The gray wolf - scavenger complex in Yellowstone National Park

by

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Abstract

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The reintroduction of gray wolves (*Canis lupus*) to Yellowstone National Park in 1995 provides a natural experiment in which to study the effects of a keystone predator on ecosystem function. Gray wolves often provision scavengers with carrion by partially consuming their prey. In this dissertation, I seek to understand the causes of partial carcass consumption by wolves and quantify the impact of this predator mediated food supply on sympatric meat eating species. In addition, I compare scavenging at human hunter killed-elk (*Cervus elaphus*) to wolf-killed elk, and predict how a changing climate will affect the scavenger complex.

I found that the percent of an elk carcass consumed by wolves increases as snow depth decreases and the ratio of wolf pack size to prey size and distance to the road increases. In addition, wolf packs of intermediate size provide the most carrion to scavengers. My results also demonstrate that wolves increase the time period over which carrion is available from pre-wolf conditions, and change the variability in scavenge from a late winter pulse dependent

primarily on abiotic environmental conditions to one that is relatively constant across the winter and primarily dependent on wolf demographics. Wolves also decrease the year-to-year and month-to-month variation in carrion availability. By transferring the availability of carrion from the highly productive late winter, to the less productive early winter and from highly productive years to less productive ones, wolves provide a temporal subsidy to scavengers.

Human hunters in the Yellowstone Ecosystem also provide resource subsidies to scavengers by provisioning them with the remains of their kills. Carrion from hunter kills is highly aggregated in time and space whereas carrion from wolf kills is more dispersed in both time and space. This provides the context for a natural experiment to investigate the response of consumers to resources with differing spatial and temporal dispersion regimes. I estimated the total amount of carrion consumed by each scavenger species at both wolf and hunter kills over four years. Species with large feeding radii [bald eagles (*Haliaeetus leucocephalus*) and ravens (*Corvus corax*)], defined as the area over which a consumer can efficiently locate and integrate resources, dominated consumption at the highly aggregated hunter kills whereas competitively dominant species [coyotes] dominated at the more dispersed wolf kills. In addition, species diversity and the evenness of carrion consumption between scavengers was greater at wolf kills than at hunter kills while the total number of scavengers at hunter kills exceeded those at wolf kills. From a community perspective, the top-down effect of predation is likely to be stronger in the vicinity of highly aggregated resource pulses as species with large feeding radii switch to feeding on alternative prey once the resource pulse subsides.

Understanding the mechanisms by which climate and top predators interact to affect community structure accrues added importance as humans exert growing influence over both climate and regional predator assemblages. In Yellowstone, winter severity and reintroduced gray wolves together determine the availability of winter carrion on which numerous scavenger species depend for survival and reproduction. I analyzed 55 years of weather data from Yellowstone and found that winters are getting shorter, as measured by the number of days with snow on the ground, because of decreased snowfall and an increase in the number of days where the temperature exceeds freezing. I demonstrate that in the absence of wolves, early snow thaw implies that late-winter carrion will be substantially reduced, potentially causing food bottlenecks to develop for scavengers. In addition, by narrowing the window over which carrion is available and thereby creating a resource pulse, climate change is expected to favor scavengers that can track food sources quickly over great distances. In the presence of wolves, however, late-winter reduction in carrion is largely mitigated. By buffering the effects of climate change on carrion availability, wolves allow scavengers to adapt to a changing environment over a longer time scale more commensurate with natural processes.

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Chapter One

Summary

C.C. Wilmers

The reintroduction of gray wolves (*Canis lupus*) to Yellowstone National Park provides a natural experiment in which to study the effects of a keystone predator on ecosystem function. The accessibility and visibility of the Northern Range of Yellowstone National Park provides a unique opportunity to observe wolves hunting, feeding, socializing and otherwise conducting the various activities that they undertake in their daily lives. When wolves were first released in Yellowstone in 1995, the scientific community did not appreciate the potential effect that wolves may have on other meat eating species by provisioning them with food from their kills. In fact, the ecology of scavenging in North America and the role of top predators in facilitating this process is poorly understood. It is the goal of this dissertation to shed light on the role of top predators in general and gray wolves specifically as mediators of food supply to scavengers.

In chapter 2, we lay the groundwork for future chapters by experimentally determining feeding rates for the primary carnivores in this study. In general, predator feeding strategies lie on a continuum between energy-maximizers who maximize the amount of energy obtained from a patch of food, and time-minimizers who minimize the time required to get a fixed ration of food from a patch. Carnivores feeding on large prey should adopt a time-minimizing strategy by maximizing their active consumption rate (ACR) if they evolved under conditions of high competition from group members, and conversely adopt an energy-maximizing strategy if they evolved under conditions of low competition from group members and were thus able to monopolize their prey. By provisioning animals with large pieces of ungulate carcasses, we measured ACR for captive gray wolves, coyotes (*Canis latrans*) and grizzly bears (*Ursus arctos*). In accordance with a conspecific competition hypothesis, ACR increased with increasing sociality. Other factors influencing ACR included subject weight and food type, with ACR on muscle and organ being significantly faster than on bone and hide. Measures of ACR are crucial to empirical and theoretical studies assessing foraging decisions and may be used as an indicator of an animal's competitive environment.

Gray wolves often provision scavengers with carrion by partially consuming their prey. In chapter 3, we examine how gray wolf foraging behavior influences the availability of carrion to scavengers by reporting on observations of consumption of 57 wolf-killed elk (*Cervus elaphus*) in which we calculated the percent of edible biomass eaten by wolves from each carcass. We found that the percent of a carcass consumed by wolves increases as snow depth decreases and the ratio of wolf pack size to prey size and distance to the road increases. In addition, wolf packs of intermediate size provide the most carrion to scavengers. Applying linear regression models to the years prior to reintroduction, we calculate carrion biomass availability had wolves been present, and contrast this to a previously published index of carrion availability. Our results demonstrate that wolves increase the time period over which carrion is available, and change the variability in scavenge from a late winter pulse dependent primarily on abiotic environmental conditions to one that is relatively constant across the winter and primarily dependent on wolf demographics. Wolves also decrease the year-to-year and month-to-month variation in carrion availability. By transferring the availability of carrion from the highly productive late winter, to the less productive early winter and from highly productive years to less productive ones, wolves provide a temporal subsidy to scavengers.

Gray wolves and human hunters in the Yellowstone Ecosystem both provide resource subsidies to scavengers by provisioning them with the remains of their kills. Carrion from hunter kills is highly aggregated in time and space whereas carrion from wolf kills is more dispersed in both time and space. This provides the context for a natural experiment which we report on in chapter 4 to investigate the response of consumers to resources with differing spatial and temporal dispersion regimes. We estimated the total amount of carrion consumed by each scavenger species at both wolf and hunter kills over four years. Species with large feeding radii [bald eagles (*Haliaeetus leucocephalus*) and ravens (*Corvus corax*)], defined as the area over which a consumer can efficiently locate and integrate resources, dominated consumption at the highly aggregated hunter kills whereas competitively dominant species [coyotes] dominated at the more dispersed wolf kills. In addition, species diversity and the evenness of carrion consumption between scavengers was greater at wolf kills than at hunter kills while the total number of scavengers at hunter kills exceeded those at wolf kills. From a community perspective, the top-down effect of predation is likely to be stronger in the vicinity of highly aggregated resource pulses as species with large feeding radii switch to feeding on alternative prey once the resource pulse subsides.

Fieldwork on the Northern Range of Yellowstone indicates that wolves facilitate carrion acquisition by scavengers, but it is unclear whether this represents a transient or permanent effect of wolf reintroduction. In chapter 5 we present a wolf-elk model with human elk harvest and use it to investigate the long term consequences of predator-prey dynamics and hunting on resource flow to scavengers. Our model shows that while wolves reduce the total amount of carrion, they stabilize carrion abundance by reducing temporal variation in the quantity of carrion and extending the period over which carrion is available. Specifically, the availability of carrion is shifted from reliance on winter severity and elk density to dependence on the strength of wolf predation. Though wolves reduce the overall abundance of carrion by lowering the elk population, this reduction is partially offset by increases in the productivity of an elk population invigorated by removal of the weakest individuals. The result of this is higher carrion production per elk in the presence of wolves. In addition, this yields an ecological explanation for the phenomena that predators increase the robustness of their prey: namely that by reducing the effect of density-dependent resource competition among elk, those that remain, even some of the older animals, are better fed and healthier as a result. Our model also suggests that human hunting has no effect on the distribution of carrion across the year but is crucial in determining the long-term abundance of carrion because of the effect of hunting on elk population levels. By reducing the proportion of cows in the annual hunt, which have historically been high in order to control the number of elk migrating north of the park, managers can allow an adequate supply of carrion without substantially reducing hunter take. The effects of a more tractable food resource is likely to benefit scavengers in Yellowstone and other areas of the world where wolves have been or are currently being considered for reintroduction.

Understanding the mechanisms by which climate and top predators interact to affect community structure accrues added importance as humans exert growing influence over both climate and regional predator assemblages. In Yellowstone National Park, winter severity and reintroduced gray wolves together determine the availability of winter carrion on which numerous scavenger species depend for survival and reproduction. In chapter 6, we analyze 55 years of weather data from Yellowstone and found that winters are getting shorter, as measured by the number of days with snow on the ground, because of decreased snowfall and an increase in the number of days where the temperature exceeds freezing. We show that in the absence of wolves, early snow thaw implies that late-winter carrion will be substantially reduced, potentially causing food bottlenecks to develop for scavengers. In addition, by narrowing the window over which carrion is available and thereby creating a resource pulse, climate change is expected to favor scavengers that can track food sources quickly over great distances. In the presence of wolves, however, late-winter reduction in carrion is largely mitigated. By buffering the effects of climate change on carrion availability, wolves allow scavengers to adapt to a changing environment over a longer time scale more commensurate with natural processes.

Chapter Two

Constraints on active consumption rates in gray wolves, coyotes and grizzly bears.

C.C. Wilmers and D. R. Stahler

Introduction

Optimal foraging theory predicts that foragers attempt to maximize their energy intake rates (Charnov 1976). Unfortunately for comparative biologists, measures of intake rate are inconsistent across studies. Many consider intake rate to be a long-term average of net energy intake, over which the animal may spend time searching, chasing, consuming and/or digesting prey (Stephens and Krebs 1986). Active consumption rate (ACR), defined as the weight of food consumed per unit time of active feeding, is often implicit in net measures yet may be more appropriate as a primary measure of feeding performance when, for example, food patches are large and concentrated. Diet selection studies on feral goats, for instance, have revealed that these animals will choose grass species that maximize their ACR over variants that are more nutritious (Illius et al. 1999). Grizzly bears (*Ursus arctos*) feeding on fruit diets have been shown to lose weight if berries are not at a high enough density to meet their maximum ACR (Rode and Robbins 2000).

Predators feeding on large prey may similarly seek to maximize ACR rather than overall energy intake (Holekamp et al. 1997). Recent modeling efforts, however, illustrate the paucity of information that exists on ACR for carnivores (Carbone et al. 1997, Carbone et al. 1999). For example, Carbone and colleagues (1997), used an estimate of wild dog (*Lycaon pictus*) ACR extrapolated from Schaller (1972), who describes one dog leaving a carcass with a full gut 8 minutes after a kill. Although this information is useful, knowledge of how ACR varies within and between species according to carnivore size, age, sex, feeding strategy and prey meat type (e.g. bone vs. muscle) is necessary for a fine grade understanding of predator foraging decisions. As an example of this fine grade approach, ACR may be used in conjunction with field observations of time spent at a carcass to determine the approximate number of calories obtained by an animal in a given feeding bout (Henschel and Tilson 1988). Models examining energetic or predator-prey interactions can then incorporate ACR into more accurate measures of assimilation efficiency and interaction strength.

ACR may also be an important predictor of feeding strategy. Predators may be thought of as either energy-maximizers who maximize the amount of energy obtained from a patch, or time-minimizers who minimize the time required to get a fixed ration of food from a patch (Schoener 1971). Griffiths (1980) suggested that these strategies lie on a continuum and correlate with the group size of the species concerned. As group size increases, competition between group members similarly increases, making the time-minimizing strategy more beneficial (i.e. intra-group competition influences feeding rate). Carnivores living in large groups, such as spotted hyenas (*Crocuta crocuta*), African lions (*Panthera leo*), wild dogs and gray wolves, feed quickly in a scramble competition for food, then leave the immediate area (Mech 1970, Kruuk 1972, Schaller 1972). Conversely solitary animals, such as leopards (*Panthera pardus*) and grizzly bears often cache large prey and may stay with them for some time (Hornocker 1970, Schaller 1972, Craighead et al. 1995).

Social species often gorge themselves at the cost of inefficient digestion (Mech 1970), whereas solitary species may take more time to feed and more efficiently digest their food. As an example of intra-specific variation in ACR, Tilson and Hamilton (1984) showed that hyenas in East Africa, which live in relatively large groups, consumed prey much more rapidly than did hyenas in the Namib dessert, which live in relatively small groups. While all species on the feeding strategy continuum should seek to maximize their energy intake, species living in large groups are predicted to have high ACR, species living in small groups intermediate ACR and solitary species low ACR. This relationship arises due to the different selection pressure on ACR imposed by differing levels of intra-specific competition. Inter-specific competition may also be an important factor driving ACR (Carbone et al. 1997) but is generally thought to be minor compared to intra-specific competition.

The present study was conducted in order to measure ACR in three common North American carrion feeders: gray wolves, who are highly social and live in large packs of 2-36 individuals (Mech 1970, Mech et al. 1998); coyotes who are moderately social and live in small packs of 2-10 individuals (Bekoff and Wells 1980, Gese et al. 1996), and grizzly bears who are solitary (Craighead et al. 1995). We tested how ACR varies with predator size, age, sex, and prey meat type. We then investigated how ACR varies between species according to levels of sociality.

Methods

Coyote feeding trials were conducted in May 2001 at the Logan, Utah, field station of the United States Department of Agriculture National Wildlife Research Center. Coyotes were caged in 0.1 ha outdoor enclosures. We fed 29 coyotes ranging in age from 2 to 12 years and in weight from 5.6 to 13.7 kg. Food was withheld from subjects for 48 hours prior to feeding in order to insure robust appetites. Gray wolf feeding trials were conducted in June 2001 at Mission Wolf, a captive wolf refuge outside of Gardner, Colorado. Wolves were caged in 0.5-2.0 ha outdoor enclosures.

We fed 15 wolves ranging in age from 6 to 12 years and in weight from 31.8 to 61.3 kg. Food was withheld for 72 hours prior to feeding. Grizzly bear feeding trials were conducted in May 2001 at the Grizzly Discovery Center in West Yellowstone, Montana. Grizzly bears were caged in 25 m^2 indoor enclosures and were rotated into a 0.5 ha outdoor habitat twice a day. We fed 7 grizzly bears ranging in age from 3 to 14 years and in weight from 158 to 425 kg. Food provisions for the bears were cut in half for 24 hours prior to the feeding trials. We chose animals representative of a wide range of weight and age, and withheld food for a period long enough to ensure robust hunger levels. We did not have weight information on coyotes until after the feeding trials, however, and the majority were very close in weight. All animals were cared for in accordance with principles and guidelines of the Canadian Council on Animal Care.

Feeding trials consisted of provisioning animals with large pieces of muscle, organ, rib cage, leg bone and hide from freshly killed mule deer (*Odocoileus hemionus*), elk and moose (*Alces alces*). We chose pieces of muscle from the hind and front quarters that were similarly dense and large enough to insure that subjects would tear at the meat as they would in the wild but not so large as to fully satiate them. Rib cage, leg bone and hide each had approximately 3cm of meat on them at the beginning of the feeding trial. We provisioned wolves and grizzly bears with rib, leg bone and hide from elk only. We fed mule deer to coyotes which had thinner bone and hide, but this did not seem to make a difference because coyotes tended to scrape the bone rather than break it. All meat was weighed and fed to the animals individually. Subjects were then timed to the nearest second until they fully consumed the meat, as was the case with muscle and organ, or for a preset time until the meat was retrieved, as was the case with all bones and hide. If meat was retrieved, we weighed the remains and subtracted this from the beginning weight in order to calculate the total weight consumed. Feeding time was defined as actively licking, tearing, stomping (grizzly bears stomp ribs in order to break them) or chewing meat. Time not actively feeding on the meat was excluded from the measure of feeding time. ACR was then calculated as the ratio of the weight of meat consumed to feeding time in grams/minute. We conducted at least 10 trials per meat type for coyotes and wolves and 7 trials per meat type for grizzly bears. In some cases, however, sample sizes were lower than 10 because of logistical problems with certain animals (e.g. certain animals, particularly certain wolves, would guard bones when we tried to retrieve them for weighing). We randomized the order in which meat type was fed to each animal. Feeding sessions were conducted over a few days for each species with the interval between sessions equal to withholding times reported above. If an animal was fed multiple meat types in the same day, we took care that the amount of food it received was small relative to its regular daily ration so as to mitigate the effect of satiation. We did not feed leg bone or organs to grizzly bears because these were unavailable. Wolves did not eat the hide we provisioned.

We calculated mean (± standard error) ACR for each species by meat type. T-tests were used to compare ACR between meat types and between sexes. We used standard linear regression models to determine the effect of age and weight on ACR.

Results

Coyotes

ACR was not significantly different between rib, leg bone and hide (RBH) or between muscle and organ (MO) (fig. 1). Differences between ACR on RBH and MO, however, were highly significant ($p<0.01$). Coyote age was negatively associated with ACR on both RBH and MO, however it was only significant on MO ($p=0.02$, $r^2=0.38$). Coyote weight was not significant by itself (fig. 2), but when controlling for age, there was a positive association between weight and ACR on both RBH and MO. Most of the coyotes tested were between 10 and 12 kg, which was too small a range to properly explore the effect of weight on coyote ACR. Coyote sex was not a significant predictor of ACR on either MO or RBH.

Wolves

As in coyotes, ACR on rib and leg bone (RB) did not differ significantly nor did ACR on muscle and organ (MO) (fig. 1). Differences between ACR on RB and MO, however, were highly significant ($p<0.01$). Although wolf weight was positively correlated with ACR on all meat types, it was only significantly correlated with ACR on muscle and organ ($p=0.05$, $r^2=0.30$) (fig. 2). ACR of female wolves was slower than males on all meat types but the difference was only significant on muscle ($p=0.05$). Wolf gender and weight were highly correlated ($r=0.88$), so that when controlled for weight, gender was no longer a significant predictor of ACR. ACR slowed with wolf age but this effect was not significant on any of the meat types.

Grizzly Bears

ACR on rib and hide (RH) did not differ significantly (fig. 1). Differences between RH and muscle, however, were highly significant ($p < 0.01$). Grizzly bear weight was positively correlated with ACR on all three meat types. It was a significant predictor of ACR on muscle ($p=0.02$, $r^2=0.67$) (fig. 2), nearly significant on hide ($p=0.08$, $r^2=0.48$) and not significant on ribs. Grizzly bear age was also a good predictor of ACR ($p=0.09$, $r^2=0.67$) on muscle, but as age was highly correlated with grizzly bear weight ($r=0.86$), it was not possible to determine the effect of age alone. Of the 7 grizzly bears tested, only one was female, so it was not possible to determine the effect of grizzly bear sex on ACR. Furthermore the female was not an obvious outlier in the data

Comparisons

Feeding technique on muscle was similar between species, with animals using their canines to tear off strips of meat. Additionally, ACR on muscle was significantly predicted by subject weight in wolves and grizzly bears. Although we suspect that this is also the case with coyotes, we were unable to demonstrate this due to the lack of variation in coyote weight. By dividing ACR for each subject by its weight, we were able to obtain a standardized ACR (ACR/weight) for comparison between species. Species levels of sociality correlated well with standardized ACR. Standardized gray wolf ACR was faster than coyote ACR (24.78 to 17.85 g/kg·min, $p=0.07$) which in turn was much faster than grizzly bear ACR (17.85 to 2.75 g/kg·min, $p<0.01$).

Discussion

When consuming a carcass, wolves eviscerate the organs, feed on the major muscle groups on the hind and front quarters and then pick the remaining muscle off the ribs, leg bones and hide (Mech 1970, Carbyn 1983). The skeleton, particularly the larger bones, and some hide usually remain after the feeding has finished. ACR at a carcass can be broken down into two distinct periods depending on the stage of consumption of the kill. Our results show that major muscle and organ is consumed at a similarly high rate while minor muscle on the bone and hide is consumed at a similarly slower rate (fig. 1). These differences may reflect feeding method. When presented muscle, all three species used their canines to tear off strips of meat. Conversely, when presented bone and hide, they turned their heads sideways, chewing and scraping the meat, and occasionally breaking bone, with their carnassial teeth.

Measures of ACR may be combined with field observations to estimate the amount of biomass consumed by an individual or a species at a particular kill site. Field measures of biomass consumed may be derived in two ways. (1) Absolute measures may be obtained by focal sampling of subjects, recording when they are actively feeding and what part of the carcass they are feeding on. Biomass consumed is the time spent feeding on each meat type weighted by ACR for those meat types. (2) Relative measures may be obtained by scan sampling of subjects at regular intervals, recording whether they are actively feeding or not, and what stage of consumption the carcass is in. Biomass consumed may then be estimated using relative feeding rates between individuals or species and an estimate of how much biomass is available (Henschel and Tilson 1988). Absolute measures are likely to be more accurate than relative measures but may be more difficult to obtain if the carcass is occasionally blocked from view or sampling effort is constrained by other research protocols.

Results presented here suggest that, within a species, ACR is likely to be affected by carnivore weight, age and sex. As carnivores increase in size, ACR tends to increase (fig. 2). Female wolves were slower feeders than males but they were also smaller, thus the ACR difference is most likely due to the sexual size dimorphism in canids. As canids get older they tend to feed more slowly, possibly due to lost or chipped teeth (Doug Smith pers. comm.). In addition, older animals are more likely to be dominant which might decrease the effect of intra-group competition on ACR. We did not test the effect of dominance on ACR, but this might be an important factor to consider in future studies. Grizzly bears, conversely, tended to feed more rapidly as they increased in age. Our sample size, however, was not large enough to tease out the effect of age from weight on ACR in grizzly bears.

At the proximate level, the differences in ACR between wolves, coyotes and grizzly bears may be due differences in gut physiology and dentition. Wolves, for instance, are able to expand their gut capacity in order to consume large quantities of meat (Mech 1970). In addition, the masticatory apparati of the wolf is adapted to eating food quickly in large packages (Hall 1978). Grizzly bears, conversely, have an elongated digestive tract designed for more efficient digestion of vegetation (Herrero 1985). Ursid molars are also longer and flatter than those of canids so that they may more efficiently grind plant matter (Kurten 1976). The grizzly bears ability to consume and digest vegetation, therefore, may cause a corresponding decrease in their ACR on meat.

Feeding strategy (time-minimizing vs. energy-maximizing) was a good indicator of ACR, which increased with the degree of sociality of the species. Though our sample size of species is small, ACR increases with species-specific group size within taxa (between coyotes and wolves), and between taxa (between canids and bears). At the ultimate level, intensity of competition between group members may drive the observed patterns in standardized ACR. Wolves in the wild feed communally at fresh kills, with as many as 13 animals feeding at once (Mech 1970). Coyotes feed in smaller groups, with no more than 5 individuals feeding at the same time (Wilmers personal observation). Grizzly bears feed singly and will generally stay at a carcass for many hours, intermittently feeding and sleeping on the carcass (Wilmers personal observation). Preliminary evidence suggests that because of intense competition from conspecifics, wolves have evolved a time-minimizing strategy by maximizing their ACR. Coyotes are also time-minimizers but because competition is less than that in wolves due to smaller group size, they feed more slowly. Conversely grizzly bears - which are solitary and thus do not face competition from group members – are able to monopolize kills and hence have evolved an energy-maximizing strategy for which selection on ACR has been relaxed.

Examination of Schaller's observation of a wild dog mentioned previously reveals a similar pattern. Assuming a gut capacity of 4.4 kg (Carbone et al. 1997) and body weight of 25 kg (Gorman et al. 1998), this wild dog would have a minimum standardized ACR of 22 g/kg·min, making wild dog ACR in accord with the values we have reported for wolves. Wild dogs are also highly social, living in packs of 2-32 animals with a mean pack size of 9-10 animals (Kruuk and Turner 1967, Schaller 1972), which is similar to reported average pack sizes for wolves (Mech et al. 1998).

Other explanations may exist for the patterns that we have observed regarding the effect of species-specific sociality on ACR. For instance, the difference in consumption rates between the three species may be due to their position along a dietary specialist-generalist continuum with wolves as specialists, coyotes as moderate generalists and grizzly bears as the ultimate generalist. Specialists may be able to maximize ACR's on one food type because they are not constrained in doing so by other dietary requirements. It is also possible that animals studied in captivity behave differently than their wild counterparts. Predators at a kill in the wild, for instance, are likely to be more vigilant and may engage in competitive interactions with conspecifics. Our study subjects, however, were fed individually. In order to control for this, our definition of ACR specifically excludes vigilance and intraspecific interactions which are most likely to vary with increasing competition. Ecologists seeking to measure biomass consumed by predators in the wild may need to be cautious, therefore, to discount time spent vigilant and interacting from total time at carcass in order to obtain active feeding times.

A carcass may be divided up into several components with regard to feeding behavior. Our results indicate, however, that from an ACR perspective, it is unnecessary to distinguish between muscle and organs for coyotes and wolves and between ribs, and/or bones and/or hide for all three species. In addition, we have shown that ACR at ungulate carcasses may (1) vary with carnivore age and weight, with larger and younger animals tending to feed more quickly in canids and larger and older animals tending to feed more quickly in grizzly bears, and (2) increase as mean species-specific group size increases. We have presented a method that may be used in conjunction with field observations to measure biomass consumed, and parameterize theoretical models on foraging behavior, energetic and predator-prey dynamics. In addition, standardized ACR is an indicator of position on the time-minimizing energy-maximizing continuum and may be indicative of an individual or species' competitive history.

Table 1. Mean ACR by meat type for all species. Data are in g/min ± SE. There was no significant difference between ACR on ribs, bone and hide (RBH) or between muscle and organ (MO) in each of the species. Differences between RBH and MO, however, where highly significant in all three species ($p<0.01$).

Meat Type	**Coyote**	**Gray Wolf**	**Grizzly Bear**
Muscle	192.45 ± 29.75	1118.79 ± 152.10	797.80 ± 245.70
Organ	208.92 ± 68.36	1029.83 ± 208.25	NA
Rib	27.57 ± 5.52	293.97 ± 67.26	62.82 ± 11.91
Bone	27.37 ± 3.77	278.78 ± 89.79	NA
Hide	35.39 ± 6.93	NA	46.23 ± 8.64

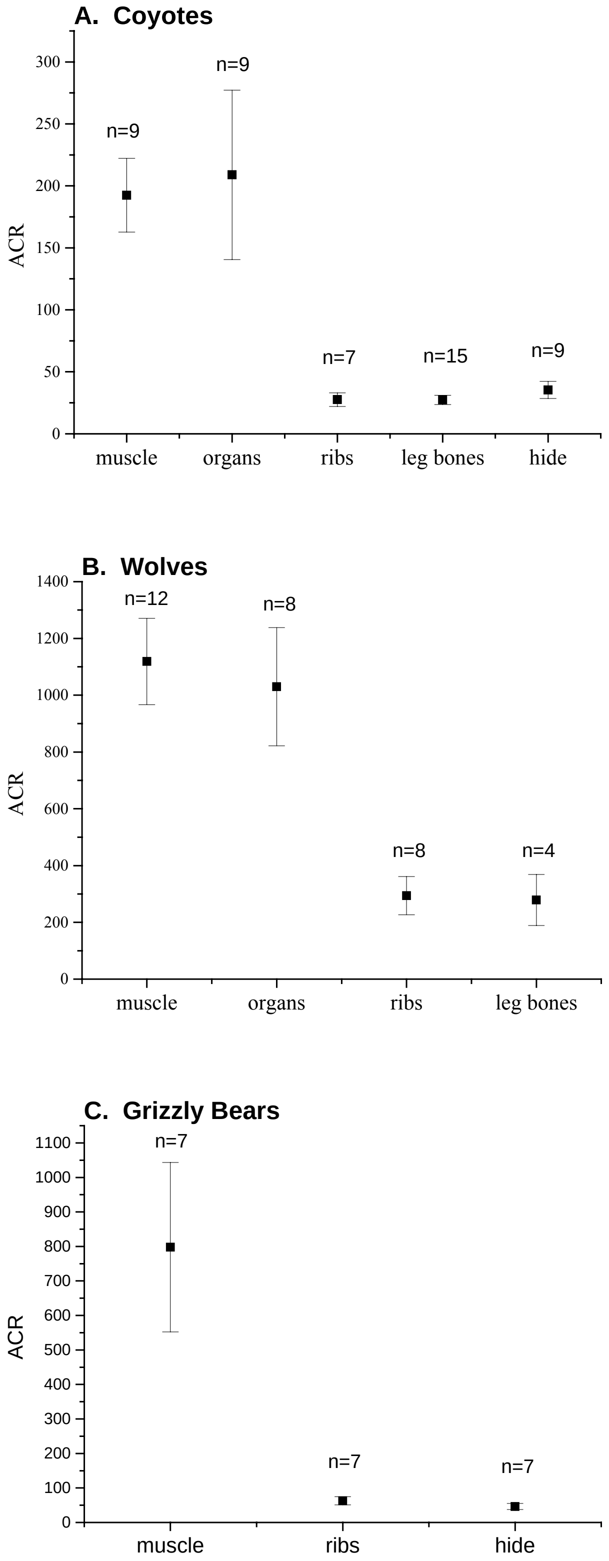

Figure 1. Active consumption rate (ACR) for A) coyotes, B) wolves and C) grizzly bears.

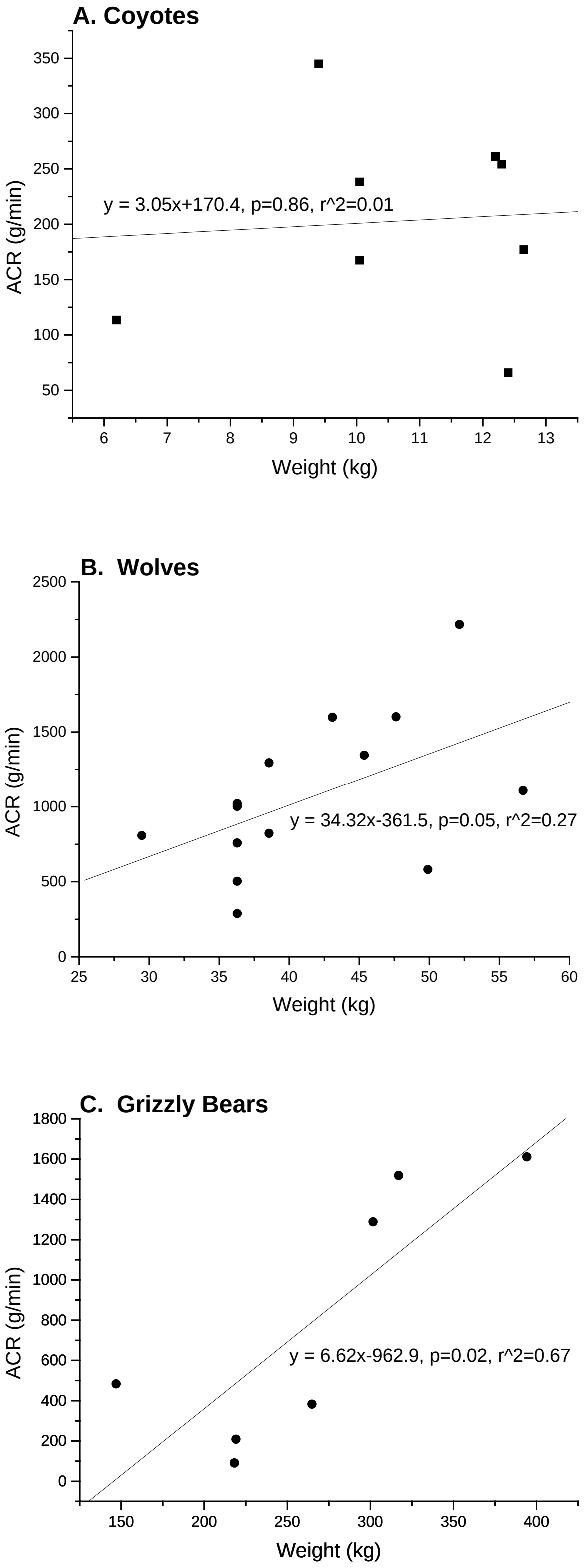

Figure 2. Relationship between subject weight and active food consumption rate (ACR) on muscle in A) coyotes, B) wolves and C) grizzly bears.

Chapter Three

Trophic facilitation by introduced top predators: gray wolf subsidies to scavengers in Yellowstone National Park.

C.C. Wilmers, R.L. Crabtree, D.W. Smith, K.M. Murphy and W.M. Getz.

Introduction

Identifying and understanding the trophic links between carnivore and herbivore guilds is critical to understanding predator-prey relations and community diversity. To this end, ecologists have traditionally focused on the effects of predator foraging behavior as they cascade down the food chain. As a major predator of large ungulates, gray wolves may suppress prey levels or alter prey behavior to the extent that they affect vegetation patterns and productivity. On Isle Royale in Lake Superior, wolf predation on moose has been shown to increase balsam fir (*Abies balsamea*) productivity (McLaren and Peterson 1994). In the long absence of wolves from the Greater Yellowstone Ecosystem, moose populations flourished, reducing willow structure and density and subsequently decreasing the number of avian neotropical migrants which nest and feed in riparian areas (Berger et al. 2001). Since wolf reintroduction to Yellowstone National Park (YNP), changes in elk foraging have resulted in the release of aspen (*Populus tremuloides*) populations in some areas (Ripple et al. 2001). While trophic cascades are a well documented mechanism by which top predators affect community process and pattern (Power 1992), less is known about the influence of top predators on fellow guild members. Here we show that gray wolves affect other meat eating species by subsidizing them with scavenge from their kills.

Recent work on resource subsidies has revealed that allochthonous input from more productive habitats may subsidize consumers in adjacent less productive habitats (Polis and Hurd 1995). Riparian lizards (*Sceloporus occidentalis*) in California, for instance, have been shown to exhibit higher growth rates in near river habitats where aquatic insect densities are high (Sabo and Power 2002). While such resource flows from high productivity to low productivity habitats have been well documented (Fagan et al. 1999), little is understood about the possible mechanisms and effects of resource exchange from highly productive time periods to a less productive ones. Such temporal subsidies are common in agricultural settings where crop watering occurs during dry periods or livestock is fed during the winter, but its occurrence in nature is not well documented.

Prior to wolf reintroduction in YNP, carrion availability was primarily a function of winter severity (Gese et al. 1996). Specifically, high snow levels and cold temperatures caused elk to weaken and die, usually at the end of winter (Gese et al. 1996). Since wolves were reintroduced to Yellowstone in 1995, however, scavenging occurs at wolf kill-sites on a year-round basis (pers. obs.). By changing the distribution and abundance of carrion availability, wolves may serve to facilitate the acquisition of food by scavengers.

Carrion is crucial to the growth and fitness of many species in the Northern Rocky Mountains. Coyotes are highly dependent on winter scavenge (Crabtree and Sheldon 1999a) and have been shown to track wolves to their kill-sites and feed despite a high risk of predation (Paquet 1992). In addition, Crabtree and Sheldon (1999b) have shown that additional elk carrion increases coyote litter size and pup survival. Raven reproduction is tied to the availability of winter carrion (Newton et al. 1982) and they adopt a foraging strategy of following wolves to locate their kills (Stahler et al. 2002). Grizzly bears are similarly dependent on spring carrion and are even known to forego hibernation altogether in Glacier National Park, Montana in favor of scavenging wolf kills (D. Boyd pers. comm.).

A group of gray wolves does not always fully consume their prey in one feeding (Mech 1970). Once satiated, they may stay to guard the carcass (Peterson 1977) and incur energetic costs associated with defense against scavengers or risk being killed by other predators such as grizzly bears and humans (Mech 1970). Alternatively, wolves may abandon the carcass and risk losing potential calories to scavengers. These costs must be balanced against the corresponding energetic output and risk of injury in acquiring their next prey item. If the cost of attaining a future prey item is less than the cost of remaining at the current carcass, wolves should abandon their kill. Partial consumption of prey by wolves has previously been linked to wolf-pack size, prey size (Paquet 1992) and winter severity (Mech et al. 2001) but little is known about the relative importance of these variables, the amount of carrion that wolves provide to other species, and how it is distributed throughout the year.

By directly observing wolves killing and consuming elk, we investigated the factors that determine partial consumption by wolves and the amount of carrion biomass they leave behind to the scavenger guild. We then use these factors to estimate the quantity and timing of this wolf-provisioned carrion subsidy to examine whether wolves have altered the temporal distribution of carrion availability to scavengers. We hypothesize that wolves (1) increase the abundance, (2) alter the timing, (3) decrease year-to-year variation and (4) change the source of the variance of carrion resource to scavengers. With its wide, open valleys, Yellowstone provides an excellent opportunity to observe wolves preying and feeding on ungulates, which has not existed in other studies where inaccessibility or forest cover severely limited viewing possibilities (e.g. in Minnesota, Denali, Isle Royale, Elsmere Island, Algonquin etc).

Study Area

This study was conducted on an 83,000-ha portion of Yellowstone National Park known as the "northern range", so named for the large aggregations of ungulates which winter along the drainage of the Yellowstone River (Houston 1982). Elevations in the park range from 1500-3400m, with the majority of the northern range falling between 1500-2400m (Houston 1982). The climate is characterized by long cold winters with snow and short cool summers. Mean monthly temperatures range from –12c to 13c (Cook 1993). Large open valleys of grass meadows and shrub steppe dominate the landscape, with coniferous forests occurring at higher elevations and on north facing slopes (Houston 1982).

During the course of the investigation, 3 to 6 groups of wolves held territories in the study area. Seven species of ungulates occur on the northern range: elk, mule deer, white-tailed deer (*Odocoileus virginianus*), moose, bison (*Bison bison*), bighorn sheep (*Ovis canadensis*) and pronghorn antelope (*Antilocapra americana*). Elk are the primary prey species of wolves (Mech et al. 2001), as well as the primary source of scavenge for many of the ecosystem's meat-eating species (Gese et al. 1996). The most conspicuous of these include grizzly bear, black bear (*Ursus americanus*), golden eagle (*Aquila chrysaetos*), bald eagle, coyote, fox (*Vulpes vulpes*), raven and magpie (*Pica pica*).

Methods

We conducted the study from January 1998 to July 2001, excluding summer periods from July 15 to October 15 when wolf predation occurs at high elevations, tall grass precludes observation and scavenging on ungulates is slight because mortality is low (Gese et al. 1996). Carcasses were located on a daily basis by tracking wolves to their kill sites using radio telemetry. We either directly observed wolves making a kill or located the kill site shortly afterwards while the wolves were still gorging themselves. We then used 15-45x Nikon spotting scopes to observe feeding activity from observational vantage points located throughout Yellowstone's northern range.

Determining Percent Consumption

In order to determine the percent of the carcass consumed by wolves, we (details follow):

(i) sampled in situ feeding times of wolves and each scavenger species at wolf kills during each stage of consumption of the carcass (Table 1);

(ii) measured active consumption rates (ACR) of wolves and common scavengers in captivity (magpies were measured in situ) in order to convert in situ feeding times into actual biomass consumed;

(iii) estimated elk live weights based on sex, age and day of the year from a model;

(iv) measured the amount of edible biomass of elk, at each stage of consumption, by butchering 14 hunter-killed elk;

(v) used feeding times and active consumption rates to determine the percent of each stage consumed by wolves and scavengers respectively. Percentage of each stage was weighted by the relative contribution of each stage to total edible biomass.

(i) Wolves typically consume the organs of their prey first, followed by the major muscle groups on the front and hind quarters, scrape meat off the bone and hide and then occasionally will eat bone and hide (Mech 1970, Carbyn 1983). Feeding activity at carcasses was sampled according to stage of consumption defined as 1 - evisceration of the stomach and organs, 2 - consumption of the major muscle mass on front and hind quarters, 3 - scraping muscle off of bone and hide, and 4 - consumption of brain, hide and bone. Within each stage, observers recorded the numbers of each predator or scavenger species feeding every 5, 10 or 15 minutes depending on the number of observers. In order to minimize observer bias, each observer was trained for at least one week.

(ii) Active consumption rates (ACR, Table 2) (i.e. rates averaged over a feeding bout in contrast to feeding rates that may be averaged over some longer time period, such as a day or month) for wolves, coyotes and grizzly bears were measured in captivity (Wilmers and Stahler 2002). ACR was also measured for ravens and eagles in captivity and for magpies in situ at Eagle Creek campground on National Forest land just north of the park. Birds were provided with large pieces of pre-weighed muscle and/or muscle on bone. We recorded the number of pecks per feeding bout in order to determine the number of grams per peck that a bird consumed or stored in its crop. We then measured peck rates for each bird species at wolf kill sites by choosing focal animals and recording the number of pecks per minute at carcass. Grams/peck were multiplied by pecks/minute to determine ACR measured in grams/minute. Captive eagles would not eat meat containing large amounts of bone. We therefore estimated eagle ACR on bone by linearly extrapolating from raven and magpie bone ACR based on average species weights (Table 2). Mammal ACRs were estimated from Wilmers and Stahler (2002) using mean Yellowstone wolf weights of 46 kg (YNP unpublished data), mean Yellowstone coyote weights of 13 kg (R. Crabtree unpublished data) and mean Yellowstone grizzly bear weights of 163 kg (Blanchard 1987).

(iii) After carcasses were fully consumed, we examined the kill site to determine cause of death (Mech et al. 2001). We determined sex from the presence/absence of antlers or pedicels. Prey age was estimated by examining annulations of the incisiform teeth (Mech et al. 2001). Carcass weights for elk were then estimated based on animal age, sex and day of the year according to a model (Murphy et al. 1997).

(iv) We determined the percent of edible biomass in each stage by butchering 14 field-dressed elk shot by hunters just north of the park during the Gardner Late Hunt (early January – mid February 2002). We weighed all muscle and fat to within 2-3 cm of the bone in order to determine stage-2 biomass. This is approximately the point at which canids and bears will change feeding technique by using their carnassial teeth to scrape and chew meat off the bone (Wilmers and Stahler 2002). The remainder of the muscle was scraped off the bones, weighed and recorded as stage-3 biomass. The brain and hide were also weighed and logged as stage-4 biomass. The remaining skeleton was also weighed. In order to determine the amount of edible stage-1 biomass, we subtracted stages 2 through 4 and skeleton weights from estimated whole weights to determine gut weights. We then weighed three intact gut piles from the late hunt in order to determine the ratio of rumen to organs and entrails.

(v) In order to determine percent biomass consumed by wolves at carcasses, we weighted the number of minutes spent feeding by each species in each stage, by relative measures of ACR between species for those stages (Wilmers and Stahler 2002). We then summed these percentages weighted by the proportion of the total carcass weight to determine percent consumed of the total available biomass for each carcass.

Additional Data

Wolves have historically been trapped and hunted by humans through much of their range in North America. As such, wolves may perceive humans as potential predators and/or competitors for food. In Yellowstone, wolves are often watched by visitors from the road. Anticipating that human disturbance could cause wolves to abandon carcasses prematurely, we measured the distance in meters of each carcass to the road (hereafter denoted as ROAD). We also examined the effects of forage quality (FORAGE), monthly averages of snow water equivalent (SWE), and minimum temperature (TMIN) (Farnes et al. 1999). Following Farnes et al. (1999) these variables are each scaled to take on values between –4 and +4 with –4 representing the most severe conditions and +4 representing the mildest ones.

Statistical analysis

The percent of a carcass consumed by a group of wolves is likely to depend on prey weight (PREYW) as well as pack size (PACKS). The relationship between resource availability and predator abundance is often better expressed on a per capita basis (Pitcairn et al. 1990), thus we also investigated how the number of wolves per kg of prey (WPKP) affects the percent of a carcass consumed by wolves (% CONSUMPTION). Additionally, foraging costs such as defense against scavengers or distance to road are likely to be balanced against the difficulty with which wolves may obtain their next prey item. Environmental conditions, particularly snow depth, may influence the condition of elk (Houston 1982, Gese et al. 1996). We used regression analyses to determine the significance of all these factors on % CONSUMPTION. Statistical analyses were conducted using S-Plus 6.0. In order to avoid dependence of the variance on the mean of our data we transformed all percentages using the arcsine function (Sokal and Rohlf 1995). We used linear and multiple linear regression techniques to assess the importance of the measured variables.

The availability of carcass biomass to scavengers prior to wolf reintroduction was measured by Gese et al. (1996) for three years in the Lamar River Valley, Yellowstone National Park, which is a large 70 km^2 site in the Northern Range. We compared these data to predictions of what would have been available had wolves been present, in order to examine how wolves may have changed the overall quantity and temporal availability of carcass biomass to scavengers. To do so, we calculated the percent of carcass biomass consumed by a pack of eight wolves and multiplied this by monthly wolf kill rates to get the total amount of scavenge available from wolf kills. Specifically, we estimated average percent consumption by wolves from our regression equation using the variables PACKS and SWE. In order to estimate the variance in percent consumption, we assumed that these variables were normally distributed with mean and standard error given from the regression analysis. We then performed Monte Carlo runs to estimate the variance associated with our estimate of percent consumption. We used actual SWE data from the three years in Gese et al.'s study and assumed a November and March kill rate 5 kg/wolf/day and 8 kg/wolf/day respectively (Smith et al. in press). December through February kill rates were estimated by linear interpolation between the two endpoints.

Results

We observed 240 wolf-killed elk carcasses during the study period for a total of 104,640 minutes. Fifty-seven of these carcasses were observed from beginning or near beginning (during stage 1 and only wolves had fed) to end of consumption during the winter period of November 1 to April 1: 8 of these were bulls, 24 were cows, 24 were calves and 1 was unknown. Estimated carcass weights varied from 101 to 269 kg and were located between 30 m and 3250 m from the road. Wolf-group size at carcasses ranged from 1 to 27 animals. Other major consumers of these carcasses included coyotes, grizzly bears, ravens, magpies, bald eagles and golden eagles.

Measurements of bird ACR on muscle were significantly different from ACR on bone for ravens (p=0.03, Table 2) and for magpies (p=0.04, Table 2). Elk dissection revealed that approximately 68% of an elk's whole weight is edible. Approximately 14% of the elk's whole weight is in stage 1, 31 % in stage 2, 15% in stage 3 and 6% in stage 4 (Table 1). The remaining 32% is comprised of rumen and inedible bone.

The percent of the carcass consumed by wolves was significantly predicted by 6 variables on their own: WPKP, PACKS, PREYW, SWE, TMIN and ROAD (Table 3).

As pack size increases, the percent consumed by a wolf pack also increases (Table 3). As prey weight increases, percent consumption decreases (Table 3) because the wolves become satiated before fully consuming the carcass. WPKP explained more of the variation in percent consumption than any other variable alone ($r^2 = 0.38$, Fig. 1A). As the number of wolves relative to kg of prey increases, the percent consumed by wolves increases (Table 3). Wolves consumed a greater percentage of their carcasses, the further away they were from the road (Fig. 1B). SWE was also a significant predictor of percentage consumed by wolves. As snow levels increase, wolves consume a smaller percentage of their kills (Fig. 1C). We found that 58 percent of the variation in percent consumption could be explained by WPKP, SWE, ROAD and the interaction between SWE and ROAD (Table 3).

The regression model was used to predict the effect of wolves on biomass availability in three consecutive winters, characterized by Gese et al. (1996) as follows: (1990-91) mild and little carcass biomass was available, (1991-92) snow arrived early and higher than normal winter severity resulted in substantially more carcass biomass throughout the winter, (1992-93) late onset of snow and a corresponding pulse of carrion biomass. By adding wolves into the model, the scenario changes considerably. During the mild winter of 1990-1991, our model reveals that wolves would have increased the amount of biomass available to scavengers from February to March in the Lamar Valley from an estimated 458 kg spanning 4 weeks to 1524 kg spanning 8 weeks (Fig. 2A – note that data collection did not begin until February that year). During the severe winter of 1991-1992, the addition of wolves results in a small increase in carrion biomass overall (4232 kg up to 5724 kg from November to March in the Lamar Valley

– Fig. 2B) with a decrease in mid-winter carrion when conditions were most severe and a small increase in carrion at the beginning and end of winter when conditions were milder. In the winter of 1992-1993, characterized by a late onset of carcass biomass, wolves would have increased the variance of carrion by providing more biomass at the beginning of winter when weather was relatively mild and possibly less biomass at the end of winter when weather was more severe and elk were significantly weakened (2910 kg spanning 13 weeks up to 4468 kg spanning 20 weeks from November to March in the Lamar Valley, Fig. 2C).

As wolf pack size changes, the amount of biomass available to scavengers also changes. Initially the amount of biomass available to scavengers should increase as wolf numbers increase and kill more but eventually should start to decline as wolf numbers increase and wolves consume a higher percentage of their kills. In Fig. 3 (dark circles) we have plotted the relationship between wolf pack size and the total amount of biomass that would have been available to scavengers from one wolf pack in winter 1992-1993. The curve reveals that wolf packs of intermediate size provide the most carcass biomass to scavengers. The peak of the curve is most likely skewed towards high wolf pack sizes, however. We use estimates of kg $wolf^{-1}day^{-1}$ derived from Smith et al. (in review) which were reported independent of pack size. As wolf pack size increases, however, kg $wolf^{-1}day^{-1}$ is likely to decrease. We also plotted the curve (Fig. 3) assuming that kill rate per wolf is a decreasing function of pack size to explore how this would affect the relationship.

Discussion

Elk carrion is an important winter food resource for many scavenger species in Yellowstone National Park (Houston 1978). By partially consuming their prey, wolves subsidize scavengers with a high calorie resource that may be essential for metabolic maintenance, growth and/or reproductive success (see Crabtree and Sheldon 1999b for coyotes). In addition, wolves change the timing of the resource from a pulsed resource at the end of severe winters to a more constant resource throughout the winter. This resource subsidy may in turn promote increased biodiversity (Johnson et al. 1996) and lead to larger populations of scavengers species. Female grizzly bears with reliable high-energy foods, for instance, have been shown to attain larger body size and have bigger litter sizes than their counterparts with less reliable and/or lower calorie foods (Blanchard 1987). Reproduction in magpies, ravens and bald eagles is also highly correlated with the timing and proximity of high quality food resources (Newton et al. 1982, Swenson et al. 1986, Dhindsa and Boag 1990).

Foraging theory provides a context in which to understand and predict the amount of wolf-provisioned carrion biomass available to scavengers. As the difference between the costs and benefits of remaining at a carcass increases, wolves become increasingly likely to abandon the carcass. As a wolf becomes more satiated, the marginal benefit of remaining at a carcass decreases with respect to future calorie gains. Deep snow causes increased energy expenditure in ungulates resulting in weakened animals that are more vulnerable to predation (Gese et al. 1996). If the next prey item is easier or less risky to attain than guarding the present one, wolves should trade available low value carcass remains for higher value organ and large muscle tissue on a fresh carcass that must be obtained at some cost. Costs of remaining increase with proximity of the carcass to the road, while the costs of acquiring the next prey item decrease with increasing snow depth, which is an indicator of prey vigor. Selection for road tolerance may occur in Yellowstone as wolves learn that humans in the park are harmless. This is likely to be balanced by selection against road tolerance outside the park, however, where wolves are sometimes shot or collide with moving vehicles.

Wolf packs of intermediate size provide the largest subsidies to the scavenger guild in YNP. The ratio of the number of wolves to kilograms of prey (WPKP) is the best indicator of how much carrion biomass wolves leave behind to the scavenger guild at a particular carcass. When wolf packs are small, they may not consume much, but their kill rates are low. Conversely, when wolf packs are large, kill rates are high but they also consume a large percentage of their prey. Wolf packs of intermediate size, however, kill at a relatively high rate but consume only part of the carcass thereby maximizing the subsidy to scavengers.

Gese et al. (1996) found that 54 % of the variation in the amount of carcass biomass available to scavengers was due to snow depth and interaction between snow depth and minimum temperature. Our results indicate that, with the reintroduction of wolves, the number of wolves present has become the primary factor determining carcass biomass availability to scavengers with environmental conditions (particularly snow depth) now a secondary factor. From a scavengers perspective, wolves appear to have changed the source of variance in carcass biomass from one dependent primarily on stochastic, climatic factors to one dependent primarily on a less stochastic, biotic factor -- the ratio of wolves to abundance of carcass biomass. The amount of carrion available to scavengers has thus shifted from one dependent primarily on environmental stochasticity to one dependent primarily on wolf demographic stochasticity. Wolves also appear to reduce the variability, within and between years, of carcass availability. Prior to wolf reintroduction, the availability of elk carrion pulsed when severe environmental conditions caused weakened elk to die and ebbed when conditions were mild. Carrion biomass is now less variable during the winter because wolves are killing throughout the year and often partially consuming their kills. In addition, by preying largely on the young and old (Mech et al. 2001), wolves reduce the pool of old weak animals and so lessen the late winter pulse of carrion when conditions get severe. In other wolf-elk systems, such as Riding Mountain National Park (RMNP) in Canada, natural mortality of elk is rare (Paquet 1992).

We have demonstrated here that wolves mediate the flow of carrion subsidy to scavenger guild members, by controlling the timing and quantity of carcasses. By decreasing the year to year variation and increasing the time over which carcasses are available during the winter, this carrion subsidy may contribute significantly to the biodiversity of the region. In RNMP, over 30 species of avian and mammalian scavengers have been documented to use wolf kills (P. Paquet pers. comm.) In addition, 57 species of beetles are known to depend on elk carrion in YNP (Sikes 1998). By removing a future meal for wolves, scavengers may in turn cause wolves to kill more often thus strengthening their top-down effect on vegetation through the control of elk populations. When wolf packs are large or winters are mild, the carrion wolf subsidy will be small. This subsidy increases for wolf packs of intermediate size and as winters become more severe.

Table 1. Carcass food resources available during successive stages of consumption.

Consumption Stage	Description[1]	Percent of whole weight[2] (SE)
1	organs and entrails	14 (2.7)
2	major muscle	31 (2.5)
3	minor muscle	15 (3.6)
4	brain and hide	8 (2.7)
inedible	rumen and skeleton	32 (6.1)

[1] stages 2-4 include some small bits of bone which are of negligible weight.

[2] based on dissection of 4 calves, 6 bulls and 4 cows.

Table 2. Active consumption rates (ACR) for birds and mammals.

species	grams/peck (SE)		pecks/min (SE)	ACR g/min (SE)	
	stage 1&2	stage 3&4		stage 1&2	stage 3&4
ravens	1.15 (0.40)	0.65 (0.03)	22	2.4 (0.15)	1.14 (0.33)
magpies	0.088 (0.0042)	0.0042 (0.0011)	26	2.4 (0.15)	1.14 (0.33)
eagles	3.15 (0.80)	-	15	63.27 (17.4)	30 (5.2)[1]
wolves[2]	-	-	-	1022 (150)	280 (40)
coyotes[2]	-	-	-	230 (60)	30 (5.6)
grizzlies[2]	-	-	-	800 (245)	62 (11.9)

[1] estimated from linear interpolation of magpie and raven rates by bird weight.

[2] estimated from average Yellowstone weights using formulas from Wilmers and Stahler (2002).

Table 3. Regression analyses on the dependent variable, percent consumed by wolves[1]. We present results for all significant one variable models and the best overall model.

independent variables[2]	d.f.	coefficient	s.e.	r^2, R^2	F-ratio	p-value
constant	55	47.7	3.54	0.38	33.47	0.0000
WPKP		150.2	25.97			0.0000
constant	55	44.4	4.55	0.31	25.2	0.0000
PACKS		1.19	0.24			0.0000
constant	55	55.8	3.61	0.16	10.37	0.0000
ROAD		0.0076	0.0023			0.0022
constant	55	54.8	3.54	0.19	13.3	0.0000
SWE		4.70	1.29			0.0006
constant	55	65.8	2.31	0.11	6.875	0.0000
TMIN		-3.21	1.22			0.0113
constant	52	29.5	4.87	0.58	16.92	0.0000
WPKP		103.14	28.1			0.0006
ROAD		0.01	0.003			0.0002
SWE		6.66	1.75			0.0004
SWE*ROAD		-0.0026	0.0011			0.0188

[1] variable is arcsine transformed; [2] WPKP - wolves per kg of prey; PACKS - pack size; ROAD - distance to road; SWE - snow water equivalent; TMIN - minimum temperature. Note that prey weight, winter severity index and forage were not significant predictors of percent consumption.

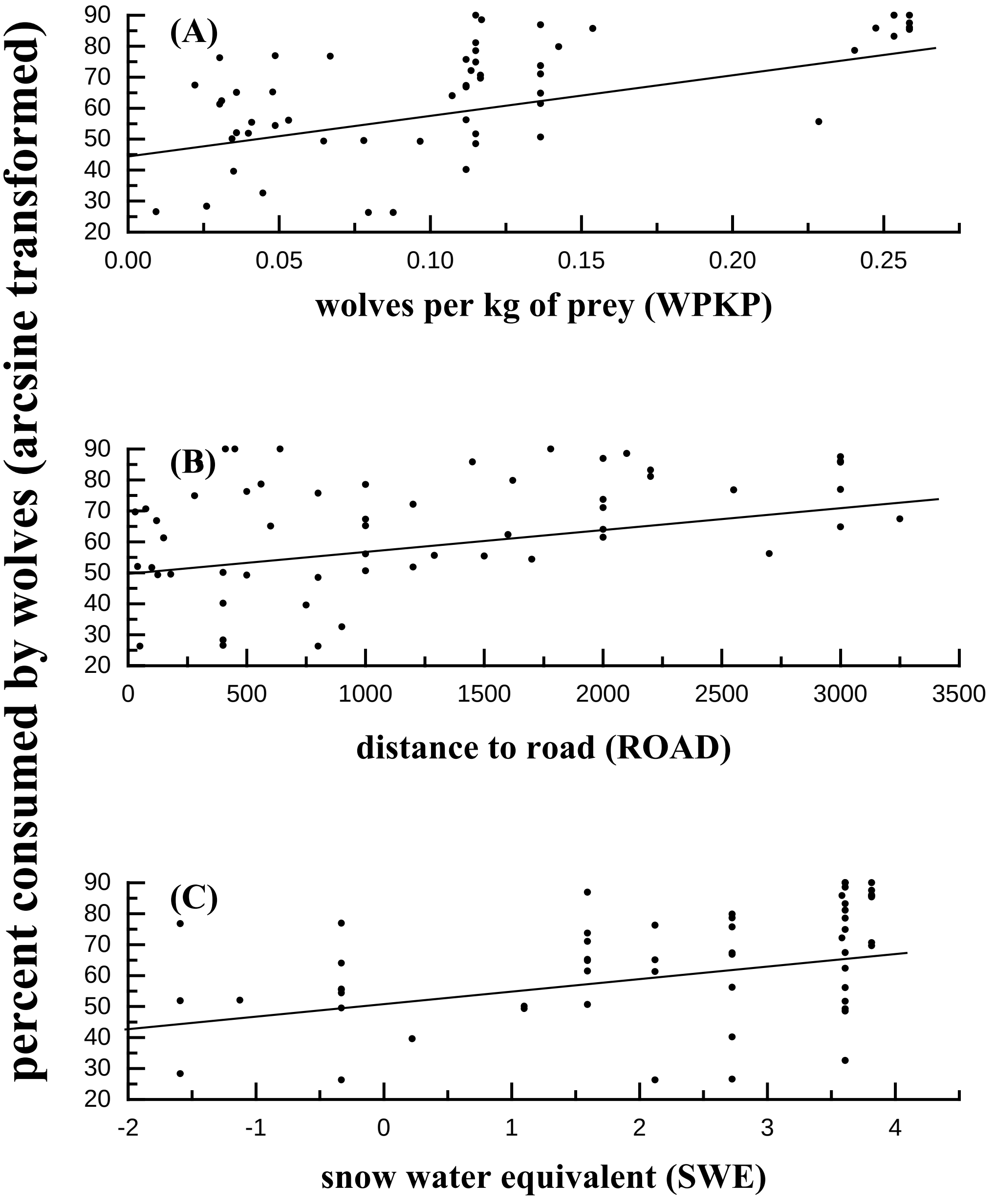

Figure 1. Relationship between the percentage of a carcass consumed by wolves and A) per capita, B) distance to road and C) snow water equivalent (SWE, note that larger values of SWE represent milder conditions and thus less snow). Percentages are arcsine transformed (20 – 90 point scale) so that they no longer represent numbers between 0 and 1.

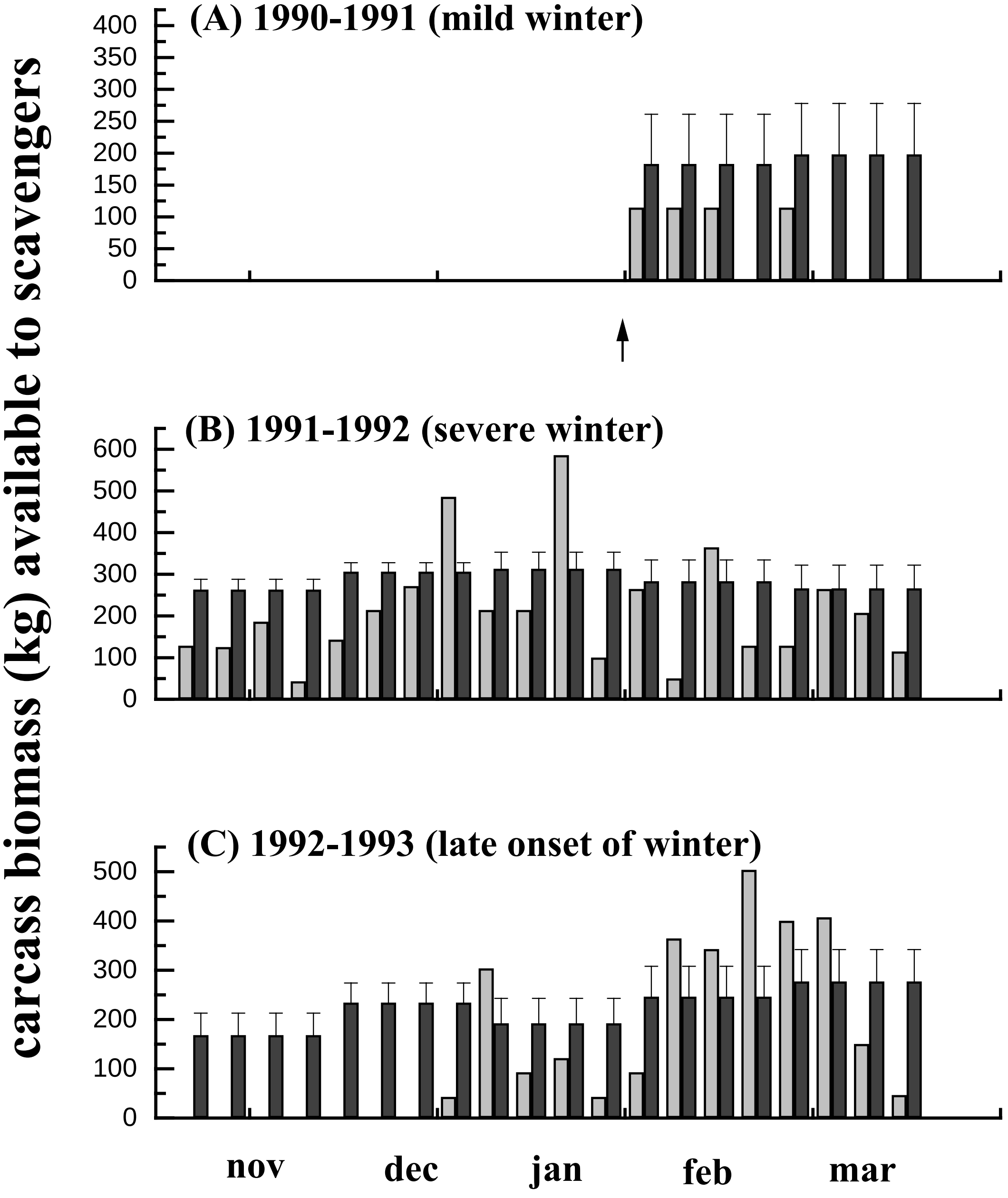

Figure 2. Comparison of biomass available in the Lamar Valley, Yellowstone National Park with and without wolves. Light gray bars represent carcass biomass without wolves as measured by Gese et al. (1996). Dark gray bars represent carcass biomass with wolves as derived from our regression model (see methods). Arrow indicates when data collection by Gese et al. (1996) began. The standard deviation of monthly carrion availability for each of the three years with and without wolves was as follows: A) 8 kg/month vs. 61 kg/month, B) 38 kg/month vs. 137 kg/month and C) 47 kg/month vs. 171 kg/month.

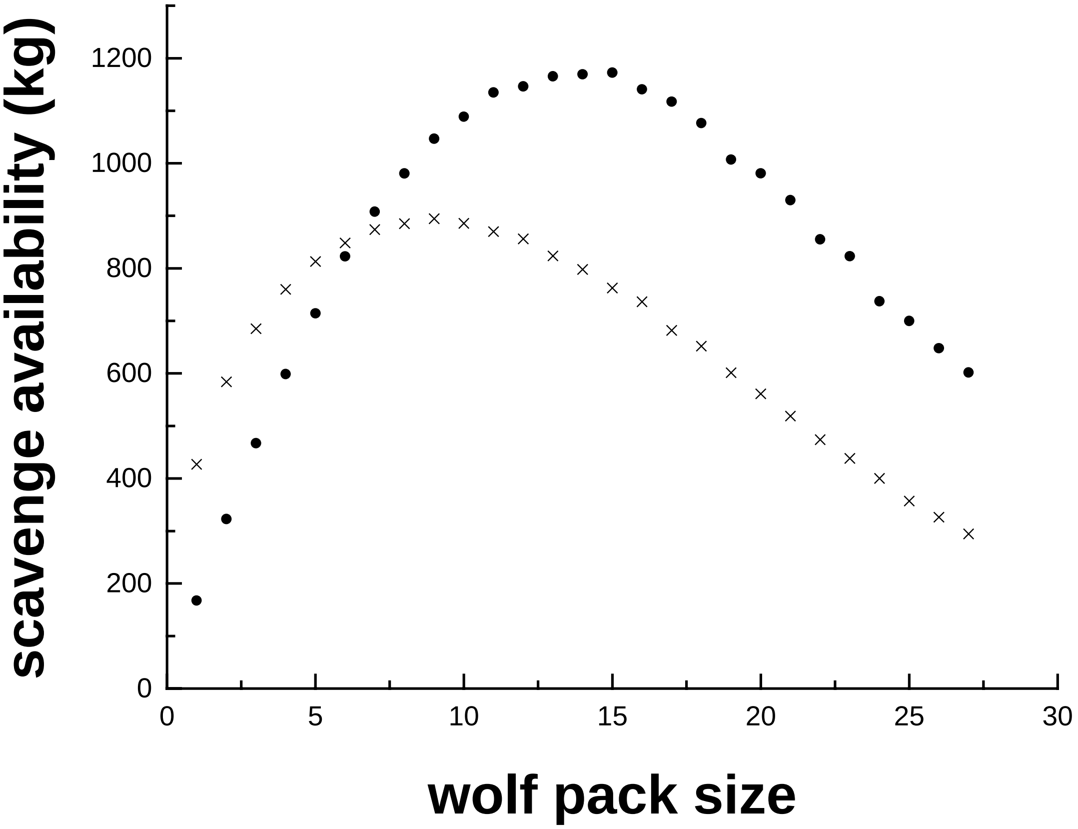

Figure 3. Carcass biomass available to scavengers for increasing wolf pack size. Circles represent estimates using data from Smith et al. (2002). Pluses represent estimates assuming a declining kill rate as wolf pack size increases.

Chapter Four

Resource dispersion and consumer dominance: scavenging at wolf- and hunter- killed carcasses in Greater Yellowstone.

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Introduction

A predictive food-web theory requires that we quantify the effects of spatio-temporal resource fluctuation on animal distributions and abundance. To this end, ecologists have recently begun to articulate the effects of temporal resource pulses on local animal populations such as mast fruiting by trees (Kelly 1994, Gonzalez and Donoso 1999), irruptions of insects (Ito 1998), and marine subsidies to terrestrial communities (Rose and Polis 1998). Consumer species that are able to respond to these sudden pulses, such as mice on acorns (Jedrzejewska and Jedrzejewski 1998), insectivorous birds on insects (Folkard and Smith 1995) and coyotes on beached whales (Rose and Polis 1998), are usually generalist species that can support themselves on alternative resources in the absence of a pulse. Positive numerical responses by consumers to such pulsed resources are often observed either through increased population growth or migration, and may have strong trophic consequences (Ostfeld and Keesing 2000). Once a pulse has dissipated, high consumer densities frequently lead to high levels of predation on alternative prey and increased competition with hetero-specifics (Ostfeld and Keesing 2000). While the temporal aspect of resource pulses has been well explored (Ostfeld and Keesing 2000), little is known regarding the response of multiple consumers to the spatial dispersion of resource pulses that have a periodic temporal component.

The 72,800 km^2 greater Yellowstone ecosystem (GYE) provides the context for a natural experiment to investigate this question. Gray wolves in the GYE provide resource subsidies to scavengers in the form of carrion from their kills (Wilmers et al. 2003a). As the ratio of wolf pack size to prey size decreases and/or snow depth increases (thus weakening ungulate populations) wolves become increasingly likely to abandon their kills before entirely consuming the carcass (Wilmers et al. 2003a). A number of avian and terrestrial scavengers are then rewarded with left over muscle meat, bone and hide. Human hunters also provide such subsidies to scavengers when they leave behind the entrails of their kills. The majority of carrion biomass provided by human hunters comes from the Gardiner Late Hunt, a permit-issued elk hunt running from early January to mid-February (Lemke et al. 1998). This hunt, which primarily targets "antler-less" elk (cows and calves) migrating from Yellowstone National Park (YNP), often produces an annual harvest exceeding 1000 individuals (Lemke et al. 1998). Whether provided by wolves or hunters, carrion is an ephemeral resource that is often consumed within hours. The spatial and temporal distribution of these two carrion sources differs markedly, however. Hunter kills are aggregated in both time and space, as hunting takes place in a tightly circumscribed area over a narrow time horizon. In contrast, wolf kills are highly dispersed in time and space, as they occur throughout the year and over the entire ecosystem.

A carcass, or group of gut piles, will initially attract scavengers from the local area. If the total amount of carrion is small, then it will be consumed primarily by those scavengers that are the first to arrive and/or competitively dominant. If the amount of carrion is larger than that which can be consumed immediately by local scavengers, then consumers should continue to recruit from more distant areas. Certain species, however, will be more capable of recruiting than others. Those species that can recruit from large geographic distances therefore, will predominate at highly aggregated resources.

The primary winter scavengers in Greater Yellowstone are, in order of dominance at carcasses, coyote, golden eagle, bald eagle, raven and magpie (see Magoun 1976 for similar dominance relationships). These species differ in their relative foraging radii, defined as the distance over which an animal can locate and integrate a resource in a given period of time. Within the group of the scavengers mentioned above, we characterize bald eagles and ravens as having the largest feeding radii because they both have excellent long distance flying capabilities (Heinrich 1988, Buehler 2000) and often roost communally where information about resource locations may be transferred (Marzluff et al. 1996, Buehler 2000, Dall 2002). Coyotes and magpies are characterized as having relatively small feeding radii because they are limited in their abilities to cover large distances quickly (Bekoff and Andrews 1978, Trost 1999). Golden eagles have similar flying capabilities to bald eagles, however unlike bald eagles, they are relatively solitary and sedentary (LeFrank Jr and Clark 1983). As such we characterize them as having smaller feeding radii than bald eagles and ravens because they lack the degree of social interaction that enhances information transfer concerning resource locations.

Here we investigate this question of resource dispersion and consumer dominance on the northern Yellowstone winter range of the GYE. Specifically, we estimate the total carrion biomass provided to scavengers by both wolves and hunters, and investigate how each species of scavenger responds to different spatial and temporal resource regimes. We hypothesize that the highly concentrated hunter-kills should be dominated by wide-ranging consumers that can track ephemeral resources over a broad geographic area, whereas the more dispersed wolf kills should be tracked most efficiently by competitively dominant local consumers.

Study Area

This study was conducted on the 1530 km^2 northern Yellowstone winter range of the GYE, so named for the large aggregations of ungulates that winter along the Yellowstone River (Houston 1982). Elevations range from 1500 to 3400 m and the climate is characterized by short, cool summers and long, cold winters, with most of the annual precipitation falling as snow. Mean annual temperature is 1.8° C, and mean annual precipitation is 31.7 cm (Houston 1982). Large open valleys of grass meadows and shrub steppe dominate the landscape, with coniferous forests occurring at higher elevations and on north facing slopes.

During the course of the investigation, three to six packs of wolves held territories in the study area. The northern range supports seven species of native ungulates: elk, mule deer, white-tailed deer, moose, bison, bighorn sheep and pronghorn antelope; and one nonnative ungulate, mountain goat (*Oreamnos americanus*). Five species of native large carnivores also exist: coyote, wolf, cougar (*Puma concolor*), grizzly bear, and black bear. Elk are the primary prey species of both wolves (Mech et al. 2001) and hunters (Lemke et al. 1998), as well as the primary source of scavenge for many of the ecosystem's meat-eating species (Murie 1940, Gese et al. 1996, Crabtree and Sheldon 1999a). It is important to note that hunting occurs in a subset of the larger area used by wolves. As such, the hunting area occurs within the same range of elevation and vegetation as the larger area used by wolves, and is populated by the same suite of scavenger species.

Methods

We conducted the wolf component of the study from November 1998 to July 2001, excluding summer periods from July 15 to October 15 when wolf predation occurs at higher elevations, tall grasses preclude observation, ungulate mortality is low (Gese et al. 1996), alternate foods are available to scavengers, and smaller prey packages are fed on, attracting fewer scavengers. Hunter-kills were observed during the Gardiner Late Hunt, which in recent years has accounted for >80% of annual hunter take (Lemke et al. 1998), in January and February 2001 and 2002. Wolf-killed carcasses (see Mech et al. 2001 for cause of death determination) were located on a daily basis by tracking wolves to their kill sites using radio telemetry. Hunter gut piles were located by communicating with hunters, scanning the landscape for bloodstains in the snow and searching for aggregations of birds. We observed all kills and gut piles from the time they were located until they were either fully consumed, dragged out of view or it became too dark to distinguish behavior. We used 15-45x spotting scopes during the day and an infrared attachment when possible at night to observe feeding activity from observational vantage points located throughout Yellowstone's northern range (for sampling details see Wilmers *et al*. in press).

Estimating total wolf provided carrion

Total wolf-killed elk biomass available to scavengers on the northern range was estimated by sampling total biomass to scavengers for the majority of northern range wolf packs and then extrapolating to packs that we did not sample. Specifically, if we let D_m be the number of days in each month m, $K_{\rho,m}$ the monthly wolf kill rate (kg/wolf/day) for each pack ρ, $W_{\rho,m}$ the number of wolves in each pack by month, $Q_{\rho,m}$ the percentage of each carcass consumed by wolves and assume that only 68% of each carcass is edible (Wilmers et al. 2003a), then the total carrion $C_{\rho,m}$ to scavengers in the months December thru March is given by,

$$C_{\rho,m} = K_{\rho,m} \cdot W_{\rho,m} \cdot D_m \cdot (1 - Q_{\rho,m}) \cdot 0.68 \,. \tag{1}$$

The kill rates of each sampled pack were estimated by the National Park Service from November 15 - December 15 and March 1-31 of each year (Smith et al. in press). We use the former period as our November kill rate and the latter as our March kill rate. Kill rates for December thru February were linearly interpolated between the November and March rates. Mean percent consumption (and standard error) by each wolf pack was calculated from previously reported multiple regression equations (Wilmers et al. 2003a) using wolf pack size and snow-water equivalent (SWE) as dependent variables.

Total carrion to scavengers from non-sampled packs and for all packs in April and May was then estimated based on multiple linear regressions relating total carrion $C_{\rho,m}$ to pack size and SWE. We did not extrapolate beyond May because wolf kill rates for the summer months are poorly documented. While wolves continue to kill adult elk that are then scavenged, they also begin killing newborn calves in June, which they generally consume entirely. The percentage of their kills that are newborns versus adults is not currently known making it hard to extrapolate the total carrion biomass they provide to scavengers.

Estimating total wolf-killed carrion to each scavenger species

We then set out to determine the total wolf-killed elk biomass consumed by each scavenger species during the winter period of January to March for comparison to hunters. To do so, we used $s = 1,...,7$ to index the seven common consumer species (1 = wolves, 2 = grizzly bears, 3 = coyotes, 4 = golden eagles, 5 = bald eagles, 6 = ravens and 7 = magpies) and $c = 1,...,4$ to represent the stage of consumption (1 = eviceration of organs, 2 = major muscle, 3 = minor muscle and 4 = brain and hide) of carcass i. We then sampled in situ feeding times to estimate the total time (individual hours) $F_{c,i}^{s}$ spent by each species at wolf kills and multiplied this by species and stage-specific consumption rates R_{c}^{s} (Wilmers and Stahler 2002, Wilmers et al. 2003a). The proportion $P_{c,i}^{s}$ of each stage of a carcass i's edible biomass, $B_{c,i}$, consumed by each species s is then given by,

$$P_{c,i}^{s} = \frac{R_{c}^{s} F_{c,i}^{s}}{B_{c,i}} \text{, where } \sum_{s=1}^{7} P_{c,i}^{s} = 1. \tag{1}$$

We determined ungulate age from its incisors and used this to determine $B_{c,i}$ using previously determined weight by stage relationships (see Wilmers *et al.* 2003).

We then pooled each species-specific stage proportion $P_{c,i}^{s}$ for carcass i and calculated the mean in order to get an overall estimate of the percentage of each stage that a species consumed during the winter. Because sampling effort varied between carcasses, percentages from heavily sampled carcasses were more likely to represent the true division of carrion than those from lightly sampled carcasses. Since sampling variance in estimating means is proportional to the reciprocal of the square root of sample size, we weighted each proportion by the square root of the number of samples n_i taken from carcass i in our pooling procedure. Specifically, mean percent consumption Ω_c^s of stage c by species s is given by

$$\Omega_c^s = \frac{\sum_i P_{c,i}^s \sqrt{n_i}}{\sum_i \sqrt{n_i}} . \tag{2}$$

For each species, s, we then sum mean percent consumption across all stages c, weighting each stage's contribution to total carcass biomass in order to get the total percent of an average carcass consumed by each species to obtain,

$$\Omega_T^s = \frac{0.14}{0.68}\Omega_1^s + \frac{0.31}{0.68}\Omega_2^s + \frac{0.15}{0.68}\Omega_3^s + \frac{0.08}{0.68}\Omega_4^s \text{ (Wilmers et al. 2003a).} \tag{3}$$

Total carrion biomass H_m^s consumed by a species per month is then,

$$H_m^s = \Omega_T^s \cdot \sum_\rho C_{\rho,m} \tag{4}$$

Estimating total hunter provided carrion

The total number of elk killed by hunters is reported each year by Montana, Fish, Wildlife and Parks. In order to estimate the total amount of elk carrion provided by hunters to scavengers, we assumed that all hunters field-dressed their carcass thus leaving behind the entrails. We used sex and age information from each kill (Lemke 2001, 2002) to estimate that animals live weight based on a model (Murphy et al. 1997). Gut weights (not including the rumen) were assumed to be 14% of live weight based on Wilmers *et al*. (2003). Total carrion to scavengers was then equal to the sum of each kill multiplied by its live weight and by 0.14.

In order to estimate the proportion of this total going to each scavenger species, we used the same procedure as we did for wolf kills except for there was only one stage of consumption. Additionally, we periodically checked all known gut piles each morning for animal tracks to account for potential consumption by nighttime foragers, such as coyotes.

Analyzing spatial distribution

In order to test for a difference in spatial distribution between wolf- and hunter-killed elk, we first estimated the center of both wolf and hunter kills respectively. To do this, we found the average *x* and *y* location for wolf kills and then did the same for hunter kills. We then calculated the distance of each wolf kill to its center and the distance of each hunter kill to its corresponding center. A Wilcoxon rank sum test was then used to test for a difference in distribution between the two sets of distances.

Results

We observed 202 wolf-killed carcasses and 28 hunter-killed gut piles for a total of 83,325 and 5,775 minutes respectively. In 98-99 and 99-00 we sampled three out of the four existing northern range wolf packs while in 00-01 we sampled four out of six.

Multiple regression analysis revealed that SWE and the square of wolf pack size accounted for 59% of the variance in carrion abundance to scavengers. We used this relationship to estimate mean monthly carrion from wolf-killed elk to scavengers +/- residual standard errors (Fig. 1). Mean seasonal (November - May) carrion provided to scavengers from wolves on the northern range was 13,220 ± 383.9 kgs. Hunters provided significantly more carrion to scavengers (January through mid - February) at 33,203 ± 993 kgs (Wilcoxon rank sum test, $p<0.05$). We documented twelve scavenger species feeding at wolf kills and four species feeding at hunter kills (Table 1). We sub-sampled the wolf kills by randomly selecting 28 wolf kills at a time to investigate the effects of sample size on common species present. This did not have an effect on the presence of common species at wolf kills. We could not determine whether the presence or absence of rare species at wolf versus hunter hills was due to a sampling artifact or biology.

The distribution of hunter provided carrion was highly aggregated in both space (Fig. 2) and time (Fig. 1) compared to that of wolves. Bald eagles, golden eagles, ravens, magpies and coyotes were common at wolf kills during the winter period whereas coyotes were absent at hunter-kills. Mammal tracks were not located at any hunter gut piles with the exception of one fox track that was located in the vicinity of the gut piles but not at any one of them in particular. Grizzly bears began to emerge from hibernation and feed on wolf kills at the very end of the sample period. Comparison to hunter gut piles is not appropriate, however, because the majority of gut piles from the Gardiner Late Hunt are fully consumed by the time of grizzly den emergence. Ravens and bald eagles consumed significantly more carrion at hunter-kills than at wolf kills (Fig. 3, $p<0.05$). Consumption by magpies and golden eagles did not differ significantly between hunter and wolf kills ($p>0.05$). The average of the maximum number of ravens and bald eagles was higher at hunter kills whereas the opposite pattern was found for magpies and golden eagles (Table 2). Average numbers of scavengers at wolf kills did not change during the human hunting period.

Discussion

We have shown that gray wolves and human hunters alike provide an enormous resource subsidy to Greater Yellowstone's scavengers. In a landscape with limited options for food, carrion is likely to lead to increased winter survival and reproduction for many of these species (Houston 1978, Newton et al. 1982, Swenson et al. 1986, Blanchard 1987, Dhindsa and Boag 1990, Crabtree and Sheldon 1999b). Hunter provided carrion arrives as a large pulse in mid-winter and is more plentiful than wolf provided carrion, which arrives consistently over the course of the entire winter. Which temporal resource regime is more beneficial to scavengers will depend on a trade off between an ability to assimilate and/or cache large amounts of resource quickly and/or tracking that resource over time.

As expected, under-dispersed and super abundant resources (hunter kills) were best tracked by consumers with higher foraging radii (*i.e.* ravens and bald eagles). Conversely, highly dispersed carrion was best tracked by competitively dominant species (e.g. coyotes). Due to the high temporal and spatial overlap of carrion at hunter kills, scavengers from the local area surrounding the gut piles are super-saturated with resource, leading consumers to recruit from larger and larger areas. Such super-saturation reduces competition and allows far ranging species to gather in high numbers. As wolf kills are spread out over time and space, carrion is under-saturating, leading the competitively dominant coyotes to dominate the resource over other scavengers. The complete absence of coyotes at hunter kills was unexpected as coyote packs are known to occur in the area. This was likely an artifact of exclusion due to the indiscriminate killing of coyotes by humans in the study area outside of YNP. If hunters did not exclude coyotes, our expectation is that they would consume an equivalent or slightly greater amount of carrion than they do at wolf kills, but would not be able to dominate this highly abundant resource. To do so would require that they recruit to the area in numbers that are larger than coyotes are capable of because they have smaller feeding radii and may be constrained by territoriality. Though coyotes would likely reduce the total amount of carrion intake by bald eagles and ravens, we expect that these two species would still consume the bulk of the resource.

The dispersion of wolf- and hunter-killed carcasses represent opposite ends of the spatio-temporal resource spectrum, allowing us to make predictions about the consumption of resources with different spatial and temporal properties (Fig. 4). Wolf kills are distributed regionally across the northern range as they are highly dispersed in time and space, and are consumed primarily by nearby animals. As such, local dynamics such as competition determines access to and consumption of carcasses (Fig. 4, panel 3). Conversely, hunter-kills have a local distribution as they are highly aggregated in time and space. Here, regional dynamics such as recruitment ability, determine the species that consume the bulk of the carrion (Fig. 4, panel 2). In panels 1 and 4, we predict that competition would determine dominance of resources because in neither case would carrion be super-saturated.

Species diversity was found to be higher at wolf kills than at hunter kills (Table 1). This was attributable to a combination of factors: the timing of hunter kills precludes hibernating or migratory species, hunter presence may exclude species wary of being shot, and larger sampling effort at wolf kills made it more likely to detect rare species. Of the common species listed in Table 1 that were not present at hunter kills, it is likely that coyotes were excluded by hunters, while grizzly bears and black bears were in hibernation at the time of the highly aggregated late hunt. Hunts at times of the year when bears are not hibernating, however, may result in their scavenging at gut piles. We did not observe any of the rare species listed in Table 1 at hunter kills so it is not possible to say whether this is merely a result of more observation minutes at wolf kills or some biological process.

The evenness of carrion consumption among species was higher at wolf kills than at hunter kills, while the abundance of consumers was higher at hunter kills than at wolf kills. These two regimes will have different implications on local community dynamics. Once all the carrion is consumed in an area, scavengers may switch to feeding on alternative prey and thus become predators (as long as they are not obligate scavengers as is the case with many vulture species in Africa). In the neighborhood of wolf kills, the trophic effects of prey switching are likely to be relatively small in magnitude and wide in the number of species participating. At hunter-kills, in contrast, the effect is likely to be strong because of the high number of ravens and bald eagles, but narrow because these two species will be doing the bulk of the predation. Food chain effects are thus likely to be stronger at highly aggregated pulses, and to be influenced by species with large feeding radii, compared to highly dispersed and short-lived resources where competitively dominant species are likely to impact the food chain.

This has important implications for conservation and management. If the alternative prey of a highly mobile species is endangered or valued for its economic worth, then conservationists and/or managers should try to avoid creating situations where resources are highly aggregated in time and space. Ravens, for instance, are a predator of the endangered sage grouse (*Centrocercus urophasianus*) (Autenrieth 1981). Managers should take care then not to have highly aggregated hunts in sage grouse habitat because this will likely attract high raven numbers, which may then suppress sage grouse populations. On the other hand, aggregation of resources benefits bald eagles which are also a species of conservation concern. The greater diversity of the scavenger community associated with wolf kills compared to human hunter kills reveals the importance of having natural ecological processes occurring in intact ecosystems. This study reveals a significant component to ongoing comprehensive research on trophic cascades in the GYE due to wolf restoration (Smith et al. 2003a).

The differential success of scavenger species to resources with varying spatial and temporal dynamics suggests an underlying cause for the evolutionary history of these respective species. Bald eagles and ravens may have developed sociality as a means to expand their foraging radii. By roosting communally, these birds are able to find out about the location of resources from conspecifics and thus more efficiently track distant resources that are highly aggregated in time and space.

From managing hunting to controlling the flow of rivers, humans have everincreasing control over the spatial and temporal dispersion of resources. If we are to properly manage these resources, knowledge of how different pulse regimes affect community composition is crucial. Previous research has shown that generalist species are the most adaptable to tracking resources pulses. Here, we add a spatial component to resource pulse dynamics and demonstrate that species-specific feeding radii (which is a function of movement capabilities and access to knowledge about food resources) influence an animals ability to track resource pulses.

Table 1. Species list of scavengers at wolf- and hunter-kills (x indicates presence).

Common Name	Scientific Name	**Wolf**	Hunter
American crow[r]	**Corvus brachyrhynchos**	x	
Bald eagle[c]	*Haliaeetus leucocephalus*	x	x
Black bear[c]	*Ursus americanus*	x	
Common raven[c]	*Corvus corax*	x	x
Clark's nutcracker[r]	*Nucifraga columbiana*	x	
Coyote[c]	*Canis latrans*	x	
Golden eagle[c]	*Aquila chrysaetos*	x	x
Gray jay[r]	**Perisoreus canadensis**	x	
Grizzly bear[c]	*Ursus arctus*	x	
Magpie[c]	*Pica pica*	x	x
Red fox[r]	*Vulpes vulpes*	x	
Turkey vulture[r]	*Cathartes aura*	x	

c - common; r - rare

Table 2. Summary statistics for the maximum number of each species found at each carcass.

Species	Wolf Kills			Hunter Kills		
	mean	S.E.	range	mean	S.E.	range
Bald eagle	1.46	0.18	0-13	10.07	2.24	0-49
Coyote	4.96	0.39	0-16	0	0	0
Golden eagle	1.26	0.19	0-13	0.31	0.14	0-3
Magpie	8.91	0.75	0-32	3.52	0.92	0-23
Raven	36.05	2.19	1-163	78.17	13.22	3-347

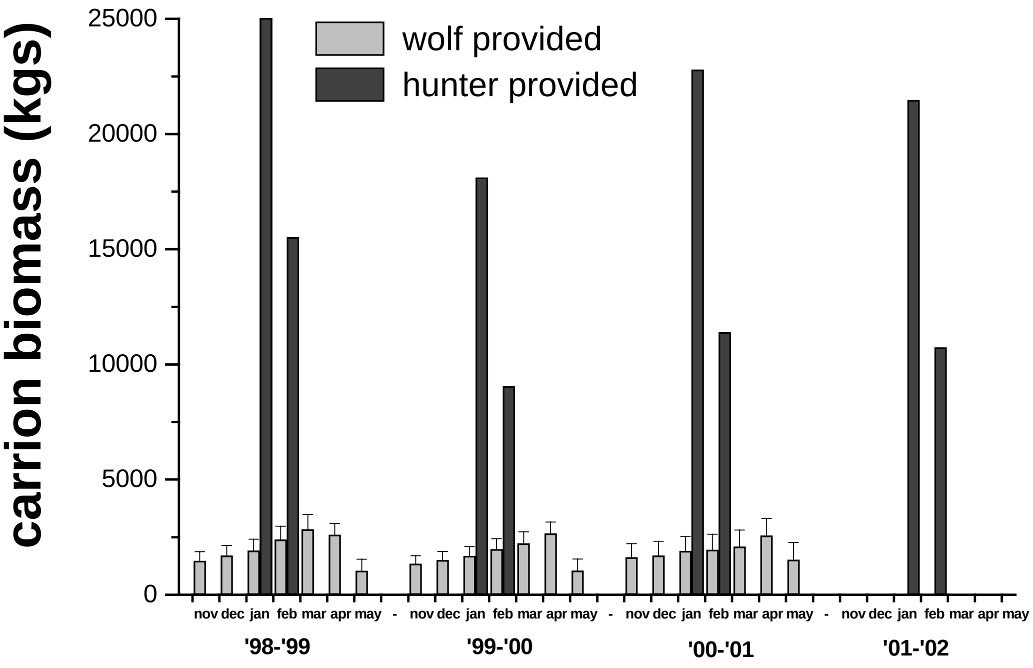

Figure 1. Estimated carrion provided to scavengers by wolves and hunters respectively for the seven months from November thru May (mean ± SE). Wolf scavenge data was not collected in 01-02.

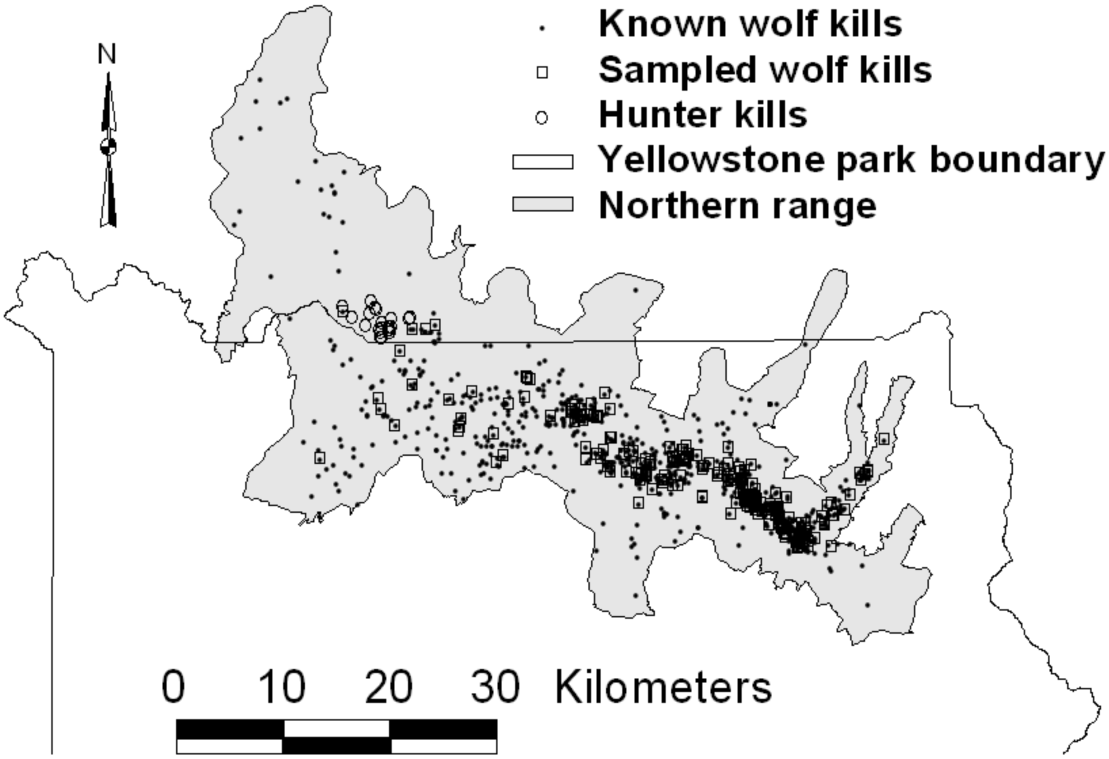

Figure 2. Spatial locations of known wolf kills and hunter kills on the northern range of Yellowstone during the study period. Wolf kills that were sampled for scavenger data are circled. Hunter kills are aggregated in space north of the park boundary because hunters are confined to designated hunting areas. In comparison, wolf kills are more scattered (Wilcoxon rank sum test, $p < 0.001$) as wolf packs are spread out over the landscape.

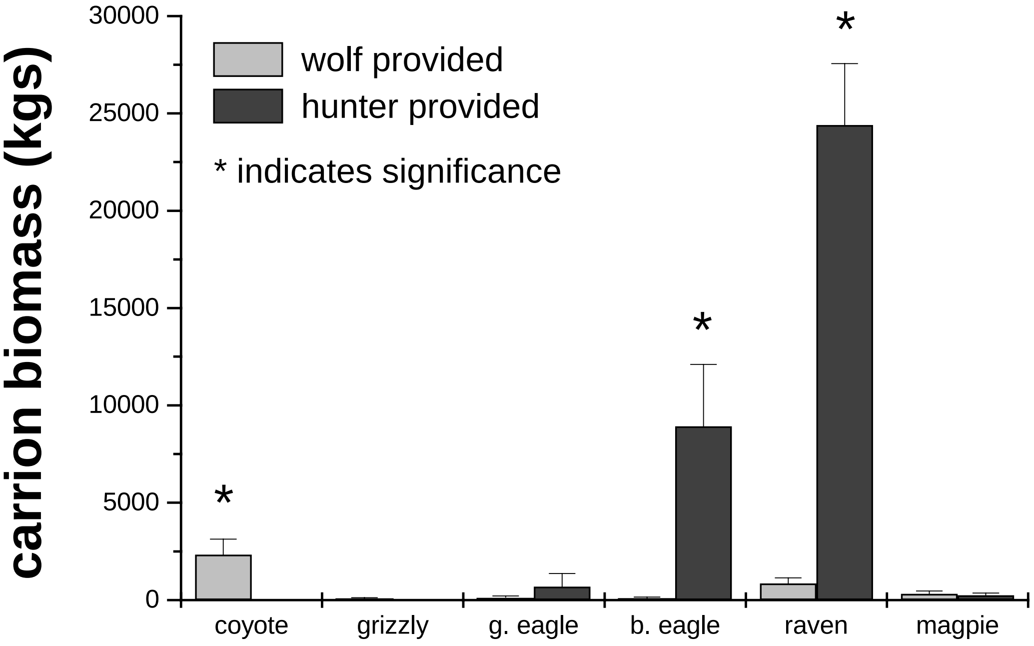

Figure 3. Estimated total carrion biomass to scavengers from wolf- and hunter-killed elk.

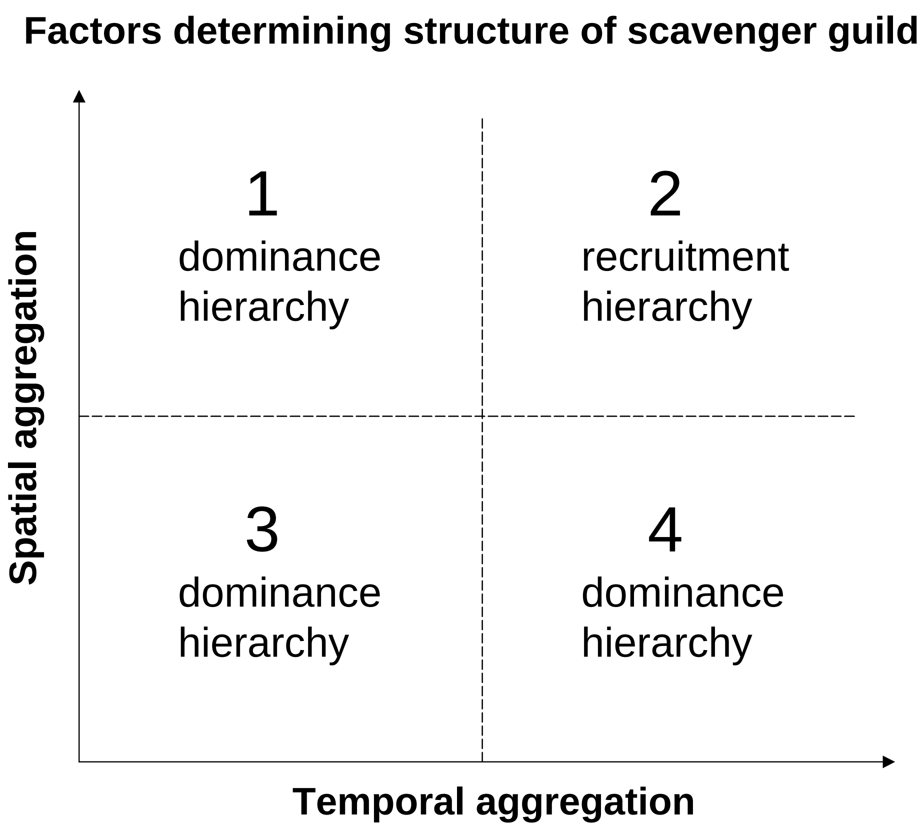

Figure 4. Predictions for the structure of the scavenger guild at a carcass given different spatial and temporal dispersion in resources. In panels 1, 3 and 4 resources are likely to be ephemeral and are thus dominated by competitively superior species in the local scavenger pool. In panel 4, conversely, resources are likely to be saturating and are thus dominated by species with superior recruitment abilities. Resource regimes characterized by recruitment hierarchies are likely to have more pronounced effects on local food chains as consumers switch to alternative prey once the primary resource is consumed (see discussion).

Chapter Five

Simulating the effects of wolf-elk population dynamics on resource flow to scavengers

C.C. Wilmers[1,2] and W.M. Getz[2].

Introduction

The management and conservation of top predators and their respective prey is often informed by community theory on predator feeding habits. By curbing the number or altering the behavior of prey, predators have been shown to cause the release of species two rungs down the food chain (Estes and Palmisano 1974, Power 1990, McLaren and Peterson 1994, Ripple et al. 2001). In addition, predators may also facilitate the coexistence of other prey species by suppressing competitive dominants (Paine 1966, Inouye et al. 1980, McNaughton 1983). While the positive indirect effects of predators eating prey on basal levels of the food chain have been well documented both theoretically and empirically, little work has been undertaken regarding the indirect effects of top predator feeding habits on other guild members. Recent studies on large carnivores have revealed that predators may also help to shape scavenger communities by mediating their supply of carrion (Carbone et al. 1997, Wilmers et al. 2003a). Understanding these effects is crucial to the proper management of ecosystems.

Reintroduced gray wolves in Yellowstone National Park (YNP) have been shown to provide a temporal subsidy to scavengers by transferring the availability of carrion from the resource-rich end of winter period to the resource-poor early winter period (Wilmers et al. 2003a). Scavengers in Yellowstone historically experienced a boom in food supply at the end of severe winters when elk weakened and died, but received very little carrion the rest of the year or in mild winters (Houston 1978, Gese et al. 1996). With the reintroduction of gray wolves to Yellowstone in 1995 (Bangs and Fritts 1996), scavenge of partially consumed wolf-killed carcasses became more constant through time and more abundant overall (Wilmers et al. 2003a). By reducing the peaks in carrion flow to scavengers (some of which is left unused by mammalian and avian scavengers), thereby increasing the troughs, we demonstrate here that the presence of wolves allows for a more predictable and reliable food supply to scavengers.

Winter carrion is crucial to the growth and fitness of many species in the Northern Rockies. As many as 31 species have been documented to feed on wolf kills (P. Paquet personal communication), but grizzly bears, black bears, coyotes, bald eagles, golden eagles, ravens and magpies are the most common visitors at wolf kills in Yellowstone. Coyotes are highly dependent on winter scavenge (Crabtree and Sheldon 1999a) and they have been shown to track wolves to their kill-sites and to feed despite a high risk of predation by wolves (Paquet 1992). In addition, Crabtree and Sheldon (1999b) found that additional elk carrion increased coyote litter size and pup survival. Raven reproduction has been tied to the availability of winter carrion (Newton et al. 1982) and they have been shown to adopt a foraging strategy of following wolves to locate their kills (Stahler et al. 2002). Grizzly bears also depend on spring carrion and occasionally forego hibernation altogether in Glacier National Park, Montana in favor of scavenging wolf kills (D. Boyd personal communication).

As wolf and elk populations grow and contract, carrion subsidies to scavengers may change both in abundance and temporal distribution (Wilmers et al. 2003a). Here we simulate the population dynamics of northern Yellowstone elk and the corresponding accrual of carrion across the year in the absence of wolves. Elk mortality is driven by winter environmental conditions and density dependence. We then add wolf harvest to the model and explore how wolves alter the distribution and abundance of carrion over time. We focus on elk because they are the most numerous ungulate in the area (Houston 1982) and because they account for well over ninety percent of the wolf's diet on the northern range (Mech et al. 2001). Further, prey switching is unlikely to occur because of the sheer magnitude of the elk population and the potential alternative, bison, are difficult to kill except under special circumstances (Smith et al. 2000).

Humans also play a major role in provisioning carrion to scavengers. Elk hunters typically dress their catch in the field, leaving behind entrails that become food to scavengers. Unlike wolf predation, however, human hunting is highly localized both in space and time due to restrictions on where and when hunting is allowed. The long-term impacts of hunting are also likely to be different from those of wolves because hunters kill a different segment of the elk population. Wolves kill primarily calves and old individuals (Mech et al. 2001) whereas hunters in the Yellowstone area kill primarily adult cows and usually do not discriminate based on age (T. Lemke personal communication). We add human hunting to the model and explore scenarios both with and without wolves and with and without human hunting in order to explore the separate and synergistic effects of wolves and hunters on scavenger populations.

Understanding how wolves affect the long-term supply of resource to scavengers in areas with and without hunting is important to conservationists seeking to restore wolf populations in other areas. In addition, insight into the interplay between wolf predation and human hunting on carrion supply to scavengers will aid managers formulating hunting policies. The essence of our problem is reduced to a two predator, one prey model that simulates the flow of carrion resource to scavengers. The model allows us to explore conservation and management scenarios (Starfield and Bleloch 1986) as well as test basic ideas about predator effects on food chains.

Methods

Pre-Wolf Model

We use a modified Leslie Matrix model with a monthly time step to simulate the population dynamics of Yellowstone elk and the corresponding accrual of elk carrion as individuals die from one month to the next. Elk calves and old adults experience density-dependent mortality in the winter (Taper and Gogan 2002) as increasing snow levels concomitantly increase metabolic activity (Parker et al. 1984) and reduce access to food (Houston 1982). Therefore we incorporate density dependence into winter survival probabilities of old adults and calves. Males and females are modeled separately to account for the fact that senescence begins much earlier in males than in females (Houston 1982). Reproduction is limited to females of three years and older and declines when females reach old age (Houston 1982).

The female components of the elk population over time t are represented by the age class vector $\mathbf{x}^f = (x_1^f, x_2^f, ..., x_n^f)'$ where the elements, x_i^f, for i = 1, …, n, are the number of females in age class i. A similar vector $\mathbf{x}^m$ defines the male population so that the combined female and male population $\mathbf{x}(t)$ at time t satisfies,

$$\mathbf{x}(t) = \mathbf{x}^f(t) + \mathbf{x}^m(t) \tag{1}$$

where we choose the units of t to be one month. We also let age classes range from 1 year olds to 20+ year olds, i.e. $n = 20$, in order to account for the full age range of Northern Yellowstone elk (Houston 1982). This adds structural realism to the model without increasing the number of parameters to estimate because we keep vital rates unchanged between most ages. Reproduction occurs once a year in June. In non-reproductive months our model takes the form,

$$\mathbf{x}^{y}(t+1) = \mathbf{A}^{y}(t)\mathbf{x}^{y}(t) \qquad \text{mod }(t,12) \neq 6,\ \ y = f \text{ or } m \tag{2}$$

where $\mathbf{A}^{y}(t)$ is the transition matrix,

$$\mathbf{A}^{y}(t) = \begin{bmatrix} P_1^y & 0 & . & . & 0 \\ 0 & P_2^y & & & \\ . & & . & & \\ . & & & . & \\ 0 & & & & P_n^y \end{bmatrix}, \tag{3}$$

and P_i^y is the probability that a member of the i^{th} age class survives to the next month. Each June, females reproduce and elk advance age classes such that,

$$\begin{aligned} \mathbf{x}^{f}(t+1) &= \left(\mathbf{R}^{f}(t) + \mathbf{T}^{f}(t)\right)\mathbf{x}^{f}(t) \\ \mathbf{x}^{m}(t+1) &= \mathbf{T}^{m}(t)\mathbf{x}^{m}(t) + \mathbf{R}^{f}(t)\mathbf{x}^{f}(t) \end{aligned} \qquad (\text{mod }(t,12) = 6), \tag{4}$$

where the reproductive, $\mathbf{R}^{y}$, and the transition, $\mathbf{T}^{y}$, matrices have the form,

$$\mathbf{R}^f(t) = \begin{bmatrix} 0 & 0 & F_3 & \dots & F_n \\ . & . & & & \\ . & & . & & \\ . & & & . & \\ 0 & & & & 0 \end{bmatrix} \tag{5}$$

and,

$$\mathbf{T}^y(t) = \begin{bmatrix} 0 & . & . & . & 0 \\ G_1^y & & & & . \\ & . & & & . \\ & & . & & . \\ & & & G_{n-1}^y & 0 \end{bmatrix}. \tag{6}$$

In these matrices, F_i is the fecundity of females and G_i^y is the probability of advancing to the next age class. Female elk in Yellowstone are highly productive in their younger years but become substantially less fecund in old age (Houston 1982). As such, we set fecundity for prime aged females $F_{i=3,\ldots,\alpha-1} = F_{\max}$ and the fecundity for old females $F_{i=\alpha,\ldots,n} = F_{\min}$. We assume a 50-50 birth sex ratio so that F_i represents half of the total value.

Senescence begins in the winter of females' α^{th} year and males' β^{th} year. In each subsequent age class, an increasing proportion γ_i^π, where $\pi = \alpha$ or β, become part of the senescent class. Guided by mortality curves published by Houston (1982), we increase γ_i^π quadratically with age such that

$$\gamma_i^{\pi} = -0.025(i - \pi + 1)^2 + 1 \quad \text{for } i = \pi,\ldots,n. \tag{7}$$

Density dependence is incorporated into the survival terms of calves and senescent adults as follows. Let V be the snow-water-equivalent (which serves as a proxy for snow depth that has been found to be strongly correlated with elk mortality (Gese et al. 1996)), B the biomass of the elk population, $P_{\max}$ the maximum survival probability, λ the half saturation level and s the shape parameter. Survival probabilities for calves and old adults during the winter time are then described by the function,

$$\begin{aligned}
P_i^f &= P_{\max}^f && i = 2,\ldots,\alpha - 1 \\
P_i^m &= P_{\max}^m && i = 2,\ldots,\beta - 1 \\
P_i^y &= \frac{P_{\max}^y (\lambda)^s}{(\lambda)^s + (V(t)^2 \cdot B(t))^s} && \begin{array}{l}\text{for } i = 1 \text{ and } \alpha,\ldots,n \text{ for females} \\ \text{for } i = 1 \text{ and } \beta,\ldots,n \text{ for males}\end{array}
\end{aligned} \tag{8}$$

This function has the properties that as elk biomass or snow-water-equivalent increase, survival decreases (Fig. 1). The half saturation parameter λ sets the point at which maximum survival is reduced by half. The shape parameter s describes the abruptness of the onset of density dependence (Fig. 1) (Getz 1996). When s is low, density dependence sets in gradually as biomass and snow-water-equivalent increase. As s increases the function approaches a step function where density dependence sets in abruptly as V^2B increases. We assume that survival decreases in proportion to the square of snow-water-equivalent because previous studies have indicated that as snow-water-equivalent increases, elk metabolism increases quadratically (Parker et al. 1984). In our simulations we use real snow-water-equivalent values collected on the Northern

Range from 1949-2001 (Farnes et al. 1999). To do so, we choose a year at random from 1949-2001. Monthly snow-water-equivalent values from that year are then assigned to the model corresponding to each winter (December through April) month. Stochasticity is thus introduced into the model via *V*.

The biomass of the entire elk population is given by

$$B(t) = \sum_{i=1}^{n} x_i^f(t) \cdot \omega_i^f(t) + x_i^m(t) \cdot \omega_i^m(t)\,, \tag{9}$$

where ω_i^f and ω_i^m are the average monthly weights (in kgs) of females and males for age *i* taken from an elk growth model (Murphy et al. 1997). Individuals that do not survive from one month to the next enter the carrion pool for that month. The amount of carrion that accumulates in the months without reproduction (in kgs) is given by

$$\begin{array}{l} C(t+1) = \sum_{i=1}^{n} \left(x_i^f(t) - x_i^f(t+1)\right) \cdot \omega_i^f(t) + \left(x_i^m(t) - x_i^m(t+1)\right) \cdot \omega_i^m(t) \\ \bmod(t,12) \neq 6 \end{array} \,. \tag{10a}$$

and,

$$
\begin{aligned}
C(t+1) = {} & \left(0.5\cdot\left(\sum_{i=3}^{\alpha-1} x_i^f(t)F_{\max} + \sum_{i=\alpha}^{n} x_i^f(t)F_{\min}\right) - x_1^f(t+1)\right)\cdot\omega_1^f + \\
& \left(0.5\cdot\left(\sum_{i=3}^{\alpha-1} x_i^f(t)F_{\max} + \sum_{i=\alpha}^{n} x_i^f(t)F_{\min}\right) - x_1^\beta(t+1)\right)\cdot\omega_1^m + \\
& \sum_{i=1}^{n}\left(x_i^f(t) - x_{i+1}^f(t+1)\right)\cdot\omega_{i+1}^f(t) + \left(x_i^m(t) - x_{i+1}^m(t+1)\right)\cdot\omega_{i+1}^m(t)
\end{aligned}
\tag{10b}
$$

$mod(t, 12) = 6$

in June to account for the effect of reproduction and age class advancement on carrion accrual.

Adding Wolves

We incorporate dynamics into the wolf population to explore the relationship between scavenge provision and elk population size as the wolf population responds dynamically to changes in its prey base. Wolves are born at the beginning of April each year, and reach sexual maturity at two years of age. As such we define three age classes of wolves: pups (w_1: 0-1 year olds), juveniles (w_2: 1-2 year olds), and adults (w_3: >2 year olds) where the minimum breeding age is set at 22 months (Haight et al. 1998). If we let $S_j, j = 1, 2, 3$, represent the survivorship of the j^{th} age class, and L_3 be the fecundity of adults then the change in wolf population $\mathbf{w}$ over the interval [t, t+1] satisfies,

$$
\mathbf{w}(t+1) = \mathbf{M}(t)\mathbf{w}(t), \quad t = 0,1,2,\ldots,(\text{months}), \tag{11}
$$

where $\mathbf{M}(t)$ is the transition matrix given by,

$$\mathbf{M}(t) = \begin{bmatrix} 0 & 0 & L_3 \\ S_1 & 0 & 0 \\ 0 & S_2 & S_3 \end{bmatrix} \quad \text{for } \mathrm{mod}(t,12) = 4, \tag{12}$$

$$\mathbf{M}(t) = \begin{bmatrix} S_1 & 0 & 0 \\ 0 & S_2 & 0 \\ 0 & 0 & S_3 \end{bmatrix} \quad \text{for } \mathrm{mod}(t,12) \neq 4. \tag{13}$$

Wolf survivorship is assumed to depend on the quantity of prey resource. If the harvest of elk by wolves exceeds their energetic requirement (allowing for losses to scavengers), then survival is at its maximum. However, if the harvest is less than this energetic requirement, then resources go into deficit, *D*, and survival begins to decline as a function of the amount of this deficit per wolf. To account for the reduced requirements of pups, we define the relative number of wolves, *W,* where pups are discounted by $a(t)$, ($0<a(t)<1$) because they are smaller and require less resources than adults, as

$$W(t) = a(t)w_1(t) + w_2(t) + w_3(t)\,. \tag{14}$$

The dependence of *a* on *t* arises because we assume that pup growth is a linear function of time with pups starting out at a fraction a_0 of full growth and becoming full-grown at 10 months, viz:

$$a(t) = a_0 + \left(\frac{1 - a_0}{10} \right) (t - 4) \qquad \mathrm{mod}(t,12) = 4,5,\ldots,12,1$$

$$a(t) = 1 \qquad \mathrm{mod}(t,12) = 2,3 \tag{15}$$

If we let $S_{\max}$ be the maximum survival probability, ν the half saturation constant, ζ the shape parameter, E the energetic requirement per wolf per month, and $K(t)$ the kill rate per wolf per month (in kgs), survivorship then becomes,

$$S_j(t) = S_{\max} \left(1 - \frac{(D(t))^{\varsigma}}{\nu_j^{\varsigma} + (D(t))^{\varsigma}} \right), \tag{16}$$

where

$$\begin{aligned} D(t) &= 0 && \text{for } E \le K(t) \\ D(t) &= E - K(t) && \text{for } E > K(t). \end{aligned} \tag{17}$$

While wolves may kill an occasional prime-aged elk, they are primarily dependent on the old and young for their sustenance (Peterson et al. 1984, Mech et al. 2001). Hence the biomass of vulnerable prey B_v is the sum of calves and senescing adults given by,

$$B_v(t) = \omega_1^m(t) x_1^m(t) + \omega_1^f(t) x_1^f(t) + \sum_{i=\alpha}^{n} \gamma_i \omega_i^f(t) x_i^f(t) + \sum_{i=\beta}^{n} \gamma_i \omega_i^m(t) x_i^m(t). \tag{18}$$

The functional form of wolf kill rate has recently been shown to depend on the ratio of the number of wolves to the number of prey (Vucetich et al. 2002). Though Vucetich et al. found that a ratio-dependent function was among the best fits to the data (Pitcairn et al. 1990), it still only explained 33% of the variance. While many factors may contribute to explaining the remaining variance, we believe that one improvement would be to make kill-rate depend on the ratio of wolves to the biomass of vulnerable prey rather than total prey numbers. This more accurately represents the segment of the prey population vulnerable to predation and the actual availability to wolves of the prey resource. Kill-rate-per-wolf in our model then is assumed to be a function of the ratio of the number of wolves to biomass of vulnerable prey given by

$$K(t) = \frac{K_{\max}\mu^{\xi}}{\mu^{\xi} + \left(\frac{W(t)}{B_v(t)}\right)^{\xi}}, \tag{19}$$

where $K_{\max}$ is the maximum kill rate per wolf, μ is the half saturation constant and ξ is the shape parameter (Fig. 2).

If the elements h_i^y of $\mathbf{h}^y$, $i = 1,...,n$ and $y = f$ or m, represent the number of additional elk harvested each month from age class i and gender class y, that would not have died in the absence of wolves, then the change in elk population over time with wolf harvesting is given by

$$\mathbf{x}^y(t+1) = \mathbf{A}^y(t)\mathbf{x}^y(t) - \mathbf{h}^y(t) \qquad \text{for } \operatorname{mod}(t,12) \neq 6 \tag{20}$$

and

$$\begin{aligned}\mathbf{x}^f(t+1) &= \left(\mathbf{R}^f(t) + \mathbf{T}^f(\mathrm{t})\right)\cdot \mathbf{x}^f(t) - \mathbf{h}^f(t) \\ \mathbf{x}^m(t+1) &= \mathbf{T}^m(t)\cdot \mathbf{x}^m(t) + \mathbf{R}^f(t)\cdot \mathbf{x}^f(t) - \mathbf{h}^m(t)\end{aligned} \qquad \text{for } \mathrm{mod}(t,12) = 6\,. \tag{21}$$

Wolf predation is assumed to be additive during times of the year when natural elk mortality would be less than wolf demands and to be compensatory during times when natural mortality would have exceeded wolf demands. The total take, H, of elk biomass killed by wolves is given by

$$H(t) = K(t)\cdot W(t)\,. \tag{22}$$

During certain times of the year, some or all of the carrion produced by wolves may have otherwise died. Hence we express the additional take, H_a, of elk biomass when wolf predation is additive by

$$H_a(t) \equiv \sum_{i=1}^{n} h_i^y = K(t)\cdot W(t) - C(t) \quad \text{for } K(t)\cdot W(t) > C(t)\,. \tag{23}$$

We then convert elk biomass to numbers by dividing the total carrion in each age class by the average weight of an individual in that age class and month of the year. Calves and senescing adults are killed in proportion to their abundance in the population. The oldest senescent adults are harvested first, followed by the next oldest and so on.

The amount of carrion available each month to scavengers C_s is simply total elk mortality less that which wolves consume: that is,

$$C_s(t) = C(t) + \sum_{i=1}^{n} h_i^y(t) - E \cdot W(t)\,. \tag{24}$$

Hunter Harvest

Human hunting of the Northern Yellowstone elk herd occurs north of the park on national forest land as animals leave the park in the winter. There are two hunts: the early hunt from September to December which is largely unregulated and the late hunt from January to February for which quotas are set. The late hunt accounts for the bulk of the total take for the entire winter hunting season (over 80% in some years) (Lemke et al. 1998) as elk are at lower elevations and less dispersed on the landscape. Late hunt quotas are set in order to regulate elk numbers and to provide sustainable public recreation (Lemke et al. 1998). Hunting permit quotas are set using adaptive harvest management (AHM) guidelines which take into account the number of elk migrating north of the park and hunter success rates (T. Lemke Personal Communication). Approximately 95% of the permits issued are antler-less. So the majority of hunters take adult cows.

We incorporate hunting into the model by assuming that all hunting occurs in the late winter period. As the number of elk wintering north of the park is likely to correlate with population size (in addition to winter severity), we simply set the hunting level, θ, as a percentage of the total population. We then specify the proportion of kills that are cows ρ_{cow}. Calves are harvested at a fixed low background proportional rate

ρ_{calf}. The proportion of bulls harvested is then $\rho_{\text{bull}} = 1 - \rho_{\text{calf}} - \rho_{\text{cow}}$. The number of individuals in each age class harvested is proportional to the abundance of that age class in the population. Based on weights of hunter gut piles (Wilmers et al. 2003a), we assume that 14% of each hunter kill becomes food for scavengers.

Actual quotas set by managers in the Yellowstone Ecosystem are based on count data and hunter success rates which have a degree of error in them. In addition, other factors affect the quota such as weather conditions and public comment. In this study, however, our goal is to understand some of the basic biological interactions between hunters and scavengers rather than to precisely model the Northern Yellowstone elk hunt.

Simulations and Sensitivity Analysis

The model was coded in Matlab 6.0.1 (Mathsoft $^{\text{TM}}$). We ran the model for 500 years with monthly time steps and deleted the first 100 years of data in order to remove the transient effects of initial conditions. We then collected basic descriptive statistics on carrion levels within and across years. In order to quantify the spread of carrion by month *j* across a single year we calculated its normalized Shannon-Weaver diversity number, *Φ*, given by,

$$\Phi = -\frac{1}{\log(12)}\sum_{i=j}^{12} Q_j \ln(Q_j) \tag{25}$$

where,

$$Q_j = \frac{C_j}{\sum_{j=1}^{12} C_j}. \qquad (26)$$

This is an index ranging between zero and one, which relates the evenness of the carrion spread across the year. A Shannon diversity number of 0 indicates that all the carrion occurs in one month of the year whereas a value of 1 indicates that the carrion is evenly distributed across each month of the year.

Sensitivity analyses were conducted using Monte Carlo methods to assess the relative effects of several parameters on model statistics (Wisdom and Mills 1997, Wisdom et al. 2000, Cross and Beissinger 2001). Specifically, for each model, 1000 random parameter sets were created by choosing model specific parameter sets from uniform distributions bounded by the values shown in Table 1. Parameter ranges were either estimated from previously published work or chosen a priori in order to test the effect of different management scenarios (such as the case with hunt level). Where specific ranges were not given in published work, we estimated a range based on our best understanding of the biology. Each parameter set was used to run the model once, for a total of 1000 runs. Mean yearly carrion levels and Shannon diversity numbers for the years 101-500 were recorded for each run and used as the dependent variable in linear regressions in which the model parameters were the explanatory variables. Model parameters were ranked according to r^2 values in order to determine which ones explained the most variance in model output statistics (Wisdom and Mills 1997, Wisdom et al. 2000, Cross and Beissinger 2001). The larger the range in a parameter, the higher its r^2 may become. As such we generally erred on the side of caution, choosing larger rather than smaller ranges so that our bias would be towards overestimating the sensitivity of an output variable to the parameter.

Each model typology was thus analyzed for parameter sensitivities. Model statistics from the pre-wolf model were then compared to parallel statistics for each successive post-wolf model by running each model through its most sensitive parameters.

Results

Carrion Accrual and Diversity

The pre-wolf model generates a changing elk population over time with a corresponding accrual of elk carrion across the year (Fig. 3a). Within year fluctuations in biomass largely reflect the changing weight of the elk population as they gain weight during the summer and lose it during the winter (Fig. 3b). Between year changes in elk biomass reflect changes in elk number or age structure. Carrion levels during the summer months are low and begin to accumulate during the winter months as snow levels increase and elk weaken and die. Though the distribution of elk carrion varies from year to year depending on the snow pack and population size, the general pattern is for carrion to build during the course of the winter and peak near March (Fig. 3b, 4a). In addition the total abundance of elk carrion roughly follows the size of the elk population. In a single run of the model, using mean values of each parameter, average winter snow depth accounts for 53%, and elk number accounts for 40% of the variance in mean yearly carrion respectively.

The addition of wolves to the model results in a reduction of the amount of late winter carrion, but extends the availability of carrion to early winter (November and December) and other times of year when carrion would not previously have been available in large quantities (Fig. 4). In addition, wolves reduce the year to year variance in carrion availability (Fig. 4). By killing continuously throughout the year, wolves provide carrion at times that it would not have been available otherwise and also reduce the pool of weak animals entering the winter. As a result, carrion is less plentiful in severe winters but more abundant in mild ones.

Abruptness Parameter

The shape parameter of density-dependent elk survival s (eq. 8) accounts for 98% of the variance without wolves in the distribution of carrion across the year as measured by our statistic Φ (Table 2, Fig. 5a). As s increases, the carrion diversity index Φ decreases which implies that the more abrupt the onset of density-dependent mortality, the more aggregated elk deaths become. Mean yearly carrion abundance and elk numbers were sensitive to changes in the onset of female senescence α, female fecundity $F_{\max}$, shape parameter s and the half saturation constant h (Table 2). The sensitivity results of carrion abundance largely parallel those of elk number (Table 2) because, on average, more elk result in more carrion.

Introducing wolves to the model reduces elk numbers and carrion levels. In addition to the four parameters affecting the sensitivity of these two variables in the pre-wolf model, mean numbers of elk and carrion levels are sensitive to changes in the wolf half-saturation kill rate μ (Table 2). As μ decreases, wolf kill rate declines at smaller ratios of wolves to prey (Fig. 2) thus allowing the elk population to attain higher average numbers. The fewer wolves there are, the more elk and hence more carrion there is. Conversely, as wolves become more efficient predators and μ increases, the elk population shrinks and there are more wolves and less total carrion as a result.

Wolves have a large impact on the distribution of carrion throughout the winter. While the carrion diversity index, Φ, is still sensitive to changes in the elk abruptness parameter s, the majority of the variance in Φ can now be explained by μ (Table 2). In addition, wolves increase Φ levels for all values of μ (Fig. 5b) indicating that the distribution of carrion in the presence of wolves is more evenly spread throughout the year. The effect of μ on Φ and mean carrion levels respectively are opposed to each other. This implies that as wolves become more efficient predators and hence attain higher population sizes, carrion is more evenly distributed throughout the year, but there is less of it. Conversely, as wolves become less efficient predators and hence attain lower population sizes, total carrion increases but the distribution becomes increasingly skewed towards late winter. With few wolves, elk mortality is primarily driven by winter conditions and density-dependent phenomena resulting in a pulse of carrion at the end of severe winters. The more wolves there are, the more additive elk mortality there is in early winter and other times of the year (Fig. 4b). This results in a more equitable distribution of carrion throughout the year but less of it because the population of elk is reduced.

Hunting

The addition of hunting to the model also results in lower carrion yields because hunting reduces the elk population. As in the pre-wolf model with no hunting, mean elk numbers and carrion levels are still sensitive to changes in α, $F_{\max}$, s, and h though the effect of these parameters is reduced. Hunt level θ, and the proportion ρ_{cow} of harvested elk that are cows are now important factors in explaining the variance in population size and carrion abundance (Table 2). The more elk that are hunted or the higher the proportion of adult females harvested, the lower the overall population. Hunting has very little effect on the distribution of carrion across the winter, however. As in the pre-wolf model, Φ is only affected by changes in the elk abruptness parameter s (Table 2).

The addition of hunting to the post-wolf model largely parallels the effect of the addition of hunting to the pre-wolf model. The elk population and mean carrion levels are reduced with both variables being sensitive to changes in hunt level and the proportion of cows that are harvested. In addition, the distribution of carrion across the year remains sensitive primarily to changes in μ as in the wolf model without hunting.

Assuming the hunt level θ remains the same, changes in the proportion ρ_{cow} of cows harvested can have a large effect on elk population size and hence carrion levels. As an example of this effect, we assume average parameter values from Table 1 and tune λ such that the pre-wolf model generates an average elk population of 17,000 individuals with a hunting level $\theta = 0.05$ and $\rho_{\text{cow}} = 0.95$. If we then add wolves with a half saturation kill rate μ tuned such that a mean of 100 wolves persists in the system, the average elk population drops to 13,000. Reducing the proportion of cows harvested by hunters %10 to $\rho_{\text{cow}} = 0.85$ would restore the elk population to its original 17,000 individuals and hence boost mean carrion levels (Fig. 6).

Survivorship

By selectively preying on old and young elk, wolves cause a decrease in the survivorship of calves and the very old (Fig. 7). By reducing the elk population overall, however, wolves cause an increase in the survivorship of individuals that have just begun to senesce (Fig. 7). By reducing the number of elk, wolves mitigate the effect of density-dependent resource competition between elk, causing elk that have just begun to senesce to be better off than they would have been in the absence of wolves. As they get older, however, this effect is overcome by predation by wolves. One effect of these changes in survivorship is that a greater turnover in the elk population occurs. This results in higher carrion yields per elk in the population.

Hunting also changes the shape of the elk survivorship curve (Fig. 7). By hunting cows indiscriminate of age, this lowers the survivorship of adult cows. In addition, by reducing the population and hence the effects of density dependence it also increases the survivorship of calves.

Discussion

Elk carrion is a crucial food resource for scavengers. Our model reveals that although wolves reduce the size of the elk population and hence the abundance of elk carrion, they smooth out the temporal distribution of carrion providing carrion throughout the year when previously carrion was only available at the end of winter. In addition, wolves reduce the year to year variance in carrion availability. Whereas prior to wolf reintroduction, carrion would have been plentiful at the end of severe winters and largely absent in mild ones, carrion is now likely to be relatively more plentiful in mild winters and less abundant in severe ones. Since wolf reintroduction, carrion represents a more reliable food resource than in the previous boom and bust cycle. The change in carrion resource availability is likely to affect scavenger species differentially. Small to medium size scavengers with small fat stores are likely to benefit from the more steady supply of carrion. Large scavengers, such as grizzly bears, may experience less of a benefit because they have large fat stores and could thus more easily track the pre-wolf boom and bust scavenge cycle. The fact that carrion is now available in the fall, however, will likely benefit bears going into hibernation by providing a high calorie food prior to denning. Thus wolves may actually facilitate average population levels of scavengers even though they reduce total annual carrion levels.

The total size of the elk population, and hence abundance of carrion, was found to be sensitive to the half saturation λ, abruptness s, fecundity of prime age females $F_{\max}$ and onset of female senescence α in the elk equations. The parameters λ and s control abundance because they control the onset and rapidity of density dependence. The parameters α and $F_{\max}$ are important parameters because they determine the proportion of the population that are prime breeders and how many of these actually give birth. Without wolves, the distribution of carrion across the year, as measured by our diversity statistic Φ, was only sensitive to s. Given a high value of s, density dependence is absent until a critical density is obtained at which point survivorship drops precipitously and a spike in carrion level occurs. Conversely, for a low value of s, the effects of density dependence set in relatively slowly and carrion accumulates at a lower rate over a longer period. The addition of wolves to the model reduces the dependence of Φ on s and results in greater variance in the distribution (Fig. 5b). This is due to the effect of wolves decreasing the elk population and hence the effects of density dependence on the herd. The degree to which wolves reduce the elk population and hence carrion abundance is primarily dependent on the fit of the wolf-kill-rate function. Fitting this function with Yellowstone data in order to estimate parameters, in particular the half-saturation parameter μ will be crucial in determining the ultimate equilibrium levels of wolves, elk and carrion. While the kill-rate per wolf is currently being estimated each year in Yellowstone (Mech et al. 2001), fitting equation 19 will require a longer-term data set.

Though wolves reduce the overall abundance of elk carrion by reducing the elk population, this is partially mitigated by the effect of wolves on the turnover of the elk population. By wolves preying selectively on old animals and thus reducing the average age of the elk population, elk productivity is increased. This in turn leads to increased carrion yield per elk in the population. This is akin to the findings of research on herbivores increasing the productivity of the plants they feed on by removing dead tissue thus allowing remaining plant tissue better access to sunlight for photosynthetic activity (McNaughton 1984).

An interesting consequence of the selective predation by wolves is that they actually increase the survival probabilities of early senescing elk. Arguments for predators strengthening prey populations have generally drawn on evolutionary arguments of predators selecting less fit individuals and thus weeding those genes out of the population (Krebs and Davies 1981). Here we present a possible ecological explanation for the same phenomenon: that by reducing the effect of density-dependent resource competition among elk, those that remain, even some of the older animals, are better fed and healthier as a result.

Hunting exerts a strong downward pressure on the elk population when cows are the prime target of hunters. Elk population numbers are especially sensitive to the survival of prime aged cows because they are responsible for the future reproductive yield of the population. An important goal of the late winter elk hunt has been to regulate the population migrating north of the park in order to avoid conflicts with livestock operations in Paradise Valley, maintain the long-term diversity and productivity of winter range vegetation and avoid the transmission of brucellosis from elk to domestic livestock (Lemke et al. 1998). Additionally, the hunt serves as a popular recreational activity important to the winter economy of the local area. Our model reveals that in addition to these concerns, hunt intensity affects the supply of carrion to scavengers. In the short term, a large hunt may provide a localized boom in carrion to scavengers, but in the long term, large hunts suppress the elk population and reduce overall carrion availability from wolf kills which are available throughout the year and throughout the northern range. With the addition of wolves to the ecosystem, the elk herd is likely to experience a reduction in equilibrium population levels. This potentially lessens the need for management actions to reduce the size of winter migration into Paradise Valley. Hunting, however, remains a vital interest among the local community. Our model reveals that by shifting the focus of the hunt away from cows, average hunt levels need not change dramatically in order to allow for a robust elk population and plenty of carrion for scavengers.

Our model builds upon the work of previous predator-prey and wolf-ungulate models (Crete et al. 1981, Hadjibiros 1981, Stocker 1981, Jensen and Miller 2001, Miller et al. 2002) by incorporating a monthly time step so that seasonal carrion biomass to scavengers may be accounted for. We also expand upon the models of Miller et al. (2002) and Jensen and Miller (2001) by incorporating human hunters into our model. By explicitly keeping track of each year class of elk, we are able to tease out the differential effects of human hunters and wolves on elk population dynamics and carrion availability to scavengers. What emerges is a community perspective of predator-prey dynamics that so far has been ignored in these types of models.

Wolf reintroduction and re-colonization in other parts of the world may likewise affect scavenger species in those areas. Though species composition may change from location to location, the dynamics of carrion availability will likely respond in the same way. As such, conservation efforts focused on small and medium sized carnivores may benefit from the presence of wolves. In addition, management of wolves and/or human hunters should consider the synergism of these two predators when setting policy.

Table 1. Parameter descriptions and data ranges.

function	parameter	description	range	source
elk	α	onset of female senescence	10-13 years	(Houston 1982)
	β	onset of male senescence	4-7 years	(Houston 1982)
	s	abruptness parameter	1-2	(Getz 1996)[1]
	λ	half saturation level	3-5 x 10^6 kgs	[2]
	$F_{\max}$	fecundity of prime aged females	0.6-0.85	(Houston 1982)
	$F_{\min}$	fecundity of senescing females	0.4-0.6	(Houston 1982)
	$P_1^y(6)$	summer calf survival	0.5-0.8	(Singer et al. 1997)
hunt	θ	proportion of population to harvest	0.025-0.06	[3]
	ρ_{cow}	proportion of cows to harvest	0.5-0.95	[3]
wolf kill rate	μ	half saturation	0.00003-0.0003	(Fuller 1989, Vucetich et al. 2002)[4]
	ξ	abruptness parameter	1-4	(Getz 1996)
wolf survival	ζ	abruptness parameter	1-2	(Getz 1996)[1]
	v_1	half saturation of pups	50-100	[5]
	$v_{2,3}$	half saturation of juveniles and adults	100-200	[5]
	E	energetic requirement	1-5 kgs/day	(Fuller 1989)
	L	fecundity	1-6	(Mech 1970)

[1] Because of the extreme sensitivity to this parameter, we confined it to this narrow range. In addition, for the reasons discussed in Getz (1996), this parameter is likely to be small (i.e. < 2) for mammals with large storage (fat) capabilities (elk) or for territorial animals (wolves).

[2] We chose half saturation levels that yielded mean elk numbers of 15,000 to 25,000 elk in the pre-wolf model.

[3] Ranges were chosen to test the effects of different management scenarios.

[4] We converted data given in numbers to biomass in order to estimate μ.

[5] We chose ranges based on intimate knowledge of the system that were larger than they probably are. This would tend to overestimate the sensitivity of this parameter.

Table 2. r^2 values of parameters with respect to three indices, mean Shannon diversity index $\overline{\Phi}$, mean elk number $\overline{x}$, and mean carrion $\overline{C}$ obtained from Monte Carlo simulations.

model	**parameter**	$\overline{\Phi}$	$\overline{x}$	$\overline{C}$
		r^2	r^2	r^2
pre wolf no hunt	α	-[1]	0.16	0.19
	$F_{\max}$	-	0.08	0.20
	s	0.98	0.29	0.21
	λ	-	0.45	0.34
pre wolf w/ hunt	α	-	0.08	0.08
	$F_{\max}$	-	0.06	0.11
	s	0.86	0.29	0.16
	λ	-	0.19	0.10
	θ	-	0.16	0.27
	ρ_{cow}	-	0.15	0.16
post wolf no hunt	α	-	0.12	0.10
	F_{max}	-	0.07	0.09
	s	0.20	0.22	0.09
	λ	-	0.25	0.12
	E	0.07	-	0.05
	μ	0.54	0.19	0.36
	ξ	0.07	-	0.05
post wolf w/ hunt	α	-	0.05	0.05
	$F_{\max}$	-	0.07	0.12
	s	0.13	0.21	0.08
	λ	-	0.18	0.09
	E	0.12	-	-
	μ	0.51	0.11	0.24
	θ	-	0.17	0.27
	ρ_{cow}	-	0.14	0.15

[1] We only report results with $r^2 \geq 0.05$.

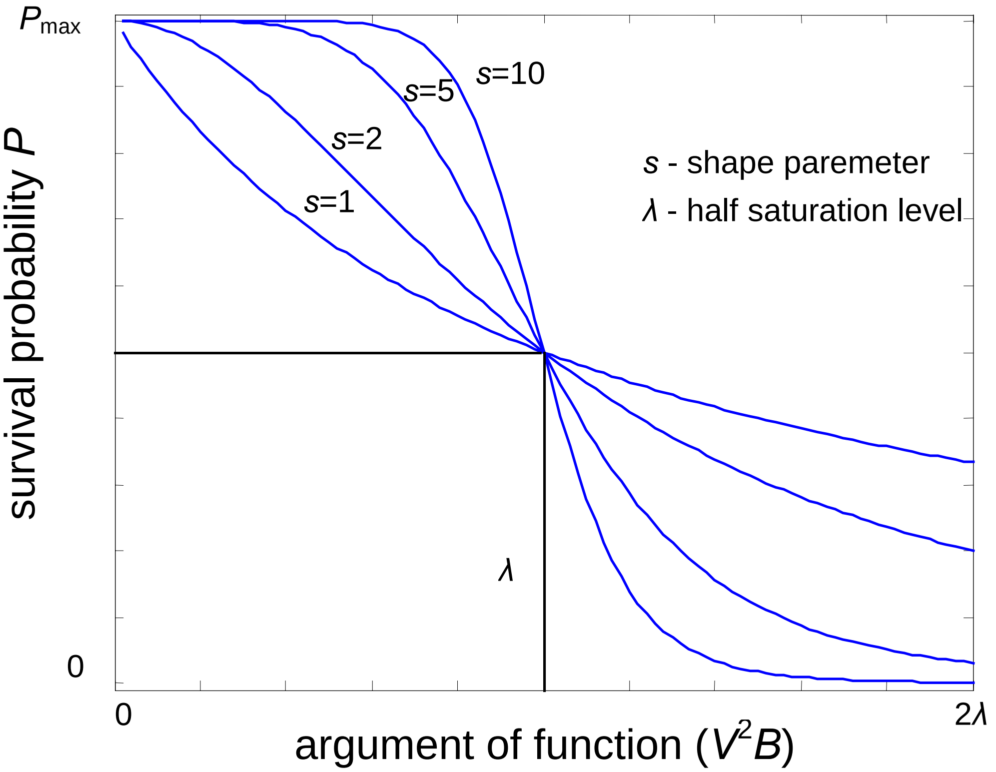

Figure 1. The sigmoid elk density-dependence function as defined in equation 8. Increasing the shape parameter, *s*, increases the abruptness of density dependence onset.

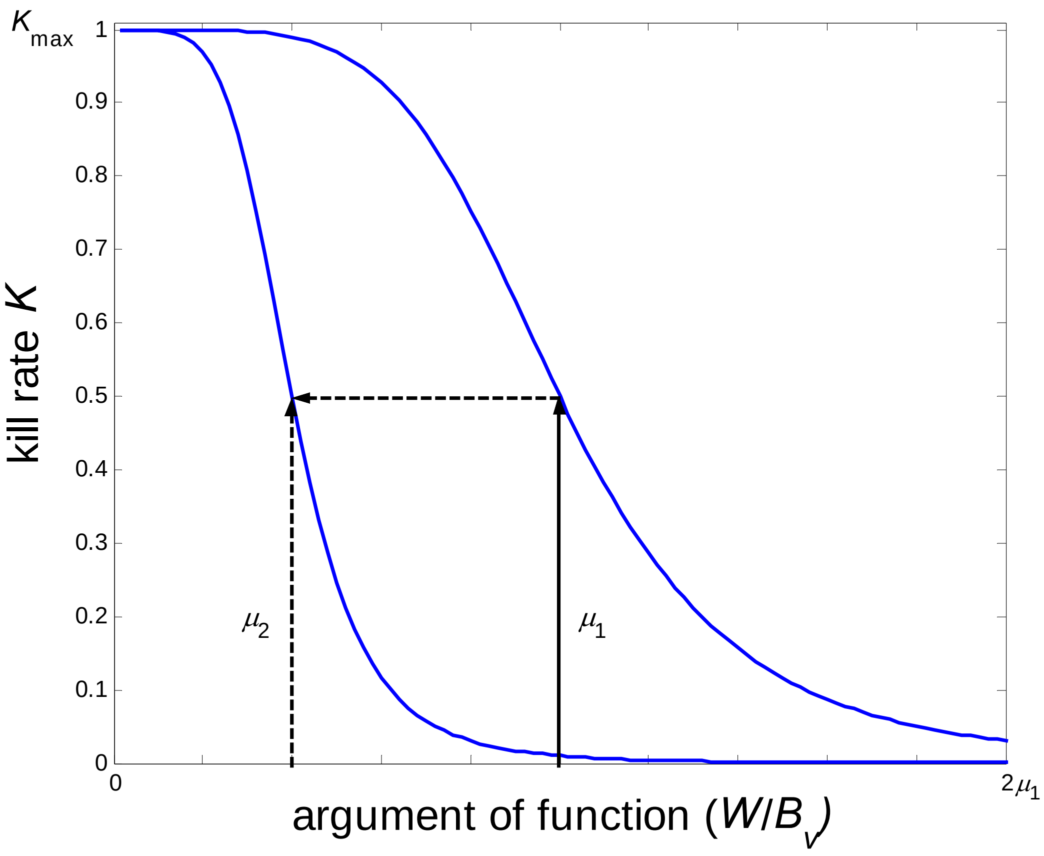

Figure 2. Pictorial representation of the wolf kill-rate function as defined in equation 19. As the half saturation level decreases from μ_1 to μ_2, wolf kill-rate K declines at lower ratios of wolves to elk.

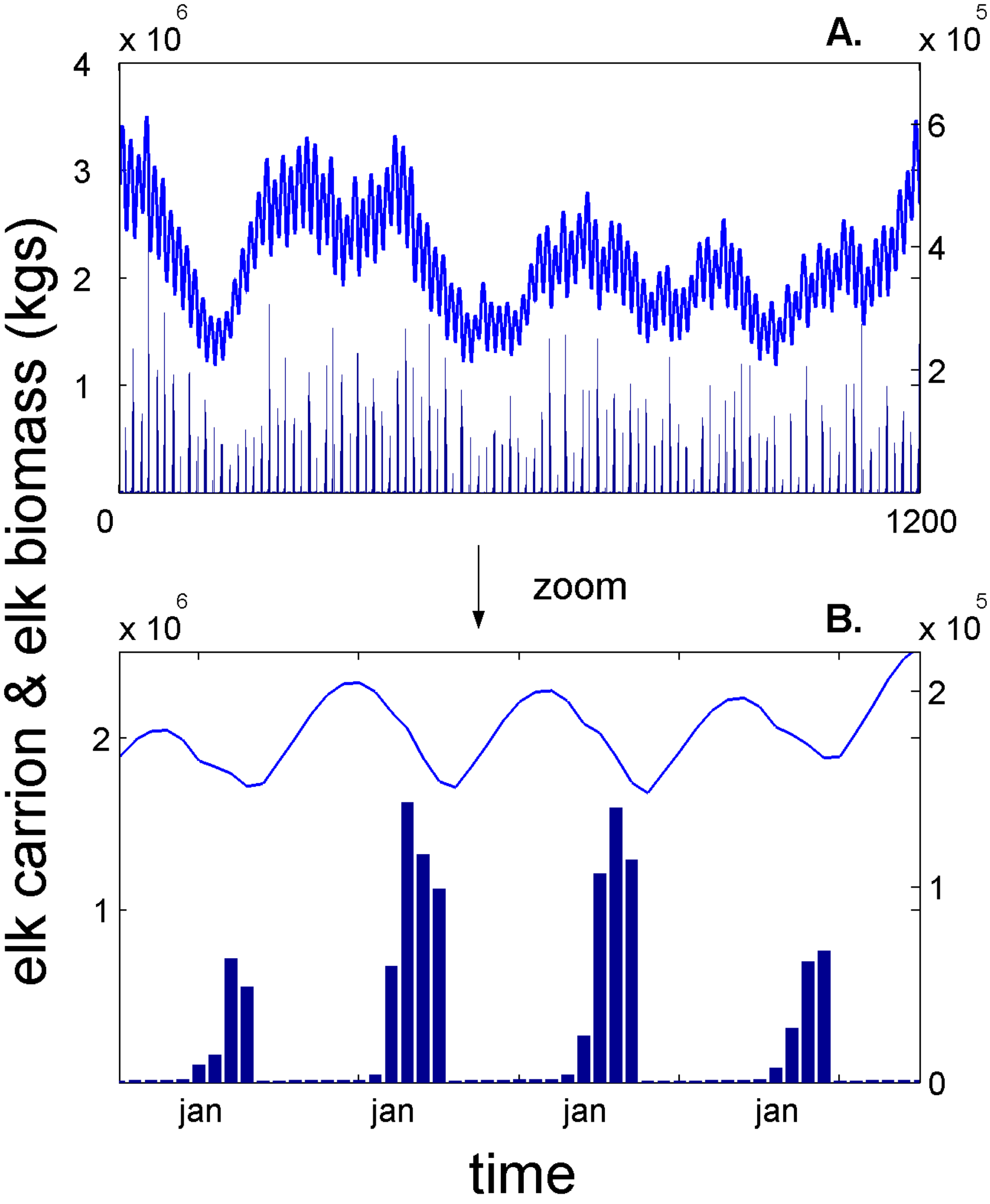

Figure 3. Output of a sample run of the model for average parameter values taken from Table 1: (a) pre-wolf elk biomass over 100 years (line with scale on left axes) and corresponding elk carrion (bars with scale on right axes); (b) 4 year subset of the full run.

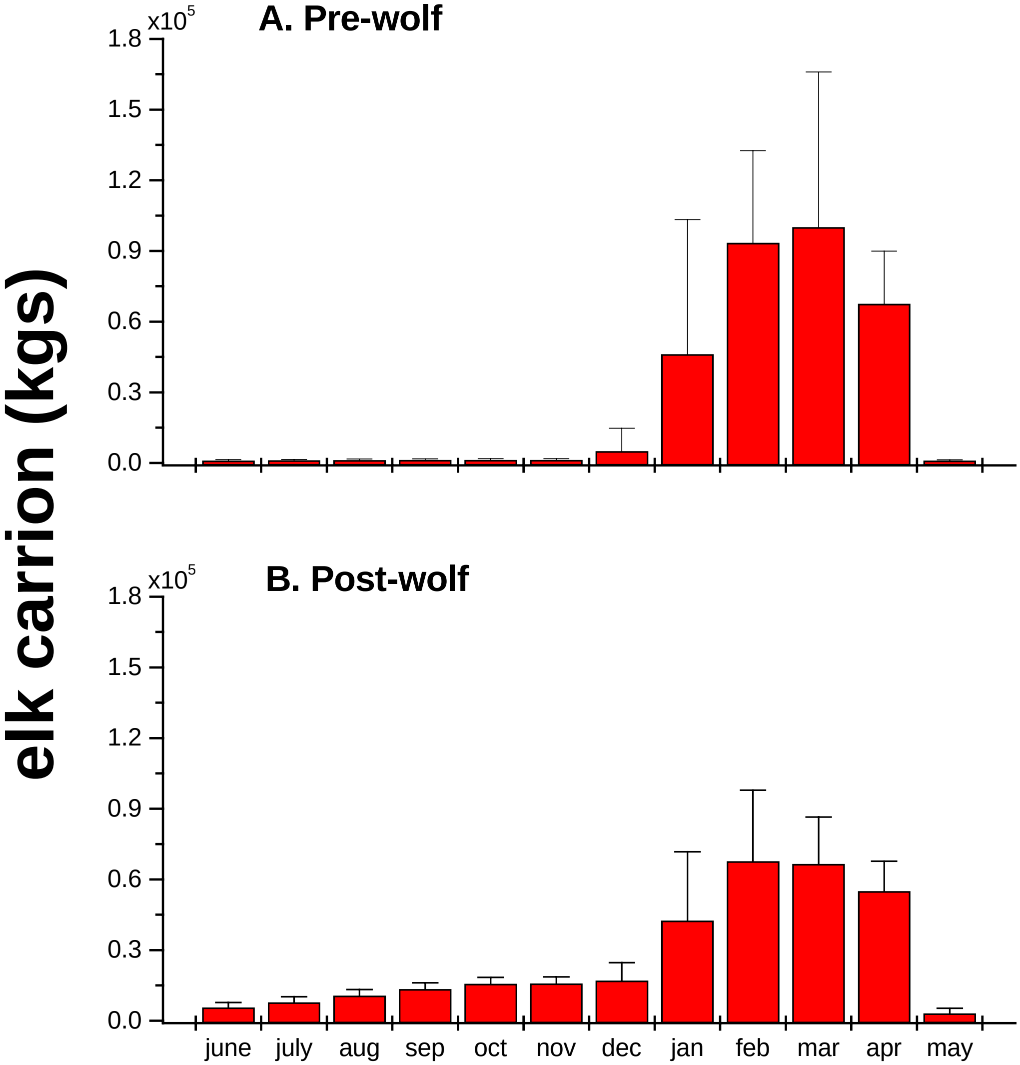

Figure 4. (a) Average pre-wolf carrion distribution generated from one run of the model with average parameter values taken from Table 1 and the half saturation parameter λ tuned so as to generate an average elk population of 17,000. (b) Average post-wolf carrion distribution generated with the same pre-wolf parameter set as in (a) and average post-wolf parameters taken from Table 1 with the wolf kill-rate half saturation parameter μ tuned so as to generate and average wolf population of 100. Error bars represent one standard deviation.

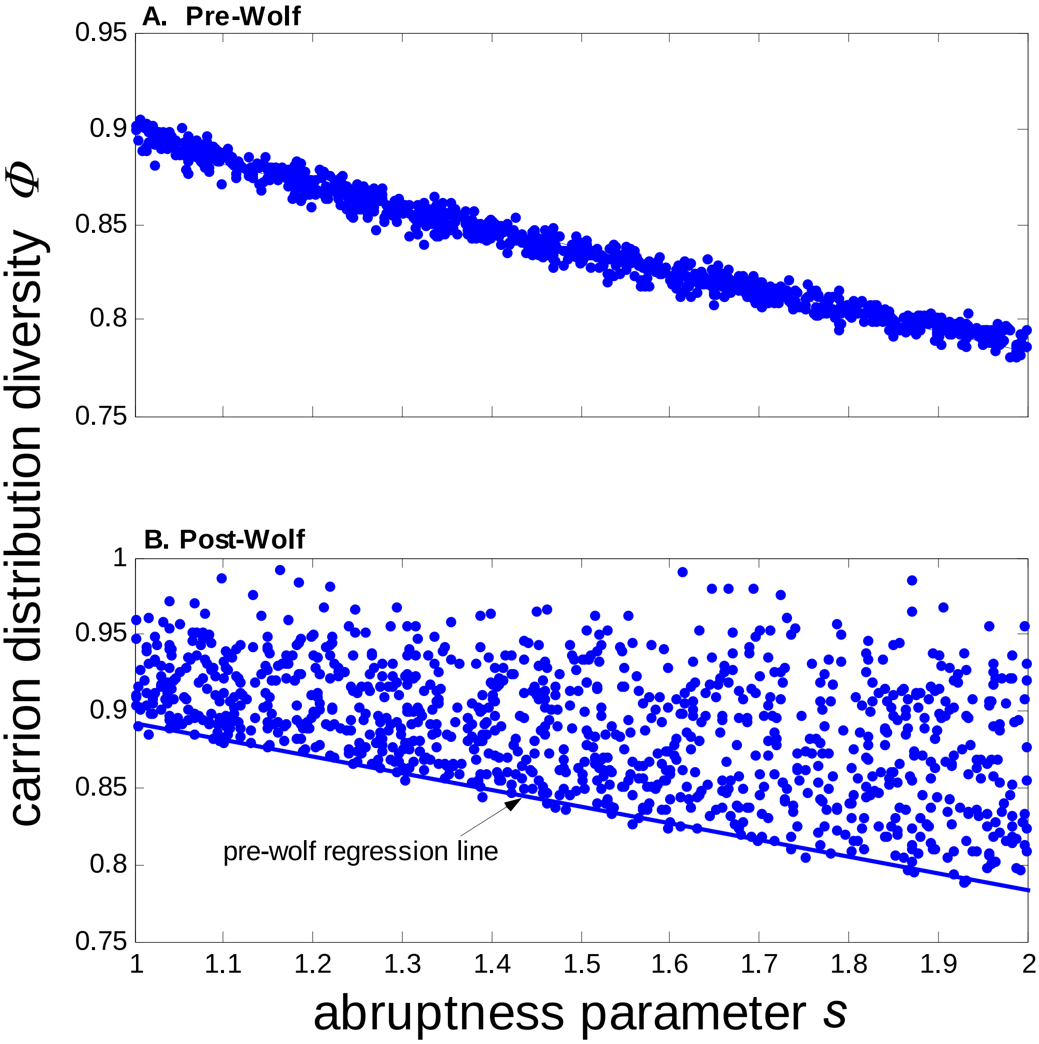

Figure 5. Carrion diversity index plotted for 1000 runs of the model, choosing parameter values from their uniform distributions (Table 1), except for the abruptness parameter *s* which has the specific values represented by the x-axis: (a) pre-wolf model; (b) post-wolf model with pre-wolf regression line plotted for purposes of comparison.

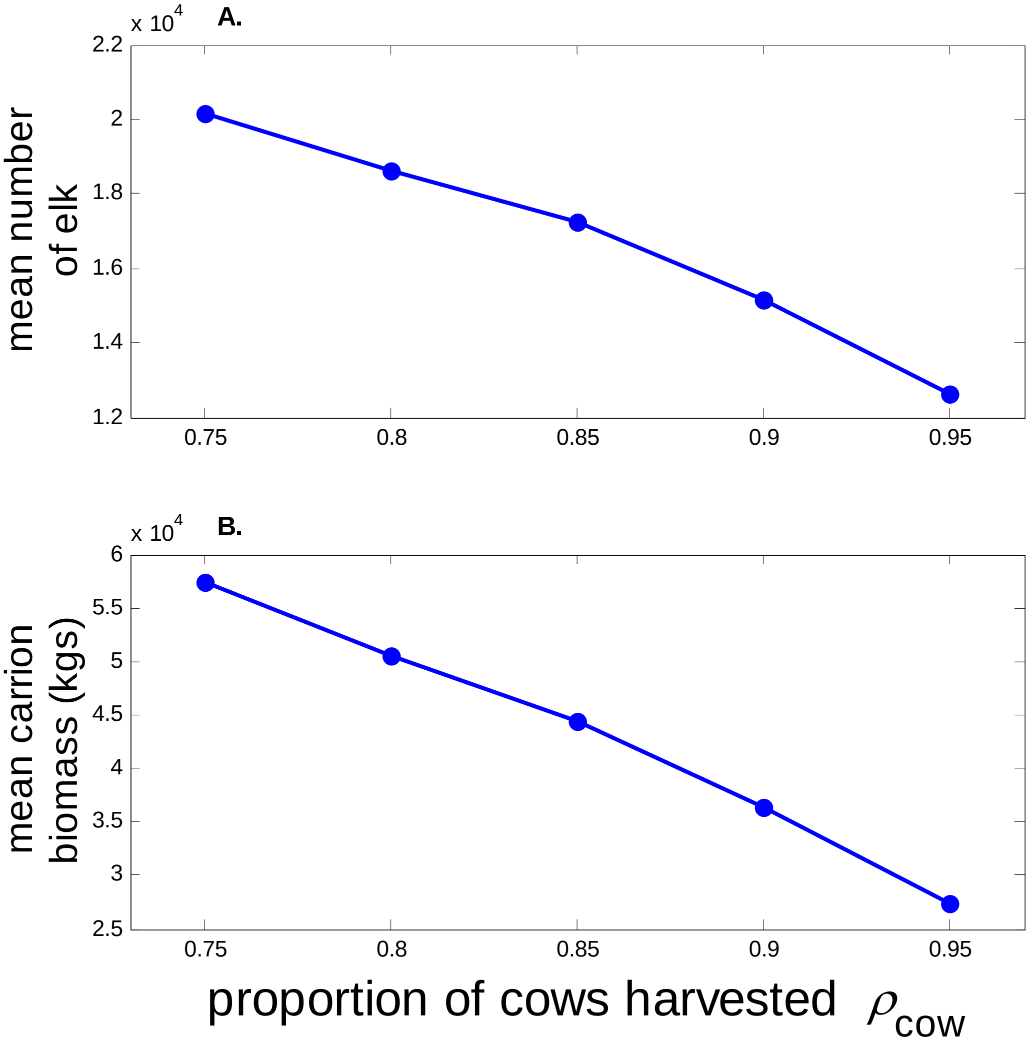

Figure 6. Comparison of (a) elk numbers and (b) carrion levels under different proportions ρ_{cow} of cows harvested. We used the same parameter set as those in fig. 4 with a hunting level $\theta = 0.05$ and ran the model for each level of ρ_{cow} represented on the x-axis. Y values represent the mean value of elk numbers and carrion levels of each run of the model respectively.

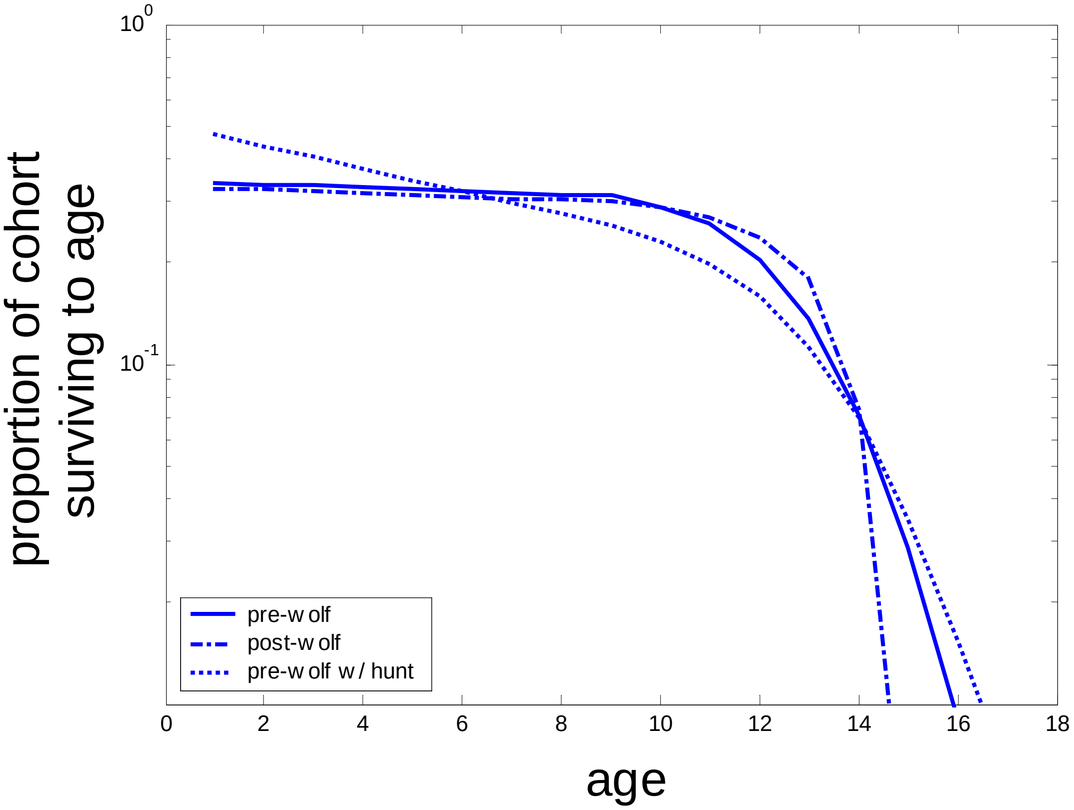

Figure 7. Comparison of female elk survivorship curves generated by following each cohort through to their deaths. We then take the average survival of each cohort for one run of the model. We use the same parameter sets as those in figure 4 with a hunt level $\theta = 0.05$ and proportions of cows harvested $\rho_{\text{cow}} = 0.95$. Survivorship curves are generated for the pre-wolf, pre-wolf with hunting and post-wolf models.

Chapter Six

Gray wolves as climate change buffers.

C.C. Wilmers[1] and W.M. Getz[2].

Introduction

Average earth temperatures have increased by 0.6 °C over the last 100 years (Walther et al. 2002) and are predicted to increase by 1.4 to 5.8 °C over the next century (Houghton et al. 2001). Commensurate with rising global temperatures are regional changes in weather patterns affecting the quantity and timing of precipitation and moisture levels. A challenge to ecologists is to understand how these changes in the abiotic environment will impact populations and communities of organisms. Already, studies have documented the effect of a changing climate on the phenology, range, reproductive success and synchrony of certain plants and animals (see Walther et al. 2002 for a comprehensive review). In addition, community level changes have been recognized when range shifts lead to the transfer of an entire assemblage of species (Barry et al. 1995).

Given such responses by individual species, we can expect consequent shifts in trophic structure and competitive hierarchies at the community scale. Studies addressing this problem have primarily focused on how species-specific responses in phenology and geographic range alter competitive balances and the timing of food availability for neonates (Beebee 1995, Visser et al. 1998, Both and Visser 2001, Visser and Holleman 2001). In Britain, for instance, winter warming has precipitated disparate responses in the breeding phenology of different amphibian species, exposing frog larvae (*Rana temporaria*), that have shown no phenological response, to higher levels of predation from newts (*Triturus* spp.) that are entering ponds earlier than before (Beebee 1995).

As predicted by community stability theory, the impact of climate change on communities may vary in relation to levels of diversity (Tilman et al. 1996, Naeem and Li 1997, McCann et al. 1998, Wilmers et al. 2002). Depauperate communities or those lacking keystone species (Paine 1969, Power et al. 1996), may be more vulnerable to the perturbing effects of climate change than fully intact communities. As such, understanding the mechanisms or pathways that confer community resistance to climate change will be important to conservationists and managers in mitigating the effect of a changing climate on community shifts and local extinctions.

The reintroduction of gray wolves to Yellowstone National Park (NP) in 1995 (Bangs and Fritts 1996) provides a research opportunity for comparing the functioning of an ecosystem with and without a keystone top predator. Wolf restoration is already realizing a change on the Yellowstone ecosystem by altering the quantity and timing of carrion availability to scavengers (Wilmers et al. 2003a). Many of Yellowstone's carnivorous species depend on winter carrion for survival and reproductive success. Prior to wolf reintroduction, winter mortality of elk, the most abundant ungulate in Yellowstone, was largely dependent on snow depth (Gese et al. 1996). Deep snows lead to increased metabolic activity (Parker et al. 1984) and decreased access to food resources, thereby causing elk to weaken and die (Houston 1982). In the absence of wolves, carrion was plentiful during both severe winters and at the end of moderate winters, but more scarce in early winter or during mild winters (Gese et al. 1996). Reintroduced wolves are now the dominant source of elk mortality throughout the year (Mech et al. 2001). Scavengers that once relied on winter-killed elk for food, now depend on kleptoparasitising wolf-killed elk (Wilmers et al. 2003a). Hence carrion availability has become primarily a function of wolf demographics, with snow depth a meaningful but secondary factor.

As global temperatures rise, evidence suggests that northern latitude and high elevation areas will experience shorter winters and earlier snow melts (Sagarin and Micheli 2001). Given the overwhelming influence of gray wolves on scavenger food webs, community-level responses to climatic changes in the absence of wolves may differ substantially from those in the presence of Yellowstone's newly restored top carnivore. We analyzed over 50 years of weather data from Yellowstone's northern range for trends in winter conditions and investigated how changes in snow pack depth and seasonality differentially affect scavengers in the presence and absence of wolves.

Study Area

The northern range of Yellowstone National Park is the wintering area of the parks largest elk herd and home to 4-6 wolf packs. Elevations range from 1500 to 3400 m with 87% of the area falling between 1500 and 2400 m (Houston 1982). The climate is characterized by short, cool summers and long, cold winters, with most annual precipitation falling as snow. Mean annual temperature is 1.8° C, and mean annual precipitation is 31.7 cm (Houston 1982). Large open valleys of grass meadows and shrub steppe dominate the landscape, with coniferous forests occurring at higher elevations and on north facing slopes.

Methods

Since 1948, meteorological data has been collected on a daily basis from two permanent weather stations on the northern range of Yellowstone NP. One is located in Mammoth Hot Springs at park headquarters near the northern entrance to the park. The other is located at the Tower Falls ranger station about 29 km east of Mammoth. Data for the period August 1, 1948 to June 1, 2003 were made available to us by the Western Regional Climate Center in Reno, Nevada.

Using linear regression we investigated trends in monthly average snow depth (SDTH) over the 55 years provided in the data set. We also examined trends in the timing of the date of first bare ground. This was defined as the first day of the year for which snow depth was zero. In order to understand changing patterns in snow depth, we analyzed average monthly snowfall (SNFL), and average monthly minimum (TMIN) and maximum (TMAX) temperatures as well as the number of days per winter that TMAX exceeded freezing.

In order to compare the effects of carrion availability to scavengers under climate change in scenarios with and without wolves, we used previously published regression equations relating snow depth S to monthly carrion availability C_p prior to wolf reintroduction given by,

$$C_p = 4 \cdot (-3.62 + 5.26 \cdot S) \text{ (Gese et al. 1996),} \tag{1}$$

and relating snow depth and wolf pack size to carrion availability C_a after wolf reintroduction obtained using,

$$C_a = K \cdot P \cdot 30 \cdot (1 - Q) \text{(Wilmers et al. 2003a),} \tag{2}$$

where K is the wolf kill rate per wolf, P is the wolf pack size, 30 is the number of days in a month and Q is the percent of the edible biomass of a carcass consumed by a wolf pack given by Wilmers et al. (2003a). To do this, we used Monte Carlo methods, as elaborated below, to reconstruct how much carrion would have been available to scavengers during each of the winter months (November - April) in the years 1950 and 2000 under scenarios with and without wolves. Specifically, for each scenario ((a) 1950 without wolves (b) 2000 without wolves (c) 1950 with wolves (d) 2000 with wolves) we drew 100 random snow depth values for each of the months, where snow depth was assumed to be normally distributed with mean and standard error for the years 1950 and 2000 given by the regression analyses of the Tower Falls weather data (Fig. 2). In the scenarios without wolves, randomly chosen monthly snow depth values for each year and each run were then inserted into Eq. 1 to yield the amount of carrion available per month. We used the same procedure for selecting snow depth in our scenario with wolves. In order to select wolf pack size, we assumed that wolf pack sizes were normally distributed with a mean (±SD) pack size of 10.6 (±5) representing the current distribution of Yellowstone wolves (Smith et al. 2003b). We then inserted our randomly chosen monthly snow depth values and wolf pack sizes into Eq. 2 to yield the amount of carrion available per month with wolves. For each run of each scenario, we recorded the reduction in monthly winter biomass available to scavengers in 2000 as a proportion of what was available in 1950.

Results

Over the past 55 years, average monthly snow depths at the Mammoth weather site show a steady decline in all winter months except November (the effect is significant at the 0.05 level for February - April and nearly significant for December and January, Fig. 1). Furthermore, the slope of the line relating snow depth to year becomes more negative with each month, indicating a more pronounced effect of climate change in late winter. The result for April, however, is confounded by a number of zeros which created a violation of the normality assumption for the linear regression. Average monthly snow depths at the Tower weather site did not indicate a strong pattern in the early winter, but showed a significant decline in the late-winter months of March and April (Fig. 2, panels E & F).

Winters in Yellowstone are getting shorter. While we did not detect a difference in the date of the arrival of the first snow, we did detect a declining trend in the date of last snow on the ground (Fig. 3, panels A & B).

At both the Tower and Mammoth weather sites, the number of days that maximum temperature exceeded freezing for the period of January - March increased significantly (Fig. 3, panels C & D). Furthermore, mid-winter snowfall is decreasing and late-winter minimum and maximum temperatures show signs of increasing in certain months (Table 1).

The presence of wolves in Yellowstone significantly mitigates the reduction in late-winter carrion expected under climate change (Fig. 4). In the scenario without wolves, late-winter carrion availability is reduced by 27% in March and by 66% in April. In contrast, the scenario with wolves reveals a reduction in carrion availability of only 4% in March and 11% in April. There was not a significant difference in the reduction of early winter carrion between the two scenarios.

Discussion

The winter period on the northern range of Yellowstone NP is shortening. Both late-winter snow depths and the overall duration of snow cover have decreased significantly since 1948 (Fig. 1-3). The cause of reduced snow pack appears to be multifaceted. Average minimum and maximum temperatures are increasing in late winter while mid-winter snowfall appears to be declining (Table 1). Compounding the effects of declining snowfalls on snow depth is an increase in the number of winter days with temperatures above freezing (Fig. 3, panels C & D).

As late-winter snow-packs decrease and the date of last snow-cover recedes, elk will recover from the detrimental winter stresses at an earlier time. Smaller snow-packs allow for easier access to food and lower energy expenditures required for movement. In addition, herbaceous plant growth usually begins within a few days to weeks of last snow cover (Inouye et al. 2000), so that elk may increase food intake and quality earlier in the year thus reducing the physiologically stressing winter period. These factors are likely to influence the timing and abundance of carrion as late-winter elk mortality declines. Thus climate change is likely to sharply reduce the amount of late-winter carrion available to Yellowstone's scavengers (Fig. 4). According to our analysis, this reduction is much less pronounced in the presence of wolves (an 11% reduction with wolves vs. a 66% reduction without wolves in April, Fig. 4). Wolves therefore buffer the effects of climate change on carrion abundance and timing.

This effect will be crucial to scavenger species in the Yellowstone area that are highly dependent on winter and spring carrion for over-winter survival and reproduction. This includes ravens, bald eagles, golden eagles, magpies, coyotes, grizzly bears and black bears. Under scenarios without wolves, these species could face food bottlenecks in the absence of late-winter carrion. The magnitude of this effect will depend on how quickly these species adapt to a changing environment and how their other food resources respond to a shortening of the winter period.

Asynchrony of organismal responses to climate change has been prevalent in other areas, leading to changes in the competitive balance between species and to food shortages at important times of year (Walther et al. 2002). Yellowstone should prove no exception. Species that respond to weather cues, such as many herbaceous plants, will simply start growing earlier in the year in response to earlier snow melt. Conversely, species that respond primarily to day length cues, such as some hibernating species, may be less plastic in their responses. Coyotes, for instance, are highly dependent on late-winter and early-spring carrion to carry them over until late spring when elk calves and ground squirrels become abundant. If late-winter carrion were to disappear without a corresponding change in the timing of elk calving or ground squirrel emergence, this could cause a serious food bottleneck to develop.

As carrion becomes more concentrated over a shorter window of the year, the relative access to carrion among different scavenger species may change. Highly aggregated resources, or pulses, saturate local communities of scavengers, thus creating a recruitment hierarchy whereby species with better recruitment abilities (animals capable of covering large distances and communicating about the location of resources such as ravens and bald eagles) dominate consumption at carcasses (Wilmers et al. 2003b). Resources that are more dispersed, conversely, do not saturate local scavenger communities so that a competitive dominance hierarchy (with grizzly bears and coyotes at the top) determines which species consume the bulk of available scavenge. Our analysis suggests that winter carrion in the absence of wolves will become increasingly pulsed during winter. Consequently, areas without wolves may see an increase in scavengers with high recruitment abilities.

As the climate warms, those species that persist will be able to adapt to differences in the environment. Late-winter carrion in Yellowstone will decline with or without wolves, but by buffering this reduction, wolves extend the timescale over which scavenger species can adapt to the changing environment.

We are just beginning to understand the interaction between top predators such as wolves and global climate patterns. On Isle Royale, trophic effects have recently been shown to be mediated by behavioral responses to climate. There, gray wolf pack size is partially controlled by climatic conditions that, in turn, affect wolf kill-rates on moose and consequent herbivory levels on balsam fir (Post et al. 1999). Here in Yellowstone, wolves act to retard the effects of a changing climate on scavenger species. Together these results begin to elucidate the expected changes that may result to boreal ecosystems as a result of climate change interactions with top predators.

Table 1. Results from regression analyses using year as the independent variable to predict mean monthly snowfall (SNFL), and average late-winter minimum (TMIN) and maximum temperature (TMAX). We present results for $p < 0.10$.

Site	Dependent variable	Month	Intercept	Slope	r^2	*P*-value
Tower	SNFL	Feb	84	-0.04	0.08	0.055
	TMIN	Mar	-148	0.08	0.08	0.04
	TMAX	Mar	-77	0.06	0.07	0.06
Mammoth	SNFL	Dec	106	-0.05	0.13	<0.01
		Jan	121	-0.06	0.11	0.02
		Feb	71	-0.03	0.07	0.056
	TMIN	Mar	-237	0.13	0.18	<0.01
	TMAX	Mar	-118	0.08	0.11	0.02

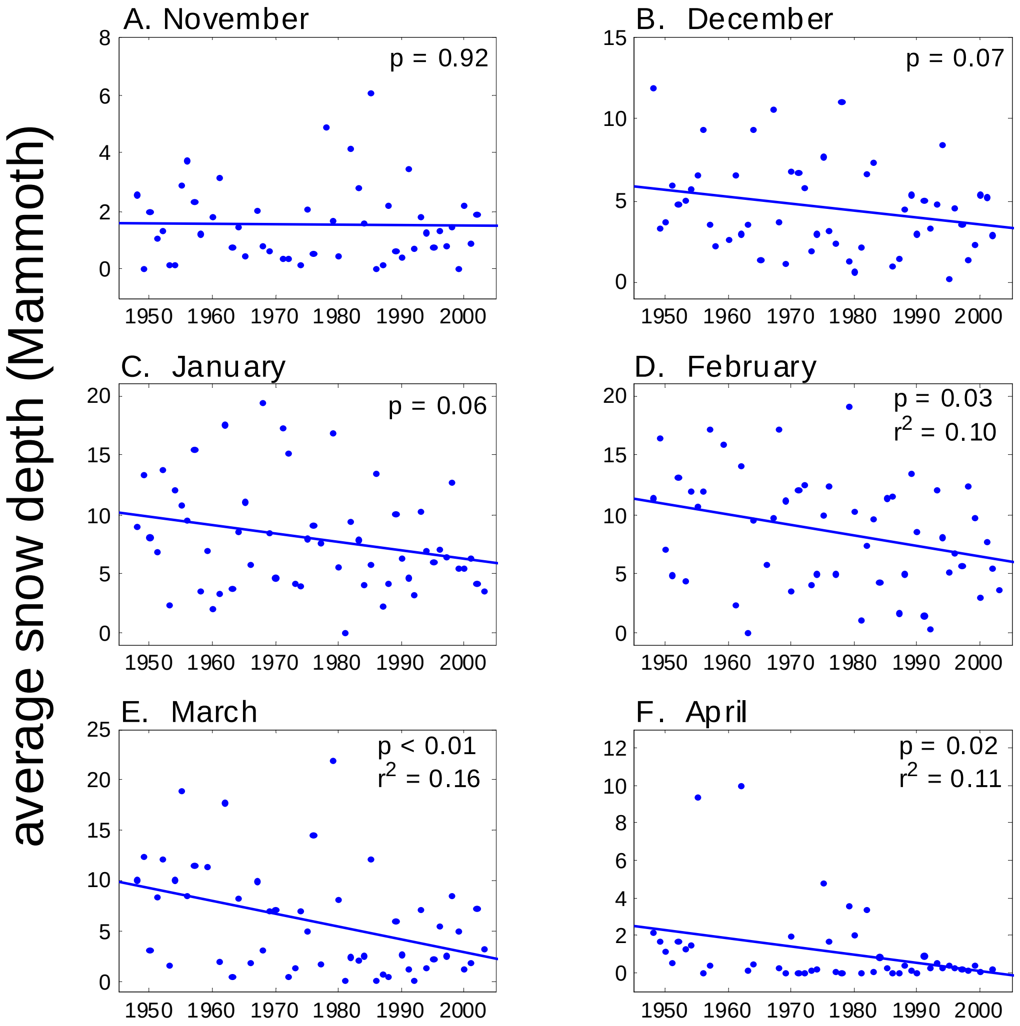

Figure 1. Average monthly snow depth for the six months November thru December for the years 1948-2003 at the Mammoth Hot Springs weather site.

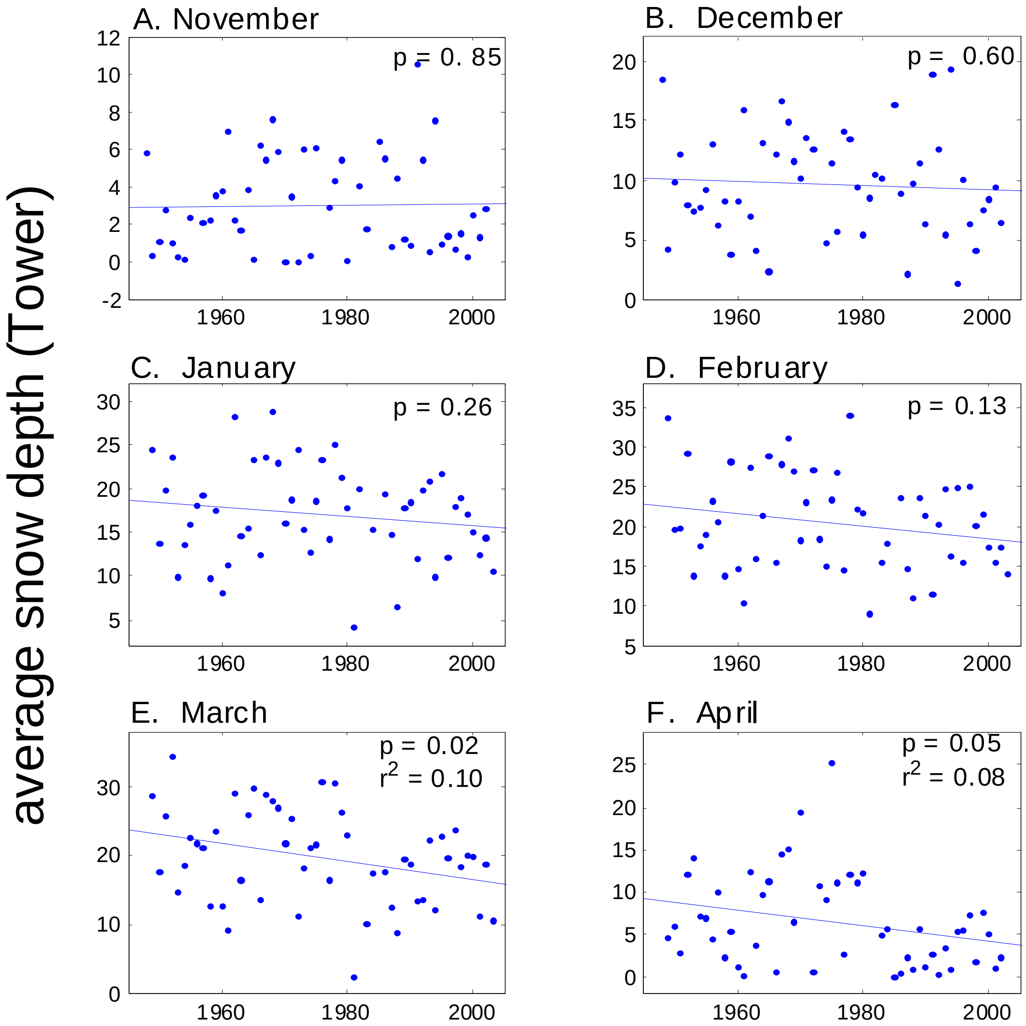

Figure 2. Average monthly snow depth for the six months November thru December for the years 1948-2003 at the Tower Falls weather site.

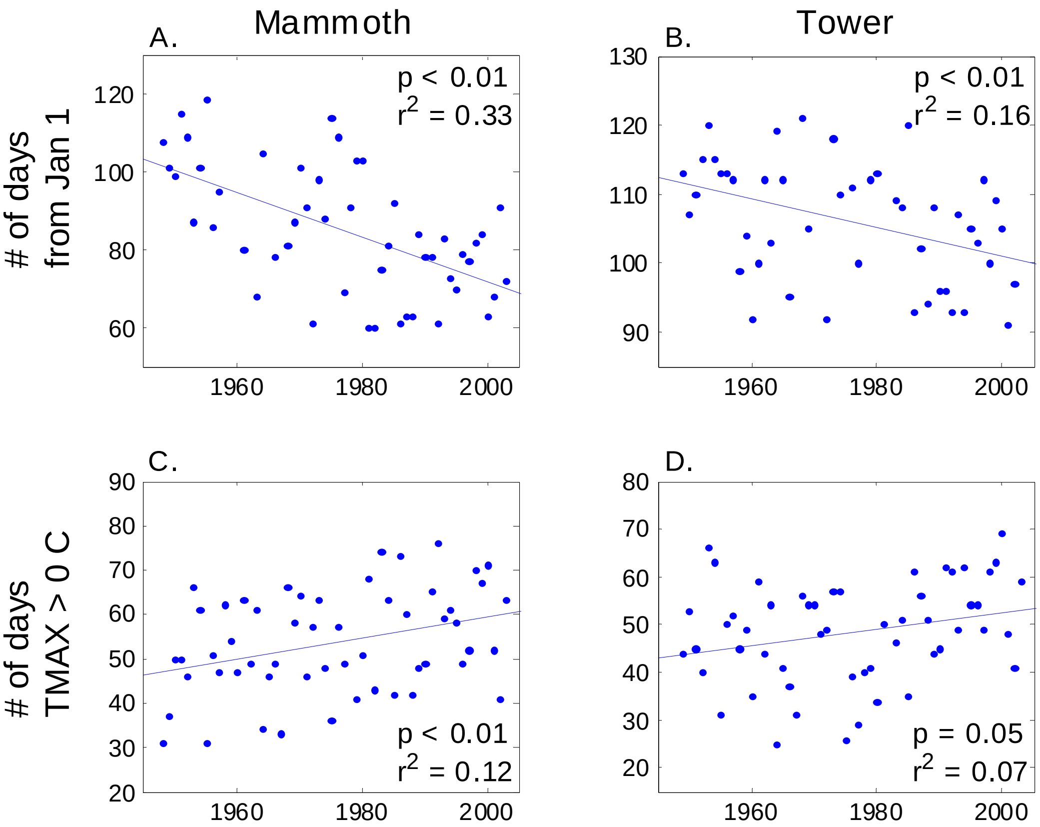

Figure 3. Changes in the last day of snow cover over the last 55 years at A) Mammoth Hot Springs and B) Tower Falls. Last day of snow cover is reported as the number of days from January 1 of that year until the first day of bare ground. Panels C & D show the number of days from January - March that temperatures exceeded freezing over the same time period at Mammoth and Tower respectively.

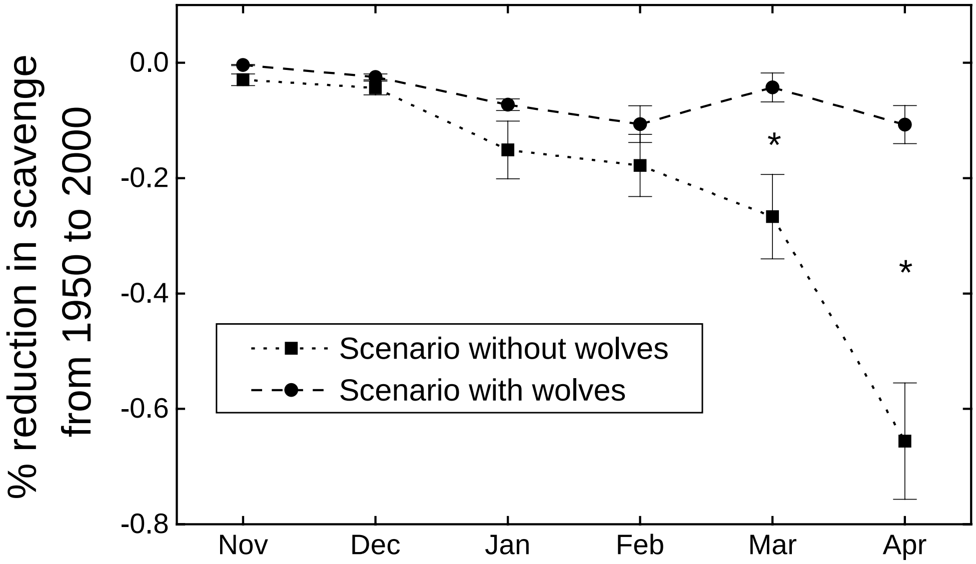

Figure 4. Reduction in winter carrion available to scavengers due to climate change from 1950 to 2000 under scenarios with and without wolves (see methods for details). Reductions are presented as proportions (±SE). The symbol * indicates significance between the two scenarios.

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