

# Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park

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## Summary

1. For large predators living in seasonal environments, patterns of predation are likely to vary among seasons because of related changes in prey vulnerability. Variation in prey vulnerability underlies the influence of predators on prey populations and the response of predators to seasonal variation in rates of biomass acquisition. Despite its importance, seasonal variation in predation is poorly understood.

2. We assessed seasonal variation in prey composition and kill rate for wolves *Canis lupus* living on the Northern Range (NR) of Yellowstone National Park. Our assessment was based on data collected over 14 winters (1995–2009) and five spring–summers between 2004 and 2009.

3. The species composition of wolf-killed prey and the age and sex composition of wolf-killed elk *Cervus elaphus* (the primary prey for NR wolves) varied among seasons.

4. One's understanding of predation depends critically on the metric used to quantify kill rate. For example, kill rate was greatest in summer when quantified as the number of ungulates acquired per wolf per day, and least during summer when kill rate was quantified as the biomass acquired per wolf per day. This finding contradicts previous research that suggests that rates of biomass acquisition for large terrestrial carnivores tend not to vary among seasons.

5. Kill rates were not well correlated among seasons. For example, knowing that early-winter kill rate is higher than average (compared with other early winters) provides little basis for anticipating whether kill rates a few months later during late winter will be higher or lower than average (compared with other late winters). This observation indicates how observing, for example, higher-than-average kill rates throughout any particular season is an unreliable basis for inferring that the year-round average kill rate would be higher than average.

6. Our work shows how a large carnivore living in a seasonal environment displays marked seasonal variation in predation because of changes in prey vulnerability. Patterns of wolf predation were influenced by the nutritional condition of adult elk and the availability of smaller prey (i.e. elk calves, deer). We discuss how these patterns affect our overall understanding of predator and prey population dynamics.

**Key-words:** additive predation, compensatory predation, GPS collar, kill rate, marrow fat, neonate predation, predator–prey, summer predation

## Introduction

Predation is a fundamental ecological process that structures communities, affects ecosystem productivity and influences biodiversity (Taylor 1984). Two perennial challenges to understanding predation dynamics are knowing whether

mortality caused by predation tends to be more additive or compensatory for prey populations (Boyce, Sinclair & White 1999; Owen-Smith 2008) and knowing how prey availability affects predator population growth rates (e.g. Vucetich & Peterson 2004; Millon & Bretagnolle 2008). Much predation research has focused on understanding the causes and consequences of interannual fluctuations in predation (e.g. Korpimäki & Norrdahl 1991; O'Donoghue *et al.* 1998;

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Vucetich *et al.* 2011). Yet, our understanding of predation will be incomplete to the extent that year-round predation patterns remain poorly documented. Fortunately, the opportunity to document and assess such annual patterns has recently been expanded through the detection of predation events, particularly during snow-free periods, at predator GPS locations (e.g. Sand *et al.* 2008; Knopff *et al.* 2010). For large terrestrial carnivores preying on ungulates, intraannual fluctuations are expected for two reasons. First, ungulates tend to be in poorer nutritional condition during the winter or dry season (Parker, Barboza & Gillingham 2009), and, second, neonates are available only in the months that follow their birthing, which tends to be most synchronous in temperate climates (Bronson 1989).

Important aspects of seasonal variation in the diet of large terrestrial carnivores are already understood. For example, the contribution of various species to the diet of African lions *Panthera leo* in Kruger National Park, South Africa differs between the dry and wet seasons (Owen-Smith 2008). Characteristics of prey composition are also known to vary among seasons for several other species, including African wild dogs *Lycan pictus* (Pole *et al.* 2004) and wolves (Peterson 1977). However, less is understood about seasonal variation in two other aspects of predation, per capita kill rate (kills per predator per unit time) and per capita rate of biomass acquisition (kg per predator per unit time).

Kill rates of cougars *Puma concolor* in west-central Alberta were highest during summer when they prey primarily on juvenile ungulates (Knopff *et al.* 2010). Conversely, kill rates were highest during winter for Eurasian lynx *Lynx lynx* preying on roe deer *Capreolus capreolus* because neonate roe deer are not particularly vulnerable to lynx predation (Nilsen *et al.* 2009). Kill rates for wolves in Poland preying primarily on red deer *Cervus elaphus* were lower during spring–summer than during autumn–winter, although predation of wild boar *Sus scrofa* piglets did tend to increase during spring–summer (Jedrzejewski *et al.* 2002). However, kill rates of wolves preying on moose *Alces alces* in south-central Scandinavia were approximately twice as high during summer, compared with winter (Sand *et al.* 2008). Except for these examples, little is known about seasonal variation in kill rates. Moreover, the diversity of patterns observed among these species and study sites is greater than our understanding of what causes this diversity.

Rates of biomass acquisition are expected to vary among seasons because of related changes in prey vulnerability (Mech & Peterson 2003). However, observations from wolves and cougars found rates of biomass acquisition that were similar in summer and winter (Sand *et al.* 2008; Knopff *et al.* 2010). Because these observations have been contrary to our expectation and the topic has only rarely been evaluated, further investigation seems warranted.

Here, we assessed seasonal variation in the species composition of wolf-killed ungulates, age and sex composition of wolf-killed elk, per capita kill rate (including only wolf-killed prey), per capita prey acquisition rate (including wolf-killed and -scavenged prey) and per capita rate of biomass (kg

acquisition for wolves living on the Northern Range (NR) in Yellowstone National Park (YNP). We assessed prey acquisition rate, in addition to kill rate, because kill rate is a poor indication of predation rate (Vucetich *et al.* 2011), and the primary value of assessing prey acquisition or kill rate is therefore to better understand the rate at which predators acquire prey, rather than understanding the impact of predators on prey populations. We documented these patterns during four seasons of the year: (i) early winter (November–December) when neonates are absent and prey are generally in good nutritional condition, (ii) late winter (March) when neonates are absent and prey are in poorer condition, (iii) spring (May) when neonates are becoming available and prey remain in poor condition, and (iv) summer (June–July) when neonates are abundant and prey condition improves. We also assessed seasonal variation in nutritional condition of wolf-killed adult elk through analyses of bone marrow fat. Characterizing the nutritional condition of wolf-killed prey provides insight into the difficulty wolves may have on capturing and killing adult prey, as well as the impact wolf predation may have on prey populations. Finally, because particularly little is known about predation dynamics during summer in temperate climates, we assessed how rates of prey acquisition during the summer were associated with the proportion of neonates ( $P_{\text{neonates}}$ ) in wolves' diet. We expected kilograms of prey acquired per wolf per day to decrease with increasing  $P_{\text{neonates}}$ , because the biomass of a neonate is small. We also assessed the relationship between the number of prey acquired per wolf per day and  $P_{\text{neonates}}$ . If wolves compensate for the small biomass of neonate prey by killing more frequently, then we would expect the number of prey per wolf per day to increase with  $P_{\text{neonates}}$ . Because the vulnerability of wolf-killed adult ungulates changes throughout summer [i.e. their nutritional condition changes (see Fig. 3)], we also expected that the above-mentioned relationships would differ between early and late summer.

While knowing how kill rate varies throughout the year is important for understanding the population dynamics of predators and their prey (see Boyce, Sinclair & White 1999), such knowledge will generally be rare. This concern may be mitigated if, for example, years with higher-than-average winter kill rates tended to coincide with higher-than-average kill rates in the previous or subsequent season. We also assessed this possibility.

## Study system

Wolves were reintroduced on the NR of YNP in 1995. Since 1995, the NR wolf population has fluctuated between 20 and 98 wolves within YNP, with an average pack size of 11 wolves (Smith & Bangs 2009). The NR is 1530 km<sup>2</sup> in size, and 1000 km<sup>2</sup> of that area lies within YNP (see Metz *et al.* 2011 for map of study area). Elevation ranges primarily between 1500 and 2400 m, with 52% of the NR within YNP between 1500 and 2100 m, 35% between 2101 and 2400 m, and 13% > 2400 m. Lower elevations are characterized by large open valleys of grass meadows and shrub steppe vegetation; upper

elevations and north-facing slopes are dominated by coniferous forests. The NR is generally characterized by long, cold winters and short, cool summers (Houston 1982).

During the study period, counts of NR elk abundance have ranged from 6279 to 16 791, and bison *Bison bison* abundance has fluctuated between 455 and 2070 (YNP, unpublished data). Within the territories of packs we monitored, bison were most abundant during winter and spring monitoring periods. During spring and summer, the portion of the NR within YNP is also inhabited by approximately 2000 mule deer *Odocoileus hemionus* (White & Garrott 2005). Less common ungulates include bighorn sheep *Ovis canadensis*, moose, mountain goat *Oreamnos americanus*, pronghorn *Antilocapra americana* and white-tailed deer *Odocoileus virginianus*. Several species of predators are also common on the NR, including black bears *Ursus americanus*, cougars, coyotes *Canis latrans* and grizzly bears *Ursus arctos*.

## Materials and methods

### DETECTION OF UNGULATE CARCASSES

Wolf predation in YNP has been investigated as part of a long-term research programme that began in 1995 (Smith & Bangs 2009). The ecology of wolf predation differs substantially between winter and summer (e.g. differences in snow cover and prey size). These differences suggest the need to employ different methods for assessing predation during these seasons. Methods associated with detecting ungulate carcasses during winter are described in Smith *et al.* (2004), and those associated with detecting ungulate carcasses during spring and summer are described in Metz *et al.* (2011). We summarize these methods here.

Approximately 35–40% of NR wolves have been outfitted with VHF (Telonics Inc., Mesa, AZ, USA) or GPS (Televilt, Lindesberg, Sweden; Lotek, Newmarket, ON, Canada) radio collars during each year between 1995 and 2009 (Smith & Bangs 2009).

During winter, we used VHF collars as a means of observing the packs to which these wolves belonged from light, fixed-wing aircraft (supercub PA-18) and from ground-based locations. Specifically, we used these observations to monitor three wolf packs for two, 30-day study periods during each winter between November 1995 and

March 2009. These study periods occurred every early winter (mid-November to mid-December) and late winter (March). During this 14-year period, we monitored 12 different packs (Table 1).

We also used 11 GPS-collared wolves as a basis for monitoring one or two wolf packs each spring (1–31 May) and/or summer (1 June to 31 July) for five different years between 2004 and 2009. In total, we monitored five different packs (Table 1). Each monitored pack included one or two GPS-collared wolves. The duration of our observations for each pack was limited by the performance of the GPS collars and averaged 74.7 days ( $\pm 12.0$  SE) of each spring–summer season.

By observing radio-collared wolves, we detected carcasses of ungulate prey which wolves acquired. From each carcass detected, we recorded the cause of death, date of death, species, sex, age and biomass of the prey (see Appendix S1, Supporting information for details). Following Wilmers *et al.* (2003), we estimated the edible biomass of each carcass to be 68% of the live weight. For adult elk that were killed by wolves, we also assessed their nutritional condition (see Appendix S1, Supporting information). During winter field seasons, we detected 942 carcasses of prey killed by monitored packs and 81 additional carcasses that these wolves scavenged. During spring and summer field seasons, we detected 296 carcasses of wolf-killed prey and 14 carcasses that wolves scavenged. We used these carcasses to assess seasonal variation in predation.

### DATA PREPARATION

We estimated three statistics related to the rate at which wolves acquire food during each of 5-month-long monitoring periods (i.e. November–December, March, May, June and July): (i) per capita kill rate, which is the number or biomass of prey killed per wolf per day, (ii) per capita rate of prey acquisition, which is number or biomass of carcasses killed or scavenged per wolf per day and (iii) the mean biomass of prey acquired per carcass. We obtained 90 estimates for each of these statistics ( $n_{\text{November–December}} = 36$ ,  $n_{\text{March}} = 36$ ,  $n_{\text{May}} = 6$ ,  $n_{\text{June}} = 7$ ,  $n_{\text{July}} = 5$ ; see Table 1).

Kill rate and rate of prey acquisition were calculated as the number and biomass of prey killed or acquired divided by the size of the pack to whom the carcass belonged and then divided by the duration of the observation period, which was typically 30 or 31 days. However, two of our June estimates were based on observation periods of 11 and 21 days because of radio-collar failure. While estimates based on shorter periods of time are sometimes characterized by large

**Table 1.** The seasons that we monitored prey composition and kill rate for various packs were late winter (L), spring–summer (S) and early winter (E). Seasons marked with a <sup>1</sup> indicate that we collected only prey composition data. For all other seasons, we collected both prey composition and kill rate data. For spring–summer 2005, ‘Leopold’ was only monitored for summer

Pack	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009
Agate													L		
Blacktail														E	L,S
Crystal	E <sup>1</sup>	L <sup>1</sup>													
Druid		E <sup>1</sup>	L <sup>1</sup> ,E	L,E	L,E	L,E	L,E	L,E	L,E	L,E			L,E	L,E	L
Everts															L,S
Geode								E	L,E	L,S,E	L				
Hellroaring											E	L,E			
Leopold		L <sup>1</sup> ,E <sup>1</sup>	L <sup>1</sup> ,E	L,E	L,E	L,E	L,E	L,E	L,E	L,E	L,S,E	L,E	L,S,E	L,S	
Oxbow													E	L,S	
Quadrant														E	
Rose	E <sup>1</sup>	L <sup>1</sup> ,E <sup>1</sup>	L <sup>1</sup> ,E	L,E	L,E	L,E	L,E	L							
Slough											L,E	L,E			

sampling variation (Hebblewhite *et al.* 2003; Knopff *et al.* 2009), our inclusion of these two estimates had no effect on the overall results or conclusions of our analysis. Pack size was determined through aerial and ground observations. During spring and summer, pack size was adjusted to account for observed pup mortality (see Metz *et al.* 2011 for details). For winter estimates, we divided by total pack size (including pups 7–11 months old), and for spring and summer, by the number of adult equivalent wolves in a pack. Pack size was calculated differently for these observation periods because during winter, pups and adults are of similar body size, but during spring and summer, pups are much smaller than adults and therefore have much different metabolic needs (see Metz *et al.* 2011 for details).

During winter, the number and biomass of prey were estimated from observed prey and an estimator based on the double-count method, which accounted for prey that went undetected. This application of the double-count method involved independent observers working from light aircraft and ground-based locations. Details are in Smith *et al.* (2004) and Kamischke (2007).

During spring and summer, the number and biomass of prey was also estimated from observed prey and an estimator based on the double-count method. This application of the double-count method involved pairs of GPS-collared wolves living in the same pack and accounts for the tendency of individual wolves to only attend a portion of the prey acquired by their pack during spring and summer. Details are in Metz *et al.* (2011).

## ANALYSIS

For each season, we observed the composition of wolf-killed prey (i.e. proportion of wolf-killed prey representing each species). We used a G-test of independence to test for seasonal differences in the frequency of deer and elk. We did not assess frequencies of other prey because they were rare among wolf kills (i.e.  $\leq 1.3\%$  of wolf-killed prey) and frequently were not observed at all during some seasons. Because most prey were elk (see Results), we also tested for seasonal differences in the frequency of elk prey belonging to each sex and age class {elk  $\leq 14$  months [i.e. neonates (0–3 months) and calves (4–14 months) combined], yearling [15–26 months], adult female, adult male; see Appendix S1, Supporting information}. Additionally, we assessed seasonal variation in the nutritional condition of adult male and adult female elk killed by wolves. More precisely, we tested for seasonal differences in the proportion of wolf-killed elk with fat-depleted bone marrow (i.e.  $\leq 70\%$  fat; Ransom 1965).

While it is known that wolf-killed prey tend to decline in nutritional condition throughout winter (e.g. Husseman *et al.* 2003), relatively little is known about when and how quickly wolf-killed prey recover during spring and summer. To assess this recovery, we developed general linear models to quantify how the per cent fat of bone marrow in wolf-killed adult elk changed with Julian Day (JD). In doing so, we took into account potential differences between sexes and between years (2004, 2005, 2007, 2008, 2009).

To gain a more precise understanding about the contribution of neonates to wolves' diet during spring and summer, we also assessed how the frequency of neonate prey (0–3 months) tended to vary with JD throughout spring and summer. To do this, we estimated the number of neonate and non-neonate carcasses for each JD for each pack ( $n = 4$ ). The estimated number of carcasses was calculated as the number detected on each day divided by the probability of detection (derived from the double-count estimator) for that pack. For context, the probability of detecting an ungulate for a pack was, on average, 93% for large ungulates and 73% for small ungulates. We then summed, across the four packs and pooled across years, the

estimated number and biomass of neonate and non-neonate carcasses for each JD and then calculated a 7-day moving average for the proportion of diet that was neonate ungulates. We limited this analysis to data from 2008 and 2009 when GPS collars acquired a high proportion of the scheduled locations (i.e. 99%, compared with 74% for other years). This high success rate allowed us to precisely estimate the date each prey was acquired. While a 74% success rate is adequate for estimating the total number of prey acquired during each month (see Metz *et al.* 2011), it is not sufficient to allow precise estimates for the Julian date on which each prey was acquired.

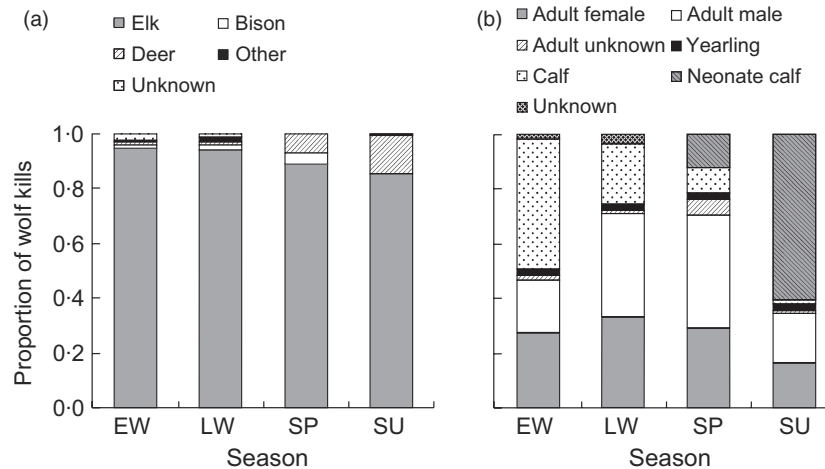
We used Kruskal–Wallis ANOVA to assess whether kill rate, rate of prey acquisition or mean biomass of prey acquired per carcass varied significantly among the months that we monitored. Multiple comparisons between months were made using a Wilcoxon rank-sum test with a Bonferroni correction. Also, to assess whether scavenged prey represented a significant portion of wolves' diet for various months of the year, we conducted one-sample *t*-tests for the hypothesis that the estimated rate of prey acquisition (for any particular month) was significantly greater than the mean kill rate for that month. We also assessed how rates of prey acquisition during the summer were associated with the proportion of neonates ( $P_{\text{neonates}}$ ) in wolves' diet. We estimated  $P_{\text{neonates}}$  and rate of prey acquisition (both derived from the double-count estimator, see above) for four packs for each 7-day period throughout early summer (30 May–3 July) and late summer (4–31 July). Because this analysis also requires knowing the Julian date on which each prey was acquired, we again used data from years with appropriately precise observations (i.e. 2008 and 2009, see above). In total, we obtained 20 estimates of  $P_{\text{neonates}}$  and rate of prey acquisition for early summer, and 16 such estimates for late summer. With these data, we calculated the correlation coefficients for each of the early and late summer associations. We then used a Chi-squared statistic to test for the equality of correlation coefficients.

Finally, we used correlation analysis to assess the tendency for the kill rate of a pack in one season to be associated with the kill rate for that pack in a subsequent season. This analysis was designed to assess, for example, the extent to which kill rate during late winter of a particular year tends to be correlated with kill rate during summer of the same year.

## Results

We identified the species for 98% of wolf-killed ungulates that we detected. We also identified the age class and sex (among adults) for 96% of wolf-killed elk that we detected. Among these carcasses,  $\geq 96\%$  of wolf-killed prey were comprised of elk during each of the winter monitoring periods. Wolves' utilization of elk declined to 89% during spring and 85% during summer (Fig. 1a). This decline was associated with an increased utilization of deer throughout spring and summer ( $P < 0.0001$ , d.f. = 3). Specifically, wolves' utilization of deer increased from 1.5% during both early and late winter to 7.1% during spring and 14.1% during summer. Bison comprised a small portion of wolf-killed prey throughout the year (1.3%) and peaked during spring (4.1%) when wolves occasionally preyed on neonate bison. If we had also included carcasses that wolves scavenged, bison represented 3% (early winter), 4% (late winter), 7% (spring) and  $< 1\%$  (summer) of the carcasses on which wolves fed.

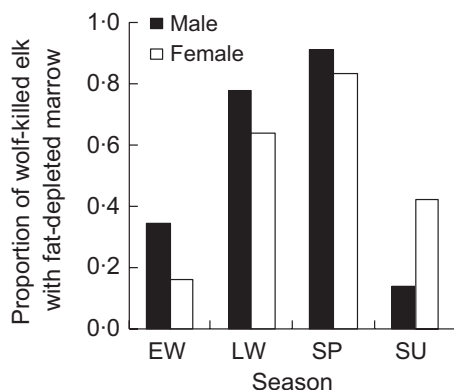
The age and sex composition of wolf-killed elk also varied significantly among seasons ( $P < 0.0001$ , d.f. = 9; Fig. 1b).



**Fig. 1.** Seasonal composition of wolf-killed prey in Yellowstone's Northern Range throughout a 14-year period (1995–2009) by (a) species and (b) age and sex of elk prey. In (a), 'Other' represents moose and bighorn sheep. Sample sizes were 401 [Early Winter (EW)], 541 [Late Winter (LW)], 98 [Spring (SP)] and 198 [Summer (SU)]. In (b), sample sizes were 378 (EW), 509 (LW), 87 (SP) and 169 (SU).

Among wolf-killed elk, adult males were most frequent during late winter (40%) and spring (41%), and least frequent during summer (18%) and early winter (20%). Adult females were more frequent during early winter (28%), late winter (34%), and spring (29%) than during summer (16%). Yearlings (15–26 months) were rare among wolf-killed elk throughout the year (3%). Elk  $\leq 14$  months (i.e. neonate calves and calves combined) were least frequent during late winter (23%) and spring (22%), and most frequent during summer (62%) and early winter (49%).

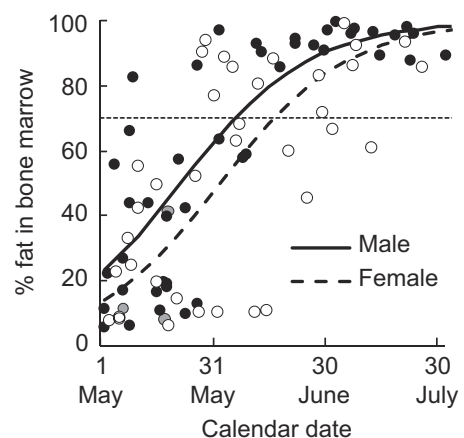
The nutritional status of wolf-killed adult elk varied significantly throughout the year, both for males ( $P < 0.0001$ , d.f. = 3) and females ( $P < 0.0001$ , d.f. = 3; Fig. 2). The frequency of elk with fat-depleted marrow was higher for males than for females during early winter ( $P = 0.01$ , d.f. = 1) and late winter ( $P = 0.01$ , d.f. = 1). However, the frequency of male and female elk with fat-depleted marrow peaked at similar levels (91% for males and 83% for females;  $P = 0.47$ , d.f. = 1) during spring. During summer, a higher



**Fig. 2.** Proportion of wolf-killed adult elk with fat-depleted bone marrow (i.e.  $\leq 70\%$ ). For males, sample sizes were 61 [Early winter (EW)], 152 [Late winter (LW)], 22 [Spring (SP)] and 22 [Summer (SU)]. For females, sample sizes were 80 (EW), 136 (LW), 18 (SP) and 19 (SU).

frequency of females had fat-depleted marrow ( $P = 0.04$ , d.f. = 1).

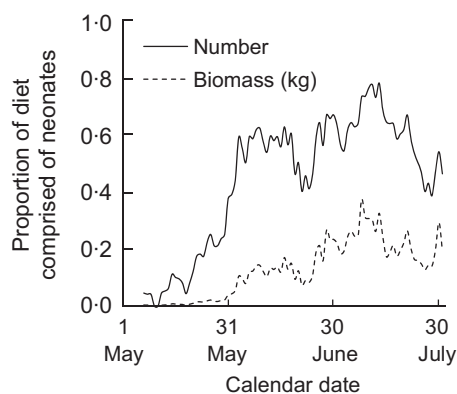
Our assessment of what factors influenced the fat content of bone marrow in wolf-killed elk during spring and summer began with a full model that included JD, year and sex as predictor variables. For that full model, JD was significant ( $P < 0.0001$ ), the year effect was not ( $P$ -values  $> 0.35$ ), and sex was marginally significant ( $P = 0.09$ ). Based on these results, we fit a reduced model that included only JD and sex. For this model, the fat content of males was on average slightly greater than that for females ( $P = 0.05$ ), and fat content increased significantly throughout spring–summer ( $P < 0.0001$ ; Fig. 3). More specifically, the model predicts an increase in fat content from about 35% in mid-May to about 70% by mid-June.



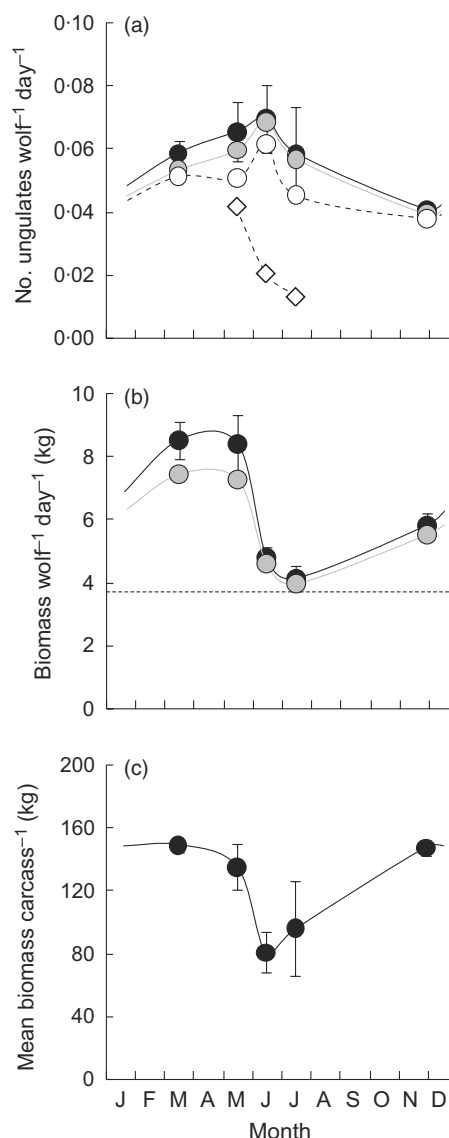
**Fig. 3.** Per cent fat in the bone marrow of wolf-killed adult elk throughout spring and summer. The curved lines depict a general linear model (conducted on logit-transformed data, and then back-transformed) that included the influence of sex and Julian day. Filled circles represent individual males, open circles represent females, and grey circles represent individuals of unknown sex. The horizontal, dotted line is a reference line and indicates the % fat associated with marrow being fat-depleted (Ransom 1965).

The frequency of neonate ungulates in wolves' diet increased substantially from mid-May through mid-June (Fig. 4), which coincides with the period when neonate elk are born and increasingly abundant (Barber-Meyer, Mech & White 2008). The biomass of neonates in the diet also increased throughout June and into July, reflecting the rapid increase in neonates' body size during this time period. From June through July, neonates comprised, on average, 61% of the carcasses in the wolves' diet and 21% of the biomass. These percentages fluctuated greatly throughout the summer (see Fig. 4). These fluctuations arise in part because when wolves feed upon a large, adult ungulate they often spend a few days feeding primarily from that one carcass.

The number of ungulate carcasses acquired (killed or scavenged) per wolf per day was least during early winter ( $0.041 \pm 0.003$  SE; Fig. 5a) and by the following June had increased by about 70% to 0.070 carcasses per wolf per day ( $\pm 0.011$ ). Between June and July, the rate decreased by about 15% from the annual maximum to  $0.058 \pm 0.015$  (Fig. 5a). These rates differed significantly among months ( $P < 0.01$ , d.f. = 4), and a *post hoc* test indicated that late winter significantly differed from early winter ( $P < 0.01$ ; see Table S1, Supporting information). Although the peak month (June) did not significantly differ from early winter ( $P = 0.16$ ), this was likely at least partially because of the relatively small sample size for June (i.e.  $n = 7$ ). By contrast, the rate of biomass (kilogram) acquired per wolf per day was lowest during July ( $4.1 \pm 0.4$ ), about 40% greater during early winter ( $5.8 \pm 0.4$ ), and peaked during late winter and spring ( $8.5 \pm 0.6$  in March and  $8.4 \pm 0.9$  in May; Fig. 5b). These rates differed significantly among months ( $P < 0.0001$ , d.f. = 4), and a *post hoc* test indicated that June and July each significantly differed from late winter ( $P = 0.02$  for June and  $P = 0.03$  for July; see Table S1, Supporting information). Kill rates, which exclude scavenged



**Fig. 4.** Estimated proportion of wolf diet comprised of neonate ungulates throughout spring and summer. The curves represent 7-day moving averages. Most (>90%) of the neonates were elk, and the remainder were deer and bison. Number (solid line) refers to the proportion of diet that is comprised of neonates in relationship to the number of prey acquired. Biomass (dashed line) refers to the proportion of diet that is comprised of neonates in relationship to the biomass of prey acquired.



**Fig. 5.** Seasonal variation in several statistics associated with the feeding ecology of wolves from Yellowstone's Northern Range (NR). Each data point represents a mean with sample sizes of 36 (November–December), 36 (March), 6 (May), 7 (June) and 5 (July). Filled circles represent prey acquisition rates (i.e. including carcasses of all ungulate species), grey circles represent kill rates (i.e. including all ungulate species, but excluding scavenged carcasses), open circles represent kill rates of elk, and diamonds represent kill rates of non-neonate elk. Diamonds are not displayed for November–December or March because neonates are not present during those months. The lines connecting adjacent data points highlight the average trend that exists between sampling periods, and the dotted line in panel (b) represents the estimated minimum daily energetic requirement for NR wolves (approximately 3.7 kg per wolf per day, see Metz *et al.* 2011). Vertical bars are standard errors. Panel (a) represents the number of ungulates acquired ( $P < 0.01$ ), the number of ungulates killed ( $P < 0.01$ ), the number of elk killed ( $P = 0.03$ ) or the number of non-neonate elk killed per wolf per day, panel (b) displays the biomass (kilogram) of ungulates acquired ( $P < 0.0001$ ) or killed ( $P < 0.001$ ) per wolf per day, and panel (c) displays the mean kilograms of ungulate prey per acquired carcass ( $P < 0.001$ ). *P*-values represent tests for the equality of rates across months, using Kruskal–Wallis ANOVA.

carcasses, followed a similar seasonal pattern for both the number and kilograms of prey. Rates of prey acquisition only significantly differed from kill rates for kilograms of prey during late winter ( $P = 0.03$ ). For all other instances,  $P$ -values were  $> 0.10$ , except for number of prey during late winter ( $P = 0.09$ ) and kilograms of prey during May ( $P = 0.10$ ). The mean biomass (kilogram) of each carcass that wolves acquired was high during early winter ( $147.6 \pm 5.2$ ), late winter ( $149.2 \pm 3.9$ ) and spring ( $135.3 \pm 14.3$ ), and low during the summer months ( $80.6 \pm 13.0$  in June and  $96.1 \pm 30.5$  in July; Fig. 5c).

Predation dynamics differed between early and late summer (Fig. 6). In particular,  $P_{\text{neonates}}$  was a significantly stronger predictor of the number of prey acquired per wolf per day during late summer than during early summer ( $R^2 = 0.74$  and  $P < 0.0001$  for late summer and  $R^2 = 0.29$  and  $P = 0.01$  for early summer;  $P = 0.06$  for a Chi-squared test for the equality of these two correlations; Fig. 6a). Also, the portion of wolves' diet comprised of neonates ( $P_{\text{neonates}}$ ) was a significant predictor of kilograms of prey per wolf per day during early summer ( $R^2 = 0.30$ ,  $P = 0.01$ ), but not late

summer ( $R^2 = 0.03$ ,  $P = 0.54$ ; Fig. 6b). More specifically, during early summer, kilograms of prey acquired tended to be less when  $P_{\text{neonates}}$  was greater.

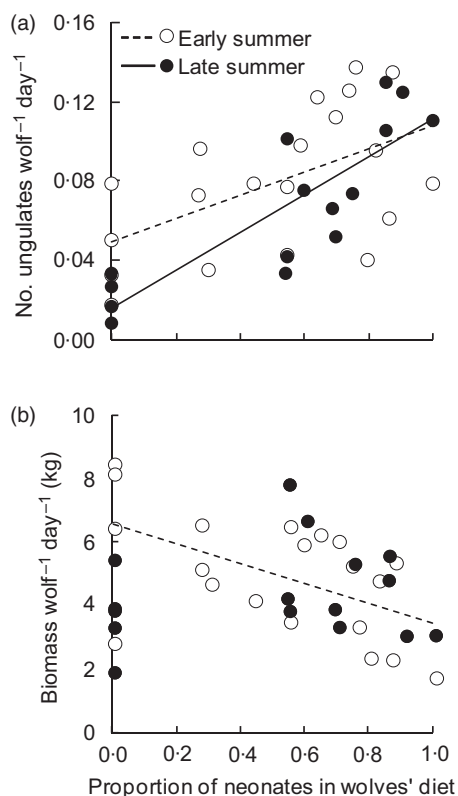
Early-winter kill rates (measured as number of ungulates per wolf per day) were significantly associated with late-winter kill rates ( $P < 0.01$ ; Fig. 7a). However, early-winter kill rates explained only a modest portion of the variation in late-winter kill rates (i.e.  $R^2 = 0.21$ ). This weak relationship indicates, for example, that observing a higher-than-average kill rate during early winter is not a good indication that kill rates during late winter will also be higher than average, compared with other late winters. Early-winter kill rates are a similarly poor indicator of late-winter kill rates when measured as kilograms per wolf per day ( $R^2 = 0.09$ ,  $P = 0.09$ ; Fig. 7c).

Late-winter kill rates seemed to have been better predictors of summer kill rates in the sense that the  $R^2$  values were relatively high [ $R^2 = 0.47$ ,  $P = 0.09$  for number of ungulates/wolf/day (Fig. 7b) and  $R^2 = 0.65$ ,  $P = 0.03$  for kg per wolf per day (Fig. 7d)]. However, these relationships were based on relatively small sample sizes (i.e.  $n = 7$  compared with  $n = 32$  for the early-winter/late-winter comparison). Moreover, we observed statistical significance only for the relationship involving kilograms per wolf per day. The relationships described here are similar to those involving other seasons (e.g. between late winter and spring) or measures of kill rate (e.g. including only elk; see Table S2, Supporting information).

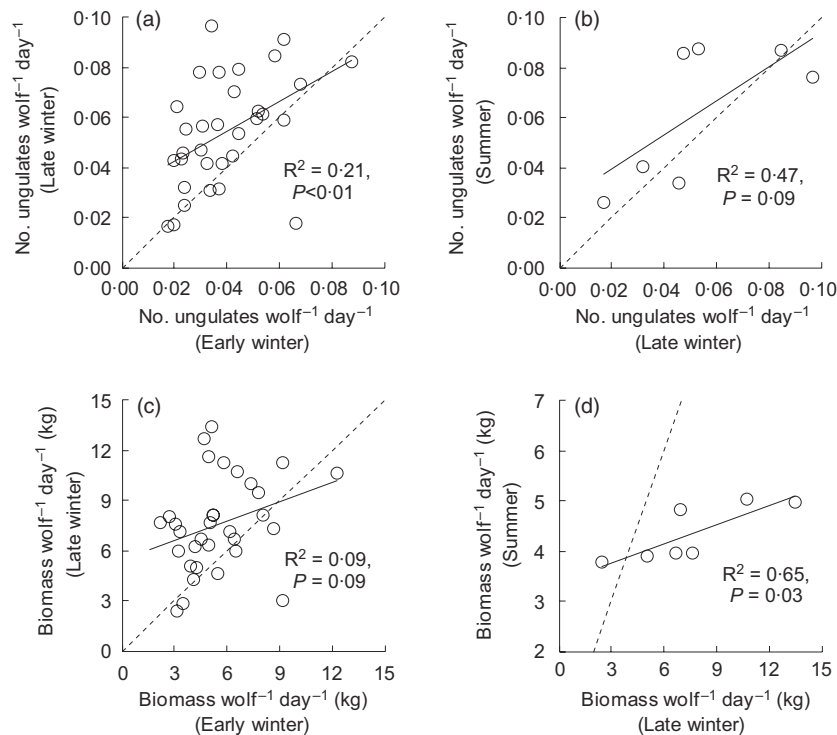
## Discussion

Each aspect of predation that we measured varied throughout the year for NR wolves. This seasonal variation was driven by changes in the availability and vulnerability of prey (Fig. 2; Houston 1982; Coughenour & Singer 1996; Barber-Meyer, Mech & White 2008). In comparison with previous work (i.e. Sand *et al.* 2008; Knopff *et al.* 2010), our work illustrates that seasonal predation patterns of large, terrestrial carnivores may exhibit significant differences among species and among populations of the same species. While previous work found that rates of biomass acquisition were similar between summer and winter, our work shows that the biomass acquired per wolf per day was twice as great during its peak in late winter and spring than during its low point in summer (Fig. 5b). Additionally, our work also indicates that one's impression of how kill rate varies among seasons may differ greatly depending on whether kill rate is expressed in terms of number or biomass of prey (compare Fig. 5a,b). Finally, our study shows that estimates of kill rate from one season may not be particularly informative of kill rate during a subsequent season (Fig. 7).

Predation dynamics may be importantly influenced by predator-prey size relationships (Owen-Smith & Mills 2008), and the NR is characterized by having three different-sized species of prey. Previous work showed that NR wolves preferred elk (medium) to bison (large) (Smith *et al.* 2004). Our work shows that elk are also the primary prey



**Fig. 6.** Influence of the estimated proportion of neonates ( $P_{\text{neonates}}$ ) in wolves' diet on weekly prey acquisition rate during early summer (30 May–3 July) and late summer (4–31 July). In panel (a),  $P_{\text{neonates}}$  is a stronger predictor of number of prey acquired per wolf per day during late summer ( $R^2 = 0.74$ ,  $P = 0.01$  for early summer;  $R^2 = 0.74$ ,  $P < 0.0001$  for late summer;  $P = 0.06$  for a Chi-squared test for equality of correlation coefficients). In panel (b),  $P_{\text{neonates}}$  is a statistically significant predictor of biomass of prey acquired per wolf per day during early summer ( $R^2 = 0.30$ ,  $P = 0.01$ ) but not late summer ( $R^2 = 0.03$ ,  $P = 0.54$ ). Lines represent the best-fitting regression, which are depicted only for statistically significant relationships.



**Fig. 7.** Correlations between kill rates estimated during different seasons. Each observation represents either the number of prey killed per wolf per day or the biomass (kilogram) of prey killed per wolf per day for a pack for a pair of subsequent seasons. Data in panels (a) and (c) represent 32 paired observations of eight different packs observed between 1997 and 2009. Data in panels (b) and (d) represent seven paired observations of five different packs observed between 2004 and 2009. Solid lines represent a simple linear regression line. Dashed lines are for reference; they pass through the origin and have a slope of one.

during spring and summer (Fig. 1a), despite an increase of deer (small) availability on the portion of the NR within YNP (Houston 1982). Besides being most abundant, elk are likely an optimal prey choice for wolves because their size makes them less dangerous than bison but also slower than deer, especially during snow-free periods. Nevertheless, wolf predation of deer increased during spring and summer, and the biomass acquired through deer may be important to NR wolves meeting their energy requirements during summer (see Fig. 5b).

Our observations indicate that seasonal variation in the age of wolf-killed elk is driven by seasonal variation in prey vulnerability. Specifically, wolves preyed most frequently on large, adult elk during late winter and spring when wolf-killed elk are in their poorest nutritional condition (compare Figs 1b and 2). Also, wolves preyed most frequently on neonate calves (0–3 months) during summer and on calves (5–14 months) during early winter when they are most abundant (Coughenour & Singer 1996; Barber-Meyer, Mech & White 2008) and wolf-killed adult elk are in good nutritional condition (Fig. 2). Interestingly, wolves rarely preyed on yearlings (15–26 months) during any season, suggesting that this age class is not particularly vulnerable to wolf predation. Although our observation that neonate calves represent approximately two-thirds of elk killed by NR wolves during summer (Fig. 1b) is not surprising, it does differ from observations in south-central Scandinavia where approximately

90% of wolf-killed moose were neonates (Sand *et al.* 2008). This difference may be attributable to adult moose, with their larger body size, being more dangerous to hunt than adult elk. The difference may also be attributable to pack sizes being larger on the NR. That is, for large packs, maximizing net energy intake may require preying more frequently on adult prey because the large amount of biomass acquired through each adult prey provides a significant opportunity for all pack members to feed.

Our observations and other recent findings indicate that the number of prey killed per predator per day peaks during summer (Fig. 5a; see also Sand *et al.* 2008; Knopff *et al.* 2010), the time when neonate prey are available in temperate climates. However, because wolf predation of neonate elk appears compensatory for systems with rich predator communities (Griffin *et al.* 2011), the most important assessment of kill rate during spring and summer for understanding the nature of wolf predation may be that of the rate at which recruited prey (i.e. prey that survive to  $\geq 6$  months) are killed. For NR wolves, kill rates of recruited prey during May are only slightly less than those observed during winter, and kill rates of recruited prey during June and July are only about half of those observed during winter (Fig. 5a; see also Vucetich *et al.* 2011). Because seasons with higher kill rates of recruited prey also tend to be seasons during which wolf-killed prey are in poor nutritional condition (compare Figs 2 and 5a), our work highlights how seasonal variation in the



characteristics of wolf predation suggests that wolf predation could often be compensatory in nature.

Our work is also important for showing that seasonal variation in the number of prey acquired per predator per day does not coincide with seasonal variation in kilograms of prey acquired per predator per day. Specifically, the number of prey acquired is highest during June when the biomass acquired by NR wolves is near its annual minimum (compare Fig. 5a,b). These seasonal patterns are decoupled because during summer each carcass, on average, provides less biomass (Fig. 5c). The patterns observed with NR wolves contrast with observations for cougars in Alberta (Knopff *et al.* 2010) and wolves in Scandinavia (Sand *et al.* 2008), where these predators acquired similar amounts of biomass during winter and summer.

This difference between wolves in NR and Scandinavia is not easy to explain, although it may also be related to how these wolf populations differ in average pack size (see above). Differences between NR wolves and cougars may be attributable to differences in hunting behaviour. Cougars are 'sit-and-wait' predators and, compared to wolves, tend to capture prey that are in better nutritional condition (Hussemann *et al.* 2003). As coursing predators, wolves' kill rates are likely more influenced by this aspect of prey vulnerability. Consequently, NR wolves obtained less biomass during periods when large ungulates killed by wolves are in better nutritional condition (compare Figs 2 and 5b). Of note, wolves also tend to have less biomass available through scavenged prey during these periods (i.e. summer and early winter). Nevertheless, because kill rates are most useful for understanding the rate at which predators acquire prey (Vucetich *et al.* 2011), it is important to also include carcasses from which wolves scavenge. What remains unknown is whether wolves' utilization of carcasses differs greatly between killed and scavenged prey, and whether those differences vary seasonally.

Sand *et al.* (2008) showed that kill rate of wolves during summer was influenced by the type of prey (i.e. small prey or moose) and JD. Aside from this, little had been known about what causes kill rate to vary during the summer. For NR wolves, the number of prey acquired per wolf per day increased with the portion of wolves' diet comprised of neonates ( $P_{\text{neonates}}$ ) (Fig. 6a). This pattern suggests that wolves compensate for neonates small size by killing more frequently. However, the relationship for late summer is stronger than early summer. These relationships differ because, when  $P_{\text{neonates}}$  is low, the number of prey acquired is higher during early summer than late summer (compare open and filled symbols on left side of Fig. 6a). The process likely underlying this pattern is that when wolves rely entirely on adults during early summer (i.e. when wolves do not kill neonates), their prey acquisition rates are higher (i.e. higher than when wolves rely entirely on adults during late summer). These rates are higher during early summer because wolf-killed adult elk tend to be in poorer nutritional condition (Fig. 3) and are therefore easier to kill than during late summer.

We expected kilograms per wolf per day to decline with increasing  $P_{\text{neonates}}$  because neonates are much smaller than adults. We observed this expected relationship during early summer (Fig. 6b). However, the relationship between kilograms per wolf per day and  $P_{\text{neonates}}$  is not significant for late summer. These relationships differ because, when  $P_{\text{neonates}}$  is low, kilograms per wolf per day is lower during late summer than early summer (compare open and closed symbols on left side of Fig. 6b.). The process likely underlying this pattern is that when wolves kill only adults during late summer (i.e. when wolves do not kill neonates), their kill rates are lower because those adults are in better nutritional condition during late summer (Fig. 3) and are therefore more difficult to kill. An important observation to draw from Fig. 6 is that predation dynamics differ importantly between early summer and late summer.

For decades, there has been a tendency to think that seasonal variation in predation is best characterized by distinguishing winter and non-winter months (e.g. Messier 1994). However, our results allow an underappreciated aspect of seasonal predation to emerge. That is, seasonal predation in temperate climates is best characterized by distinguishing among at least four seasons: early winter, late winter, spring and summer. Because our work demonstrates that both prey composition and kill rate differ importantly among seasons, accounting for such variation would enhance our understanding of a predator's influence on ungulate population dynamics (Boyce, Sinclair & White 1999; Owen-Smith 2008).

For understanding the population dynamics of any organism, it is important to know what time of year is limiting (e.g. Parker, Barboza & Gillingham 2009). For wolves in Yellowstone, summer appears to be that limiting time (Fig. 5b). If this pattern holds for many wolf populations, it would be frustrating because most of what we know about wolves is based on studying them during winter. For example, winter kill rates for Isle Royale wolves explain only about 20% of the variation in their annual population growth rate (Vucetich & Peterson 2004). Perhaps, this poor relationship between kill rate and growth rate is because summer, not winter, is the season that matters most. Moreover, Fig. 5b also exhibits how wolves' life histories are adapted to seasonal changes in food acquisition (Visser, Holleman & Gienapp 2006). That is, the annual peak in the rate of biomass acquisition (late winter and spring) coincides with a time of peak energetic demands for reproducing female wolves (i.e. gestation, lactation), and the per capita biomass acquired becomes significantly less when pups are weaned at the beginning of June. Given these considerations, knowledge of interannual variation in seasonal biomass acquisition would likely allow for an improved understanding of predator population dynamics.

However, because year-round estimates of kill rates are rare, it would be beneficial to our understanding of predation if a kill rate collected during one season was a reliable predictor of a kill rate during a subsequent season. For NR wolves, kill rate during early winter was a poor indicator of kill rate during late winter (Fig. 7a,c). This is attributable to

conditions (i.e. winter severity and nutritional condition of prey) during late winter varying greatly from year to year, and to kill rate being sensitive to variation in such conditions (Post *et al.* 1999; Mech *et al.* 2001; Nilsen *et al.* 2009). By contrast, these conditions exhibit less interannual variation during early winter.

Late-winter kill rates might be better indicators of summer kill rate (Fig. 7b,d). This speculation is similar to speculation that winter conditions may influence kill rates for lynx preying on roe deer during the subsequent summer (Nilsen *et al.* 2009). Ultimately, because many ecological relationships are non-stationary and tend to reveal more variation and covariation as sample size increases (Ariño & Pimm 1995; Vucetich, Peterson & Nelson 2010), we have too little data to know whether late-winter kill rates are good indicators of summer kill rates. However, the question is important enough to merit further attention. If winter kill rates are poor indicators of summer kill rate, and if understanding predation requires understanding how predator and prey populations are affected by predation on neonates or adults during the summer (see Boyce, Sinclair & White 1999), then an adequate understanding of interannual variation in kill rate may require estimating kill rate at least three times a year: early winter, late winter or spring, and summer (Figs 5 and 7).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Characteristics of ungulate carcasses.

**Table S1.** Results for *post hoc* tests assessing wolf feeding ecology statistics.

**Table S2.** Correlation analysis results for pairs of kill rates estimated during different seasons.

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