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The causes and consequences of partial prey consumption by wolves preying on moose

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Abstract For a wide range of taxa, partial prey consumption (PPC) is a frequent occurrence. PPC may arise from physiological constraints to gut capacity or digestive rate. Alternatively, PPC may represent an optimal foraging strategy. Assessments that clearly distinguish between these causes are rare and have been conducted only for invertebrate species that are ambush predators with extra-intestinal digestion (e.g., wolf spiders). We present the first strong test for the cause of PPC in a cursorial vertebrate predator with intestinal digestion: wolves (*Canis lupus*) feeding on moose (*Alces alces*). Previous theoretical assessments indicate that if PPC represents an optimal foraging strategy and is not caused by physiological limitations, then mean carcass utilization is negatively correlated with mean kill rate and the utilization of individual carcasses is uncorrelated with time between kills. Wolves exhibit exactly this pattern. We explore how the typical portrayal of PPC by wolves has been not only misleading but also detrimental to conservation by promoting negative attitudes toward wolves.

Keywords *Alces alces* · *Canis lupus* · Numerical response · Optimal foraging · Predator–prey dynamics

Introduction

Predators from a wide range of taxa commonly consume only portions of the prey they capture (e.g., zooplankton

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(Conover 1966), spiders (Pollard 1989; Samu 1993), predaceous mites (Metz et al. 1988), insects (Johnson et al. 1975; Loiterton and Magrath 1996), shrews (Haberl 1998), weasels (Ehrlinge et al. 1974; Oksanen et al. 1985), marsupials (Chen et al. 2004), canids (Patterson 1994), and bears (Reynolds et al. 2002). Analogous behaviors have even been described for modern humans living in western societies (Rathje 1984; Gillisa et al. 1995). Despite being commonplace and despite continued interest to document and describe partial prey consumption (PPC), the causes and consequences of PPC are not well understood.

PPC is predicted by three different hypotheses. Two hypotheses are focused on proximate mechanisms and predict that PPC is caused by satiation (Holling 1966; Johnson et al. 1975) or by limited rates of digestion (Griffiths 1982). The third hypothesis predicts that PPC is a behavioral "decision" within an optimal foraging strategy (Cook and Cockrell 1978; Sih 1980). This hypothesis rises from logic analogous to that used in patch foraging models (Charnov 1976). Specifically, a prey carcass is like a patch, and a predator decides to either continue feeding on the carcass or stop and begin searching for another carcass. If capturing another prey is relatively easy, and if the net energetic gain from continuing to feed on the carcass is low enough, it may be optimal to only consume a portion of the carcass. The proximate models indicate that PPC arises from a physiological constraint. The optimal foraging explanation indicates that PPC is an intricate and superficially counterintuitive behavioral adaptation shaped by natural selection.

Various aspects of PPC have been described. For example, the propensity to partially consume prey has a heritable, genetic component for a desert spider, *Agelenopsis aperta* (Maupin and Riechert 2001). PPC by predators with extra-intestinal digestion is constrained by evaporation of

prey fluids, which reduces the uptake rate of such fluids by making them more viscous (Pollard 1989). PPC by antlion larvae (*Myrmeleon* sp.) can be manipulated by changing the type of substrate where predation occurs (Loiterton and Magrath 1996), and PPC depends on how nutritional properties vary throughout the carcass of a prey item (Lang and Klarenberg 1997; Chen *et al*. 2004). Despite these insights, few studies have been able to discern what process is ultimately responsible for PPC as it is observed in nature (e.g., Lounibos *et al*. 2008). Exceptions are the study of Lucas (1985), which suggests that PPC by antlion larvae is best explained by optimal foraging theory, and Samu's (1993), which suggests that PPC by the wolf spider (*Pardosa hortensis*) is best explained by limitations in the rate of digestion.

The nature of PPC depends greatly on whether a predator lives under conditions where satiation is a real and regular condition, not merely a hypothetical possibility (Lucas and Grafen 1985). While laboratory experiments have assessed species and environments where satiation occurs regularly (Holling 1966; Johnson *et al*. 1975; Nakamura 1977) and where it does not (Cook and Cockrell 1978; Sih 1980; Lucas 1985), the nature and cause of PPC have never been assessed for a predator exposed to naturally varying levels of prey availability. Causes of PPC have also been assessed only for invertebrate species that are ambush predators with extra-intestinal digestion (e.g., wolf spiders and antlion larvae).

We assessed the hypothesis that PPC is an optimal foraging strategy for wolves (*Canis lupus*) feeding on moose (*Alces alces*) in Isle Royale National Park, USA. We observed natural patterns of carcass utilization by these wolves during each of 14 consecutive winters (1995–2008). If PPC is an optimal foraging strategy, then one expects carcass utilization to be lower during periods when kill rates are higher, and one expects carcass utilization to be unrelated to the number of days since the previous kill (Lucas and Grafen 1985). In the absence of these patterns, PPC is expected to have some alternative explanation (Lucas and Grafen 1985).

Partial prey consumption may, at least in principle, impact population dynamics. For example, theoretical analyses suggest PPC can promote the coexistence of competing predator species (Mittler 1997). Also, a wide range of models consider how PPC affects the functional response (e.g., Nakamura 1974; Abrams 1982; Juliano 1989; Cosner *et al*. 1999), which is a fundamental determinant of population dynamics. Population dynamics are also fundamentally influenced by the numerical response, which is the relationship between kill rate and growth rate of the predator population (Bayliss and Choquenot 2002). The numerical response is a key point of connection between predator and prey population

dynamics, as kill rate represents simultaneously a source of mortality for prey and a source of food for predators. In most predation models, what predators consume is generally presumed to equal what they kill. If kill rate, however, is inversely related to carcass utilization, as predicted by optimal foraging theory (also see "Results"), then consumption rate would be a decreasing portion of kill rate as kill rate increases. Consequently, the relationship between consumption rate and predator population growth rate would differ from the numerical response, which may weaken the connection between the population dynamics of predator and prey. We use data from the Isle Royale wolf–moose system to assess the possible significance of this difference.

The study system

The observations reported here were made on Isle Royale, an island (544 km^2) in North America's Lake Superior. Isle Royale is inhabited by populations of wolves and moose that interact essentially as an isolated single predator–single prey system (Peterson *et al*. 1998; Vucetich and Peterson 2004b). Immigration and emigration are virtually zero or practically negligible. Moose comprise more than 90% of the biomass for the diet of Isle Royale wolves (Peterson and Page 1988); other moose predators are absent, and hunting is prohibited on the island. Predation is the proximate cause of ~60% of deaths of moose >9 months old. Most other moose deaths are associated with nutritional restriction during spring.

Wolves typically hunt and feed on prey larger than themselves. On Isle Royale, the average-sized adult moose (~400 kg) is ~11 times larger than the average-sized wolf (~35 kg). Wolves also hunt and feed in groups called packs. On Isle Royale, the wolf population typically includes three or four packs, each typically comprised of between three and eight individuals.

The kill rates of wolves, which represent the amount of food available for their immediate consumption, are highly variable. Kill rates during plentiful winters are two to four times greater than kill rates during winters of food shortage (Fuller *et al*. 2003). The median kill rate during January and February on Isle Royale is 0.20 kills per wolf per week. Among packs, the coefficient of variation for kill rates is 47%, and the upper quartile (0.28) is about two times greater than the lower quartiles (0.15). Between a fifth and a third of that variation is associated with spatial and temporal variation in prey density and the ratio of predator to prey (Vucetich *et al*. 2002; Jost *et al*. 2005). The remaining variation is attributable to a variety of factors, including pack size (Vucetich *et al*. 2004), winter severity, and variation in hunting abilities of different packs.

In a typical year, between 10% and 39% of the Isle Royale wolf population dies (interquartile range 10–39%, median 23%). The most common causes of death are starvation and being killed by other wolves in territorial disputes. Moreover, wolf life expectancy (4 year; Peterson et al. 1998) is only about one third of the potential life span. These observations suggest that wolves are not generally satiated (see below).

Field measurements and data preparation

We counted the size of each wolf pack on Isle Royale annually from a fixed-wing aircraft each January and February (Peterson et al. 1998). Confidence in accuracy is provided by the frequent visibility of entire wolf packs at a single location and time and making several complete counts during each winter survey.

Each January and February between 1995 and 2008, we observed the number of moose killed by wolves during a period of ~44 days (median 44 days, interquartile range= [38, 47] days). Sites where moose had been killed were detected from fixed-wing aircraft by direct observation and by following tracks left in the snow by wolf packs (Mech 1966; Peterson 1977). From these observations, we estimated the per capita kill rate as the number of kills divided by the pack size divided by the observation period.

During the winters between 1995 and 2008, we conducted necropsies for which we recorded observations relating to the degree of carcass utilization. We attempted to necropsy each wolf-killed moose detected during the winter aerial surveys. We never conducted a necropsy before first observing from the aircraft that the wolves had left the site. Weather and other logistical constraints prevented us from autopsying some carcasses until the summer following our winter surveys. These carcasses were not included in our analysis.

We were able to perform 293 autopsies within several days after each moose's death (median=7 days, interquartile range=[4, 13] days, range=[1, 41] days). We did not systematically record the time between a necropsy and the time that wolves first left the carcass. Below, we assess, and account for, the effect of time since death and utilization index.

Estimating carcass utilization

Assessing conditions that cause wolves to utilize more or less of moose carcasses requires measuring aspects of utilization that vary from carcass to carcass. For all the carcasses that we examined, wolves had eaten all organs within the thoracic and abdominal cavities. In most cases, wolves had also consumed more than approximately 90% of the soft tissue, not including the hide (see below).

Bone and hide represent approximately 25% of a moose's total body mass (Calder 1984). The small pieces of soft tissue that are close to and between bones, e.g., along the vertebral column and the lower legs, represent ~5% of a moose's total body mass. These are the portions of a carcass whose utilization varies greatly. Though bones are not easy to consume or digest, fresh bone and its marrow are, by composition, 15–20% protein and 15–20% fat (McCay 1949). A diet, comprised entirely of fresh bone alone, can sustain a wolf for a long time (Peterson and Ciucci 2003).

We documented substantial variation in carcass utilization by assessing: (1) the presence of certain bones, (2) the degree to which these bones were still articulated to one another, and (3) the amount of hair and hide still remaining or connected to certain bones. We searched for carcass remains by following wolf tracks in the snow that trace back to the kill site. We followed tracks up to approximately 150 m from the kill site. The degree of disarticulation and number of bones missing is an indication of the amount of time wolves spent consuming the bones and the smaller portions of soft tissue close to these bones. When wolves spend time in this way, they tend to scatter the bones far from the kill site, and these bones go undetected.

More precisely, we constructed an index of carcass utilization that entailed summing several values. These values are one point for each of the following bones which were present: skull, each mandible, each of the 12 largest limb bones, each scapula, and pelvis. We assigned half a point if we found half a pelvis or if approximately half of the skull had been consumed. One point is also assigned for each of these points of articulation: skull articulated to vertebral column, pelvis articulated to vertebral column, and if the rear legs were articulated to the carcass. A point was assigned if the bones of each leg were mostly articulated to each other, and another if the vertebral column was mostly intact. One point was also assigned if hide was present on the skull. Some fraction of a point was assigned to correspond to the proportion of hide remaining on the legs. Finally, an additional point was assigned if another hide was present.

The maximum number of points that could be assigned is 27. Because a carcass index is most intuitive when small values refer to relatively little utilization, we obtained a utilization index subtracting the number of points assigned to each carcass from 27. Next, we scaled the index to range between 0 and 1, by dividing the values by 27.

In general, carcasses that were least utilized had all bones present; these bones were articulated, and much hide was left. For somewhat more utilized carcasses, all the bones were present, but not the hide, and there was some disarticulation. The most utilized carcasses had no hide, little articulation, and some or many bones were missing.

Previous work provided a basis for understanding how the utilization index relates to the proportion of edible biomass consumed. In the winter of 1990, we weighed the carcass remains of 14 moose killed by wolves after they had finished feeding on the carcasses. Percent utilization was estimated by comparing the remains to mean weights for entire carcasses, excluding rumen contents, which are inedible for wolves and can represent 16% of a moose's mass. Mean weights for Isle Royale moose are 363 kg (adult males), 306 kg (adult females), and 134 kg (calves; Peterson 1977; Vucetich et al. 2004).

Visual inspection of the relationship between utilization index and proportion of edible biomass utilized by wolves suggests that the relationship would be well represented by either an exponential function or a second order polynomial. In fact, the exponential model explained 94% of the variation ($p<10^{-4}$), and the second-order polynomial explained 89% of the variation ($p<10^{-4}$). We converted values of utilization index into estimates of proportion of biomass utilized by using the weighted average of these two models (Fig. 1), where Aikaike weights ($w_{\text{exponential}}=0.84$; $w_{\text{polynomial}}=0.16$) were the weights assigned to each model (Burnham and Anderson 2010). For 15 (of 293) instances, the utilization index was between 0 and 0.02, outside the range of observed data in Fig. 1. Because the slope of this relationship (Fig. 1) is very steep for low values of the utilization index, the modeled value is likely an unreliable basis for estimating proportion of biomass consumed for such low values. Therefore, we set the proportion of edible biomass utilized for these observations equal to 0.70, which seemed appropriately lower than the next lowest
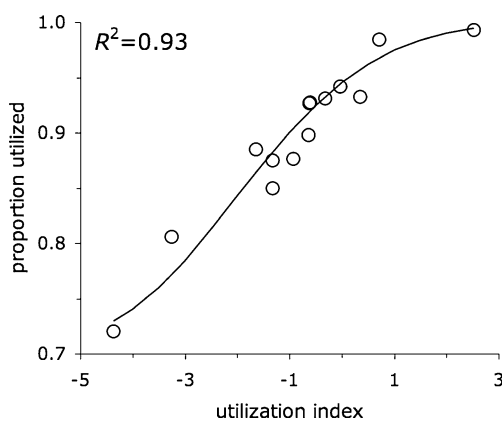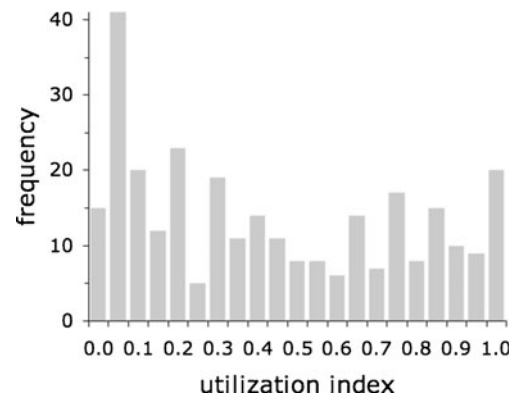

Fig. 2 The frequency distribution of 293 estimates of proportion of edible biomass consumed by wolves on Isle Royale feeding on moose carcasses

observed values (see Fig. 1 and note that these 15 observations are in the left-most column in Fig. 2).

Analysis and results

The cause of partial prey consumption

The median proportion of carcass utilized was 91%; the interquartile range was [0.84, 0.96]; and the 10th and 90th percentiles were 0.73 and 0.98 (Fig. 1). Of the 29 observations below the 10th percentile, 21 occurred during winter 1996, the most severe in this region for more than a century. Moose density in 1996 was also the highest ever documented in 50 years. During this winter, moose abundance declined by ~80%.

The degree of carcass utilization did not vary with the number of days between the moose's death and the necropsy ($R^2=0.01$; $P=0.06$), and the mean number of days between moose death and necropsy did not vary among years ($p=0.20$). Therefore, patterns of carcass utilization are not an artifact of variation in the time elapsed between prey death and necropsy.

Mean proportions of carcass utilization declined with increasing kill rate (Fig. 3a, $P=0.02$, $R^2=0.40$). Moreover, for 237 carcasses, we were able to assess both the degree of utilization and d, the number of days that had passed since the pack which had killed the moose had made their next previous kill. Degree of utilization was not well correlated with d ($P=0.12$, $R^2=0.01$; Fig. 4). These two relationships (Figs. 3a and 4) suggest that PPC is the result of an optimal foraging strategy.

Because wolves are group foragers, it is valuable to know that results in Figs. 3a and 4 are not affected by accounting for pack size. Specifically, carcass utilization was correlated with pack size for the 293 observations depicted in Fig. 4 ($P<0.01$). More importantly, however, d
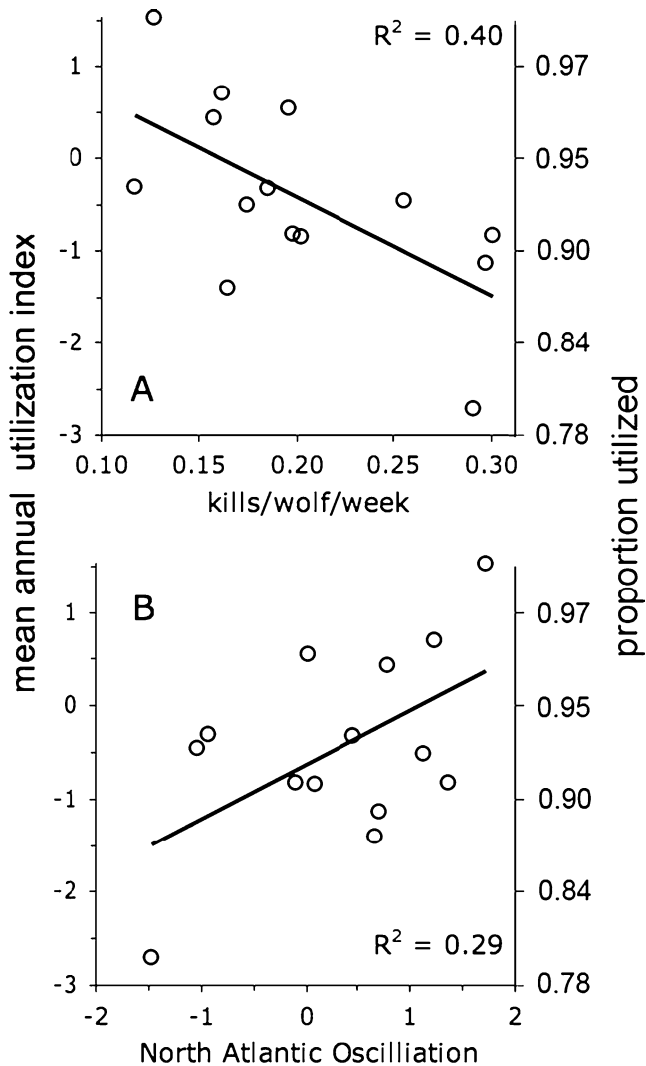

Fig. 1 The relationship between utilization index and proportion of edible biomass consumed by wolves feeding on moose carcasses on Isle Royale. The *curve* represents the weighted average between an exponential model ($R^2=0.94$) and a second-order polynomial ($R^2=0.89$). This relationship is the basis for converting 293 other observed values of utilization index into estimates of proportion of edible biomass consumed

Fig. 4 The number of days since the previous kill (*d*) in relationship to the proportion of edible biomass consumed by wolves feeding on moose carcasses (p=0.12, R^2=0.01)

Fig. 3 **a**, **b** Mean proportion of edible biomass consumed by wolves feeding on moose carcasses in relationship to kill rate and the North Atlantic Oscillation, an index of winter severity. In each *panel*, the 14 *open circles* correspond to observations from Isle Royale for each winter between 1995 and 2008. The *filled circle* in (**a**) is an observation from Scandinavian wolves (Sand *et al.* 2005; see also the "Discussion"). The R^2 value in the *upper panel* refers only to the Isle Royale data. The *solid lines* are best-fitting linear models for the Isle Royale data. The *dotted line* is the best-fitting linear model when the Scandinavian observation is included. Severe winters are indicated by low values of the North Atlantic Oscillation

was unrelated to utilization (P=0.12) when included in a multiple regression model with pack size. Also, mean proportions of carcass utilization (Fig 3a) were not related to average annual pack size (P=0.55).

That PPC might be an optimal foraging strategy is premised, in part, on the idea that in some instances, capturing a new prey is more profitable than completely consuming an already captured prey item. While prey density and kill rate are useful indices of how easy it is to find and kill another prey (Vucetich *et al.* 2002), winter
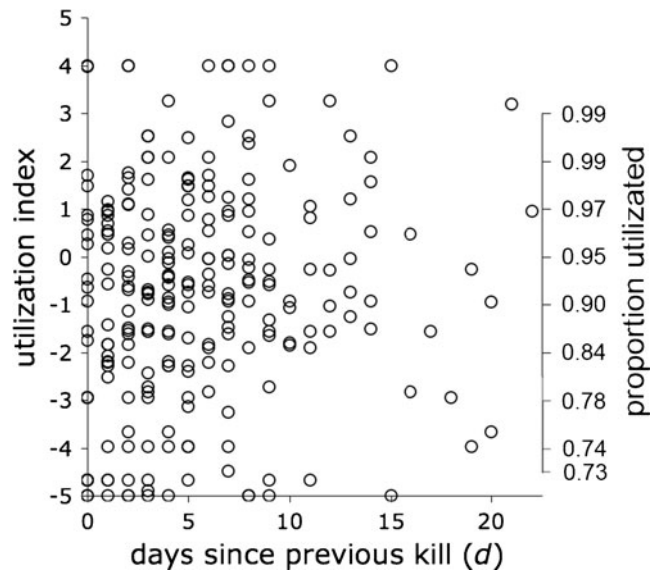
severity can also affect the vulnerability of prey. An important index of winter severity for ungulate population dynamics is the North Atlantic Oscillation (NAO) (Vucetich and Peterson 2004a, b). As would be predicted by the optimal foraging hypothesis, carcass utilization also increased with increasing NAO, i.e., decreasing winter severity (Fig. 3b, P=0.05, R^2= 0.29). Using multiple linear regression, we found that kill rate and NAO together explained 54% of the variation in carcass utilization.

Population dynamics

The expected relationship between winter kill rate in year t (kr_t) and wolf population growth rate (r_t) is characterized reasonably well by a log-linear relationship (p<0.01, R^2=0.19; solid line in Fig. 5). To compare this kr_t–r_t relationship (the numerical response) to the relationship between consumption rate (cr_t) and r_t, we regressed estimates of r_t onto estimates of cr_t, where cr_t is the kill rate multiplied by the mean consumption rate (cu_t), given the kill rate (i.e., the expected relationship in Fig. 3a, which is cu_t=0.984−0.413kr_t). Compared to the stochasticity in the numerical response, the expected kr_t–r_t relationship differs trivially from the cr_t–r_t relationship (dashed line in Fig. 5).

Some managers and stakeholders are concerned that relatively high rates of PPC are an indication that wolves have a particularly large impact on prey populations. The most useful indicator of predation's impact on ungulate populations is the predation rate (proportion of prey killed by predators; Vucetich *et al.* 2011). Using predation rate data from Vucetich *et al.* (2011), we found no association
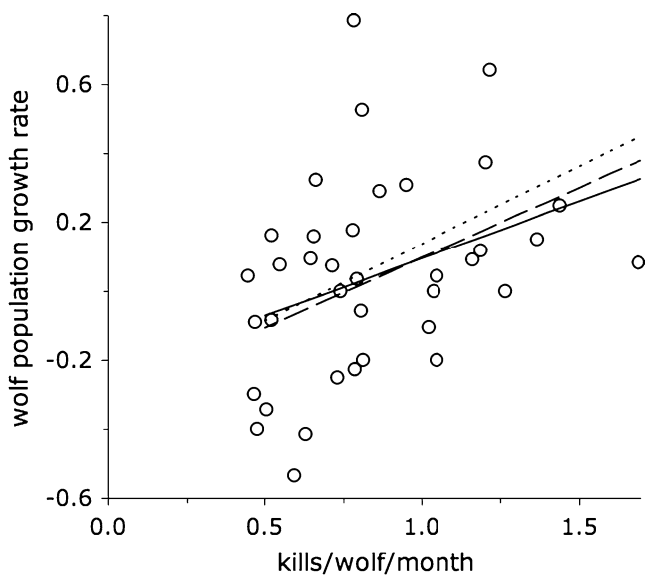
Fig. 5 The relationship between per capita kill rate and wolf population growth rate for Isle Royale wolves, 1971–2010. The *solid curve* is the best-fitting log-linear regression model. The *dashed line* represents the relationship between consumption rate and predator population growth rate, where consumption rate is a function of kill rate and degree of carcass utilization. See "Population dynamics" for details

between naturally occurring variation in carcass utilization and predation rate ($p=0.32$).

Discussion

Wolves consume, on average, smaller portions of captured prey during winters characterized by higher kill rates (Fig. 3a). However, the extent to which an individual carcass is utilized is not importantly associated with time since the previous kill (Fig. 4). These patterns are consistent with the hypothesis that PPC is driven by adaptive behaviors that maximize foraging efficiency, and inconsistent with hypotheses that PPC is merely the result of limitations in gut capacity or rates of digestion (Lucas and Grafen 1985). Moreover, assuming that wolves are not typically satiated (see "The study system"), then the kill rate/utilization relationship (Fig. 3a) is sufficient to conclude that PPC by wolves is driven primarily by the fitness value of maximizing foraging efficiency.

This result is significant because few studies have offered strong tests for the cause of PPC. Specifically, PPC is thought to have been caused by limits in the rate of digestion for a study on wolf spiders (Samu 1993), by foraging efficiency for a study of antlions (Lucas 1985), and probably by foraging efficiency for another species of spider (Maupin and Riechert 2001). Our results represent the first strong test for a species that is not an ambush predator that employs extra-intestinal digestion.

Wolves consume greater proportions of prey carcasses during milder winters (Fig. 3b). Although kill rates are somewhat lower during milder winters (Post *et al.* 1999), the pattern we observed is independent of the kill rate. During milder winters, ungulate prey are less confined to thick conifer stands where snow cover is less. Consequently, wolves likely spend more energy traveling to find prey. Ungulate prey also tend to be in better physical condition during milder winters, so that wolves likely spend more energy trying to kill prey once they have been found. The tendency for increased utilization during mild winters (Fig. 3b) may be associated with increased energetic costs of finding and killing prey.

While wolves are consuming a carcass, ravens (*Corvus corax*; and foxes (*Vulpes vulpes*), to a lesser extent) also utilize the carcass. Two considerations relieve concern that scavenger utilization confounds the conclusion that PPC maximizes foraging. First, our estimates of carcass utilization were based on behaviors that wolves exhibit, but ravens and foxes do not. For example, ravens and foxes do not disarticulate vertebrae, remove large bones from the site of a kill, or consume significant portions of frozen hide. Second, previous work indicates that scavenging decreases with increasing pack size (Vucetich *et al.* 2004). Insomuch as pack size reflects scavenger utilization, it is relevant that the central results of this analysis account for the influence of pack size: (1) pack size was not associated with mean annual carcass utilization, and (2) the conclusion that utilization is unaffected by time since previous kill (Fig. 4) is based on an analysis that accounts for the effect of pack size.

Generality

With the overall mean proportion of carcass utilization being 0.90, one might wonder: *Does this high rate of carcass utilization even count as PPC?* While carcass utilization is high, we documented significant co-variation between utilization and kill rate (Fig. 3a). That covariation means that wolves on Isle Royale are regularly not consuming all that they can from prey carcasses. Partial prey consumption seems an apt description for that behavior.

The high degree of carcass utilization observed on Isle Royale raises the question of whether these patterns of carcass utilization are relevant for understanding systems where carcass utilization may be substantially lower. For Scandinavian wolves preying on moose, the rate of carcass utilization was only about 70% (Sand *et al.* 2005). However, kill rates by Scandinavian wolves are also substantially higher (Sand *et al.* 2005). Higher kill rate among Scandinavian wolves can be explained by a higher ratio of moose to wolves (Sand *et al.* unpublished data).

Moreover, the kill rate and carcass utilization of Scandinavian wolves matches almost exactly what would be expected if the kill rate/carcass utilization relationship on Isle Royale were extended to account for the higher kill rates observed in Scandinavia (Fig. 3a).

Whereas Isle Royale wolves do not risk being killed by humans, wolves in most populations face a non-trivial risk of being legally harvested or poached by humans. This risk may reduce carcass utilization by causing wolves to abandon carcasses upon being discovered by humans. The frequency of such behavior is unknown. If such behavior is frequent, human persecution would be important in causing wolves to forage in an energetically inefficient manner. It also remains unknown whether premature carcass abandonment would cause wolves to kill more frequently.

Surplus killing

The persistent documentation of what wolf biologists call "surplus killing" seems to reflect a fascination with the phenomenon (Pimlott et al. 1969; Mech and Frenzel 1971; Kruuk 1972; Peterson and Allen 1974; Bjärvall and Nilson 1976; Eide and Ballard 1982; Carbyn 1983; Miller et al. 1985; DelGiudice 1998). This fascination may have been inherited from some of the earliest wolf research, which was influenced by folklore as well as reliable observation about wolf predation on wild prey (e.g., Young and Goldman 1944). For wolves, the phenomenon entails extremely high kill rates (usually over several days to a couple of weeks) and extremely low utilization of the resulting carcasses. In some cases, carcasses are not utilized at all. When subsequent observations are made, which is often not the case, these carcasses are found to be more thoroughly utilized in the days and weeks that follow such events (Mech et al. 1998; Krebs et al. 2001; Mech and Peterson 2003; Vucetich and Peterson, unpublished observations of wolf-killed deer carcasses in upper Michigan).

When "surplus killing" is reported, it is often during late winter or on calving grounds—situations where vulnerable prey are especially abundant. For example, Miller et al. (1985) reported wolves killing 34 caribou (Rangifer tarandus) calves within the span of a few minutes. After 24 h, wolves had consumed nothing on about half of the calves and only small portions of the other half. Those authors attributed the behavior to the calves being especially abundant and easy to kill.

"Surplus killing" certainly involves substantially lower carcass utilization than what we observed on Isle Royale. However, the basic pattern is the same: carcass utilization is higher when kill rates are higher (Fig. 3a) and when prey are more vulnerable (Fig. 3b). This pattern suggests that "surplus killing" may well represent an extreme and fleeting manifestation of wolves foraging optimally in an environment where vulnerable prey are unusually abundant. Because "surplus killing" is a relatively rare event, rarely lasting more than a few weeks, it is far from obvious that such a rare event would have an important influence on mean annual carcass utilization or mean annual kill rates of an entire wolf population.

Conservation implications

While PPC is an important behavioral phenomenon, we were unable to detect any important consequences of PPC for population-level interactions between the predator and the prey (see "Population dynamics"). These findings (and other considerations described above in "Surplus killing") offer a basis for allaying the concerns that PPC represents evidence of wolf predation's impact on prey populations.

PPC is hardly a distinctive wolf behavior. Rather, PPC appears to be an optimal foraging strategy in many organisms (see "Introduction"). PPC even appears to be an adaptive behavior shared by both wolves and humans (Rathje 1984; Gillisa et al. 1995). Despite the apparently generic nature of this behavior, ecologists more commonly use terms like "surplus killing" and "excessive killing" to describe PPC when it is exhibited by predators that consume prey that humans also like to consume, especially ungulates. Phrases like surplus killing and excessive killing—which connote wastefulness, gluttony, and wantonness—are poor metaphors for the phenomenon they aim to describe because PPC probably represents an optimal foraging strategy shaped by natural selection. In addition to being poor descriptions, these terms also underlie some hatred and persecution of wolves by humans.

One of the greatest threats to wolf conservation is the negative attitudes that many humans hold against wolves (Boitani 2003), and our attitudes about nature and conservation can be importantly influenced by the words we choose in describing nature (Chew and Laubichler 2003). It may be wise to refrain from using the terms surplus killing and excessive killing to describe partial prey consumption in wolves.

Ethical Standards   This work complies with the current Michigan Technological University Institutional Animal Care and Use Committee guidelines, which are guided by the US federal regulations and ethical principles, intended to ensure the humane care and use of animals in research.

Conflict of Interest Statement   The authors declare that they have no conflict of interest.

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