

BEHAVIORAL RESPONSES OF ELK (*Cervus elaphus*) TO
THE THREAT OF WOLF (*Canus lupus*) PREDATION

by

John Arthur Winnie, Jr.

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

of

Doctor of Philosophy

in

Biological Sciences

Montana State University
Bozeman, Montana

April, 2006

© Copyright

by

John Arthur Winnie, Jr.

2006

All rights reserved

APPROVAL

of a dissertation submitted by

John Arthur Winnie, Jr.

This dissertation has been read by each member of the dissertation 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.

Dr. Scott Creel

Approval for the Department of Ecology

Dr. David Roberts

Approval for the Division of Graduate Education

Dr. Joseph J. Fedock

STATEMENT OF PERMISSION TO USE

In presenting this dissertation in partial fulfillment of the requirements for a doctoral degree at Montana State University, I agree that the Library shall make it available to borrowers under rules of the Library. I further agree that copying of this dissertation is allowable only for scholarly purposes, consistent with "fair use" as prescribed in the U.S. Copyright Law. Requests for extensive copying or reproduction of this dissertation should be referred to ProQuest Information and Learning, 300 North Zeeb Road, Ann Arbor, Michigan 48106, to whom I have granted "the exclusive right to reproduce and distribute my dissertation in and from microform along with the non-exclusive right to reproduce and distribute my abstract in any format in whole or in part."

John Arthur Winnie, Jr.

April, 2006

TABLE OF CONTENTS

LIST OF TABLES	vi
LIST OF FIGURES	vii
1. BEHAVIORAL RESPONSES OF ELK TO THE THREAT OF WOLF PREDATION: INTRODUCTION	1
2. BEHAVIORAL RESPONSES OF ELK TO THE THREAT OF WOLF PREDATION: SEX SPECIFIC CONSTRAINTS.....	4
Abstract.....	4
Introduction	5
Methods.....	11
Study Area	11
Wolves	12
Determining Wolf Presence and Temporal Variation in Predation Risk.....	12
Elk.....	13
Elk Distributions, Herd Sizes and Herd Compositions	14
Elk Behavior.....	16
Kill Locations and Carcass Marrow Fat Determination	18
Statistical Methods.....	19
Results.....	22
Herd Dynamics and Distributions.....	22
Marrow Fat and Predation Risk.....	24
Moving, Bedding and Other Behavior	26
Vigilance and Grazing Behavior	27
Discussion	30
3. RULES FOR HABITAT SELECTION BY ELK ARE SIMPLIFIED BY THE PRESENCE OF WOLVES.....	39
Abstract.....	39
Introduction	40
Methods.....	43
Study Area	43
Elk.....	44
Wolves	45
Habitat Composition at Elk Locations	46

TABLE OF CONTENTS continued

Environmental Variables	48
Statistical Analysis	49
Independent Variables	51
Results and Discussion	53
4. SUMMARY AND SOME CAVEATS	61
Summary	61
Trophic Cascades.....	63
Influences of indirect Costs on Prey Population Dynamics.....	66
REFERENCES CITED	68
APPENDIX A: Model Parameters in Best Models	76

LIST OF TABLES

Table	Page
1.1. Herd size changes in relation to wolf presence	24
1.2 Associations between elk behavior and sex, location, position within herd, and wolf presence. Part b presents an analysis separate from the main factorial ANOVA, addressing the effects of distance to timber	27
2.1. Habitat attributes of elk GPS locations with wolves present and absent, and global model goodness-of-fit.....	54
2.2. Coefficients and their standard errors from model averaging using AICc weights (ω_i).....	57
2.3. Relative importance values from AICc.....	57

LIST OF FIGURES

Figure	Page
1.1. Effect of wolf presence on the distance between elk herds and woodland edges (protective cover).....	23
1.2. Sex differences and winter changes in physical condition, as measured by femur marrow fat concentration.	25
1.3. Vigilance differences between the sexes in behavioral responses to the presence of wolves.....	29
1.4. Grazing differences between the sexes in behavioral responses to the presence of wolves.....	29
2.1 Summary of the best models of habitat selection by elk.....	56

CHAPTER 1

BEHAVIORAL RESPONSES OF ELK TO
THE THREAT OF WOLF PREDATIONIntroduction

The effects of predators on prey population dynamics have traditionally been viewed, and modeled, as direct offtake (Lotka 1925; Bergerud and Elliot 1986, 1998; Berryman 1992; Boyce 1993; Hayes and Harestad 2000). However, prey respond to the mere threat of predation risk and these responses carry costs (Morgantini & Hudson 1979, 1985; Werner et al. 1983; Lima and Dill 1990; Illius and Fitzgibbon 1994; Abramsky et al. 1996). Prey responses to predation threat range from shifts in habitat use with associated reductions in food quality or quantity (Morgantini & Hudson 1979, 1985; Heithaus & Dill 2002), to changes in individual and grouping behaviors that reduce feeding rates or locally increase intraspecific competition for food (Elgar 1989; Roberts 1996).

Because most prey (not just those individuals about to be killed by predators) respond to the threat of predation, the costs of risk reduction are likely to manifest themselves at both the individual and the population level, and may even exceed direct offtake (Ives and Dobson 1987; Bolnick and Preisser 2005). Differences between individual prey in behavioral responses that can be attributed to differences in physiological constraints will give an indication of the costs associated with antipredator behaviors. If these costs are sufficiently large

in terrestrial vertebrates, then efforts should be made to incorporate them into future models of predator-prey interactions. The following work addresses elk behavioral responses to the threat of wolf predation, responses that are likely to carry costs, and singly or in concert, manifest themselves through changes in elk population dynamics.

Each of the two main sections are papers currently in review, and both are continuations of work already published (Creel and Winnie 2005, Creel et al 2005). There is some overlap in the introductions and methods sections and each section has its own abstract. Because of this, the main sections (chapters 2 and 3) can be read as stand-alone works, or viewed as part of the larger body of work.

The first main section, *Sex-specific behavioral responses of elk to spatial and temporal variation in the threat of wolf predation*, addresses elk anti-predator behavior at the scale of individual behaviors (time budgets), and landscapes (distribution within a drainage). We found sex specific behavioral responses to threat that appear to be constrained by body condition, implying that antipredator behaviors carry caloric costs. In addition to these results, the dichotomy between cow and bull behavior lends insights into the mechanisms driving sexual segregation in elk, and here we propose a simple explanation for this phenomenon.

The second main section, *Rules for Habitat Selection by Elk are Simplified by the Presence of Wolves*, compares elk decision making processes during high versus low risk periods. Although this chapter addresses habitat use decisions, it

does not directly deal with landscape level issues. Rather, it investigates the environmental variables that elk respond to when making habitat use decisions. The results from this section point to constraints on the elk decision making process that possibly reducing elk foraging and movement efficiency when wolves are present in a drainage. As such, this section addresses subtle, and heretofore undressed, costs associated with predator avoidance.

Throughout a manuscript I use the term “we” because the work involved extensive collaboration between myself, my advisor Dr. Scott Creel, fellow graduate student David Christianson, and Dr. Bruce Maxwell and his students and lab personnel in the LRES department at Montana State University.

CHAPTER 2

SEX-SPECIFIC BEHAVIORAL RESPONSES OF ELK TO SPATIAL AND
TEMPORAL VARIATION IN THE THREAT OF WOLF PREDATIONAbstract

We studied individual and herd level behavioral responses of elk to spatial and temporal variation in the risk of predation by wolves over three winters in the Upper Gallatin drainage, Montana. Within a given drainage, elk of both sexes moved into or closer to protective cover (timber) in response to wolf presence. Cow elk responded to elevated risk by increasing vigilance in exchange for foraging, and large mixed (cow, calf, spike) herds substantially decreased in size. In contrast, when wolves were present, bulls did not increase vigilance levels, nor decrease feeding, and small bull-only groups slightly increased in size. As a consequence, small bull-only herds and large mixed sex herds converged on a similar size when wolves were present. We believe this response is a balancing of the benefits of risk dilution with increased detectability or attractiveness of larger herds to wolves. Based on proportions in the population, wolves overselected bulls and underselected cows as prey. Thus, bulls showed weaker antipredator responses than cows, despite facing a greater risk of predation. Using marrow fat content from elk killed by wolves as an indicator of body condition, bulls were in significantly worse body condition than cows throughout the winter, and condition deteriorated for both sexes as winter progressed.

Overall, we conclude that: anti-predator behaviors carry substantial foraging costs; bulls, due to their poorer body condition, are less able to pay these costs than cows; and differences in ability to pay foraging costs likely explain sex specific differences in anti-predator behaviors.

Introduction

Anti-predator behavior is well documented across a wide variety of taxa, at many spatial and temporal scales. At relatively broad scales, prey often alter their use of habitats in response to predation risk, trading security for a reduction in forage quality, quantity, or both. Bottlenose dolphins (*Tursiops aduncus*) avoid shallow, productive foraging areas during seasons when tiger sharks (*Galeocerdo cuvier*) are present, but favor these areas when sharks are absent (Heithaus & Dill 2002). Elk (*Cervus elaphus*) move out of open grassy habitats into less nutritionally profitable closed, forested habitats during human hunting seasons (Morgantini & Hudson 1985). When faced with the threat of predation by trained barn owls (*Tyto alba*), desert gerbils (*Gerbillus allenbyi* and *G. pyramidum*) limit their foraging activity and avoid open areas, foraging under cover in brushy habitats (Abramsky et al. 1996). In experimental studies, the presence of predatory large mouth bass (*Micropterus salmoides*) limited small bluegill sunfish (*Lepomis macrochirus*) to vegetated habitats near shore, significantly reducing their growth rate (Werner et al. 1983).

At finer temporal and spatial scales, prey often alter their behavior in response to changes in predation risk. Among the most studied of these

responses are changes in vigilance levels, group formation, and interactions between the two (Elgar 1989; Lima & Dill 1990; Roberts 1996). Individuals may increase vigilance in response to elevated threat, and as with habitat shifts, this response often carries a foraging cost, typically paid with a reduction in foraging time (Jennings & Evans 1980; Underwood 1982; Berger & Cunningham 1988; Lima 1998; Abramsky et al. 2002).

Prey may benefit by grouping through multiple mechanisms, which may interact: collective vigilance (Pulliam 1973; Powell 1974; Kenward 1978; Roberts, 1996); confusion of attacking predators or cooperative defense (Cresswell 1994; Krause & Godin 1995); dilution of individual risk (Lima & Dill 1990; Cresswell 1994); and attack abatement (Turner & Pitcher 1986; Uetz & Hieber 1994). Individual vigilance levels often decline with increasing group size, which implies that prey do indeed perceive themselves as safer in larger groups (Roberts 1996; but see Elgar 1989, for a critical review).

The benefits of grouping are reduced (and potentially reversed) if predators can detect large groups more easily, or prefer to attack them. Several authors have reported that larger groups are more often detected and attacked, but some have shown that despite this - and sometimes despite higher predator success when attacking large groups - individual prey in larger groups are still safer, due to offsetting benefits of dilution (Creel & Creel 2002; Hebblewhite & Pletscher 2002), collective detection or cooperation in escape (Krause & Godin 1995), or combinations of these effects (Cresswell 1994; Uetz & Hieber 1994).

Predation risk varies in space and time. In the absence of constraints, prey would respond to risk and minimize predation rates in all places at all times. However, anti-predator behaviors commonly carry foraging costs (Lima & Dill 1990; Lima, 1998), and when prey must exchange food for security, constraints on both foraging and antipredator behaviors are inevitable. Constraints vary among individuals depending on nutritional status, and vulnerability to predation should similarly vary (Lima & Dill 1990; Sinclair & Arcese 1995; Lima 1998). Consequently, an individual's physical condition is likely to affect its behavioral response to variation in risk. Nutritionally compromised individuals should be less responsive if they are unable to pay the costs associated with reducing predation risk (Bachman 1993; Lima 1996). Notably, despite the widespread assumption that elevated vigilance confers greater security, few studies have directly shown higher predator attack rates upon, or higher mortality rates for, individuals displaying lower vigilance (but see Fitzgibbon 1988, 1990; and Scheel 1993 for a comparison of species).

Differences in behavioral responses that can be attributed to differences in physiological constraints will give an indication of the costs associated with antipredator behaviors. Because most prey (not just those individuals about to be killed by predators) respond to the threat of predation, the costs of risk reduction are likely to manifest themselves at both the individual and the population level, and may even exceed direct offtake (Ives and Dobson 1987; Bolnick and Preisser 2005). If these costs are sufficiently large in terrestrial

vertebrates, then efforts should be made to incorporate them into future models of predator-prey interactions.

We know of no field studies that have attempted to directly assess behavioral responses of prey to interactions between body condition, spatial variation in risk, and temporal variation in risk. This is particularly true for studies in which true predation risk varied naturally across space and through time, rather than using simulated risk or experimentally controlled predation. Here we examine the vigilance, grouping and cover seeking responses of elk (*Cervus elaphus*) to fine scale variations in both spatial (distance to protective cover [timbered areas], position in herd) and temporal (wolf [*Canis lupus*] presence) risk, and further ask how these behaviors are constrained by prey physical condition.

Because it was not possible to sample physical condition for the general elk population, we compared the behavior of two classes that prior research indicates are under different energetic constraints through winter: bulls (branch antlered males with brow tines) and cows (females > 1 year old). Bull elk enter winter weakened by the fall rut, having lost as much as 20% of their pre-rut (August) body mass by mid-November, and continue to lose weight more rapidly than cows throughout the winter (Anderson et al. 1972; Mitchell et al. 1976; Geist 2002; Hudson et al. 2002). In contrast, cow elk typically lose less than 10% of their body mass between August and May, ending most winters with proportionally less weight loss than bulls experience prior to winter's onset. It should be noted that in most populations over 80% of cows are pregnant each

winter, and a cow's spring weight includes that of her developing fetus - so most cows' personal over winter weight losses are greater than 10%. However, fetus growth is approximately exponential, with the majority of fetal weight gain occurring in the spring, so cow weight loss is typically low for most of winter (Hudson et al. 2002; Geist 2002; Cook et al. 2004). Here we attempt to confirm differences in body condition by comparing the bone marrow of wolf-killed bulls and wolf-killed cows. The chief limitation to this approach is that wolf-killed elk do not represent a random sample of the population at large. We do not assume in our analyses that marrow fat is the same in the sample of killed animals as in the general population. We do assume that any differences in condition between live elk and wolf killed elk are the same for males and females. In other words, the data force an assumption that loss of body condition would increase the risk of predation in the same manner for cows and bulls.

We tested the hypotheses that:

1. Vigilance levels for elk would increase when wolves were present, for both sexes (i.e. elk are sensitive to short term temporal variation in risk).
2. Vigilance would decrease with increasing group size (assuming that elk find greater security in larger groups).
3. Vigilance would increase with distance to timber (i.e. elk are sensitive to fine-scale spatial variation in risk). Here we assume that elk perceive timber as protective cover, because we have previously used the distribution of kill sites to show that risk increases with distance to timber (Creel & Winnie 2005).

4. Vigilance is higher on the periphery of herds since these animals might be the first to encounter attacking wolves (Jennings & Evans 1980; Berger & Cunningham 1988; Fitzgibbon 1990).
- 5A. Bulls in our study area would display a *greater* increase in vigilance than cows when wolves were present. Several studies of wolf-ungulate interactions have found that males are preferentially selected by wolves in winter (Kolenosky 1972; Huggard 1993; Mech et al. 2001). Our evaluation of this hypothesis includes testing whether or not bulls are preferentially preyed upon in this population. For this hypothesis we assume variation in risk is the primary driver of variation in vigilance in elk.
- 5B. In direct opposition to hypothesis 5A, bulls would show a *smaller* increase in vigilance if they were in poorer condition than cows, when wolves were present. Our evaluation of this hypothesis includes testing whether bulls are in poorer condition than cows in this population. For this hypothesis we assume that variation in constraints is the primary driver of variation in vigilance in elk.

Evaluating hypotheses 5A and 5B constitutes a test of the relative strengths of predation risk and foraging costs, in their effects on elk behavior. A priori, it is difficult to know whether variation in antipredator responses will be more closely associated with variation in risk, or with variation in the costs of response. Logic cannot resolve this question: it must be addressed empirically.

Methods

Study Area

Our study area covers 125.8 km² in four drainages along the upper Gallatin River (Porcupine [30.3 km²], Taylor [56.0 km²], Tepee [13.1 km²] and Daly [26.4 km²]), on a combination of National Forest, National Park, State, and private land. South-facing slopes and valley bottoms are generally a mixture of open sage (*Artemisia spp.*) and grassland (dominated by Idaho fescue *Festuca idahoensis* and bluebunch wheatgrass *Agropyron spicatum*) with riparian areas bordering small creeks and the upper Gallatin River. North-facing slopes and higher elevations are primarily coniferous forest (lodgepole pine and Douglas fir: *Pinus contorta* & *Pseudotsuga menziessii*) broken by occasional small meadows. Elevation runs from 1975 m to 2432 m above sea level.

Two properties of the upper Gallatin drainage provided good conditions with which to test our hypotheses. First, a short growing season and harsh winters mean that elk face energetically difficult conditions that produce notable differences between cows and bulls during the winter study season (see Results). Second, wolves enter and leave each of the four drainages many times per winter, creating substantial variation in predation pressure within and among drainages.

The data analyzed here were collected during periods that elk were on their winter range, beginning around January 1 each year and ending at melt out in late May or early June over three winters (2001 - 2003).

Wolves

Wolves colonized the study area in 1997. During the study, we had 1, 3, and 2 packs per year using the study area. The total number of wolves using the study area each year ranged from 12 to 16. The Chief Joseph pack's territory overlapped most of the Tepee, Daly and Taylor drainages, plus extensive areas inside Yellowstone National Park that were outside of the study area. Frequent movements of the Chief Joseph pack on and off the study site produced substantial short-term variation in predation risk. This pack held 12, 7 and 12 wolves in the winters of 2000-01, 2001-02 and 2002-03, respectively and denned in the Daly Creek drainage each spring. Two smaller packs attempted to den in the study area, one in Porcupine (2001), which apparently failed, and the other in the Taylor Fork drainage (2002 and 2003). The Taylor Fork wolves (Sentinel pack) successfully bred both years, producing ≥ 3 pups both years.

Determining Wolf Presence and Temporal Variation in Predation Risk

While walking fixed transect routes, and during daily visits to drainages, we continuously checked for signs that wolves were present within a drainage on that day. We considered wolves present within a drainage if we located them via VHF radiotelemetry, found a fresh kill, fresh scat, or fresh tracks in snow, mud or

loose soil. The number of radiocollared wolves in the study area varied within and between years due to mortality and dispersal. In the Chief Joseph pack, 0-6 wolves carried radiocollars. In the Sentinel pack, 0-2 carried radiocollars, and no wolves were collared in the short-lived pack in the Porcupine drainage. If wolves denned in a drainage (typically near April 15th), we scored all days during the denning period as having wolves present. Because not all wolves in the study area were radiocollared and we undoubtedly missed some physical evidence of their presence, it is likely that we failed to detect wolves on some days. This classification is conservative – failure to detect wolf presence might mask responses by elk to wolves (Type II errors), but should not create apparent differences where none exist (Type I errors).

Elk

Elk in the study area are part of a seasonally migratory population (averaging 1725 ± 63 SE: minimum and maximum counts of 1214 and 3028 since 1928) that winters along the tributaries of the upper Gallatin River from the northwest corner of Yellowstone National Park, north to Big Sky, Montana. Summer range for most of the population is at higher elevations within western Yellowstone National Park. The migration route and winter range have changed little over the past 75 years (Brazda 1953; Peek et al. 1967; Peek & Lovaas 1968; Winnie & Creel unpublished data).

Most elk herds were small (mean = 13.9 ± 0.67 SE, max = 253 elk: ground counts of 1143 herds in winter) and concentrated in the four study area drainages, avoiding the steep, rocky terrain typical of the rest of the region. Based on VHF radio telemetry and GPS telemetry data, elk rarely moved between drainages during the study period (20,400 fixes from 47 individuals over 2 years).

Moose (*Alces alces*), mule deer (*Odocoileus hemionus*) and white tailed deer (*Odocoileus virginianus*) were present in the study area at low densities. Elk comprised more than 90% of our ungulate observations, and more than 90% of wolf kills we detected were elk (Creel & Winnie 2005).

Elk Distributions, Herd Sizes and Herd Compositions

Within every two-week interval from mid- January until the end of May, we surveyed fixed areas (viewsheds) in each of the four drainages, beginning at first light. Survey routes were chosen to maximize the area scanned in each drainage while minimizing disturbance caused by our presence. During a survey we scanned from fixed highpoints, using a tripod mounted 40-56X Nikon ED spotting scope, and used 10X binoculars while moving between highpoints. Each drainage was divided into 6-8 fixed zones, based upon viewsheds. Even though these are not comprehensive counts of all elk within a drainage, we refer to these bi-weekly counts as censuses. In addition to this formal sampling regimen, we attempted to visit each drainage on every day of the winter-spring study period, in either the morning or evening, usually traversing part of our fixed

sampling routes. These ad-lib samples provided additional information on herd sizes and compositions, and wolf presence.

Upon sighting elk we noted the following: UTM location; herd size; composition (calves [young of the year, either sex], bulls [adult males with brow tines], cows [females > 1 year old], spikes [one year-old antlered males with no brow tine and usually no branching], and unknown); distance to timber in four classes (0-30 m, 31-100 m, 101-300 m, and 301+ m); primary activity (vigilant, grazing, moving, bedded, other); and habitat type (timber, grass, riparian, sage, combinations, other). Over three winters, we recorded these data for 1143 elk herds.

We regularly checked among observers (three individuals) for agreement on calf classification and our assessments were consistent. Our criteria as to what constituted separate herds were also tested and consistent. Rather than apply a simple rule to define herd membership (i.e. all elk within 5 body lengths of each other comprise a herd), we chose to let elk behavior define herds. Early in the study, we made preliminary observations and developed the following criteria to define herds as groups that behave as discrete units: inter-elk spacing tends to be consistent within herds; individuals tend to be oriented and moving in the same direction; individuals tend to move at the same speed within herds or to be simultaneously stationary; and large gaps that well exceeded intra-group spacing defined separate groups. Using this definition, most herds of 2 or more elk (732 out of 992) had mean intra-group spacing of 5 body lengths or less. Small, widely scattered herds typify the Gallatin population (mean herd size =

13.9 elk, SE = 0.67, maximum = 253; median distance between observed herds = 1.40 km, mean = 1.66 km, SE = 47.5 m) – inter-herd distances were two to three orders of magnitude greater than intra-herd spacing for most (74%) herds.

In our demographic classifications, we did not combine spikes (yearling males) with bulls, because of important behavioral and physiological differences. Bulls often segregate themselves from cow-calf herds, while spikes usually do not. Spikes rarely breed, and consequently avoid the energetic costs of rutting and concomitant survival costs later in the winter (Geist 2002). We did not distinguish yearling cows from older cows. Yearling cows often breed, placing them under similar energetic constraints to older cows (Cook et al., 2004). Moreover, we could not reliably distinguish yearlings and older cows under field conditions.

We estimated herd distances to timber in the field using a combination of GPS fixes and USGS topographic maps rather than using GIS, because ground truthing of US Forest Service raster maps of habitat types revealed that locations of habitat edges were often not accurate.

Elk Behavior

We gathered behavioral data in every two-week period in each of the 4 drainages from mid-January to the end of May, in 2002 and 2003. To avoid affecting the animals' behavior, we made observations at distances of approximately 0.5 to 2 km through spotting scopes or binoculars. If a herd retreated from observers or showed other signs of being affected by our

presence (such as vigilance directed towards us), or if it became apparent that we were mis-classifying the herd due to terrain features that hid some individuals from us for part of the session, we stopped observations and discarded the entire session's data. In addition to the following behavioral data, we recorded all of the data described above in *Elk Distributions, Herd Sizes and Compositions*.

We used instantaneous scan sampling, which provides an accurate and unbiased measure of the proportion of time spent engaged in each behavior (Altmann 1974; Hanson et al. 1993; MacDonald et al. 2000). At five minute interval, for a minimum of six and a maximum of 13 intervals, we scanned through herds noting: sex and age (cow, calf, bull, spike, unknown); position within the herd (peripheral or interior); and behavior (grazing, moving, vigilant, bedded, other) of every animal in the herd.

We defined interior animals as those that a predator from outside the herd could not approach without first encountering another herd member. Peripheral animals were those individuals that could first be encountered by a predator that approached from outside the herd. We classified a set of mutually exclusive behaviors as follows: *Grazing* animals were those standing with their heads down in forage or a hoofed-out crater in snow; *Moving* animals were either walking or running; *Vigilant* animals were standing or bedded (see note below), head erect, with ears cocked forward in the direction of gaze; *Bedded* animals were lying down, often ruminating, and rarely, sleeping; *Other* includes relatively infrequent behaviors such as grooming or sparring. We collected behavioral data on 88 herds, and logged 11,287 instantaneous individual behaviors. A note regarding

vigilance: As with many African ungulates (Underwood 1982), elk vigilance is performed to the exclusion of foraging – even if an elk has a mouth full of food, it normally stops chewing while vigilant. Moreover, elk feeding behavior is not limited to grazing and browsing, but also includes extended periods of rumination that are essential and often performed while bedded (Cook 2002). Because time spent vigilant while bedded interrupts rumination, it is likely to carry nutritional costs, so we pooled animals that were vigilant while bedded with other vigilant animals.

Kill Locations and Carcass Marrow Fat Determination

We located wolf kills using a combination of techniques: scanning for signs of wolf chases and kill sites from transects and high points; backtracking wolves through snow; following or scanning for scavengers (ravens, eagles, magpies and coyotes); and investigating sites where wolves congregated for more than a few hours (usually determined using VHF telemetry). Upon finding a carcass, we recorded the same information as described above for live elk observations. We also examined the carcass to determine the likely cause of death, estimated when death occurred, extracted an incisor for aging using dental cementum annuli (Matson Labs, Milltown, Montana), and cut an approximately 8 cm section from the middle of a femur to obtain a marrow sample. Marrow fat is a commonly used indicator of body condition in ungulates. This is the last fat reserve tapped by ungulates, and substantial declines in

percent fat indicate an animal is, or has been, operating at a caloric deficit (Neiland 1970; Sinclair & Arcese 1995).

We stored the femur sections in sealed plastic bags in a deep freezer until analysis the following summer. We used a Soxhlet extractor and the method described by Neiland (1970) to extract and determine percent marrow fat of wet weight, with one modification: we exchanged the solvent until the samples stopped losing weight (some of the samples with higher proportions of fat required 4 solvent changes before all fat was removed). Out of 59 definite and probable wolf kills, 33 provided marrow samples from animals that we could determine were bulls or cows (bulls, n=23; cows, n=10).

Statistical Methods

The dependent variables in our analyses of behavior were total proportion of time spent vigilant, grazing, moving, bedded, and other. We arcsin-transformed these proportions to obtain normality (Zar, 1999). All independent variables were categorical: wolf presence, sex, herd position, and distance to timber.

We hypothesized *a priori* that sex, wolf presence, herd position, and distance to timber might affect vigilance through main effects or interactions. However, distance to timber was not significantly associated with vigilance as a main effect or in any interactions in exploratory analysis. Because of this result (which is somewhat surprising and discussed later), we used information content (AICc) to determine which independent variables to include in our primary

analyses (Burnham and Anderson 2002, Stephens et al. 2005). Based on AICc, the best model included wolf presence, sex, and position in herd. A model with these effects and distance to timber was 3.5 AICc units worse. Therefore, we removed distance to timber from our primary analyses and used fixed effect factorial ANOVA. We tested for differences in behavioral responses between the four drainages and found none, so we pooled the data across drainages.

We addressed potential pseudoreplication in three ways. First, our basic unit of observation was the herd. Elk herd sizes and compositions changed frequently on our study site, relative to the two-week interval at which we recorded behavioral observations (as also reported by Shoensmith, [1980] in his study of 236 marked elk on Yellowstone's Mirror Plateau). Consequently, it was not possible to make repeated observations on specific herds: a set of individuals that formed a herd at one time were very unlikely to be aggregated in the same way during the next two week interval. Consequently, we considered each herd a unique observation and the degrees of freedom for ANOVA were based on the number of herds observed. Second, repeated scans within one observation period produced a single data point. That is, we pooled across individuals and scans within each herd to derive a single proportion of time spent in each behavior for each of the age by sex by position classes in each herd observed. Finally, we evaluated our assumption that the behavior of different age-sex classes was functionally independent in our data set. Of the 88 herds we observed, only 14 (16%) held both cows and bulls. Sexual segregation is common among ungulates (Clutton-Brock et al. 1987; Main & Coblentz 1990).

Of the 14 mixed-sex herds, 6 (6.8%) occurred when wolves were present, and 8 (9%) when wolves were absent, with moderate positive (but not significant at $\alpha = 0.05$) correlations between cow and bull vigilance in both cases ($r^2=0.393$, $P = 0.183$, & $r^2 = 0.17$, $P = 0.309$, respectively). Also, if positive correlations exist in mixed herds, they will tend to mask differences between bull and cow behavior, creating conservative, Type 2 errors. Given these patterns, we pooled the 14 integrated herds with the 74 segregated herds. For the purposes of our analyses, the main point is that 84% of behavioral observations came from single-sex herds, so that correlations between the behaviors of bulls and cows have relatively little effect.

To test whether vigilance levels respond to herd size, we used simple linear regression, using arcsin transformed proportion of vigilance (Zar, 1999), as the dependent variable and herd size as the independent variable.

We used contingency tables (Zar 1999) to test whether the presence of wolves affected the number of herds (and individuals) seen at various distances to timber.

The dependent variable in our marrow fat analysis was proportion fat, and the independent variables were sex (bull or cow) and time of year (Early = January 15 – March 31; Late = April 1 – June 15).

Gathering data through ground observations limited our ability to detect both live elk and wolf kills within heavily timbered areas. Consequently, our hypotheses do not extend to wolf-elk interactions within these areas.

Results

Herd Dynamics and Distributions

Wolf presence had a strong effect on the distance between elk herds and timbered areas (protective cover). Fewer herds (and individuals) than expected by chance were far from timber when wolves were present and more herds (and individuals) than expected were far from timber when wolves were absent (Fig. 1.1. Herds: $\chi^2 = 8.047$, $df = 3$, $P = 0.045$. Individuals: $\chi^2 = 586$, $df = 3$, $P < 0.001$).

In addition to this redistribution of elk in response to wolf presence, the number of elk counted in each census zone was lower by a factor of two when wolves were present (wolves present: 3.03 elk \pm 9.024 SD, $N = 204$ census zones; wolves absent: 6.2 elk \pm 14.92 SD, $N = 467$ census zones; $t = 3.387$, $P < 0.001$). Data from VHF and GPS telemetry indicated that elk were not leaving their drainage in response to wolf presence. In conjunction with the significant pattern for elk to move closer to timber when wolves were present we interpreted this reduction in the number of elk counted to be an indication that elk moved into timbered areas when wolves were present (a response confirmed by GPS telemetry: Creel et al. 2005).

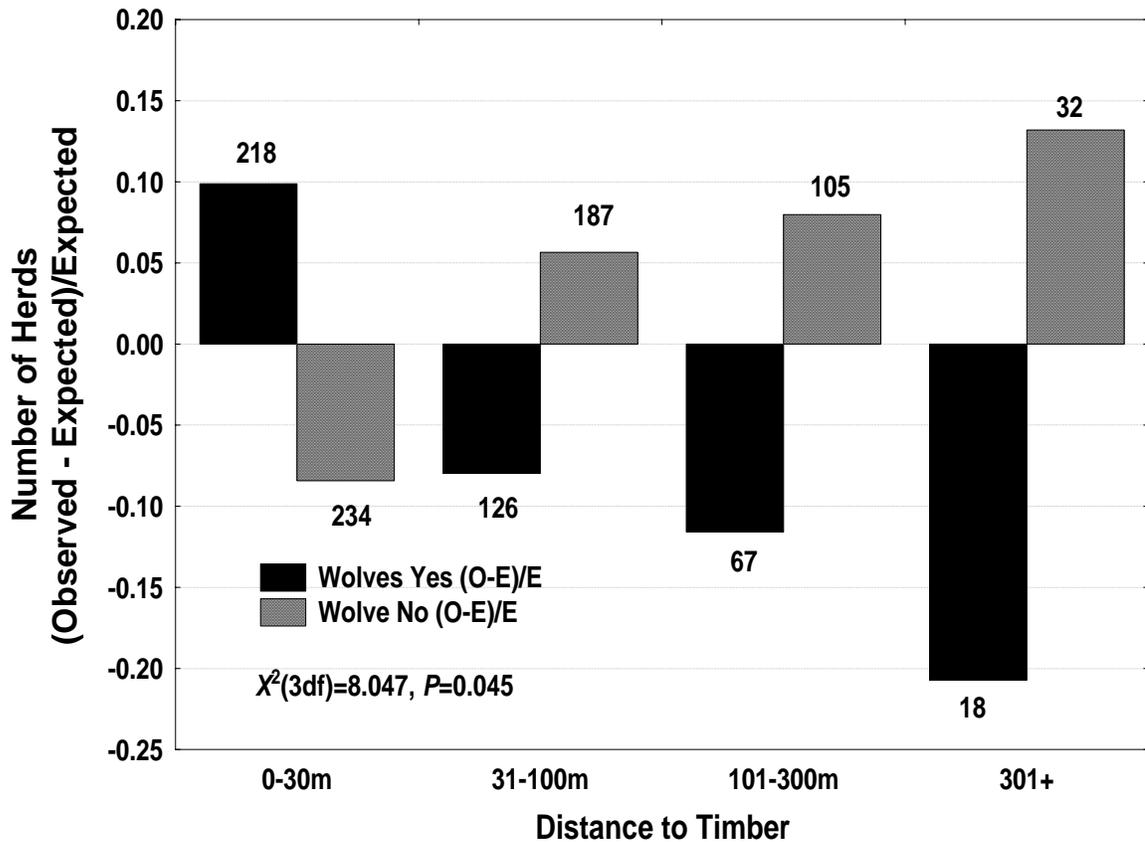


Figure 1.1. Effect of wolf presence on the distance between elk herds and woodland edges (protective cover). Numbers with bars = number of herds.

Overall, mean herd sizes were halved when wolves were present (Creel & Winnie 2005). All-bull herds were smaller than cow-calf-spike herds (Table 1.1. $t=84, P<0.001$). All-bull herds became slightly larger in response to wolf presence (Table 1.1. $F_{1,310} = 5.70, P=0.018$), in contrast to cow-calf-spike herds, which became smaller when wolves were present (Table 1.1. $F_{(1,610)}=31.12, P<0.001$). Bull herds and cow-calf-spike herds differed by a mean of 16.1 individuals (a 4.6-fold difference) when wolves were absent, but by only 3.1 individuals (a 1.5-fold difference) when wolves were present. Because initially small bull herds became larger, and initially large cow-calf-spike herds became

smaller, herds of all compositions converged to mean sizes of 6-9 elk when wolves were present. In other words, variation in herd size decreased in response to the presence of wolves.

	Overall	Wolves Absent	Wolves Present
Bull-only Herds	5.12, (4.48, 5.76)	4.472, (3.75, 5.19)	6.03, (4.88, 7.18)
Cow, Calf, Spike Herds	15.14, (13.08, 17.2)	20.58, (17.8, 23.4)	9.14, (6.22, 12.06)

Table 1.1. Herd size changes in relation to wolf presence (mean, 95% CI).

Marrow Fat and Individual Predation Risk

Wolf-killed bulls were in poorer condition than wolf-killed cows throughout the winter, as measured by marrow fat concentration (Fig 1.2: $F_{1,29} = 22.55$, $P < 0.001$). Overall, the mean marrow fat content in bulls (0.35 proportion fat by mass, 95% CI = 0.27, 0.42) was half that of cows (0.70, 95% CI = 0.57, 0.83). Marrow fat reserves in wolf-killed individuals of both sexes declined from early winter to spring ($F_{1,29} = 23.704$, $P < 0.001$, early mean = 0.70, 95% CI = 0.61, 0.90; late mean = 0.34, 95% CI = 0.22, 0.46). The interaction between the effects of sex and season on marrow fat was weak (Fig. 1.2. $F_{1,29} = 1.86$, $P = 0.183$).

Differences in body condition mirrored the patterns of predation reported by Creel and Winnie (2005), where rates of predation differed from expected for all age-sex classes ($\chi^2 = 39.21$, $df = 2$, $P < 0.001$). Adult females were killed one-third as often as expected by chance, while bulls and calves were killed 2.2-fold

and 2.5-fold more often than expected by chance, respectively. From the perspective of an individual elk, the risk of being killed by wolves was 6.3 times higher for a bull than for a cow. Because our marrow data are not a random sample of the population at large, in isolation they do not allow a strong conclusion that bulls are in worse condition than cows. However, when considered alongside the work of others indicating that live bulls are in worse condition than live cows in the winter (Anderson et al. 1972; Mitchell et al. 1976; Geist 2002; Hudson et al. 2002), these data reasonably lead to the conclusion that bulls in this population (as elsewhere) face stronger winter foraging constraints than cows.

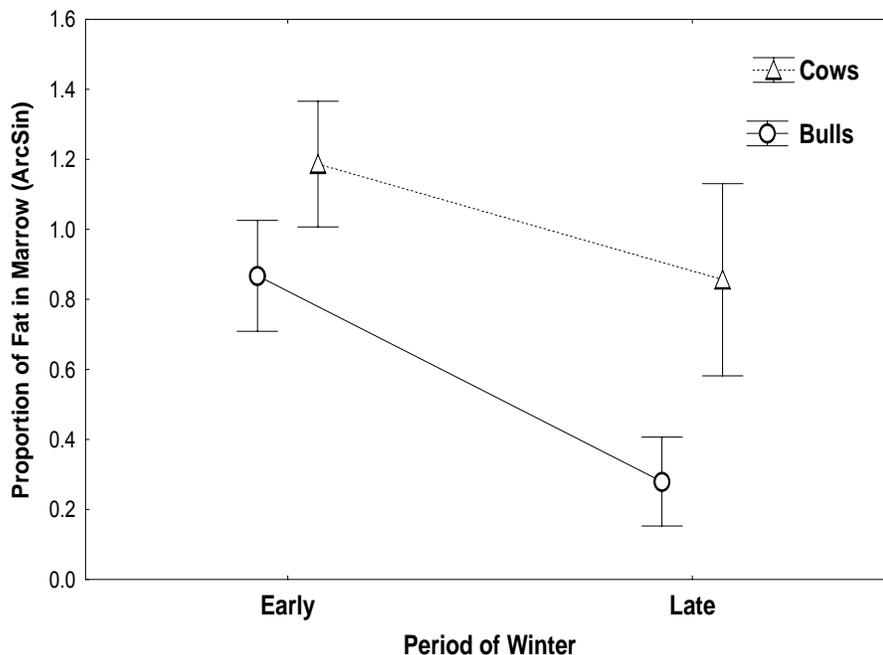


Figure 1.2. Sex differences and winter changes in physical condition, as measured by femur marrow fat concentration.

Moving, Bedding and Other Behavior

Moving, bedding and *other* behaviors accounted for 8.6%, 12.1%, and 2%, of behavioral time budgets, respectively. The proportion of time spent moving and bedding were unaffected by wolf presence, position in herd, or sex (Table 1.2). There was an overall decrease in *other* behaviors when wolves were present, driven primarily by bulls (Table 1.2. $F_{(1, 160)}=6.8848$, $P=0.0095$), and while we did not formally break *other* down into sub-classes, our field notes indicate this was probably due to bulls not sparring when wolves were present. Because our study period was well past the fall rut, the sparring we observed tended to be a relatively gentle but noisy rattling of antlers, limited to all-bull herds.

The proportion of time spent moving did not change with distance to timber (Table 1.2b). However, there was an interaction between wolf presence, sex, and distance to timber (Table 1.2b. $F_{(3,79)}=3.19$, $P=0.028$), driven by high cow movements in the 0 to 30 m class when wolves were absent. A possible explanation for this is that areas near timber are more heavily grazed than those far from timber when wolves are present (Fig. 1.1) and that elk are simply more likely to be moving through this zone to preferred foraging areas farther from timber when wolves are absent. Because our data collection was not structured to address this issue, it does not affect our general conclusions.

A	Vigilance	Grazing	Moving	Bedding	Other
Wolf Presence	$F_{(1, 160)}=1.145$, $P=0.286$	$F_{(1, 160)}=0.301$, $P=0.584$	$F_{(1,160)}=0.16$, $P=0.69$	$F_{(1,160)}=0.09$, $P=0.76$	$F_{(1,160)}=7.33$, $P=0.008$
Sex	$F_{(1, 160)} = 9.19$, $P=0.0028$	$F_{(1, 160)}=1.63$, $P=0.2$	$F_{(1,160)}=0.01$, $P=0.91$	$F_{(1,160)}=0.65$, $P=0.42$	$F_{(1,160)}=0.05$, $P=0.82$
Position	$F_{(1, 160)}=2.81$, $P=0.0956$	$F_{(1, 160)}=2.85$, $P=0.093$	$F_{(1,160)}=0.95$, $P=0.33$	$F_{(1,160)}=0.24$, $P=0.63$	$F_{(1,160)}=0.25$, $P=0.62$
Wolf Presence x Sex	$F_{(1, 160)}=5.27$, $P=0.023$	$F_{(1, 160)}=4.79$, $P=0.03$	$F_{(1,160)}=2.14$, $P=0.15$	$F_{(1,160)}=2.22$, $P=0.14$	$F_{(1,160)}=6.88$, $P=0.01$
Wolf Presence x Position	$F_{(1, 160)}=1.47$, $P=0.227$	$F_{(1, 160)}=0.35$, $P=0.554$	$F_{(1, 160)}=0.43$, $P=0.51$	$F_{(1, 160)}=.07$, $P=0.79$	$F_{(1,160)}<0.01$, $P=0.99$
Sex x Position	$F_{(1, 160)}=0.08$, $P=0.78$	$F_{(1, 160)}=0.48$, $P=0.49$	$F_{(1, 160)}=0.1$, $P=0.76$	$F_{(1, 160)}=0.22$, $P=0.64$	$F_{(1,160)}=0$, $P=1.0$
Wolf Pres. x Sex x Position	$F_{(1, 160)}=0.59$, $P=0.442$	$F_{(1,160)}=0.09$, $P=0.77$	$F_{(1, 160)}=0.09$, $P=0.76$	$F_{(1, 160)}=0.5$, $P=0.48$	$F_{(1,160)}=0.71$, $P=0.4$
B					
Distance to Timber	$F_{(3, 79)}=0.09$, $P=0.965$	$F_{(3, 79)}=0.627$, $P=0.6$	$F_{(3, 79)}=0.406$, $P=0.749$	$F_{(3, 79)}=1.148$, $P=0.34$	$F_{(1,160)}=0.05$, $P=0.95$
Wolf Presence x Dist. To Timber	$F_{(3, 79)}=1.36$, $P=0.26$	$F_{(3,79)} = 0.81$, $P=0.492$	$F_{(3,79)} = 2.258$, $P=0.088$	$F_{(3,79)} = 1.52$, $P=0.216$	$F_{(1,160)}=1.55$, $P=0.22$
Sex x Dist. to Timber	$F_{(3, 79)}=0.07$, $P=0.98$	$F_{(3, 79)}=0.55$, $P=0.65$	$F_{(3, 79)}=0.528$, $P=0.664$	$F_{(3,79)} = 0.425$, $P=0.736$	$F_{(1,160)}=0.44$, $P=0.65$
Wolf Pres. x Sex x Dist. to Timber	$F_{(3, 79)}=1.05$, $P=0.375$	$F_{(3, 79)}= 0.56$, $P=0.65$	$F_{(3, 79)}= 3.19$, $P=0.028$	$F_{(3,79)} = 1.643$, $P=0.186$	$F_{(1,160)}=0.26$, $P=0.77$

Table 1.2. Associations between elk behavior and sex, location, position within herd, and wolf presence. Part b presents an analysis separate from the main factorial ANOVA, addressing the effects of distance to timber (see methods for details).

Vigilance and Grazing Behavior

Vigilance is the behavior most often traded with foraging (Lima & Dill 1990; Lima 1998), and our results confirm this relationship. An increase in the proportion of time spent vigilant can reasonably be considered a direct response

to elevated risk, and the corresponding decrease in foraging time as a cost of this vigilance. Vigilance and grazing accounted for 15.8% (bedded vigilant: 4.9%; standing vigilant: 10.9%) and 61.5% of all behaviors we recorded respectively. Overall mean levels of vigilance and grazing did not change in response to wolf presence (main effects: vigilance: $F_{1, 160} = 1.145$, $P = 0.286$; grazing: $F_{1, 160} = 0.301$, $P = 0.584$) and the proportion of time spent grazing did not differ between cows and bulls ($F_{1, 160} = 1.63$, $P = 0.20$). However, there was an interaction between gender and wolf presence. Vigilance was higher in cows than in bulls ($F_{1, 160} = 9.19$, $P = 0.003$). The difference in vigilance between the sexes was driven by cows increasing their vigilance when wolves were present, while bulls did not (Fig. 1.3. wolf x sex interaction: $F_{1, 160} = 5.2733$, $P = 0.023$). There was a corresponding decrease in the proportion of time cows spent grazing when wolves were present (Fig. 1.4. wolf x sex interaction: $F_{1, 160} = 4.79$, $P = 0.03$).

Overall, elk on the periphery of herds tended to be more vigilant and graze less than interior animals, (vigilance: $F_{1, 160} = 2.81$, $P = 0.096$; grazing: $F_{1, 160} = 2.850$, $P = 0.093$). Vigilance and grazing did not change with distance to timber (vigilance: $F_{3, 79} = 0.091$, $P = 0.965$; grazing: $F_{3, 79} = 0.627$, $P = 0.60$). Similarly, vigilance and grazing did not vary with herd size (vigilance: $r^2 = 0.007$, $F_{(1,86)} = 0.64$, $P = 0.43$; grazing: $r^2 = 0.008$, $F_{(1,86)} = 0.70$, $P = 0.40$).

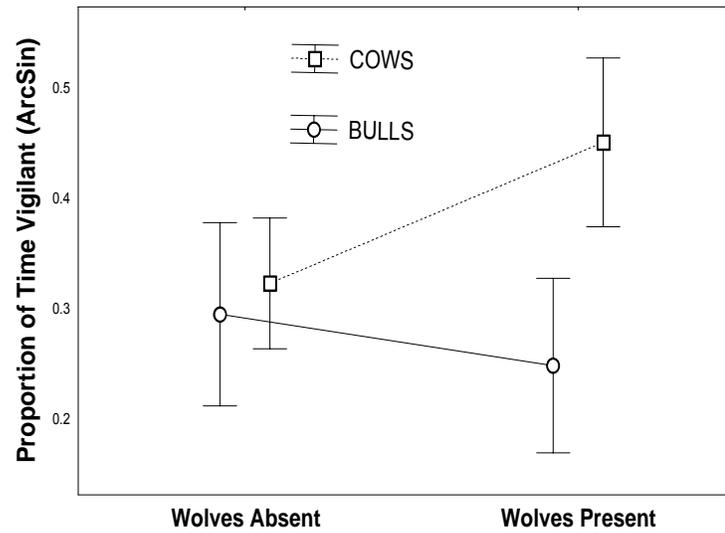


Figure 1.3. Vigilance differences between the sexes in behavioral responses to the presence of wolves.

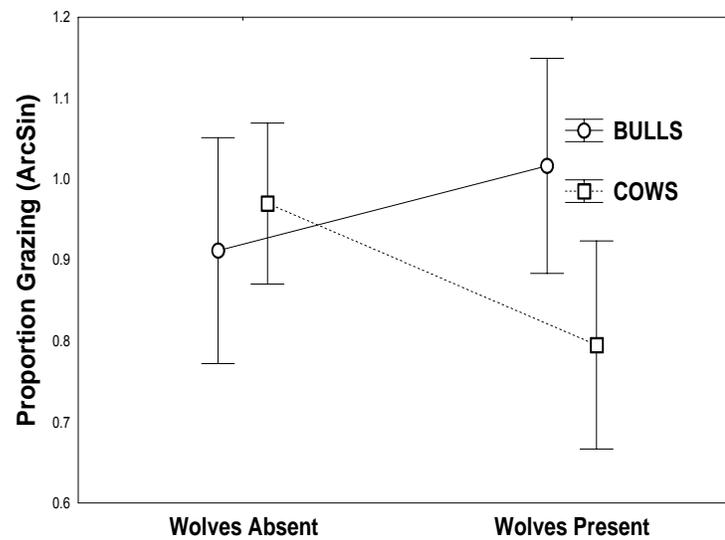


Figure 1.4. Grazing differences between the sexes in behavioral responses to the presence of wolves.

Discussion

Our results show that elk do not categorize areas far from timber as inherently dangerous, because mean vigilance levels do not increase with distance to timber. This is surprising in light of our previous work indicating that elk in our study area were disproportionately likely to be killed in open areas far from timber (Creel & Winnie 2005). These areas are used primarily when the temporal risk of predation is low (Fig. 1.1), and vigilance levels only increase (in cows) when temporal risk is high (Fig. 1.3). The antipredator behavior of elk is sensitive to both temporal and spatial variation in risk, so that areas that are only dangerous in the presence of wolves do not provoke an increase in vigilance (with its associated decrease in foraging) when wolves are absent. Moreover, temporal variation in risk produces stronger antipredator responses in cows than in bulls (Fig. 1.3), as expected based on cows' greater latitude to pay the associated foraging costs (Hudson et al. 2002; Geist 2002; Cook et al. 2004) (Fig. 1.2). These patterns suggest that antipredator responses are quite sensitive to variation in both costs and benefits.

Because herd size *decreases* when wolves are present (Creel & Winnie 2005), it is clear that elk do not aggregate for increased security when far from timber. This response is somewhat surprising in light of the large number of studies that document antipredator benefits to grouping, and suggests that elk may disaggregate to reduce the likelihood of being detected by wolves. An

individual's risk of predation can be broken into 4 components that comprise the sequence of predation (Creel & Creel 2002):

- 1) *Encounter rates* — the probability of being encountered by a predator.
- 2) *Attack preferences* — the probability that the predator will hunt, upon encountering prey.
- 3) *Hunting success* — the probability that the predator will make a kill, upon hunting.
- 4) *Dilution of risk* — the probability that a given individual will be the victim, upon a kill being made.

Predation risk is the product of these four conditional probabilities. Each of the first three probabilities can be altered by changes in individual and group vigilance, habitat types occupied by prey, or a combination of these. All four can be altered by group size. We would expect prey to attempt to minimize the product of these probabilities through behavior responses (if available), depending on the associated costs and ability of individuals to pay. However, behavioral responses that reduce one or more of the above probabilities may result in an offsetting, or partially offsetting, increase in one or more of the remaining probabilities, as when increases in group size benefit individuals through dilution of risk, but also increase encounter, attack, and predator success rates (Creel & Creel 2002; Hebblewhite & Pletscher 2002). Factors affecting hunting success and dilution of risk are relatively well studied, but we know surprisingly little about the ways that prey change their behavior to manipulate encounter and attack rates (Creel & Creel 2002). Logically, we would expect

antipredator behavior to be directed to the first two stages in predator-prey systems in which hunting success (stage 3) is difficult or energetically expensive for prey to reduce.

When wolves were present in drainages, habitats far from timber were substantially more dangerous for elk, and ground census data show that herd sizes decreased at all but the nearest distance to timber category, where they already tended to be small (Creel & Winnie 2005). GPS telemetry shows that elk move into timbered areas when wolves are present (Creel et al. 2005). The results presented here further indicate that elk are taking refuge in and near timber, and thus probably perceive this cover as protective rather than obstructive (Lazarus & Symonds 1992). Without behavioral observations of elk and wolves in timber, we cannot say with certainty which of the first three probabilities are affected by reducing herd size and dispersing into timber, but it is likely that these responses reduce the risk of detection. Moreover, these responses clearly come at the expense of dilution (at the level of single herds), because herd sizes are smaller in the presence of wolves.

Hebblewhite and Pletscher (2002) found that wolves in Alberta encountered larger groups of elk more than expected. Similar findings with wild dogs and their prey in Africa (Creel & Creel 2002), spiders and parasitoid wasps (Uetz and Hieber 1994), and cichlids and guppies (Krause and Godin 1995), suggest that at least one reason for elk to reduce herd size is to reduce encounters with wolves. However, the mechanics of encounter and attack reduction remain unclear: elk may be reducing their detectability by scattering

into timber; or wolves may be aware of these scattered small groups and avoid hunting them due to the increased effort (reduced profitability) involved in approaching and testing multiple small groups before a vulnerable individual is found; or elk may gain tactical advantages that influence wolves' decisions whether or not to attack; or some combination of these.

Regardless of the mechanisms involved, the above discussion begs the question, "if reducing group size reduces individuals' encounter probabilities, why be in groups at all?" If aggregation is a response to predation risk, the answer is probably dilution of risk. Dilution benefits accrue rapidly as group size increases above one, with the biggest gains occurring with the first few added individuals. However, wolf hunting behavior indicates that there is an increase in detectability or attractiveness to wolves as elk group size increases (Hebblewhite & Pletscher 2002), and this probably forces elk to balance these opposing effects. Trade-offs between encounters with predators and dilution provide a coherent explanation for the herd size responses of bull versus cow-calf-spike herds (recall that, when wolves were present, bull herds increased slightly from 4.5 to 6, whereas cow-calf-spike herds decreased from 20.5 to 9.1). These two types of herds make different behavioral responses to the threat of predation to arrive at a common solution – intermediate herd sizes of 6-9 elk. These results suggest that groups of roughly 6-9 individuals may provide a balance between detectability (or attractiveness to wolves) and dilution.

A large body of theoretical and empirical work has established that foraging decisions and risk taking should both depend on body condition (Houston & McNamara 1982; McNamara & Houston 1992; Bachman 1993; Sinclair & Arcese 1995). In the Gallatin, wolves killed bulls more often than expected by chance (Creel & Winnie 2005), and overselection of males in winter is common in other studies of predation on large ungulates (Huggard 1993; Mech et al. 2001). The poor condition of bulls during winter that we observed offers insight into sex-differences in behavioral responses, and incidentally, the mechanisms that might be driving sexual segregation. Wolf-killed bulls were in worse physical condition than wolf-killed cows throughout the winter. Bulls were significantly less vigilant than cows; did not respond to wolf presence with increased vigilance; and formed groups less than half the overall mean herd size. Our previous work has shown that individual bulls are roughly 6 times more likely than cows to be killed by wolves (Creel & Winnie 2005), yet despite this relatively high level of personal risk, bulls do not increase vigilance in response to wolf presence. Bachman (1993) reported similar results where experimentally starved ground-squirrels reduced vigilance levels in exchange for increased foraging time, and were less responsive to the warning calls of conspecifics. If the differences between wolf-killed bulls and live bulls are similar to differences between wolf-killed cows and live cows, as previous research indicates they probably are (Anderson et al. 1972; Mitchell et al. 1976; Geist 2002; Hudson et al. 2002), then the above behavioral patterns suggest that bulls are less able to pay the foraging costs of responding to wolf presence by increasing vigilance.

Despite the slight increase in herd size in response to elevated risk, bull groups tended to be small, regardless of wolf presence (Table 1.1). This may be driven by their lower ability to pay the costs of increased numbers of encounters. Other studies suggest that large groups are encountered and attacked by predators more often than expected by chance (Creel & Creel 2002; Hebblewhite & Pletscher 2002; Krause and Godin 1995). Consequently, bulls may need to avoid large groups (despite the benefits of risk-dilution) for two reasons. First, encounters with wolves carry energetic costs that bulls are ill prepared to pay due to poor condition. Second, the benefits of risk dilution are probably not distributed evenly within herds. There is probably a set of relatively vulnerable individuals within most herds from which the victim is selected, and rut-weakened bulls, if present in these herds, are likely to be in this subset (Geist 2002). The combination of the cost of more frequent encounters, and their relative vulnerability given an encounter (hence reduced dilution benefits), may be sufficient to keep bulls out of larger cow-calf-spike herds, thus promoting sexual segregation.

There may be differences in the way that wolves select bulls and cows based on condition. Bulls, about 30% larger than cows and carrying antlers, may represent a more dangerous adversary than cows, so that wolves do not risk attacking them until they are in worse condition. Given our data, we can not directly assess this aspect of prey selection, but the fact that wolf-killed bulls have significantly lower marrow fat than wolf-killed cows suggests that wolves may select males only when they fall below a threshold of vulnerability.

Furthermore, this threshold of vulnerability may be relative – depending on the current condition of otherwise more vulnerable cows.

In contrast to bulls, cows employ a broad set of responses to elevated threat that operate at multiple scales: cows increase individual vigilance levels at the expense of grazing, reduce group size, and move closer to or into timber. Despite the behavioral responses of cows, calves suffer higher rates of predation than expected by chance (Creel & Winnie 2005). Calves are dependent upon their mothers and do not have the option of leaving large mixed herds, as bulls do, when wolves are present (Creel & Winnie 2005). When these herds are attacked (despite the behavioral responses of the cows), calves may be singled out by attacking wolves. The high vulnerability of calves to predation may in part contribute to the strong behavioral responses of cows seeking to protect not just themselves, but also a substantial reproductive investment in their current calf.

We cannot assess the absolute effectiveness of cow behavioral responses, but in parallel with their behavioral responsiveness, they experience a low rate of predation in comparison to bulls. If the antipredator behavior of cows is relatively effective when compared to bulls, this may be all that is necessary. Savino and Stein (1989) examined the effects of prey behavioral responses and habitat selection on predation rates in fish. In an environment containing 2 species each of predators and prey, the prey species that shifted from open to closed habitats markedly decreased its risk of predation, while the prey species that did not respond suffered increased predation. Elk of different sexes display a similar dichotomy of behavior, with a similar pattern of predation. The lack of

effective behavioral responses by bulls may increase the effectiveness of cow responses – cows make themselves unavailable to wolves *relative* to bulls. Bulls then bear the brunt of wolf predation because of their inability to pay the costs associated with more effective anti-predator behavior.

Grazing and vigilance levels were unaffected by herd size or distance to timber (main effects, Table 1.2). It appears that, regardless of local elk density or habitat quality, Gallatin elk consistently attempt to maximize forage intake in winter, and only when faced with imminent danger (the presence of wolves in the drainage), are they willing to reduce feeding time in exchange for increased vigilance (cows), or compromise forage quality by moving nearer and into timber (both sexes).

Elk in the upper Gallatin assess spatial variation in predation risk at fine scales, on the order of meters, and temporal variation in risk on the order of a single day (or less). Moreover, spatial and temporal variation in risk interact and this is reflected in the behavioral responses of elk. These variations in risk drive a suite of anti-predator behavioral responses that depend on gender and physical condition, apparently constrained by individuals' ability to pay the associated cost in foraging time. Despite heavy over-selection by wolves in our study system, bulls did not increase vigilance when wolves were present in a drainage. This implies that the foraging costs of increased vigilance are substantial, yet these foraging costs are being paid by cows at a time when most are carrying developing fetuses (Cook 2002; Hudson et al. 2002; Cook et al. 2004). These

antipredator responses create indirect costs of predation which may affect prey demography through survival or reproduction.

All of these responses occur on a time scale that corresponds to the comings and goings of wolves, and a spatial scale defined by the movements of elk on that time scale, which is substantially smaller than a complete wolf territory. These results are relevant to current debate over wolf-elk-plant trophic cascades in the Yellowstone ecosystem: to date, direct data on the responses of elk to wolves have been lacking, making it difficult to disentangle elk effects from myriad other influences on surrounding plant communities. This emphasizes the necessity of observing prey behavioral responses to risk on the scales at which important variation in risk actually occurs.

CHAPTER 3

ELK DECISION-MAKING RULES ARE SIMPLIFIED
IN THE PRESENCE OF WOLVESAbstract

The risk of predation drives many behavioral responses in prey. However, few studies have directly tested whether predation risk alters the way *other* variables influence prey behavior. Here we use information theory (AICc) in a novel way to test the hypothesis that the decision-making rules governing elk behavior are simplified by the presence of wolves. With elk habitat use as the dependent variable, we test whether the number of independent variables (i.e. the size of the models) that best predict this behavior differ when wolves are present versus absent. Thus, we use AICc scores simply to determine the *number of variables* to which elk respond when making decisions. We measured habitat use using 2288 locations from GPS collars on 14 elk, over two winters (14 elk winters), in the Gallatin Canyon portion of the Greater Yellowstone Ecosystem. We found that use of three major habitat components (grass, conifer, sage) was sensitive to many variables on days that wolves were locally absent, with the best models ($\Delta\text{AICc} \leq 2$) averaging 7.4 parameters. In contrast, habitat use was sensitive to few variables on days when wolves were present: the best models averaged only 2.5 parameters. Because fewer variables affect elk behavior in the presence of wolves, we conclude that elk use

simpler decision-making rules in the presence of wolves. This simplification of decision-making rules implies subtle, but potentially important, constraints that predation risk imposes on prey behavior, by reducing prey's ability to optimize foraging and movement.

Introduction

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

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

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

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

In the winter, elk in the Upper Gallatin River drainage respond to short-term changes in the threat of wolf predation at multiple scales: individual, herd and landscape. When wolves are present in a drainage, some individuals (females) increase vigilance at the expense of foraging (Winnie and Creel, in

review), mean herd size decreases and herd composition changes (Creel and Winnie, 2005), and elk leave open grassy areas and move into the protective cover of timbered areas (Creel et al 2005). These responses appear to be constrained by body condition, indicating that antipredator behaviors carry foraging costs (Winnie and Creel in review).

Regardless of the presence of wolves, elk move about the landscape to forage, and we would expect that foraging and movement are affected by variables other than risk. Net energy and protein content differ between woody browse and grasses (Christianson and Creel in press), and both the availability of plants and foraging costs are affected by interactions between growth form and snow conditions (Jenkins and Wright 1987). Thus, we might expect elk behavior to be affected by differences in snow depth and snow density across local landscapes (Sweeney and Sweeney 1984). Elk of both sexes face a negative energy budget in winter, but males appear to face stronger energetic constraints because they enter winter with depleted energy stores following the fall rut (Geist 2002; Winnie & Creel in review). Consequently, we might expect gender to play a role in behavior. Winter weather in the Northern Rockies can be extreme even for cold-adapted species, so we might expect rules for selection of open and closed habitats to be sensitive to temperature and wind speed (Merrill 1991; Jones et al 2002).

Differences in elk decision making rules should be reflected in differences in models that best describe their behavior. Here, we test the hypothesis that the rules by which elk select habitats are simplified by the presence of wolves

Specifically, when elk are unconstrained by predation risk, models describing behavior should contain more parameters, and conversely, when risk is high, models should contain fewer parameters.

Methods

Study Area

Our study area is a mosaic of National Forest, National Park, State, and private land, covering 125.8 km² in four drainages along the upper Gallatin River (Porcupine [30.3 km²], Taylor [56.0 km²], Tepee [13.1 km²] and Daly [26.4 km²]). South-facing slopes and valley bottoms are generally a mixture of open sage (*Artemisia spp.*) and grassland (dominated by Idaho fescue and bluebunch wheatgrass: *Festuca idahoensis* & *Agropyron spicatum*) with riparian areas bordering creeks. North-facing slopes and higher elevations are primarily coniferous forest (lodgepole pine and Douglas fir: *Pinus contorta* & *Pseudotsuga menziessii*) broken by occasional small meadows. Elevation runs from 1975 m ASL to 2432 m ASL.

We surveyed fixed areas (viewsheds) in each of the four drainages, beginning at first light, every two-weeks from mid- January, 2002 until the end of May, 2002, and during the same period in 2003, and recorded all wolves, elk and elk carcasses located in these surveys. Survey routes were chosen to maximize the area scanned in each drainage while minimizing disturbance caused by our presence. During a survey, we scanned from fixed highpoints and while walking fixed routes between highpoints. Each drainage was divided into 6-8 viewsheds.

In addition to this formal sampling regimen, we attempted to visit each drainage on every day of the winter-spring study period, in either the morning or evening, usually traversing part of our fixed sampling routes. These ad-lib samples provided additional information on wolf presence (see *Wolf Presence* below).

Elk

The elk in the study area are part of a largely migratory population (averaging 1725 [se 63] and varying from 1214 to 3028 animals annually since 1928) that winters along the upper Gallatin River and its tributaries from the northwest corner of Yellowstone National Park, north to Big Sky, Montana (Brazda 1953; Peek et al 1967; Peek and Lovaas 1968). Both the migration route and winter range encompass state, private, and federal lands, while the summer range for most of the elk lies within western Yellowstone National Park.

We designed and built data-logging GPS units based on SiRFstar I GPS engines (SiRF Technology, San Jose, California) and riveted them to the tops of conventional VHF radio collars equipped with timed drop-off mechanisms (Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA). We collared 7 elk each winter (10 adult females, 4 adult males) for a total of 14 elk winters. Each collar was set to fix every 2 hours, and the mean realized fix rate was 61.7% (mean fix interval of 3.24 hours), yielding 18,317 fixes. Of these fixes, 2288 fell in winter periods in study drainages at times for which we data on wolf presence or absence. We tested for differences in fix rate between forested and open habitat types and found no significant differences (forested $F=1.67$, $P=0.196$;

open $F=0.88$; $P=0.35$). Wolf presence or absence in a drainage did not detectably alter the fix rate ($F = 0.88$, $P = 0.35$).

Wolves

Wolves colonized the upper Gallatin drainage in 1997, and during the course of this study, 2 packs (12-16 wolves) used the study area each year. We used a combination of direct observations, conventional VHF collars, snow tracking, and detection of scats and wolf kills to determine wolf presence in each of the study drainages on each day. While walking survey routes or collecting ad-lib behavioral observations, we continuously checked for signs of wolves. We considered wolves present within a drainage on a given day if we located them via VHF radiotelemetry, found a fresh kill, fresh scat, or fresh tracks in snow, mud or loose soil. We considered wolves absent from a drainage if we surveyed and detected no sign of wolf presence for that day. For days that a drainage was not surveyed, we excluded the GPS data. If wolves denned in a drainage (near April 15th both years), we scored wolves as present in that drainage on all days during the denning period. Because not all wolves in the study area were radiocollared and we undoubtedly missed some physical evidence of their presence, it is likely that we failed to detect wolves on some days. This failure to detect wolf presence might mask responses by elk to wolves (Type II errors), but should not create apparent differences where none exist (Type I errors), so tests comparing data from wolf present and wolf absent conditions are conservative.

Our work in this study system (Creel & Winnie 2005; Creel et al. 2005; Winnie & Creel in review) has shown that elk respond to the presence and absence of wolves at the scale of our data and analyses, both temporally (days and hours) and spatially (drainages, broad habitat types measured at 30m pixels). Of course, this does not mean that elk do not also respond to wolves at other spatial and temporal scales (see Discussion).

Habitat Composition at Elk Locations

To assess habitat types at elk GPS locations, we applied logistic regression models for the probability of occurrence of dominant plant species, developed for Yellowstone's Northern Range (Rew et. al., 2005; Rew et al, in press). These regressions were selected using AICc via single term deletions from a full model including slope, elevation, sine (E/W) and cosine (N/S) of aspect, and seven bands of Landsat 7 ETM reflectance data. Model selection via single term additions yielded the same result in all cases. We validated the regression models using 315 sampling locations stratified by drainage and elevation across the Gallatin study site. To simplify the analysis of habitat selection by elk, we combined probabilities of occurrence for all conifer species (lodgepole pine, limber pine, subalpine fir, Douglas fir, and Englemann spruce) into one habitat component (*conifers*), combined the probabilities of occurrence for the two dominant native grasses (bluebunch wheatgrass and Idaho fescue) into a second component (*grass*), and combined sage species (big sage, *Artemisia tridentata* and silver sage *A. cana*) into a third component (*sage*).

Using ArcGIS, each elk location was assigned separate probabilities of conifer occurrence, grass occurrence, and sage occurrence. The use of three probabilities is probably an oversimplification of how elk perceive habitats, but our previous work (Creel et al 2005; Winnie and Creel in review) has shown that these probabilities (dependent variables) do respond to wolf presence in this system. To test the hypothesis that the complexity of decision-making rules responds to predation risk, all that is required are dependent variables known to be affected by risk.

Each habitat component is modeled independently of the other two components, so the three probabilities of occurrence need not sum to 1. This is appropriate, because many locations have a high likelihood of more than one habitat component being present. This approach incorporates continuous spatial variation in preferred food (grass), protective cover (conifers), and sage, which is associated with food but also may provide limited cover. Incidental properties of this approach are that the probability of occurrence for each habitat component on any pixel (30m x 30 m) was never 1 or 0 (the model was never absolutely certain that a habitat component did or did not occur in a given pixel), and probabilities did not share the same scale from model to model, i.e. relative probabilities of occurrence are consistent across locations within a habitat model, but probabilities of occurrence cannot be directly compared across habitat models. This method of mapping habitat components is more descriptive than simply categorizing habitats into three exclusive types, because it is unlikely that elk perceive locations categorically, as one habitat type or another. Locations

are mixtures of food and cover that vary along continuous scales, and multiple plant components can and do occur in the same patch (in the case of our models, 30 x 30m pixels).

Environmental Variables

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

across the study site using a design stratified by drainage, elevation and habitat type, we preferred them to daily data on snow-water-equivalent accumulation from regional NRCS SNOTEL sites.

Statistical Analysis

To test our hypothesis, we compared the complexity of models that best fit data on elk behavior in high and low risk conditions. We did this via model selection using Akaike's Information Criterion (AICc), applied in a novel way. Typically, AICc is used to distinguish among competing hypotheses, each framed as a regression model. Here, we used AICc simply to test whether well-supported models included a larger set of independent variables when wolves were absent. That is, we used AICc scores to identify models with good support from the data, so that the number of parameters in these models could be used in the next step.

Using the models identified by AICc, our intention shifted from identifying strong models to testing hypotheses about the differences between model sets. We performed three one-tailed t – tests, one for each habitat component. Each t-test compared the mean number of parameters in the best models (within 2 AIC units of the best model) when wolves present versus wolves absent (H_0 : the number of parameters equal or greater when wolves present; H_a : fewer parameters when wolves are present). Degrees of freedom were based on the number of models within 2 AIC units of the best model, calculated conservatively using a method that penalizes for high sample variance (Devore and Peck 2001).

Overall, the logic of our analysis is as follows. We hypothesized that the presence of wolves (high predation risk) imposes constraints on habitat selection rules. The models of habitat use selected when wolves are present identify the number of variables to which elk respond when constrained by immediate risk. Similarly, the models of habitat use selected when wolves are absent identify the number of variables to which elk respond without the constraints of immediate predation risk. We hypothesized that models would be larger (more complex) when elk were unconstrained by predation risk and smaller when wolves were present. We used 'best subsets' modeling, allowing elk to tell us how many environmental variables were important to them when making habitat use decisions. Because this approach yields a large model list, we limit all subsequent inferences (including model averaging and calculating relative variable importance) to models within 2 AIC units of the best model. Best subsets modeling has been criticized as data dredging, in the normal context of using AIC to compare a set of models, each of which represents a hypothesis of direct interest (Burnham & Anderson 2002, Stephens et al. 2005). But we use AIC only to determine the complexity of the best models under two conditions. The hypothesis we test is that the model sets differ in the size of the models that receive support from the data – a test to which the data-dredging criticism does not apply.

To test how predation risk affected habitat selection rules, we divided the elk GPS locations into two data sets based on differences in short-term predation risk: wolves present versus wolves absent from that drainage on that day. For

each of the data sets (wolves present, wolves absent) we used model selection based on information theory (using Akaike's Information Criterion with sample size correction, AICc) to identify the models that best predicted the probabilities of occurrence of grass, sage, and conifer at elk locations. Thus, we compared models of habitat selection for three dependent variables (habitat components), each under two conditions (wolves present = high risk, wolves absent = low risk), for a total of six model-selection analyses. We applied a log-odds transformation to the dependent data $\log(y/(1-y))$ that yielded an approximately normal distribution, and specified an identity link to the independent variables.

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

- *Previous location.* The attributes of an elk's current location are related to the attributes of its location two hours earlier, so treating all of the GPS fixes as independent data points would cause pseudoreplication. To avoid this, we used autoregression, including the value of the dependent variable for the previous location in the time series as a predictor. We tested whether the inclusion of more than one time lag improved the model, but AICc scores strongly supported the single-lag model (Creel et al. 2005). This procedure accounts for repeated measures and temporal autocorrelation in the data while retaining all of the GPS fixes for maximum valid power.

- *Sex*. Our previous work revealed behavioral differences between bulls (branch antlered males) and cows (females > 1 year old) in their responses to wolves (Winnie and Creel in review).
- Minimum recorded *temperature* in each drainage for that day.
- Maximum *wind speed* in each drainage on that day.
- *Temperature x Wind Speed* interaction (minimum x maximum, respectively).
- *Depth* of snow in the *open*.
- *Depth* of snow in *timber*.
- *Density* of snow in the *open*.
- *Density* of snow in *timber*.
- *Day of year*, beginning January 1st. This variable incorporates three effects that we did not measure directly. Forage quality declines as winter progresses (Demarchi, 1968). Forage quantity also declines because this was a winter study, and there was no plant re-growth after grazing and browsing. Finally, body condition declines, due to the interaction of the declining forage quantity and quality with high winter metabolic demands. Declining body condition through winter has been reported in other ungulate studies, and we have presented evidence for elk in this system (Winnie and Creel in review). This factor is problematic because it is correlated with temperature and snow depth, and thus contributes to overdispersion in models that also contain these variables.

Because regression models (and parameter estimates) can be expected to differ from one data set to another, it is important to keep in mind that these analyses use six discrete data sets (predicting 3 habitat variables under two levels of risk). Thus, differences in parameter estimates between models should be interpreted cautiously and we limit our inferences to overall differences between sets of model-averaged parameters.

Results and Discussion

The attributes of elk GPS locations and global model goodness-of-fit, when wolves were present and absent are summarized in Table 2.1. Model selection revealed marked and consistent differences in the number of parameters that influenced elk behavior when wolves were present versus absent. The probability of occurrence of all three habitat components at elk GPS locations was best predicted by models with many environmental parameters when wolves were absent, and fewer parameters when wolves were present: conifers wolves present mean 2.2, wolves absent mean 7.2, ($t_{0.05(1), 22} = 12.6$, $p < 0.0001$); sage wolves present mean 2.2, wolves absent mean 6.7 ($t_{0.05(1), 33} = 11.9$, $p < 0.0001$); grass wolves present mean 2.0, wolves absent mean 8.2 ($t_{0.05(1), 7} = 21.4$, $p < 0.0001$).

Wolves Absent							Global Model		
Log Odds	N	Mean	Min.	Max.	SD	CV	R ²	F (10 DF)	P
Conifer	1604	-2.31	-4.42	0.15	1.03	44.35	0.09	14.9	<0.0001
Grass	1604	-0.32	-2.22	1.53	0.74	229.73	0.06	10.01	<0.0001
Sage	1604	-0.40	-3.24	2.14	1.14	282.98	0.04	6.5	<0.0001
Wolves Present									
Log Odds	N	Mean	Min.	Max.	SD	CV	R ²	F (10 DF)	P
Conifer	684	-1.69	-4.50	0.52	1.19	70.09	0.06	4.22	<0.0001
Grass	684	-0.82	-2.32	2.50	0.78	95.30	0.04	2.75	0.0030
Sage	684	-1.15	-3.46	1.93	1.24	107.16	0.06	3.68	<0.0001

Table 2.1. Habitat attributes of elk GPS locations with wolves present and absent, and global model goodness-of-fit. ¹Lower log-odds indicate a lower probability of occurrence of a habitat component. * Autocorrelation in these data are accounted for in the analysis, see methods.

When wolves were absent, several models within two AIC units of the best model included 8 or more parameters (overall wolves absent: mean = 7.42 parameters in the top models: Figures 2.1a, b, c). For conifers, the global model (10 parameters) was in the set of best models. In particular, parameters describing snow conditions significantly affected the occurrence of all three habitat components at elk locations, and appeared in most of the top models when wolves were absent (Appendix A).

When wolves were present, the best models describing elk behavior were much simpler. Most of the top models contained 2 parameters, and none had more than 4 (wolves present: mean = 2.46 parameters). For all three habitat components, *previous location* alone was the best model, based on AICc scores (Figure 2.1a, b, c and Appendix A). Given this, the worst Δ AICc score that any two parameter model could attain when wolves were present was two AIC units worse than *previous location* alone. Consequently, for all of the two parameter

models with $\Delta AICc$ values near 2, the second parameter has relatively little effect on habitat use (Tables 2.2 & 2.3, Appendix A). This is reflected in the parameter estimates and their standard errors (Table 2.2), and in relative importance values (Burnham & Anderson 2002) for each variable (Table 2.3). No factors other than previous location had significant effects on habitat use at $\alpha = 0.05$ (Table 2.2), and no factors other than previous location had relative importance approaching 1 when wolves were present (Table 2.3).

Differences in the complexity of the models suggest differences in the rules that elk use to make decisions about habitat use. In the absence of wolves, elk respond to many environmental factors, particularly snow conditions, when making habitat use decisions. On days that wolves were absent, the probability of both conifer and grass occurrence at elk locations is sensitive to snow depth and density in both open and forested areas (Tables 2.2 & 2.3). Sensitivity to environmental conditions is probably a response to the combination of poor winter food quality and the energetic costs of moving and foraging in snow. Frequent adjustments to movements and foraging locations based on fine temporal and spatial scale information about snow conditions may be necessary to optimize trade-offs between energy expenditure and intake. For elk in winter, facing a long-term negative energy budget (Cook 2002, Hudson et al 2002), selection pressures on this optimization are likely to be strong.

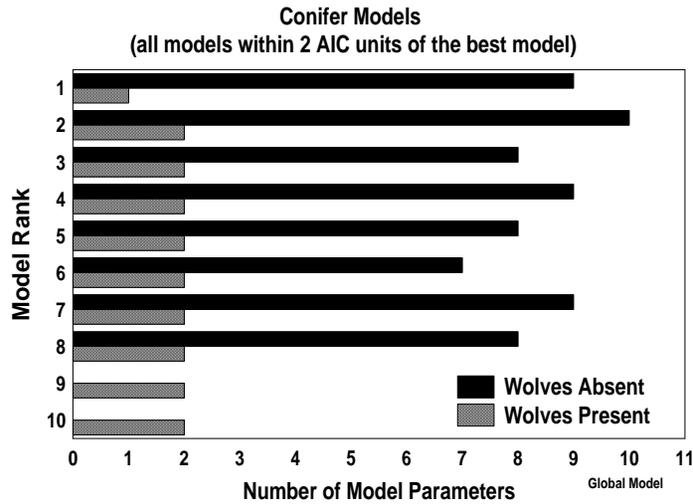


Figure 2.1a.

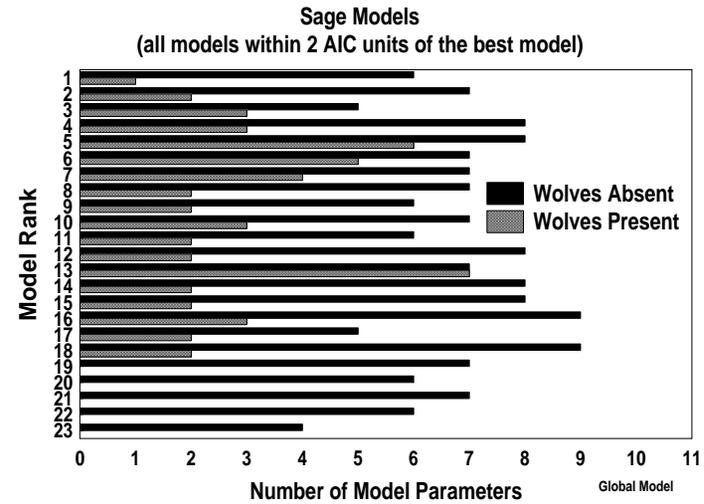


Figure 2.1c.

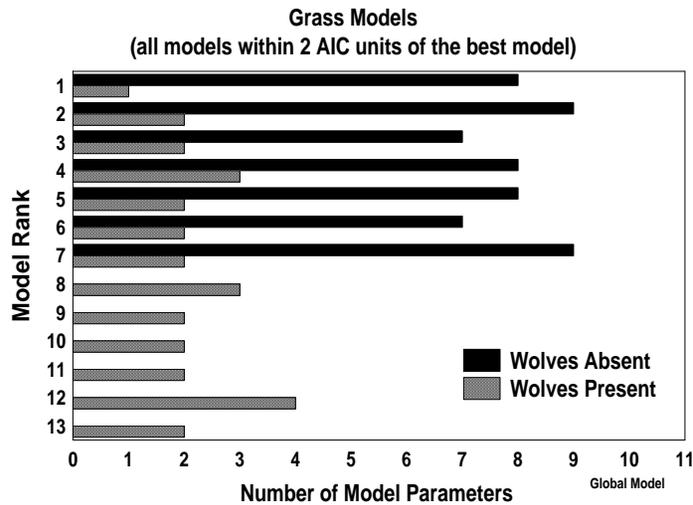


Figure 2.1b.

Figure 2.1a, b, c. Summary of the best models of habitat selection by elk, identified via Akaike's Information Criterion. Each panel summarizes the set of best models for a given habitat component, for data with wolves absent (black bars) and present (crosshatched bars). (a) conifers, (b) grassland, (c) sage. See Appendix A for details of each model.

Parameter Estimates from Model Averaging (bold indicates 95% CI does not contain 0)												
Parameter	Conifer				Grass				Sage			
	Wolves Absent		Wolves Present		Wolves Absent		Wolves Present		Wolves Absent		Wolves Present	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Previous Location	0.214	0.025	0.250	0.038	0.183	0.025	0.118	0.133	0.147	0.025	0.201	0.039
Sex	-0.115	0.042	0.000	0.056	0.060	0.031	0.014	0.038	0.046	0.046	-0.035	0.059
Day of Year	0.004	0.003	0.001	0.002	-0.004	0.002	0.000	0.001	-0.006	0.003	0.004	0.006
Temperature	-0.008	0.006	0.001	0.008	0.003	0.004	-0.004	0.006	0.008	0.006	-0.005	0.010
Wind Speed	-0.012	0.007	0.003	0.012	0.006	0.005	0.007	0.008	0.015	0.008	0.000	0.013
Temp. x Wind	-0.003	0.001	0.001	0.002	0.001	0.001	-0.002	0.001	0.002	0.001	-0.001	0.002
Snow Depth Open	0.012	0.004	-0.001	0.002	-0.010	0.003	0.059	0.075	-0.010	0.004	0.025	0.017
Snow Depth Timber	-0.012	0.004	0.000	0.003	0.007	0.003	-0.003	0.339	0.006	0.005	-0.037	0.024
Snow Density Open	0.272	0.111	-0.206	0.226	-0.214	0.081	0.097	0.153	-0.199	0.123	0.574	0.383
Snow Density Timber	-0.405	0.158	-0.149	0.337	0.277	0.116	0.165	0.226	0.303	0.177	-0.844	0.757

Table 2.2. Coefficients and their standard errors from model averaging using AICc weights (ω_i). Coefficients reported separately for each habitat component under each predation-risk condition. Bold entries indicate parameters that differ from zero at $\alpha = 0.05$. Deviance/DF (\hat{c}) for each global model is reported in parentheses under wolf presence headings.

Parameter	Relative Importance					
	Conifer		Grass		Sage	
	Wolves Absent	Wolves Present	Wolves Absent	Wolves Present	Wolves Absent	Wolves Present
Previous Location	1.000	1.000	1.000	1.000	1.000	1.000
Sex	1.000	0.081	0.901	0.062	0.232	0.043
Day of Year	0.677	0.081	1.000	0.059	0.900	0.151
Temperature	0.427	0.081	0.216	0.132	0.367	0.118
Wind Speed	0.581	0.083	0.287	0.082	0.931	0.038
Temp. x Wind	0.923	0.094	0.600	0.117	0.774	0.082
Snow Depth Open	1.000	0.083	1.000	0.194	1.000	0.360
Snow Depth Timber	1.000	0.081	1.000	0.191	0.278	0.368
Snow Density Open	1.000	0.113	1.000	0.195	0.557	0.424
Snow Density Timber	1.000	0.086	1.000	0.067	0.804	0.344

Table 2.3. Relative importance values from AICc.

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

The results of model selection for sage are not as clear as the results for conifers and grass (Figure 2.1c.). This is not due to sage being uniformly distributed among elk locations, because sage probability of occurrence has a higher CV than either grass or conifer (Table 2.1). At the risk of telling *Just So Stories* (Kipling 1902), we believe this is because sage offers neither preferred foraging habitat when wolves are absent, nor preferred cover when wolves are present. When unconstrained by snow or predation risk, elk strongly prefer

grazing to browsing (Christianson and Creel in press), and when faced with elevated predation risk they move to timber (Creel et al 2005, Winnie and Creel in review). Anecdotally, from substantial experience walking on this study site, moving through sage is particularly difficult. The complex plant structure collects snow and creates suspended surfaces that collapse when weighted. When walking surveys, the most difficult stretches to traverse were consistently patches with sage.

For grass and sage, coefficients of variation (CV) were smaller in the data with wolves present (Table 2.1). This creates the possibility that simpler models are supported for data with wolves present simply because there is less variation to be explained. However, the CV for conifer probability of occurrence was greater when wolves were present than when they were absent. Despite this, the data with wolves absent supported a set of very complex models, suggesting that the differences in complexity are real.

The overall differences between the wolf present and wolf absent models sets indicates that predator avoidance may carry costs beyond forced diet changes due to habitat shifts (Morgantini and Hudson, 1985; Christianson and Creel in press). Because elk are more sensitive to environmental factors when not constrained by wolves, this implies that there are benefits to environmental sensitivity, such as increased foraging or movement efficiency. Conversely, lack of response to environmental factors that results in decreased foraging and movement efficiency could add to, or compound, the negative effects of a diet shift. However, it is conceptually possible that environmental sensitivity is only

beneficial when elk are unconstrained by predation risk. That is, the dietary shift that accompanies a habitat shift in response to elevated risk might negate the need for environmental sensitivity. For example, moving from the open into timber may reduce snow's influence on movement efficiency, and the corresponding diet shift from grass to woody browse may reduce the influence of snow pack on foraging efficiency. If this is the case, then diet shifts are likely to be the primary cost of habitat shifts, and the loss of environmental sensitivity in response to wolves would carry little cost.

The higher sensitivity of elk to environmental factors in the absence of wolves may lend some insight into current discussion surrounding trophic cascades in the Greater Yellowstone Ecosystem. Our data on elk locations with 'wolves absent' were not gathered before wolf reintroduction, but it is reasonable to believe that our analysis underestimates elk sensitivity to environmental conditions prior to wolf reintroduction (because the risk of wolf predation probably never truly drops to zero as it was before wolf reintroduction). If habitat use and foraging decisions are based on a complex suite of environmental factors when wolves are absent, then changes in these environmental factors would result in changes in elk habitat use and foraging patterns. Consequently, it would be prudent to consider patterns of snow depth and density when evaluating the drivers of trophic cascades from wolves to elk to plants.

CHAPTER 4

SUMMARY AND SOME CAVEATSSummary

In response to the threat of wolf predation, elk altered their behavior at every scale we measured. At the scale of landscapes, elk shifted from open, grassy habitats to timbered areas associated with woody browse (Creel et al 2005). At the herd level, overall group size decreased and herd compositions changed (Creel and Winnie 2005), while bull-only groups increased slightly in size. Cow elk increased vigilance at the expense of feeding. At finer scales, elk sensitivity (or responses) to environmental conditions appeared to decrease in response to wolf presence.

Each behavioral response noted above carries probable costs, either in diet shifts, time spent feeding, increased movement and foraging costs, or in some combination. However, our results don't directly rule out the possibility of compensating behavioral mechanisms reducing the costs of predator avoidance. For example, we measured vigilance and feeding and expressed them as proportions of time observed, but did not measure total time spent feeding in a day. Elk tend to feed in bouts with interspersed periods of ruminating, resting, and moving (personal observation). They might compensate for reduced feeding rates within a bout by increasing bout length, increasing the number of bouts in a day, or both. In field experiments using sheep (*Ovis aries*), individuals that had

feeding time artificially limited were only able to compensate (by extending feeding bout length) for the temporal shortfall when food availability was very high (Iason et al. 1999) . When food availability was low, the sheep were unable to compensate for lost grazing time. Given the low quality of winter food on our study area and the relatively high costs of foraging in snow, it seems likely compensating feeding behavior (if present) can only reduce, but not entirely eliminate, the negative fitness effects of the predation avoidance behaviors we have documented in elk.

We have no data comparing wolf hunting success in timbered versus open habitats. If risk reduction explains why elk move into timber, and it works, elk habitat shifts should have a negative effect on wolf hunting success and this would obviously benefit individual elk by reducing their probability of death. However, because possible death is not the only cost of an encounter with wolves (being chased is undoubtedly costly to elk that survive an attack), a reduction in the probability of death is not necessary to explain habitat shifts. Suppose the average cost of an encounter (to elk surviving an attack) exceeds the average cost of a habitat shift. If elk breaking into smaller groups and scattering into timber reduces encounter probabilities, then even if this behavior does not reduce an individual's probability of death, it should be favored. This scenario is possible if an individual elk's probability of death is the product of encounter probability and probability of death given an encounter (dilution). Upon detecting wolves, elk go from being in fewer large groups to multiple small groups. If each group's probability of encounter is reduced, then because dilution

benefits are simultaneously reduced, an individual's probability death could potentially remain constant while its probability of encounter was reduced.

Thus, some elk behavioral responses to the threat of predation may not be specifically directed at reducing the risk of dying, but rather directed at reducing the need for costly, escalated responses that arise from encounters with predators. This idea deviates from our implicit assumption that elk are engaging in certain behaviors solely to reduce risk, and that these behaviors *carry costs*, and raises the possibility that some responses to the threat of predation are attempts to *reduce* predation avoidance costs. This does not mean that habitat shifts are cost-free, but instead implies that elk may be engaging in a sophisticated balancing of costs associated with predator avoidance – balancing the cost of predator avoidance in the open with the costs of a habitat shift combined with reduced probability of encounter.

Trophic Cascades

Ungulate density and distribution can influence plant communities (McNaughton 1985) and this has led to speculation that wolves may initiate a trophic cascade, indirectly influencing Yellowstone plant communities through their effects on elk behavior (Smith et al 2003). Recent research addressing this issue has either used a bottom-up approach, examining current and pre-wolf browse patterns on willows and aspen (Ripple and Larson 2000; Ripple and Beschta 2003, 2004), or indirect measures of elk habitat use and risk such as pellet counts (Hernandez and Laundre 2005), or seasonal assessment of risk

inferred from wolf utilization distributions (Fortin et al 2005). These lines of inquiry have led to the conclusion that wolves have indirectly affected plant communities through their influence on elk behavior, specifically, that wolves have caused elk to reduce consumption of willow and aspen (woody browse). Implicit in all of these studies is the assumption that elk eat more browse when they are unconstrained by risk. This is interesting because in a meta-analysis of over 80 studies of elk dietary preferences, Christianson and Creel (in press), found that when elk are unconstrained by either risk or snow, they strongly prefer grass to woody browse. (It should be noted that in most studies in the meta-analysis the source of risk was humans and a difference to different predators is possible. However, the habitat shifts we documented in response to wolves are similar to reported elk responses to humans.) Thus the purported effect of wolves on elk diet composition is not what one would expect from a broad survey of elk dietary preferences and the effect of predation risk on the diet. Our studies presented in this dissertation, as well as work we have published elsewhere (Creel and Winnie 2005; Creel et al. 2005), indicate that when wolves are absent elk are found in areas dominated by grass, and when wolves are present elk are found in areas associated with woody browse. These results suggest that the threat of wolf predation should lead to an increase in woody browse in elk diets on our study site, rather than a reduction. Our data do not specifically address elk browsing aspen and willow versus other woody species. It is possible that aspen and willow are perceived differently from other browse species (notably conifers and sage) by elk, and may be foods that are preferred similarly to grass.

However, in every trophic cascade study in the Greater Yellowstone Ecosystem to date, despite substantial evidence to the contrary, such preferences have been assumed.

So why do these discrepancies exist? There are several possibilities. If they are occurring, trophic cascades could be driven by changes in elk density, changes in elk behavior, or both. Since wolf reintroduction, elk populations have fallen steadily both on Yellowstone's northern range and in the Gallatin drainage (where most research on trophic cascades has been done) (Creel et al in review). Fewer elk could mean reduced competition for preferred food (grass), resulting in an overall lower incidence of browsing. Weather changes provide another possible explanation. Changes in winter range snow pack may affect the relative availability of grass and browse (Christianson and Creel in press), and if post-wolf reintroduction weather has increased grass availability, then elk may have reduced their browsing. Decreased elk density and weather changes could further interact, leading to a synergistic (greater than additive) reduction in browsing. These possible explanations address influences that operate over large areas at long time scales. The relatively short time and small space scale behavioral responses that we have documented may act to partially offset these effects, by periodically increasing elk browsing. Clearly, more work needs to be done before the nature of trophic cascades in the Yellowstone Ecosystem, and mechanisms that drive them, are understood. The discrepancies in the implications and findings of current studies surrounding trophic cascades highlight the need to test alternative hypotheses, as well as the value of

integrating plant, weather, elk population, and elk behavior and distribution, data gathered at multiple temporal and spatial scales.

Influences of Indirect Costs on Prey Population Dynamics

How the costs of predator avoidance influence elk population dynamics has not been established. However, recent work in invertebrate systems indicates that indirect effects of predators on prey population dynamics can be substantial. In field experiments, the presence of predators incapable of killing prey (surgically altered damsel bugs – *Nabis spp.*) reduced aphid (*Acyrtosiphon pisum*) population growth rates by approximately 30%. In comparing the effects of threat and direct offtake in two trials, threat represented 80% and 39% of the total effect predators had on aphid population growth (Nelson et al. 2004). In a meta-analysis of 166 mostly aquatic invertebrate studies, Preisser et al. (2005) found that indirect effects of predators on prey population dynamics were “...at least as strong as direct consumption...”.

Field experiments involving vertebrates have yielded similar, but not as striking, results. In pond experiments, predator induced habitat shifts resulted in reduced growth rates in juvenile blue gill sunfish (*Lepomis macrochirus*) (Werner et al. 1983). Because the number of eggs produced are positively correlated with body size in fish, these habitat shifts are likely to result in population level consequences. In field experiments, when elk were repeatedly disturbed (but not killed) by humans during calving season, projected population growth fell from 7% annually to 0 (Phillips and Aldredge 2000). Preliminary data from the upper

Gallatin and neighboring study areas indicates that pregnancy rates may be negatively correlated with increased wolf activity (Creel unpublished data). The exact mechanism for the apparent decrease in pregnancy rates is not clear. It could be due to interference from wolves during mating season; direct behavioral responses by cow elk seeking to avoid the added burden of a pregnancy in a high risk environment; increased stress levels that interfere with some aspect of pregnancy; decreased food quality or availability because of behavioral constraints (this raises the interesting possibility of the threat of predation decreasing prey K) or a combination of factors.

The multi-scale suite of elk behavioral responses to the threat of predation, and their likely costs, indicates that the effects of wolves on elk populations can not be adequately described by offtake alone. Our work, considered with the above cited field experiments and other empirical and theoretical work (Ives and Dobson 1987; Formanowicz and Bobka 1988; Bolnick and Preisser 2005), suggests that indirect effects of predators on prey are substantial, and may influence elk population dynamics.

REFERENCES CITED

- Abramsky, Z., Strauss, E., Subach, A., Kotler, B.P., 1996. The effect of barn owls (*Tyto alba*) on the activity and microhabitat selection of *Gerbillus allenbyi* and *G. pyramidum*. *Oecologia* 105:313-319.
- Abramsky, Z., Rosenzweig, M.L., Subach, A., 2002. The costs of apprehensive foraging. *Ecology* 83:1330-1349.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour* 49:227-267.
- Anderson, A.E., Medin, D.E., Bowden, D.C., 1972. Indices of carcass fat in a Colorado mule deer population. *Journal of Wildlife Management* 63:579-594.
- Bachman, G.C., 1993. The effect of body condition on the trade-off between vigilance and foraging in Belding's ground squirrels. *Animal Behaviour* 46:233-244.
- Berger, J., Cunningham, C., 1988. Size-related effects on search times in North American grassland female ungulates. *Ecology* 69:177-183.
- Bergerud, A. T., Butler, H. E. & Miller, D. R. 1983. Antipredator tactics of calving caribou: dispersion in mountains. *Canadian Journal of Zoology* 62:1566-1575.
- Bergerud, A.T., Elliot, J.P., 1986. Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology* 64:1515-1529.
- Bergerud, A.T., Elliot, J.P., 1998. Wolf predation in a multiple-ungulate system in northern British Columbia. *Canadian Journal of Zoology* 76:1551-1569.
- Berryman, A.A., 1992. The origins and evolution of predator-prey theory. *Ecology* 73:1530-1535.
- Blumstein, D. T. & Daniel, J.C. 2002. Isolation from mammalian predators differentially affects two congeners. *Behavioral Ecology* 13:657-663.
- Bolnick, D.A., Preisser, E.L., 2005. Resource competition modifies the strength of trait-mediated predator-prey interactions: a meta-analysis. *Ecology* 86(10): 2771-2779.

- Boyce, M.S. 1993. Predicting the consequences of wolf recovery to ungulates in Yellowstone National Park. In Cook, R.S., ed. *Ecological issues on reintroducing wolves into Yellowstone National Park*. National Park Service, Denver, Colorado. NPS/NRYELL/NRSM-93/22
- Brazda, A.R., 1953. Elk migration patterns, and some of the factors affecting movements in the Gallatin River drainage, Montana. *Journal of Wildlife Management* 17:9-23.
- Burnham, K.P., Anderson, D.R. 2002. *Model Selection and Multimodel Inference, A Practical Information Theoretic Approach*. Second edition. Springer.
- Christianson, D., Creel, S., In review. A review of environmental factors affecting elk winter diets.
- Clutton-Brock, T.H., Iason, G.R., Guinness, F.E., 1987. Sexual Segregation and density-related changes in habitat use in male Red deer (*Cervus elaphus*). *Journal of Zoology* 211:275-289.
- Cook, J.G., 2002. Nutrition and Food. In: *North American Elk, Ecology and Management*. Smithsonian Institution Press, Ed. Toweill, D.E., and Thomas, J.W.
- Cook, J.G., Johnson, B.K., Cook, R.C., Riggs, R.A., Delcurto, T., Bryant, L.D., Irwin, L.L. , 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs*, 155.
- Creel, S. and Creel, N.M., 2002. *The African Wild Dog: Behavior, Ecology and Conservation*. Princeton, New Jersey: Princeton University Press.
- Creel, S., Winnie, J., Jr., 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour* 69:1181-1189.
- Creel, S., Winnie, J., Jr., Maxwell, B., Hamlin, K, Creel, M., 2005. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 86:3387-3397.
- Cresswell, W. 1994. Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. *Animal Behaviour* 47:433-442.
- Demarchi, R., 1968. Chemical composition of bighorn winter forages. *Journal of Range Management* 21(9):385-388.
- Elgar, M.A., 1989. Predator vigilance and group size in mammals and birds: a critical review of empirical evidence. *Biological Review* 64:13-33.

- Fitzgibbon, C.D., 1988. A cost to individuals with reduced vigilance in groups of Thompson's gazelles hunted by cheetahs. *Animal Behaviour* 37:508-510.
- Fitzgibbon, C.D., 1990. Why do hunting cheetahs prefer male gazelles? *Animal Behaviour* 40:837-845.
- Formanowicz, D.R. & Bobka, M.S. 1988. Predation risk and microhabitat preference: an experimental study of the behavioral responses of prey and predator. *American Midland Naturalist* 121:379-386.
- Geist, V. 2002. Adaptive and behavioral strategies. In: *North American Elk, Ecology and Management*. Smithsonian Institution Press, Ed. Toweill, D.E., and Thomas, J.W.
- Hanson, M.B., Bledsoe, L.J., Kirkevold, B.C., Casson, C.J., Nightengale, J.W., 1993. Behavioral time budgets of captive sea otter mother-pup pairs during pup development. *Zoo Biology* 12:459-477.
- Hayes, R.D., Harestad, A.S., 2000. Wolf functional responses and regulation of moose in the Yukon. *Canadian Journal of Zoology* 78:60-66.
- Hebblewhite, M. & Pletscher, D. H. 2002. Effects of elk group size on predation by wolves. *Canadian Journal of Zoology* 80:800-809.
- Heithaus, M.R., Dill, L.M., 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology* 83:480-491.
- Houston, A.I., McNamara, J.M., 1982. A sequential approach to risk-taking. *Animal Behaviour* 30:1260-1261.
- Hudson, R.J., Haigh, J.C., Bubenik, A.B. 2002. Physical and physiological adaptations. In: *North American Elk, Ecology and Management*. Smithsonian Institution Press, Ed. Toweill, D.E., and Thomas, J.W.
- Huggard, D.J., 1993. Prey selectivity of wolves in Banff National Park. II. Age, sex, and condition. *Canadian Journal of Zoology* 71:140-147.
- Hughes, J.J. & Ward, D., 1993. Predation risk and distance to cover affect foraging behaviour in Namib Desert gerbils. *Animal Behaviour* 46:1243-1245.
- Hutchinson, J.M.C., Gigerenzer, G., 2005. Connecting behavioural biologists and psychologists: Clarifying distinctions and suggestions for further work. *Behavioural Processes* 69:159-163.

- Iason, G.R., Mantecon, A.R., Sim, D.A., Gonzalez, J., Foreman, E., Bermudez, F.F., Elston, D.A., 1999. Can grazing sheep compensate for a daily foraging time constraint? *Journal of Animal Ecology* 68:87-93.
- Illius, A.W. & Fitzgibbon, C., 1994. Costs of vigilance in foraging ungulates. *Animal Behaviour* 47:481-484.
- Ives, A.R., Dobson, A.P. 1987. Antipredator behavior and the population dynamics of simple predator-prey systems. *The American Naturalist* 130(3): 431-447.
- Jenkins, K.J., Wright, R.G., 1987. Dietary niche relationships among cervids relative to winter snowpack in northwestern Montana. *Canadian Journal of Zoology* 65:1397-1401.
- Jennings, T., Evans, S.M., 1980. Influence of position in the flock and flock size on vigilance in the starling, *Sturnus vulgaris*. *Animal Behaviour* 28:634-635.
- Jones, P.F., Hudson, R.J., Farr, D.R., 2001. Evaluation of a winter habitat suitability index model for elk in west-central Alberta. *Forest Science* 48(2):417-425.
- Kemp, S., 2005. Simple Optimisation. *Behavioural Processes* 69:131-132.
- Kenward, R.E., 1978. Hawks and doves: factors affecting success and selection in goshawk attacks on woodpigeons. *Journal of Animal Ecology* 47:449-460.
- Kipling, R. 1902. *Just So Stories*. London MacMillan & Co.
- Kolenosky, G.B., 1972. Wolf predation on wintering deer in east-central Ontario. *Journal of Wildlife Management* 36:357-369.
- Krause, J., Godin, J.J., 1995. Predator preferences for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk. *Animal Behaviour* 50:465-473.
- Lazarus, J. & Symonds, M. 1992. Contrasting effects of protective and obstructive cover on avian vigilance. *Animal Behaviour* 43:519-521.
- Lima, S.L., 1996. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* 67:377-385.
- Lima, S.L., 1998. Nonlethal effects in the ecology of predator-prey interactions. *Bioscience* 48:25-34

- Lima, S.L., Dill, L.M., 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619-640.
- Lotka, A.J., 1925. *Elements of physical biology*. Williams and Wilkins, Baltimore, Maryland, USA.
- MacDonald, D.W., Stewart, P.D., Stopka, P., Yamaguchi, N., 2000. Measuring the dynamics of mammalian societies: an ecologist's guide to ethological methods. In: *Research Techniques in Animal Ecology: Controversies and Consequences*. Boitani, L. and Fuller, T. K. eds. Columbia University Press, NY.
- Main, M. B., Coblentz, B. E. 1990. Sexual segregation among ungulates: a critique. *Wildlife Society Bulletin* 18:204-210.
- Matson Labs. P.O. Box 308, Milltown, Montana, 59851
- McNamara, J.M., Houston, A.I., 1992. Risk sensitive foraging: A review of the theory. *Bulletin of Mathematical Biology* 54:355-378.
- McNaughton, S.J., 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs* 55(3):259-294.
- Mech, D.L., Smith, D.W., Murphy, K.M., MacNulty, D.R., 2001. Winter severity and wolf predation on a formerly wolf-free elk herd. *Journal of Wildlife Management* 65:998-1003.
- Merrill, E.H., 1991. Thermal constraints on use of cover types and activity time of elk. *Applied Animal Behaviour Science* 29, 251-267.
- Mitchell, B., McCowan, D., Nicholson, I.A., 1976. Annual cycles of weight and condition in Scottish Red deer, *Cervus elaphus*. *Journal of Zoology, London*, 180:107-127.
- Morgantini, L.E., Hudson, R.J., 1979. Human disturbance and habitat selection in elk. In: *North American elk: ecology, behavior, and management*. University of Wyoming, Ed. Boyce, M.S., Hayden-Wing, L.D.
- Morgantini, L.E., Hudson, R.J., 1985. Changes in diets of Wapiti during a hunting season. *Journal of Range Management* 38:77-79.
- Neiland, K.A., 1970. Weight of dried marrow as indicator of fat in caribou femurs. *Journal of Wildlife Management* 34:904-907.
- Nelson, E.H., Matthews, C.E., Rosenheim, J.A., 2004. Predators reduce prey population growth by inducing changes in prey behavior. *Ecology* 85(7):1853-1858.

Peek, J.M., Lovaas, A.L., 1968. Differential distribution of elk by sex and age on the Gallatin winter range, Montana. *Journal of Wildlife Management* 32:553-565.

Peek, J.M., Lovaas, A.L., Rouse, R.A., 1967. Population changes within the Gallatin elk herd, 1932-65. *Journal of Wildlife Management* 31:304-316.

Phillips, G., Alldredge, A.W., 2000. Reproductive success of elk following disturbance by humans during calving season. *Journal of Wildlife Management* 64(2):521-530.

Powell, G.V.N., 1974. Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in relation to predation and foraging. *Animal Behavior* 22:501-505.

Preisser, E.L., Bolnick, D.I., Benard, M.F., 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86(2):501-509.

Pulliam, H.R., 1973. On the advantages of flocking. *Journal of Theoretical Biology* 38:419-422.

Rew, Lisa J.; Maxwell, Bruce D.; Aspinall, Richard; 2005. Predicting the occurrence of nonindigenous species using environmental and remotely sensed data. *Weed Science* 53:236-241.

Rew, Lisa J.; Maxwell, Bruce D.; Dougher, Frank, L., Aspinall, Richard, In Press. Searching for a needle in a haystack: evaluating survey methods for non-indigenous plant species. *Biological Invasions Special Issue*.

Ripple, W.J., Bechsta, R.L., 2003. Wolf reintroduction, predation risk and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management* 184:299-313.

Ripple, W.J., Bechsta, R.L., 2004. Wolves, elk, willows and trophic cascades in the upper Gallatin Range of South-western Montana, USA. *Forest Ecology and Management* 200: 161-181.

Ripple, W.J., Larsen, E.J., 2000. Historic aspen recruitment, elk and wolves in northern Yellowstone National Park. *Biological Conservation* 95:361-370.

Roberts, G., 1996. Why individual vigilance declines as group size increases. *Animal Behaviour* 51:1077-1086.

Savino, J.F., Stein, R.A., 1989. Behavioural interactions between fish predators and their prey: effects of plant density. *Animal Behaviour* 37:311-321.

Scheel, D., 1993. Watching for lions in the grass: the usefulness of scanning and its effects during hunts. *Animal Behaviour* 46:695-704.

Shoensmith, M.W., 1980. Seasonal movements and social behavior of elk on the Mirror Plateau, Yellowstone National Park. In: *North American Elk: Ecology, Behavior and Management*. University of Wyoming Press, Ed. Boyce, M.S. and Hayden-Wing, L.D.

Sih, A. & McCarthy, T.M. 2002. Prey responses to pulses of risk and safety: testing the risk allocation hypothesis. *Animal Behaviour* 63:437-443.

Sih, A. Krupa, J., Travers, S. 1990. An experimental study on the effects of predation risk and feeding regime on the mating behavior of the water strider. *The American Naturalist* 135:284-290.

Sinclair, A.R.E., Arcese, P., 1995. Population consequences of predation sensitive foraging: the Serengeti wildebeest. *Ecology* 76:882-891.

Smith, D.W., Peterson, R.O., Houston, D.B., 2003. Yellowstone after wolves. *Bioscience* 53(4):330-340.

Turner, G.F., Pitcher, T.J., 1986. Attack abatement: a model for group protection by combined avoidance and dilution. *The American Naturalist* 128:228-240.

Stephens, P.A., Buskirk, S.W., Hayward, G.D., Martinez Del Rio, C., 2005. Information Theory and hypothesis testing: a call for pluralism. *Journal of Applied Ecology* 42:4-12.

Sweeney, J.M., Sweeney, J.R. 1984. Snow depths influencing winter movements of elk. *Journal of Mammalogy* 65(3):524-526.

Turner, G.F., Pitcher, T.J., 1986. Attack abatement: a model for group protection by combined avoidance and dilution. *The American Naturalist* 128:228-240.

Uetz, G. W., Hieber, C.S., 1994. Group size and predation risk in colonial web-building spiders: analysis of attack abatement mechanisms. *Behavioral Ecology* 5:326-333.

Underwood, R., 1982. Vigilance behaviour in grazing African antelopes. *Behaviour* 79:81-107.

Werner, E.E., Gilliam, J.F., Hall, D. J., Mittelbach, G.G., 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540-1548.

Zar, J. H., 1999. *Biostatistical Analysis*, 4th Edition. Upper Saddle River, New Jersey: Prentice-Hall.

APPENDIX A

MODEL PARAMETERS IN BEST MODELS

Appendix A. Specific parameters in each of the models in Figure 2.1, with $\Delta AICc$ scores.

(a) Wolves present.

Rank	Sage Wolves Present							Delta AIC
	1	2	3	4	5	6	7	
1	Prev Loc							0
2	Prev Loc	Dense Opn						0.14
3	Prev Loc	Depth Opn	Depth Tmbr					0.332
4	Prev Loc	Dense Opn	Dense Tmbr					0.732
5	Day	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr		0.764
6	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr			0.943
7	Prev Loc	Depth Opn	Depth Tmbr	Dense Tmbr				1.185
8	Prev Loc	Depth Tmbr						1.563
9	Prev Loc	Sex						1.74
10	T x W	Prev Loc	Dense Opn					1.822
11	Day	Prev Loc						1.877
12	T x W	Prev Loc						1.883
13	Day	Temp c	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr	1.885
14	Prev Loc	Dense Opn						1.889
15	Prev Loc	Dense Tmbr						1.919
16	Temp c	Prev Loc	Dense Opn					1.944
17	Temp c	Prev Loc						1.998
18	Wind sp	Prev Loc						2

(a) Wolves present continued.

Rank	Grass Wolves Present							Delta AIC
	1	2	3	4	5	6	7	
1	Prev Loc							0
2	T x W	Prev Loc						0.606
3	Wind sp	Prev Loc						1.318
4	Prev Loc	Depth Opn	Depth Tmbr					1.492
5	Prev Loc	Dense Opn						1.539
6	Temp c	Prev Loc						1.669
7	Prev Loc	Dense Tmbr						1.709
8	T x W	Prev Loc	Dense Opn					1.835
9	Prev Loc	Sex						1.869
10	Prev Loc	Depth Opn						1.928
11	Day	Prev Loc						1.983
12	T x W	Prev Loc	Depth Opn	Depth Tmbr				1.987
13	Prev Loc	Depth Tmbr						2
Rank	Conifer Wolves Present							Delta AIC
	1	2	3	4	5	6	7	
1	Prev Loc							0
2	Prev Loc	Dense Opn						1.317
3	T x W	Prev Loc						1.701
4	Prev Loc	Dense Tmbr						1.879
5	Prev Loc	Depth Opn						1.936
6	Wind sp	Prev Loc						1.945
7	Temp c	Prev Loc						1.991
8	Prev Loc	Depth Tmbr						1.996
9	Day	Prev Loc						1.997
10	Prev Loc	Sex						2

(b) Wolves absent.

Rank	Sage Wolves Absent										Delta AIC	
	1	2	3	4	5	6	7	8	9	10		
1	Day	Wind sp	T x W	Prev Loc	Depth Opn	Dense Tmbr						0
2	Day	Wind sp	T x W	Prev Loc	Depth Opn	Dense Opn	Dense Tmbr					0.12
3	Day	Wind sp	T x W	Prev Loc	Depth Opn							0.275
4	Day	Wind sp	T x W	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr				0.45
5	Day	Wind sp	T x W	Prev Loc	Depth Opn	Dense Opn	Dense Tmbr	Sex				0.683
6	Day	Temp c	Wind sp	Prev Loc	Depth Opn	Dense Opn	Dense Tmbr					0.997
7	Day	Wind sp	T x W	Prev Loc	Depth Opn	Dense Tmbr	Sex					1.195
8	Day	Wind sp	T x W	Prev Loc	Depth Opn	Depth Tmbr	Dense Tmbr					1.242
9	Day	Temp c	Wind sp	Prev Loc	Depth Opn	Dense Tmbr						1.277
10	Day	Temp c	Wind sp	T x W	Prev Loc	Depth Opn	Dense Tmbr					1.435
11	Wind sp	T x W	Prev Loc	Depth Opn	Dense Opn	Dense Tmbr						1.488
12	Day	Temp c	Wind sp	T x W	Prev Loc	Depth Opn	Dense Opn	Dense Tmbr				1.512
13	Day	T x W	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr					1.54
14	Day	Temp c	Wind sp	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr				1.628
15	Day	Temp c	Wind sp	Prev Loc	Depth Opn	Dense Opn	Dense Tmbr	Sex				1.683
16	Day	Wind sp	T x W	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr	Sex			1.707
17	Day	Temp c	Wind sp	Prev Loc	Depth Opn							1.759
18	Day	Temp c	Wind sp	T x W	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr			1.793
19	Day	Temp c	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr					1.799
20	Day	Temp c	Wind sp	T x W	Prev Loc	Depth Opn						1.817
21	Wind sp	T x W	Prev Loc	Depth Opn	Dense Opn	Dense Tmbr	Sex					1.827
22	Day	Wind sp	T x W	Prev Loc	Depth Opn	Sex						1.848
23	Wind sp	T x W	Prev Loc	Depth Opn								1.968

(b) Wolves absent continued.

Rank	Grass Wolves Absent										Delta AIC	
	1	2	3	4	5	6	7	8	9	10		
1	Day	T x W	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr	Sex				0
2	Day	Wind sp	T x W	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr	Sex			0.618
3	Day	Prev Loc	Depth Opn	Snow Depth Timber	Dense Opn	Dense Tmbr	Sex					0.752
4	Day	Temp c	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr	Sex				1.274
5	Day	Wind sp	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr	Sex				1.466
6	Day	T x W	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr					1.73
7	Day	Temp c	T x W	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr	Sex			1.904
Rank	Conifer Wolves Absent										Delta AIC	
	1	2	3	4	5	6	7	8	9	10		
1	Day	Wind sp	T x W	Prev Loc	Depth Opn	Dense Tmbr	Dense Opn	Dense Tmbr	Sex			0
2	Day	Temp c	Wind sp	T x W	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr	Sex		0.644
3	Wind sp	T x W	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr	Sex				0.672
4	Day	Temp c	T x W	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr	Sex			1.04
5	Day	T x W	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr	Sex				1.042
6	Temp x Wind	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr	Sex					1.492
7	Temp c	Wind sp	T x W	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr	Sex			1.933
8	Day	Temp c	Prev Loc	Depth Opn	Depth Tmbr	Dense Opn	Dense Tmbr	Sex				1.971