost foraging in the open. However, this would require a pattern of foraging that would be unusual for elk, because in a meta-analysis of elk diet preferences, Christianson and Creel (in press) found that elk strongly preferred grazing in open habitats rather than browsing when unconstrained by risk or snow. In a study examining foraging patterns of moose, Edwards (1983) found that cow moose with calves ate significantly more herbs of low preference, and fewer shrubs of high preference, when they confined their movements to islands on Lake Superior that were free from wolves, thus trading safety for a less nutritional diet. Morgantini & Hudson (1985) found that elk shifted away from grazing and increased browsing when exposed to risk from human hunters, then shifted back to a grass-dominated diet when the hunting season ended.

Other factors that were not examined in this study may influence elk vigilance levels, such as differences in responses to wolves in the daytime versus the nighttime, or in the winter versus the summer, and the effects of other predators of elk on their behavior. Because this study was done in the winter months we have no data concerning vigilance levels of elk in the summer. Vigilance levels may differ in the summer for several reasons. First, because forage quality and quantity are greater in the summer, elk do not face as great of an energetic constraint as they due in the winter, and this may allow more time to be allocated towards vigilance. Second, elk are exposed to bears during the summer months and bears are known to prey on elk calves (Gunther and Renkin 1990). Due to the added risk of bear predation and the higher nutritional state of elk they may allocate more time towards vigilance. Vigilance of elk may differ between night and day. Due to logistical constraints we have no data examining vigilance levels at night. The value of vigilance in detecting predators may decrease at night due to low light conditions, however little is known on the sensory capabilities of elk (Toweill and Thomas 2002), and it is not known whether changes in light levels would alter the benefits of vigilance. Cougars are known to prey on elk throughout the winter months and thus pose an added threat to elk that may favor different behaviors than those that reduce the risk of predation by wolves (Murphy 1998). However cougar densities are much lower than wolves, and our results show that elk lower vigilance levels as they move into forested areas where cougar predation is higher (Smith et al. 2003). This suggests that the patterns that we observed are not appreciably altered by the presence of cougars, which is logical, given that wolves impose a much larger predation pressure on elk.

Indirect Influence of Predators on Prey Demography

It has often been argued that not only direct consumption by predators can reduce prey populations, but the mere presence of predators can induce behaviors in prey that affect their population dynamics (Shmitz 1998; Presser et al. 2005). Nelson et al. (2004) showed that the presence of damsel bugs (*Nabis* spp.) can suppress population growth of pea aphids (*Acyrthosiphon pisum*). In this study they surgically manipulated the mouthparts of damsel bugs making them unable to kill the pea aphid. They then monitored pea aphid population growth and found population growth decreased by 30% in the presence of the manipulated damsel bugs compared to controls where no damsel bugs were present. They found that the population decrease was a result of pea aphids altering their foraging behavior in the presence of the damsel bugs. A meta-analysis looking at the effects of predators on prey in 166 species (mostly aquatic insects), found that the indirect effects of predators on prey were generally as strong as the direct consumption effects on prey dynamics (Preisser et al. 2005).

Examples from vertebrates are less common and the results are not as definitive. In a semi-field experiment looking at the effects of a snake predator (*Demansia psammophis*) on its lizard prey (*Lampropholis guichenoti*), Dowens (2001) found that lizards raised in an environment with predator scent were smaller at maturity (body mass and total length), produced smaller clutches, and had offspring of smaller size, than lizards raised with a control scent. Therefore Dowens concluded that the predatory snake was likely to have a negative indirect effect on population dynamics of lizards. Many species of rodents are known to suppress breeding in the presence of predators (Ruxton and Lima 1997). Ylonen (1989) found that bank voles (*Clethrionomys glareolus*) held in an enclosure with a caged weasel (*Mustela nivalis*) significantly reduced their breeding effort. None of the four pairs of voles held in an enclosure with a weasel breed, whereas three of the four pairs of voles held in enclosures without weasels breed. Another example in vertebrates comes from a study examining the effects of human disturbance on elk population growth rate. When human researchers continually disturbed cow elk (approached and displaced the elk) during parturition they found that elk population growth rates went from 7% annually to 0% over a course of two years. However, population growth rates returned to pre-disturbance levels within two years after the disturbance (Shively et al. 2005).

Finally results from our study system have shown that the presence of wolves alone can negatively impact elk demography (Creel et al. 2007). Here we showed that antipredator responses carry costs that were measured by changes in reproduction and demography. We found that pregnancy rates (measured by fecal progesterone) were associated with a elk:wolf ratio. The lowest pregnancy rates were found in elk that had the highest wolf predation pressure, and this in turn lead to the lowest cow:calf ratio (6:100) recorded for that site in 20 years over a 57 year period. In areas where wolves were less common, mean progesterone levels were higher, and cow:calf ratios exceeded 30:100. The above results from both invertebrates and vertebrates show that predators can negatively impact prey populations by direct consumption, but also through indirect effects which in turn can substantially influence prey populations. Repeated analyses of elk dynamics in northern Yellowstone have shown that calf recruitment is an important driver of population dynamics (Houston 1982, Singer et al 1997, Taper & Gogan 2002).

The successful reintroduction of wolves into Yellowstone National park is one of conservation's greatest achievements. This had lead to many studies examining the effects of a top predator on its prey populations, all the way down to the plant community. While we have gained a lot of understanding on specific behavioral responses of elk due to predation pressure from wolves, there is still a lot to be known on what effect these behaviors might have. Some researchers have speculated that wolves had modified elk behavior in ways that allowed the aspen and willow communities to rebound (Ripple and Larsen 2000; Ripple and Beschta 2003, 2004). While this may be true other factors might have allowed this rebound. In the areas where this research has been preformed elk densities have declined substantially since the reintroduction of wolves. In the northern range of YNP Elk densities have gone from 17,000 in 1995 (White and Garrott 2005) to approximately 6,700 in 2006 (US Fish and Wildlife Service Gray Wolf Recovery Web Site). Less elk could mean reduced intraspecific competition for the preferred forage (grass) and lead to less browsing. Another factor that could be complicating the picture is climate. If climate during post-wolf reintroduction has lead to less snow pack on winter ranges, available grass may have become more common and this could also result in less browsing, due to the fact that elk prefer grass to browse (Christianson and Creel in press). To gain a better understanding of the effect of wolves on elk, and potentially other organisms in YNP, researchers must look at finer spatial and temporal scales. We have been able to show that elk can adjust their behavior on time scales of days to perhaps hours, and on spatial scales of less than a kilometer (Liley and Creel in review; Winnie and Creel 2007; Winnie et al. 2006; Creel et al. 2005).

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APPENDICES

APPENDIX A

MODEL PARAMETERS IN *A PRIORI* MODEL LIST

Parameters in each of the models, with AICc score, ΔAICc, and Akaike weights. The *Model Type* column identifies the type of variables included in the model (EL = prey variables, W = predator variables, EN = environmental variables). Bold entries indicate the best model with variables from only one of the three categories (predator, prey, or environment). The order of variables (1-9) within a single model

Model Type	Model #	Var 1[a]	Var 2	Var 3	Var 4	Var 5	Var 6	Var 7	Var 8	Var 9	DF	k	AICc	ΔAIC	weight
EL and W	1	# Wolves	Pro. Cow	Pro. Calves	Herd Size	Dist. to Wolves					5	6	-124.9252	0	0.1989298
EL, W, and EN	2	SWE	# Wolves	Pro. Cow	Pro. Calves	Herd Size	Dist. to Wolves	Dist. to Forest	Kill Pres./Abs.		11	12	-124.4097	0.51543	0.1537357
EL, W, and EN	3	SWE	Snow Cover	Pro. Cow	Pro. Calves	Dist. to Wolves	Dist. to Forest				9	10	-123.7067	1.21845	0.1081725
EL and W	4	# Wolves	Pro. Cow	Pro. Calves	Herd Size	Dist. to Wolves	Kill Pres./Asb.				6	7	-123.5308	1.39441	0.0990623
EL and W	5	# Wolves	Pro. Cow	Pro. Calves	Dist. to wolves	Kill Pres./Abs.					5	6	-123.4986	1.42655	0.0974827
EL and W	6	Pro. Cow	Pro. Calves	Dist. to Wolves							3	4	-123.0653	1.85986	0.078494
EL and W	7	Pro. Cow	Pro. Calves	Herd Size	Dist. to Wolves						4	5	-122.4168	2.50841	0.0567551
EL, W, and EN	8	SWE	Snow Cover	# Wolves	Pro. Cow	Pro Calves	Herd Size	Dist. to Wolves	Dist. to Forest	Kill Pres./Abs.	12	13	-122.1399	2.78528	0.049418
EL and W	9	Pro Cow	Pro Calves	Dist. to Wolves	Kill Pres./Abs.						4	5	-121.9628	2.96235	0.0452307
EL and W	10	Day of Year	# Wolves	Pro. Cow	Pro. Calves	Herd Size	Dist. to Wolves	Pro. Peripheral	Kill Pres./Abs.		8	9	-121.5925	3.33264	0.037586
EL and W	11	Pro. Cow	Pro. Calves	Herd Size	Dist. to Wolves	Kill Pres./Abs.					5	6	-121.0922	3.83298	0.029267
EL and W	12	Day of Year	Pro. Cow	Pro. Calves	Herd Size	Dist. to Wolves	Pro. Peripheral				6	7	-120.8013	4.1239	0.025305
EL, W, and EN	13	Pro. Cow	Pro. Calves	Dist. to Wolves	Dist. to Forest						7	8	-118.9905	5.9347	0.0102329
EL, W, and EN	14	Snow Cover	Pro. Cow	Pro. Calves	Dist. to Wolves	Dist. to Forest					8	9	-118.9601	5.96509	0.0100785
EL and W	15	# Wolves	Pro. Cow	Pro. Calves							3	4	-109.0229	15.9023	7.007E-05
EL	16	**Pro. Cow**	**Pro. Calves**								2	3	-108.7761	16.1491	6.194E-05
EL	17	Pro. Cow	Pro. Calves	Herd Size							3	4	-108.5755	16.3496	5.603E-05
EL	18	Day of Year	Pro. Cow	Pro. Calves	Herd Size	Pro. Peripheral					5	6	-107.3868	17.5383	3.092E-05
EL and W	19	Pro. Cow	Pro. Calves	Kill Pres./Abs.							3	4	-107.3693	17.5559	3.065E-05
W	20	**Dist.to Wolves**									1	2	-95.43222	29.493	7.841E-08
EL and W	21	Herd Size	Dist. to Wolves								2	3	-94.86785	30.0573	5.913E-08

Model Parameters in *a priori* Model List Continued

W	22	Dist. to Wolves	Kill Pres./Abs.				2	3	-93.55102	31.3742	3.061E-08
EL, W, and EN	23	SWE	Snow Cover	Herd Size	Dist.to Wolves	Dist. to Timber	8	9	-93.20633	31.7188	2.577E-08
W	24	# Wolves	Dist. to Wolves	Kill Pres./Abs.			3	4	-92.95185	31.9733	2.269E-08
EL and W	25	# Wolves	Herd Size	Dist. to Wolves	Kill Pres./Abs.		4	5	-92.23736	32.6878	1.587E-08
EL, W, and EN	26	Snow Cover	Herd Size	Dis. to Wolves	Dist. to Timber		7	8	-91.7218	33.2034	1.227E-08
EL, W, and EN	27	Herd Size	Dist. to Wolves	Dist. to Timber			6	7	-91.56118	33.364	1.132E-08
EL	28	Pro. Peripheral					1	2	-89.61185	35.3133	4.271E-09
W	29	# Wolves					1	2	-88.14781	36.7774	2.054E-09
EL	30	Herd Size					1	2	-87.98739	36.9378	1.896E-09
EL	31	Day of Year					1	2	-87.98295	36.9422	1.891E-09
EN	32	**SWE**					1	2	-87.54038	37.3848	1.516E-09
W	33	Kill Pres./Abs.					1	2	-87.31781	37.6074	1.356E-09
EN	34	Snow Cover					1	2	-87.18497	37.7402	1.269E-09
EL and W	35	# Wolves	Herd Size				2	3	-86.7554	38.1698	1.024E-09
EL and W	36	Herd Size	kill present				2	3	-86.15941	38.7658	7.6E-10
EN	37	Dist. to Timber					4	5	-84.7106	40.2146	3.683E-10
EN	38	SWE	Snow Cover	Dist. to Timber			6	7	-81.59585	43.3293	7.76E-11

APPENDIX B

DEPENDENT AND INDEPENDENT VARIABLES INCLUDED IN THE *A PRIORI* MODELS

Dependent and Independent variables

Dependent	**Independent**
Proportion Vigilant	Day of year
	Proportion Cow
	Proportion Calf
	Herd Size
	Pro. Peripheral
	Distance to Wolves
	# of Wolves
	Kill Present/Absent
	Distance to Forest
	% Snow Cover
	SWE