

# Trophic facilitation by introduced top predators: grey wolf subsidies to scavengers in Yellowstone National Park

CHRISTOPHER C. WILMERS\*, ROBERT L. CRABTREE†, DOUGLAS W. SMITH‡, KERRY M. MURPHY‡ and WAYNE M. GETZ\*

\*Department of Environmental Science, Policy and Management, University of California, Berkeley, CA 94720–3112, USA, †Yellowstone Ecological Research Center, 7500 Jarmen Circle, Suite 2, Bozeman, MT 59715, USA, and ‡Yellowstone Center for Resources, Wolf Project, PO Box 168, Yellowstone National Park, WY 82910, USA

## Summary

1. The reintroduction of grey wolves *Canis lupus* (L.) to Yellowstone National Park provides a natural experiment in which to study the effects of a keystone predator on ecosystem function.
2. Grey wolves often provision scavengers with carrion by partially consuming their prey.
3. In order to examine how grey wolf foraging behaviour influences the availability of carrion to scavengers, we observed consumption of 57 wolf-killed elk *Cervus elaphus* (L.) and determined the percentage of edible biomass eaten by wolves from each carcass.
4. We found that the percentage 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.
5. 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.
6. 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.

*Key-words:* *Canis lupus*, community stability, keystone species, optimal foraging, trophic dynamics.

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## 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 behaviour as they cascade down the food chain. As a major predator of large ungulates, grey wolves may suppress prey levels or alter prey behaviour to the extent that they affect vegetation

patterns and productivity. On Isle Royale in Lake Superior, wolf predation on moose *Alces alces* (L.) has been shown to increase balsam fir *Abies balsamea* (L.) productivity (McLaren & 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* (Michaux) 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

Correspondence: C. C. Wilmers, Department of Environmental Science, Policy and Management, 201 Wellman Hall #3112, University of California, Berkeley, CA 94720–3112, USA. Tel: 510-381-8640; Fax: 510-642-7428; E-mail: cwilmers@nature.berkeley.edu

guild members. Here we show that grey wolves affect other meat eating species by subsidizing them with scavenger 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 & Hurd 1995). Riparian lizards *Sceloporus occidentalis* (Baird) in California, for instance, have been shown to exhibit higher growth rates in near river habitats where aquatic insect densities are high (Sabo & Power 2002). While such resource flows from high productivity to low productivity habitats have been well documented (Fagan, Cantrell & Cosner 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, Ruff & Crabtree 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 (C. C. Wilmers *et al.* personal observation). 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 *Canis latrans* (Say) are highly dependent on winter scavenger (Crabtree & 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 & Sheldon (1999b) have shown that additional elk carrion increases coyote litter size and pup survival. Raven *Corvus corax* (L.) reproduction is tied to the availability of winter carrion (Newton, Davis & Davis 1982) and they adopt a foraging strategy of following wolves to locate their kills (Stahler, Heinrich & Smith 2002). Grizzly bears *Ursus arctos* (L.) are similarly dependent on spring carrion and are even known to forego hibernation altogether in Glacier National Park, Montana in favour of scavenging wolf kills (D. Boyd personal communication).

A group of grey 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 defence 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).

## Methods

### 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 to 3400 m, with the majority of the northern range falling between 1500 and 2400 m (Houston 1982). The climate is characterized by long cold winters with snow and short cool summers. Mean monthly temperatures range from  $-12$  to  $+13$  °C (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, three to six groups of wolves held territories in the study area. Seven species of ungulates occur on the northern range: elk, mule deer *Odocoileus hemionus* (Rafinesque), white-tailed deer *Odocoileus virginianus* (Zimmerman), moose, bison *Bison bison* (L.), bighorn sheep *Ovis canadensis* (Shaw) and pronghorn antelope *Antilocapra americana* (Ord). Elk are the primary prey species of wolves (Mech *et al.* 2001), as well as the primary source of scavenger 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* (Pallas), golden eagle *Aquila chrysaetos* (L.), bald eagle *Haliaeetus leucocephalus* (L.), coyote, fox *Vulpes vulpes* (L.), raven and magpie *Pica pica* (L.).

We conducted the study from January 1998 to July 2001, excluding summer periods from 15 July to 15 October 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 15–45× Nikon spotting scopes to observe feeding activity from observational vantage points located throughout Yellowstone's northern range.

#### DETERMINING PERCENTAGE CONSUMPTION

In order to determine the percentage of the carcass consumed by wolves, we:

1. sampled *in situ* feeding times of wolves and each scavenger species at wolf kills during each stage of consumption of the carcass (Table 1);
2. 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;
3. estimated elk live masses based on sex, age and day of the year from a model;
4. measured the amount of edible biomass of elk, at each stage of consumption, by butchering 14 hunter-killed elk;
5. 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.

#### Feeding times

Wolves typically consume the organs of their prey first, followed by the major muscle groups on the front- and

hindquarters, 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 hindquarters; 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 min depending on the number of observers. In order to minimize observer bias, each observer was trained for at least 1 week.

#### Active consumption rates

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 & 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 preweighed 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

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

Consumption stage	Description*	Percentage of whole mass† (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)

\*Stages 2–4 include some small bits of bone which are of negligible mass.

†Based on dissection of 4 calves, 6 bulls and 4 cows.

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

Species	Grams peck <sup>-1</sup> (SE)		Pecks min <sup>-1</sup> (SE)	ACR g min <sup>-1</sup> (SE)	
	Stages 1 & 2	Stages 3 & 4		Stages 1 & 2	Stages 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)*
Wolves†	–	–	–	1022 (150)	280 (40)
Coyotes†	–	–	–	230 (60)	30 (5.6)
Grizzlies†	–	–	–	800 (245)	62 (11.9)

\*Estimated from linear interpolation of magpie and raven rates by bird mass.

†Estimated from average Yellowstone masses using formulas from Wilmers & Stahler (2002).

bone. We therefore estimated eagle ACR on bone by linearly extrapolating from raven and magpie bone ACR based on average species masses (Table 2). Mammal ACRs were estimated from Wilmers & Stahler (2002) using mean Yellowstone wolf masses of 46 kg (YNP unpublished data), mean Yellowstone coyote masses of 13 kg (R. Crabtree, unpublished data) and mean Yellowstone grizzly bear masses of 163 kg (Blanchard 1987).

#### *Elk live masses*

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 masses for elk were then estimated based on animal age, sex and day of the year according to a model (Murphy, Felzien, Hornocker & Ruth 1997).

#### *Edible biomass of elk*

We determined the percentage 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 & 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 to 4 and skeleton masses from estimated whole masses to determine gut masses. We then weighed three intact gut piles from the late hunt in order to determine the ratio of rumen to organs and entrails.

#### *Percentage consumed*

In order to determine percentage 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 & Stahler 2002). We then summed these percentages weighted by the proportion of the total carcass mass to determine percentage 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 metres 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, Heydon & Hansen 1999; P. Farnes personal communication). 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 percentage of a carcass consumed by a group of wolves is likely to depend on prey mass (PREYM) as well as pack size (PACKS). The relationship between resource availability and predator abundance is often better expressed on a per capita basis (Pitcairn, Getz & Williams 1990), thus we also investigated how the number of wolves per kg of prey (WPKP) affects the percentage of a carcass consumed by wolves (% CONSUMPTION). Additionally, foraging costs such as defence 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 percentage 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 & 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 3 years in the Lamar River Valley, Yellowstone National Park, which is a large 70 km<sup>2</sup> site in the Northern Range. We compared these data with 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 percentage 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 percentage consumption by wolves from our regression equation using the variables PACKS and SWE. In order to estimate the variance in percentage 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 percentage consumption. We used actual SWE data from the 3 years in Gese *et al.*'s study and assumed November and March kill rates of 5 and 8 kg wolf<sup>-1</sup> day<sup>-1</sup>, respectively

(Smith *et al.* 2003). December to February kill rates were estimated by linear interpolation between the two endpoints.

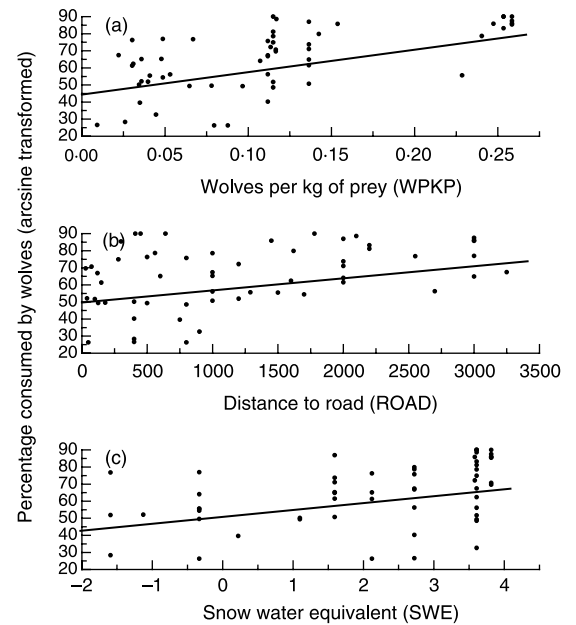
## Results

We observed 240 wolf-killed elk carcasses during the study period for a total of 104 640 min. 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 1 November to 1 April: 8 of these were bulls, 24 were cows, 24 were calves and 1 was unknown. Estimated carcass masses varied from 101 to 269 kg and were located between 30 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 mass is edible. Approximately 14% of the elk's whole mass is in stage 1, 31% in stage 2, 15% in stage 3 and 6% in stage 4 (Table 1). The remaining 32% comprises rumen and inedible bone.

The percentage of the carcass consumed by wolves was significantly predicted by six variables on their own: WPKP, PACKS, PREYM, SWE, TMIN and ROAD (Table 3). As pack size increases, the percentage consumed by a wolf pack also increases (Table 3). As prey mass increases, percentage consumption decreases (Table 3) because the wolves become satiated before fully consuming the carcass. WPKP explained more of the variation in percentage consumption than any other variable alone ( $r^2 = 0.38$ , Fig. 1a). As the number of wolves relative to kg of prey increases, the percentage

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% of the variation in percentage consumption could be explained by WPKP, SWE, ROAD and the interaction between SWE and ROAD (Table 3).



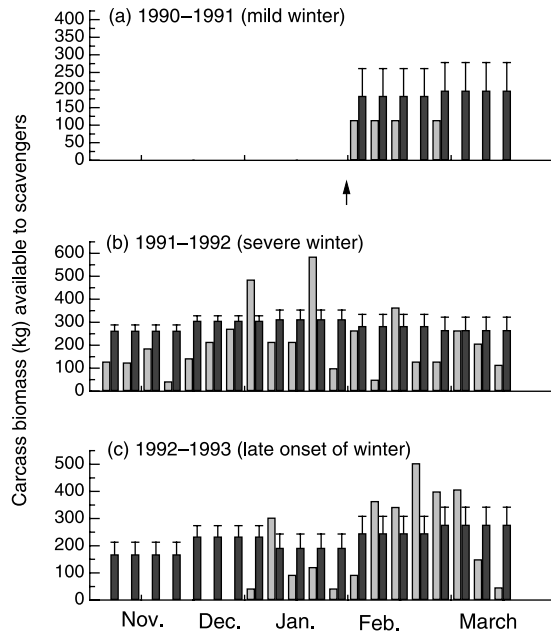
**Fig. 1.** Relationship between the percentage of a carcass consumed by wolves and (a) per capita, (b) distance to road and (c) snow water equivalent (SWE, note that larger values of SWE represent milder conditions and thus less snow). Percentages are arcsine transformed (20–90 point scale) so that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

**Table 3.** Regression analyses on the dependent variable, percentage consumed by wolves. \* We present results for all significant one variable models and the best overall model

Independent variables†	d.f.	Coefficient	SE	$r^2$ , $R^2$	$F$ -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

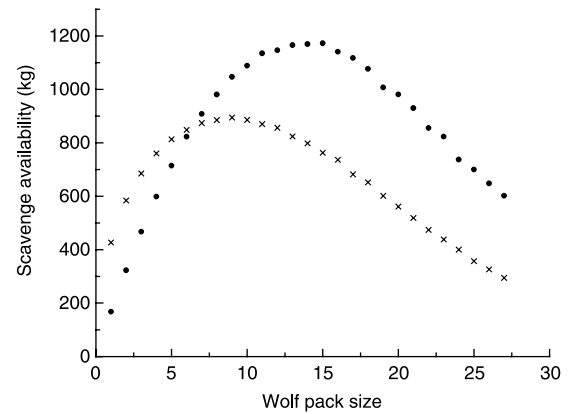
\*Variable is arcsine transformed.

†WPKP – wolves per kg of prey; PACKS – pack size; ROAD – distance to road; SWE – snow water equivalent; TMIN – minimum temperature. Note that prey mass, winter severity index and forage were not significant predictors of percentage consumption.



**Fig. 2.** Comparison of biomass available in the Lamar Valley, Yellowstone National Park with and without wolves. Light grey bars represent carcass biomass without wolves as measured by Gese *et al.* (1996). Dark grey 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 vs. 61 kg month<sup>-1</sup>, (b) 38 vs. 137 kg month<sup>-1</sup> and (c) 47 vs. 171 kg month<sup>-1</sup>.

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 1990–91, 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 1991–92, 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 1992–93, 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



**Fig. 3.** Carcass biomass available to scavengers for increasing wolf pack size. Circles represent estimates using data from Smith *et al.* (2003). Pluses represent estimates assuming a declining kill rate as wolf pack size increases.

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 1992–93. 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 used estimates of kg wolf<sup>-1</sup> day<sup>-1</sup> derived from Smith *et al.* (2003) which were reported independent of pack size. As wolf pack size increases, however, kg wolf<sup>-1</sup> day<sup>-1</sup> 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 & 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 scavenger 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, Alt & Eng 1986; Dhindsa & 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 vigour. 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 scavenger's 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, personal communication). 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.

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