

Predicting prey population dynamics from kill rate, predation rate and predator–prey ratios in three wolf-ungulate systems

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Summary

1. Predation rate (PR) and kill rate are both fundamental statistics for understanding predation. However, relatively little is known about how these statistics relate to one another and how they relate to prey population dynamics. We assess these relationships across three systems where wolf–prey dynamics have been observed for 41 years (Isle Royale), 19 years (Banff) and 12 years (Yellowstone).

2. To provide context for this empirical assessment, we developed theoretical predictions of the relationship between kill rate and PR under a broad range of predator–prey models including predator-dependent, ratio-dependent and Lotka–Volterra dynamics.

3. The theoretical predictions indicate that kill rate can be related to PR in a variety of diverse ways (e.g. positive, negative, unrelated) that depend on the nature of predator–prey dynamics (e.g. structure of the functional response). These simulations also suggested that the ratio of predator-to-prey is a good predictor of prey growth rate. That result motivated us to assess the empirical relationship between the ratio and prey growth rate for each of the three study sites.

4. The empirical relationships indicate that PR is not well predicted by kill rate, but is better predicted by the ratio of predator-to-prey. Kill rate is also a poor predictor of prey growth rate. However, PR and ratio of predator-to-prey each explained significant portions of variation in prey growth rate for two of the three study sites.

5. Our analyses offer two general insights. First, Isle Royale, Banff and Yellowstone are similar inasmuch as they all include wolves preying on large ungulates. However, they also differ in species diversity of predator and prey communities, exploitation by humans and the role of dispersal. Even with the benefit of our analysis, it remains difficult to judge whether to be more impressed by the similarities or differences. This difficulty nicely illustrates a fundamental property of ecological communities. Second, kill rate is the primary statistic for many traditional models of predation. However, our work suggests that kill rate and PR are similarly important for understanding why predation is such a complex process.

Keywords: functional response, numerical response, predation rate, predator–prey, regulation

Introduction

Predation and other consumer–resource relationships are among the most fundamental of all ecological relationships and have been the focus of ecology since its inception. The population biology of predation is comprised of two basic elements: the kill rate and the predation rate (PR) (Holling 1959; Taylor 1984). Kill rate (KR) is the number of prey

killed per predator per unit time and represents the predator's supply of food. In this sense, kill rate is the predator population's perspective of predation. Predation rate is the proportion of the prey population killed by predation and represents the pressure of predation on the prey population. In this sense, PR is the prey population's perspective of predation. Understanding predation dynamics requires understanding the predator's rate of food acquisition (KR) and the mortality rate of prey that arises from predation (PR). Despite the fundamental role that KR and PR each

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play, KR seems to receive more attention (Dale, Adams & Bowyer 1994; Bergstrom & Englund 2004; Nilsen *et al.* 2009). Some studies highlight the difficulties of understanding predation dynamics from assessments that focus on KR and neglect PR (Marshall & Boutin 1999; Jost *et al.* 2005).

The tendency to focus on KR may have arisen largely from the tradition, established by seminal ecologists, to express predator–prey models in terms of per capita kill rate (Lotka 1925; Volterra 1926; Holling 1959; Rosenzweig & MacArthur 1963). That is, prey dynamics are assumed to arise largely from the processes that determine kill rate (i.e. the functional response), and predator dynamics are largely considered some function of the kill rate (i.e. the numerical response (NR), by which we mean the relationship between KR and predator growth [see May 1981; Bayliss & Choquenot 2002]:

$$dN/dt = f(N) - kr(\bullet) \times P \quad \text{eqn 1a}$$

$$dP/dt = g(kr(\bullet)) \times P, \quad \text{eqn 1b}$$

where $f(N)$ is some function of prey density and possibly other arguments that represent prey growth in the absence of predation, $kr(\bullet)$ is some function that represents the kill rate, and $g(\bullet)$ is the NR, a function whose arguments include the kill rate, and P is predator abundance. In this way, kill rate, especially its relationship to the functional and NR, is conventionally considered the primary determinant of predator–prey dynamics. This convention is likely responsible for apparent confidence about the extent to which empirical assessments of the functional and NRs can, by themselves, explain predator–prey dynamics (e.g. Messier 1994). The appropriateness of treating KR as the fundamental process of predation is further supported inasmuch as PR may be expressed in terms of KR. Specifically, $PR = (KR \times P)/N$, where P is the total number of predators and N is the total number of prey. This seemingly simple relationship between KR and PR obfuscates what is in reality a far more complex relationship between the two processes.

Here, we first review theoretical models to show how the relationship between KR and PR depends on the nature of predator–prey dynamics, for example, whether dynamics are more influenced by top-down or bottom-up processes. These theoretical results give reason to think KR is a poor predictor of PR. We then test the theoretical predictions with empirical observations from three North American study sites – Isle Royale National Park (IRNP), Yellowstone National Park (YNP) and Banff National Park (BNP) – where long-term observations have been made on wolf (*Canis lupus*) and ungulate dynamics.

For many real populations, estimates of KR or PR are unavailable, but estimates for the ratio of predator-to-prey are available. While this ratio is sometimes considered a useful indicator of predation's effect on prey population dynamics (Eberhardt 1997), these ratios have been criticized as misleading indicators of predation (Theberge 1990; Abrams 1993; Person, Bowyer & Van Ballenberghe 2005). Here, we show how, for our study sites, these ratios are reasonably good indicators of PR and prey growth rate.

Materials and methods

STUDY AREAS

Isle Royale National Park (48°00'N, 89°00'W) is an island (544 km²) in North America's Lake Superior, covered by transition boreal forest (*Abies balsamea*, *Picea glauca*, *Betula spp.*) with relatively little variation in elevation (200–400 m). The Bow Valley of Banff National Park (BNP) is a Montane area (1801 km²) on the eastern slope of the extreme topography (1400 to 3400 m) of the Canadian Rocky Mountains (51°15'N, 116°30'W), with densely forested highlands (*Pinus contorta*, *Picea engelmannii*) and interspersed grassy and shrubby meadows amongst forested (*Pinus*, *Picea*, *Populus tremuloides*) Montane valleys. The Northern Range of YNP is also a montane area (1531 km²) located in the central Rocky Mountains (44°50'N, 110°30'W), with forested highlands (*Pseudotsuga menziesii*, *Pinus contorta*, *Picea engelmannii*), grass-covered valleys and elevations ranging from 1500 to 2200 m.

Each study site has been the focus of long-term research on wolves (*Canis lupus*), and their prey and additional details can be found elsewhere (Hebblewhite, Pletscher & Paquet 2002; Vucetich, Peterson & Schaefer 2002; Smith *et al.* 2004). The wolves of IRNP prey on moose (*Alces alces*), which interact essentially as an isolated single predator–single prey system (Peterson *et al.* 1998). These wolves are the only moose predator, moose comprise more than 90% of the biomass in wolf diet (Peterson & Page 1988), and the remainder of the diet is comprised of beaver (*Castor canadensis*). Although YNP and BNP are both multi-prey systems, elk comprise approximately 90% of wolf diet in YNP and approximately 50% of the wolf diet in BNP (Hebblewhite *et al.* 2004; Smith *et al.* 2004). Adult elk are about 80% the body size of moose (114, 261, and 330 kg for calf, cow and bull moose in winter; 113, 223, and 262 kg for calf, cow and bull elk). Also, elk are social-living ungulates, and moose on IRNP are solitary. The remainder of wolf diet for these study sites is largely comprised of bison (*Bison bison*; YNP), white-tailed deer (*Odocoileus virginianus*), moose, mule deer (*O. hemionus*), bighorn sheep (*Ovis canadensis*) and mountain goat (*Oreamnos americanus*). YNP and BNP are also multi-predator systems, where important causes of elk death include cougars (*Felis concolor*), coyotes (*Canis latrans*), grizzly bears (*Ursus arctos*) and black bears (*Ursus americanus*).

On IRNP, humans do not hunt moose or wolves. In BNP, humans are an important cause of death for elk and wolves. In YNP, humans are an important cause of death for elk (Vucetich & Peterson 2004), and a minor cause of death for wolves. Comparatively, wolf and prey densities were greatest in YNP (27–48 wolves per 1000 km², 5–8 elk/km², 1150–1760 kg of elk km⁻²), intermediate in IRNP (32–51 wolves per 1000 km², 1.4–2.4 moose km⁻², 380–650 kg of moose per km² [ranges are interquartile ranges]) and lowest in BNP (6–11 wolves per 1000 km², 0.4–1.4 elk km⁻², 42–355 kg of elk km⁻²).

All three systems are characterized by cold, snowy winters and warm summers that are moist (IRNP) or dry (BNP, YNP). Moreover, interannual climatic variation has an important influence on the wolf–prey dynamics of all three systems (Vucetich & Peterson 2004; Hebblewhite 2005; Vucetich, Smith & Stahler 2005).

THEORETICAL PREDICTIONS

To provide context for understanding empirical relationships described below, we first investigate how theoretical relationships between KR and PR depend on the underlying predator–prey model, drawing from the most commonly used models in the literature. First, we considered a set of models for which predator dynamics

depend largely on bottom-up processes. That is, for each model, predator abundance is a function of prey abundance (Boyce 2000):

$$dN/dt=f(\bullet) - KR \times P \quad \text{eqn 2a}$$

$$P=g(N), \quad \text{eqn 2b}$$

where $f(\bullet)$ is any function describing the prey's relationship with its forage, KR is the per capita kill rate, and $g(N)$ is the NR, a function of N describing the relationship between N and P . The relationship between KR and PR depends on the nature of the KR and $g(N)$, but is independent of $f(\bullet)$. For example, consider the case for a linear, prey-dependent functional response ($KR = aN$) and a linear NR $P = (\alpha_0 + \alpha_1 N)$, where a and the α s are coefficients that relate N to KR and P . To understand how KR and PR are related, begin with $PR = KR \times P/N$, which is true for any predator-prey model. Into this equation replace model-specific expressions for KR and P and perform algebraic manipulations until the relationship between KR and PR is clear. Specifically, replacing KR with aN and P with $(\alpha_0 + \alpha_1 N)$ yields $PR = aN \times (\alpha_0 + \alpha_1 N)/N$ which reduces to $PR = a(\alpha_0 + \alpha_1 N)$. Because PR and KR each increase linearly with N , it is the case that PR increases linearly with increasing KR (line 1 in Fig. 1a). The same result occurs if the functional response depends asymptotically on prey density (see Supporting Information).

The KR - PR relationship differs, however, when the NR is nonlinear or if the functional response is ratio dependent. Each circumstance is shown in Fig. 1a and demonstrated in the Supporting Information using similar algebraic techniques to those described above. Specifically, the KR - PR relationship is asymptotic when the NR is linear and the functional response is a linear function of prey density (Fig. 1a, line 2). The KR - PR relationship is unimodal when the NR is asymptotic and the functional response is an asymptotic function of prey density (Fig. 1a, line 3). PR is independent of KR when the functional response is a linear function of the ratio of prey to predator (Fig. 1a, line 4). Finally, the KR - PR relationship is negative for dynamics characterized by an asymptotic, ratio-dependent functional response (Fig. 1a, line 5).

We also considered three more complex models of predator-prey dynamics, where top-down processes are stronger (Ginzburg 1998):

$$dN/dt=f(\bullet) - KR \times P \quad \text{eqn 3a}$$

$$dP/dt= KR \times cP - mP, \quad \text{eqn 3b}$$

where c is a conversion coefficient and m is the mortality rate of predators in the absence of prey. We assessed the relationship between KR and PR directly from numerical solutions obtained with Excel and the Runge-Kutta method. We assessed a form of eqn 3 that represents classic Lotka-Volterra dynamics (Lotka 1925; Volterra 1926), where $f(\bullet) = rN$ and $KR = aN$. In this case, KR and PR are related to each other approximately as a circle (Fig. 1b, line 6). We also assessed a more stable form of eqn 3 where prey growth is density dependent, $f(\bullet) = r(1 - N/K)N$, and the functional response is prey-dependent and asymptotic, $KR = b_0 N/(b_1 + N)$. In this case, KR and PR spiral around the KR - PR plane as it settles towards its equilibrium value (Fig. 1b, line 7). Generally, KR and PR will cycle out of phase, for any set of equations where the populations cycle out of phase (e.g., Fig. 1b). Finally, we assessed eqn 3 for the case where prey growth is density-dependent growth and the functional response is ratio-dependent, $f(\bullet) = r(1 - N/K)N$ and $KR = b_0 N/(P + b_1 N)$. In this case, PR decreases with increasing KR (Fig. 1b, line 8).

Finally, we considered a set of models that include environmental stochasticity. We selected a model structure whose salient features

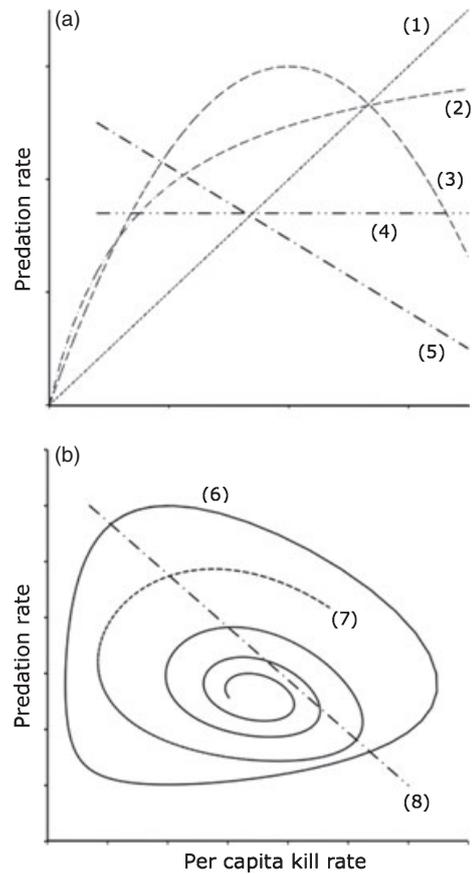


Fig. 1. The relationship between kill rate (kills/predator/unit time) and predation rate (proportion of prey killed by predation per unit time) depends on the structure of the predator-prey model and the nature of the numerical response (NR) and functional response (FR). Panel (a) represents models where predator density is a function of prey abundance, and Panel (b) represents models where predator growth rate is a function of prey abundance. The various curves are characterized by a linear NR and prey-dependent FR (1), an asymptotic NR and a linear, prey-dependent FR (2), an asymptotic NR and asymptotic, prey-dependent FR (3), a linear, ratio-dependent FR (4), an asymptotic, ratio-dependent FR (5), classic Lotka-Volterra dynamics (6), an asymptotic, prey-dependent FR and density-dependent prey growth (7), and an asymptotic, ratio-dependent FR and density-dependent prey growth (8). These models are further specified in *Theoretical Patterns*. The P -values for each relationship are < 0.01 , except where noted.

were general, inasmuch as they include a functional response, NR and density-dependent prey growth:

$$r_{i,\text{prey}} = [r_{\text{int}} N_i (1 - (N_i/K)^\theta) - ((KR_i + e_1) \times P_i)/N_i] + e_2 \quad \text{eqn 4a}$$

$$r_{i,\text{predator}} = [a_1 \ln(KR_i + e_1) - a_2] + e_3, \quad \text{eqn 4b}$$

where r_{int} is the intrinsic growth rate of the prey population, K is the carrying capacity, θ is a coefficient describing nonlinearity in density dependence (Gilpin & Ayala 1973), the a s are coefficients relating kill rate to growth rate in the predator population, and the e s are normally distributed error terms with a mean of zero and standard deviation of s_1 , s_2 and s_3 , respectively. The form of the eqns 4 – i.e. theta-logistic density dependence and a nonlinear NR – is justified by both theoretical (Ginzburg 1998) and empirical considerations (Eberhardt & Peterson 1998; Vucetich & Peterson 2004). To obtain realis-

tic results, we parameterized eqns 4 using data from IRNP, which has the most information related to this model structure (see Supporting Information for details).

We ran eight sets of simulations based on eqn 4. The sets of simulations represented various combinations of the two kinds of functional response (i.e. Type II prey dependent and Type II ratio dependent), two values of θ (i.e. 1 and 4) and two variance structures (i.e. where the functional response is a relatively strong source of stochasticity and where it is a weak source of stochasticity). Although IRNP system is better characterized by a ratio-dependent functional response (Vucetich, Peterson & Schaefer 2002), prey-dependent functional responses are still important to consider (Abrams & Ginzburg 2000). Similarly, while $\theta = 4$ corresponds to nonlinear density dependence that characterizes ungulates (Eberhardt & Peterson 1998), $\theta = 1$ is also important to consider because it represents linear density dependence. To make the functional response a relatively strong source of stochasticity, we increased s_1 relative to s_2 and s_3 . Additional details regarding other parameter values are described in the Supporting Information. For each set of simulations, we observed several correlations among predation-related statistics for 1000 simulated populations. Each population was represented by time series that were 25 years in length.

For these simulations, the correlation between kill rate and PR depended importantly on the form of the functional response and on whether the functional response was an important source of stochasticity. Specifically, kill rate exhibited (Fig. 2a): (i) strong, positive correlations with PR when the functional response is a weak source of stochasticity, (ii) weak, negative correlations with PR when the functional response is prey-dependent and a strong source of stochasticity and (iii) strong, negative correlations with PR when the functional

response is ratio-dependent and a strong source of stochasticity. We could continue to test this model with other parameter settings, or entirely different predation models. Doing so, however, would most likely not change the salient observation: theoretical models provide reason to think that KR will be well correlated with PR on some occasions and not on other occasions. KR is, consequently, an unreliable predictor of PR and prey growth rate (Figs 1 and 2).

The simulations also indicated that the kill rate and prey growth rate tended to exhibit weak, negative correlations that were not statistically significant (Fig. 2b). However, the simulated predator-to-prey ratio exhibited a strong positive correlation with PR (Fig. 2c), and a moderately, strong negative correlation with prey growth rate (Fig. 2d). These simulated relationships indicate the value of assessing empirical relationships between wolf-to-prey ratio and prey growth rate.

EMPIRICAL RELATIONSHIPS BETWEEN KILL RATE AND PREDATION RATE

Given these predictions about the nature of the relationship between kill rate and PR under different predator-prey models, we next tested predictions by comparing empirical relationships from IRNP, BNP and YNP. The empirical data are estimates of per capita kill rate (KR_t , whose units are kills per wolf per unit time), wolf abundance (P_t) and prey abundance (N_t) for a 41-year period from IRNP (1971–2011), 11 years during a 12-year period from YNP (1997–2008) and 17 years during a 19-year period from BNP (1986–2005). From these data, we also calculated prey growth rate as $r_t = (N_{t+1} - N_t)/N_t$ and predator growth rate as $PR_t = (KR_t \times P_t)/N_t$. Although the estimates of KR_t , P_t and N_t used here have all been published elsewhere (BNP: Hebblewhite, Pletscher & Paquet 2002; YNP: Smith

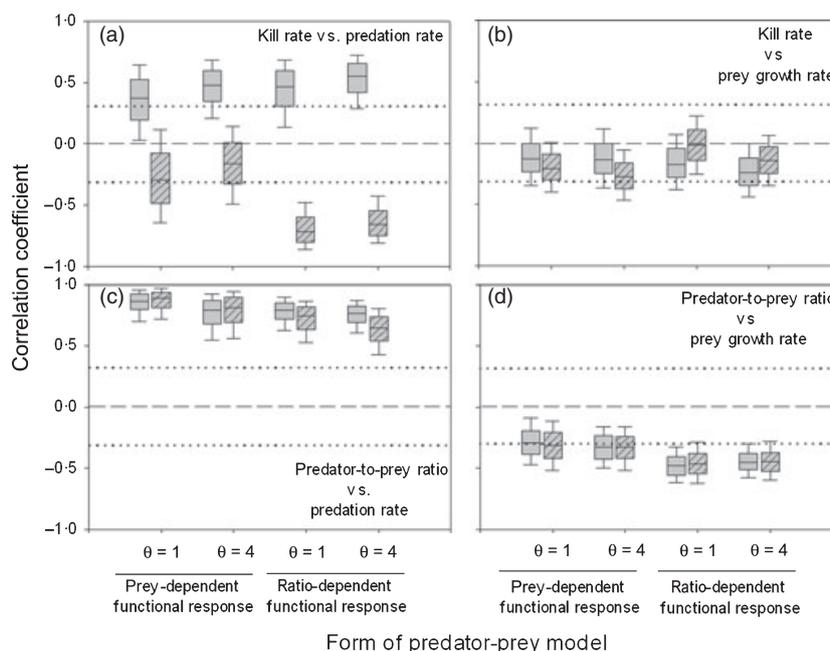


Fig. 2. The distribution of correlation coefficients between various population parameters for 1000 simulated predator-prey systems (eqn 4), each represented by time series with 25 consecutive, annual observations. Each panel describes the correlation between a different pair of parameters. Each pair of bars (hatched and unhatched) within each panel corresponds to a predator-prey model with prey growth that is either linearly ($\theta = 1$) or nonlinearly ($\theta = 4$) density dependent, and with either a ratio-dependent or prey-dependent functional response. Unhatched bars represent simulations where the functional response is a relatively minor source of stochasticity, and hatched bars represent simulations where the functional response is an important source of stochasticity. The lines within the boxes are medians, the boxes indicate the interquartile range, and the whiskers indicate the 10th and 90th percentiles. The dashed lines represent a correlation coefficient of zero, and the dotted lines represent the values of coefficient that are statistically significant at the critical value of 0.05.

et al. 2004; Vucetich, Smith & Stahler 2005; IRNP: Vucetich, Peterson & Schaefer 2002), we briefly review these methods in the next sections. The regression models that we built were evaluated on the basis of P -values, R^2 , and Akaike Information Criterion (AIC_C).

Isle Royale

We counted the entire wolf population annually from a fixed-wing aircraft each January and February (Peterson *et al.* 1998). Confidence in census accuracy was provided by the frequent visibility of entire wolf packs at a single location and time, and by making several complete counts during each winter survey. Moose abundance was estimated annually from 1997 to 2011 by aerial survey and a stratified design that involves counting moose on ninety-one, 1-km² plots from fixed-wing aircraft (Peterson & Page 1988). From 1971 to 1996, moose abundance was estimated by a method of cohort analysis that is similar to that described by Solberg *et al.* (1999). Each January and February between 1971 and 2011, 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).

Yellowstone

Wolf abundance and kill rates in YNP were estimated by methods similar to those used in IRNP. In YNP, wolf abundance was estimated between mid-November and mid-December (Smith *et al.* 2004). Counts are based on frequent aerial observations during this period (> 10 observations/pack) and almost daily counts (> 20 observations per pack) from ground-based observations. Kill rates were estimated each winter from approximately 60 days of observation during two periods, mid-November through mid-December and during March (Smith *et al.* 2004). During these periods, each pack was located, with the aid of radio telemetry, by either aerial observation or ground-based observers. We estimated the number of kills during the observation period as those observed from the air or ground. Annual estimates of elk abundance are based on observations of four fixed-wing planes flying over different portions of the elk range on the same day. Flights were typically conducted in early winter (mid-December). See Lemke, Mack & Houston (1998), for additional details.

Banff

We estimated wolf kill rates, wolf abundance and prey abundance starting in 1986 when wolves recolonized the Bow Valley of BNP (Hebblewhite, Pletscher & Paquet 2002). Wolves were intensively studied via radiotelemetry after capturing and radiocollaring 1–4 wolves per year with VHF or, more recently, with GPS radiocollars in the Bow Valley wolf pack; wolves were captured using foot-hold trapping, aerial darting or net gunning (Hebblewhite *et al.* 2004). Collared wolves were used to study predation by the entire Bow Valley wolf pack. Winter (Nov 1 to April 30) wolf kill rates were estimated using a ratio-estimator developed from snow backtracking wolves over continuous periods of time, on average, 7-days in length (Hebblewhite *et al.* 2004). On average, 31% of each winter was continuously estimated, and kill rates averaged 0.33 kills day⁻¹ per pack, and 0.23 elk day⁻¹ per pack. We determined annual wolf abundance in the Bow Valley using a combination of ground tracking, aerial telemetry and observations to record maximum pack size. Elk abun-

dance was determined by Parks Canada biologists using aerial helicopter surveys in late winter through low elevation winter range. Surveys were conducted along systematic survey routes at 80–120 m above ground level in early morning by trained observers. Aerial counts were adjusted for an average 11% sightability bias using a sightability model developed in BNP (Hebblewhite 2000). See Hebblewhite *et al.* (2004) and Hebblewhite, Pletscher & Paquet (2002) for more details.

Annual predation rates

For all three sites, we estimated PR for sampled periods during winter. These estimates represent the proportion of prey killed for each period of observation. Estimating the annual predation from winter PRs requires understanding and accounting for how PRs tend to fluctuate seasonally. The most general evidence suggests per capita wolf kill rates of recruited prey (i.e. moose > 6 months of age) during non-winter periods (May–October) are 71% of those observed during winter months (Messier 1994). Because more specific data from YNP suggest that this conversion factor is appropriate for wolf-elk systems (see Supporting Information), we used it to estimate annual PRs from the winter PRs observed for BNP and YNP. More specific information suggests a conversion factor of 50% for IRNP (see Supporting Information). The purpose of converting seasonal PRs to annual PRs is to foster a basis for visually comparing graphs that depict PR for each of the study sites (see Figs 3 and 4) and to offer an approximate sense of what total annual wolf PR may be.

It is critical to understand that these conversions factors do not affect the inferences we make in this paper, which entail comparing the ability of KR to predict PR among the study sites. More precisely, our inferences are not confounded by the use of any scaling factor because the correlation between KR and PR is identical to the correlation between KR and PR $\times X$, where X is a scaling constant.

Results

The purpose of the theoretical models is to provide a basis for anticipating and interpreting empirical relationships between KR and PR. Kill rate was a poor predictor of PR for all three study sites (Fig. 3a,b,c). More precisely, KR exhibited no relationship to PR for IRNP ($P = 0.27$, $R^2 = 0.17$, $n = 41$), a marginally significant, positive relationship to PR for BNP ($P = 0.13$, $R^2 = 0.15$, $n = 17$), and a marginally significant, positive relationship to PR for YNP ($P = 0.10$, $R^2 = 0.27$, $n = 11$). However, the ratio of predator-to-prey was a strong indicator of PR for all three study sites (Fig. 3d,e,f; $P < 0.001$, $R^2 = 0.63$ for IRNP; $P = 0.009$, $R^2 = 0.49$ for BNP, and $P < 0.001$, $R^2 = 0.89$ for YNP).

Next, we assessed the extent to which prey growth rate was associated with kill rate and PR. Kill rate was also a poor predictor of prey growth rate (Fig. 4a,b,c). More precisely, KR and prey growth rate were unrelated for YNP ($P = 0.82$) and BNP ($P = 0.66$), and weakly related for IRNP ($P = 0.05$, $R^2 = 0.11$). The lack of significance for the YNP and BNP relationships may be attributable to their smaller sample sizes.

Predation rate was a good predictor of prey growth rate for IRNP (Fig. 4d, $P < 0.01$, $R^2 = 0.67$), a weaker predictor for BNP (Fig. 4f, $P = 0.02$, $R^2 = 0.31$), and bore

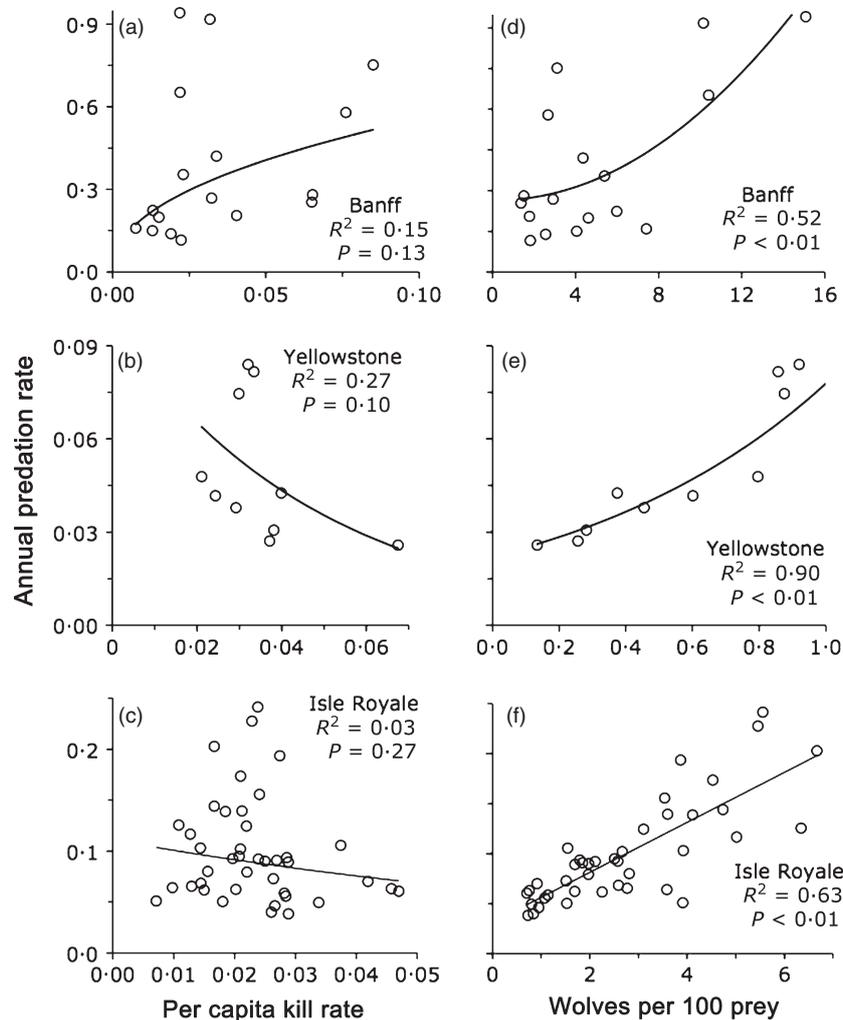


Fig. 3. The associations that kill rate (kills per wolf day⁻¹) and wolves: 100 prey have with predation rate (proportion of prey killed by wolves) for three study sites in North America. The lines in each panel represent the best fitting model, according to AICc criterion, from among those tested (linear, quadratic, logarithmic, exponential and power; see Supporting Information). Panel a is a power function, Panels b, c and e are exponential models, and panels d and f are linear functions. Note that predation rates for Banff were relatively high because the ratio of wolves per hundred prey in was relatively high in Banff.

no statistically significant relationship for YNP (Fig. 4e, $P = 0.35$, $R^2 = 0.11$). Differences in sample size and observed range of PR may be an important explanation for this pattern among sites.

The ratio of wolf-to-prey abundance performed similarly to PR in terms of its ability to predict prey growth rate (Fig. 4g,h,i). That is, the relationship was strongest for IRNP ($P < 0.01$, $R^2 = 0.56$), intermediate for BNP ($P = 0.03$, $R^2 = 0.23$) and weakest for YNP ($P = 0.33$, $R^2 = 0.12$). The ratio of wolf to prey and PR are also similar in the sense that, for IRNP and BNP, the ratio predicted prey growth rate about as well as PR did.

Discussion

Empirical observations seem to indicate that observed kill rate, which represents the predator population's perspective on predation, is a poor predictor of PR, which represents the prey population's perspective on predation (Fig. 3a–c). Our

complementary theoretical analyses of a wide variety of predator–prey models give good theoretical reason to expect these empirical results (Figs 1 and 2). Different theoretical models of predator–prey dynamics (prey dependent, ratio dependent, etc.) provided a diverse array of predictions about the predicted relationship between KR and PR (Fig. 1). Given these empirical and theoretical patterns, it is not surprising that KR is also a poor predictor of prey growth rate (Fig. 4a,d,g). Although empirical estimates of KR are critical for understanding the population biology of predators (i.e. the NR, eqn 1b), theoretical and empirical results show how kill rate is not very useful for understanding how prey are affected by predation. That is, kill rate is not a useful indicator of predation pressure. However, the theoretical analyses presented here give reason to think that predator:prey ratios would be a good predictor of PR and prey growth rate (Fig. 3d,e,f), and our empirical analyses suggest that the ratio is the best predictor of these statistics (Fig. 4g,h,i).

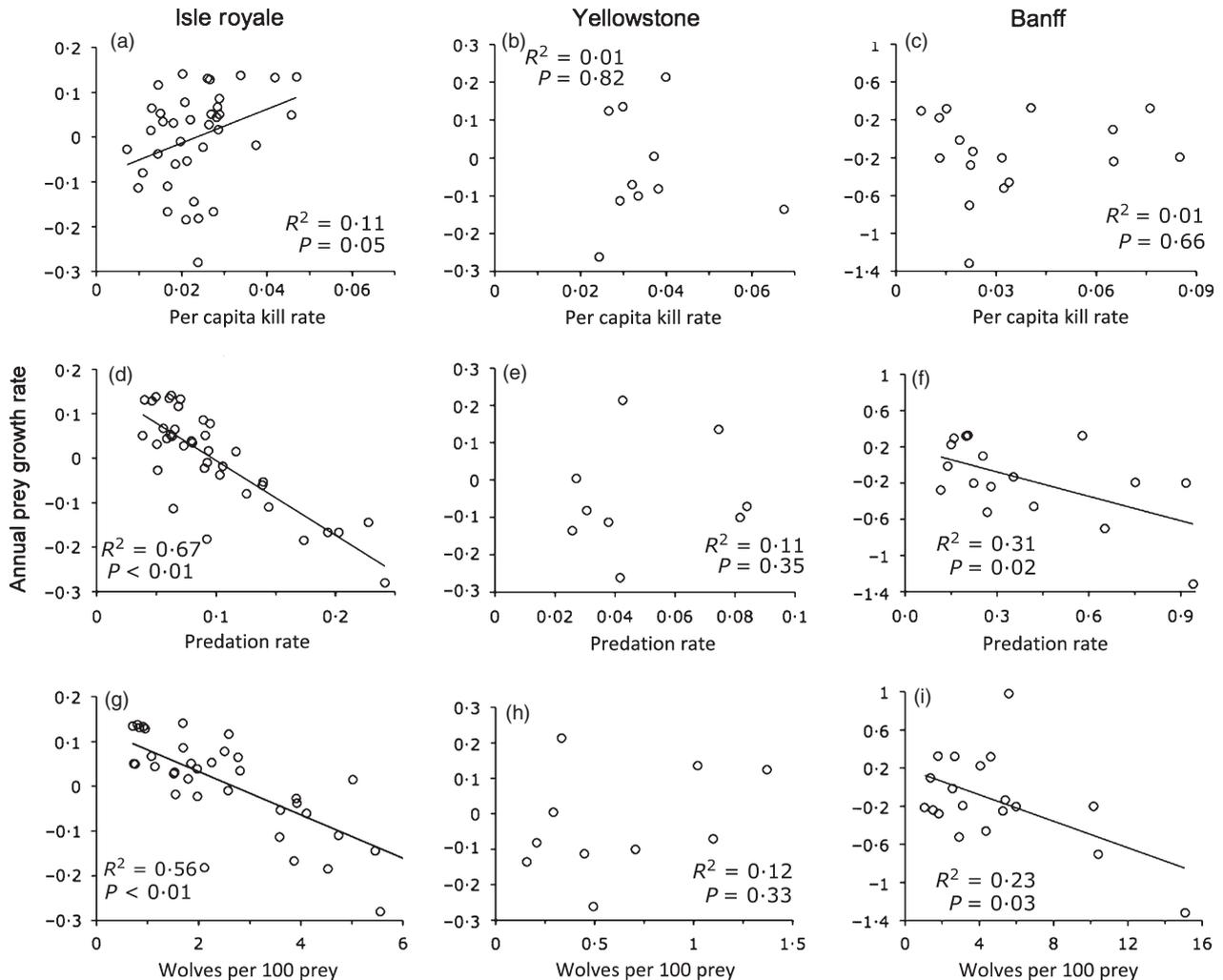


Fig. 4. The association between annual population growth rate of prey and various predation statistics showing the relationship between wolf kill rate (a, b, c), predation rate (d, e, f) and predator-prey ratio (g, h, i) for Isle Royale (a, d, g), Yellowstone National Park (b, e, h) and Banff National Park (c, f, i).

The explanation for the contrasting abilities of empirical estimates of KR and the ratio of predator:prey to predict kill rate relates to the fundamental relationship between KR and PR (i.e. $PR = KR[P/N]$). That PR is well predicted, in real systems, by P/N but not KR (Fig. 3) suggests that much of the variation in PR is attributable to variation in P/N , not KR. Logic like this also explains why KR–PR correlations differ among simulated populations with respect to the relative contributions of kill rate and population growth rate to stochasticity (i.e. the relative values of the s_1 , s_2 and s_3 in eqn 4; see Fig. 2a). Moreover, the weak positive KR–PR relationship for BNP (Fig. 3a) suggests KR may be a relatively weak source of stochasticity for the BNP system, compared with YNP and IRNP, where the KR–PR relationships were negative (Fig. 3b,c).

IRNP and YNP were similar inasmuch as PR exhibited a strong, positive relationship with wolves-per-prey and weak, negative relationship with kill rate (Fig. 1). Moreover, BNP differed from IRNP and YNP in that PR exhibited a weaker positive relationship with wolves-per-prey, and a positive

(though statistically insignificant) relationship with kill rate (Fig. 1a,d). These inter-site differences are consistent with the proposition that the number of wolves-per-prey is a more important (relative to kill rate) source of variation in PR for IRNP and YNP than for BNP.

The relationship between prey growth rate and various predation statistics was also strongest for IRNP and weakest for YNP (Fig. 4). The strength of the IRNP relationships (Fig. 4b,c) may correspond to IRNP being the only site of the three where wolves are the sole predator of moose, and moose represent about 90% of wolf diet. The somewhat weaker relationships observed in BNP (Fig. 4h,i) may correspond to wolves being only one of several predators for the elk in that system and the importance of human harvest on elk and wolves. The weakness of the YNP relationships (Fig. 4d–f) likely corresponds to PR and wolves-per-prey having been low and varied little during the period of observation (cf., the x-axes of Fig. 4b,e,f and compare the axes labels of Fig. 4c,f,i). Compared to the other sites, YNP is likely farthest from

its equilibrium because wolves have been present in that system only since the mid-1990s.

IRNP, YNP and BNP are fundamentally similar inasmuch as they involve wolves preying on large prey in temperate climates. However, they are also fundamentally different in important respects, including dispersal in and out of the study sites, species diversity of predator and prey communities, and human exploitation. How these differences translate into the differences that we observed in patterns of predation (Figs 3 and 4) is very difficult to know. More generally, it is difficult to judge what is more striking, the similarities in patterns of predation among the three sites, or the differences. This difficulty represents one of the perennial challenges in ecology.

Although predator–prey ratios have been an important basis for predicting the effect predators will have on prey (e.g., Keith 1983; Fuller 1989; Gasaway *et al.* 1992), their use for such purposes has been criticized (Theberge 1990; Abrams 1993; Person, Bowyer & Van Ballenberghe 2005), and basic theoretical considerations offer additional reason to justify the criticism (Theberge 1990; Abrams 1993; Person, Bowyer & Van Ballenberghe 2005). Although our empirical results suggest that predator-to-prey ratios are *relatively* good predictors of prey growth, they also suggest how these ratios may be inadequate for the interest of reliably predicting or controlling predator–prey systems. Even in the best case (IRNP, Fig. 4g), the predator–prey ratio accounts for only 56% of the variance in prey growth rate. Although prey population growth rate is expected to be zero when there are 2.9 wolves per 100 moose on IRNP, the 80% confidence interval for the predator-to-prey ratio corresponding to $r_{\text{prey}} = 0$ is [0.8, 4.9]. That is, a prey population that is stationary (in the statistical sense) seems to be associated with a very wide range of predator-to-prey ratio. Knowing the predator-to-prey ratio, even in this best-case scenario, offers only a vague idea about prey growth, probably too vague to be of much value for controlling or precisely predicting predator–prey dynamics. The inability to reliably predict prey growth from predator-to-prey ratio likely arises from factors such as interannual variation in climate, prey age structure, and extent to which predation is compensatory.

Moreover, even knowing that predator–prey ratio is correlated with PR or prey growth rate does not, by itself, indicate that predation is additive, and therefore the ultimate cause of prey dynamics. The correlations we observed here are also consistent with the prospect that some other process (e.g. environmental stochasticity in the form of a severe winter) causes both prey decline and high PR. In other words, a correlation between PR and prey growth rate does not, without additional information, allow one to distinguish between predation being an additive or compensatory source of prey mortality, or allow one to conclude that predation is responsible for lowering prey density. In most cases, data on predator–prey ratio or even PR will be inadequate for reliably inferring whether predation is causing prey population declines. Nevertheless, such inferences are the kinds that are typically used to judge the appropriateness of predator

control (Theberge 1990; Abrams & Ginzburg 2000). The limited value of such inferences suggests the need to develop alternative strategies for making such judgments.

The results presented here do not indicate that kill rate is unimportant for understanding predator–prey dynamics. On the contrary, understanding kill rate – that is, its causes and consequences – is important for understanding the energetics and dynamics of predator populations (Scheel 1993; Fuller & Sievert 2001; Vucetich, Peterson & Waite 2004; Packer *et al.* 2005). Nevertheless, our results may feel like a set-back for those hoping that some easily measured predation statistic, such as kill rate, might reliably indicate a prey population's growth rate or the impact of predation on prey dynamics.

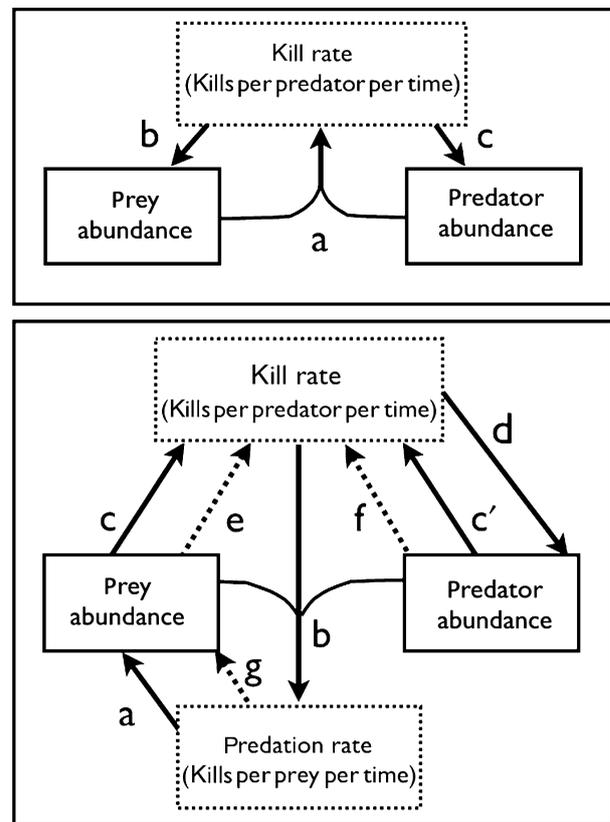


Fig. 5. Two conceptual models that both arise from many mathematical models of predation. Processes are represented by dotted outlined boxes, states of the system by solid outlined boxes and causal relationships by arrows. More specifically, in the upper panel, the letter *a* represents the functional response or potential causes of kill rate, *b* represents the prey's response to predation, or the second term of eqn 1a, and *c* represents the numerical response (NR) or immediate consequence of the kill rate (i.e., eqn 1b). In the lower panel, the letter *a* represents the empirical patterns shown in the second row of Fig. 4, *b* shows how the three factors feeding into predation rate make it importantly different from kill rate (i.e., $PR = (KR \times P)/N$), *c* and *c'* represent the functional response, and *d* represents the NR. Dotted lines depict how predation is affected, not only by abundance, but also by other dynamic properties of a prey population (e.g. age structure, mean body condition and non-lethal effects of predation). These effects add further complexity that tend not to be captured by conventional mathematical models of predation. For simplicity, neither conceptual model accounts for the influence of abiotic processes such as climate.

However, our results do represent an opportunity to develop how it is that we commonly think about predation. That is, conventional mathematical models of predation (e.g. eqns 1a,b) are typically expressed in a manner that seem to generate conceptual models (i.e. thoughts we hold in our minds about predation) where kill rate is the central process of predation (Fig. 5a). Our results suggest that a better conceptual model would depict the kill rate and PR, each as a fundamental process (Fig. 5b). Although this second conceptual model is substantially more complex, both arise from the same mathematical models (e.g. eqn 1). The two conceptual models are just different ways of thinking about the same set of equations. The more complex conceptual model should motivate the allocation of greater effort to understand the causes of variation in PR and its consequences. The added complexity of the lower conceptual model also helps one better intuit how complex dynamics can arise from what can otherwise appear to be a relatively simple set of equations.

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References

- Abrams, P.A. (1993) Why predation rate should not be proportional to predator density. *Ecology*, **74**, 726–733.
- Abrams, P.A. & Ginzburg, L.R. (2000) The nature of predation: prey dependent, ratio dependent, or neither? *Trends in Ecology and Evolution*, **15**, 337–341.
- Bayliss, P. & Choquenot, D. (2002) The numerical response: rate of increase and food limitation in herbivores and predators. *Philosophical Transactions of the Royal Society B*, **357**, 1233–1248.
- Bergstrom, U. & Englund, G. (2004) Spatial scale, heterogeneity and functional responses. *Journal of Animal Ecology*, **73**, 487–493.
- Boyce, M.S. (2000) Modeling predator-prey dynamics. *Research Techniques in Animal Ecology: Controversies and Consequences* (eds L. Boitani & T.K. Fuller), pp. 253–287. Columbia University Press, New York.
- Dale, B.W., Adams, L.G. & Bowyer, R.T. (1994) Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. *Journal of Animal Ecology*, **63**, 644–652.
- Eberhardt, L.L. (1997) Is wolf predation ratio-dependent? *Canadian Journal of Zoology*, **75**, 1940–1944.
- Eberhardt, L.L. & Peterson, R.O. (1998) Predicting the wolf-prey equilibrium point. *Canadian Journal of Zoology*, **77**, 494–498.
- Fuller, T.K. (1989) Population dynamics of wolves in north-central Minnesota. *Wildlife Monographs*, **105**, 1–41.
- Fuller, T.K. & Sievert, P.R. (2001) Carnivore demography and the consequences of changes in prey availability. *Carnivore Conservation* (eds J.L. Gittleman, S.M. Funk, D. MacDonald & R.K. Wayne), pp. 163–178. Cambridge, UK.
- Gasaway, W.C., Boertje, R.D., Grangaard, D.V., Kellyhouse, D.G., Stephenson, R.O. & Larsen, D.G. (1992) The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildlife Monographs*, **120**, 1–59.
- Gilpin, M.E. & Ayala, F.J. (1973) Global models of growth and competition. *Proceedings of the National Academy of Sciences of the United States of America*, **70**, 3590–3593.
- Ginzburg, L.R. (1998) Assuming reproduction to be a function of consumption raises doubts about some popular predator-prey models. *Journal of Animal Ecology*, **67**, 325–327.
- Hebblewhite, M. (2000) *Wolf and Elk Predator-Prey Dynamics in Banff National Park*. Master of Science Thesis, 130 pp. Wildlife Biology Program, School of Forestry, University of Montana, Missoula, Montana.
- Hebblewhite, M. (2005) Predation interacts with the North Pacific Oscillation (NPO) to influence western North American elk population dynamics. *Journal of Animal Ecology*, **74**, 226–233.
- Hebblewhite, M., Pletscher, D.H. & Paquet, P.C. (2002) Elk population dynamics in areas with and without predation by recolonizing wolves in Banff National Park, Alberta. *Canadian Journal of Zoology*, **80**, 789–799.
- Hebblewhite, M., Paquet, P.C., Pletscher, D.H., Lessard, R.B. & Callaghan, C.J. (2004) Development and application of a ratio-estimator to estimate wolf killing rates and variance in a multiple prey system. *Wildlife Society Bulletin*, **31**, 933–946.
- Holling, C.S. (1959) The components of predation as revealed by a study of small-mammal predation of the European sawfly. *The Canadian Entomologist*, **91**, 293–320.
- Jost, C., Devulder, G., Vucetich, J.A., Peterson, R.O. & Ardit, R. (2005) The wolves of Isle Royale Display Scale-Invariant Satiation and Ratio-Dependent Predation on Moose. *Journal of Animal Ecology*, **74**, 809–816.
- Keith, L.B. (1983) Population dynamics of wolves. *Wolves in Canada and Alaska: Their Status, Biology and Management* (ed. L.N. Carbyn), pp. 66–77. Canadian Wildlife Service, Edmonton, Alberta.
- Lemke, T.O., Mack, J.A. & Houston, D.B. (1998) Winter range expansion by the northern range Yellowstone elk herd. *Intermountain Journal of Sciences*, **4**, 1–9.
- Lotka, A.J. (1925) *Elements of physical biology*. reprinted in 1956 by Dover Publications, New York.
- Marshall, J.P. & Boutin, S. (1999) Power analysis of wolf-moose functional responses. *Journal of Wildlife Management*, **63**, 396–402.
- Mech, L.D. (1966) *The Wolves of Isle Royale*, US Government Printing Office, Washington, DC.
- Messier, F. (1994) Ungulate population models with predation: a case study with the North American Moose. *Ecology*, **75**, 478–488.
- Nilsen, E.B., Linnell, J.D.C., Odden, J. & Andersen, R. (2009) Climate, season, and social status modulate the functional response of an efficient stalking predator: the Eurasian lynx. *Journal of Animal Ecology*, **78**, 741–751.
- Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmschurst, J., Mduma, S. & Sinclair, A.R.E. (2005) Ecological change, group territoriality, and population dynamics in Serengeti Lions. *Science*, **307**, 390–393.
- Person, D.K., Bowyer, R.T. & Van Ballenberghe, V. (2005) Density dependence of ungulates and functional responses of wolves: effect on predator-prey ratios. *Alces*, **37**, 253–273.
- Peterson, R.O. (1977) Wolf ecology and prey relationships on Isle Royale. *U.S. National Park Service Science Monograph Series*, **11**, 1–210.
- Peterson, R.O. & Page, R.E. (1988) The rise and fall of Isle Royale wolves, 1975–1986. *Journal of Mammalogy*, **69**, 89–99.
- Peterson, R.O., Thomas, N.J., Thurber, J.M., Vucetich, J.A. & Waite, T.A. (1998) Population limitation and the wolves of Isle Royale. *Journal of Mammalogy*, **79**, 828–841.
- Rosenzweig, M.L. & MacArthur, R.H. (1963) Graphical representation and stability conditions of predator-prey interactions. *American Naturalist*, **97**, 209–223.
- Scheel, D. (1993) Profitability, encounter rates, and prey choice of African Lions. *Behavioral Ecology*, **4**, 90–97.
- Smith, D.W., Drummer, T.D., Murphy, K.M., Guernsey, D.S. & Evans, S.B. (2004) Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995–2000. *Journal of Wildlife Management*, **68**, 153–166.
- Solberg, E.J., Sæther, B.-E., Strand, O. & Loison, A. (1999) Dynamics of a harvested moose population in a variable environment. *Journal of Animal Ecology*, **68**, 186–204.
- Taylor, R.J. (1984) *Predation*, Chapman Hall, New York.
- Theberge, J.B. (1990) Potentials for misinterpreting impacts of wolf predation through prey: predator ratios. *Wildlife Society Bulletin*, **18**, 188–192.
- Volterra, V. (1926) Fluctuations in the abundance of a species considered mathematically. *Nature*, **118**, 558–560.
- Vucetich, J.A. & Peterson, R.O. (2004) The influence of prey consumption and demographic stochasticity on population growth rate of Isle Royale wolves (*Canis lupus*). *Oikos*, **107**, 309–320.
- Vucetich, J.A., Peterson, R.O. & Schaefer, C.L. (2002) The effect of prey and predator densities on wolf predation. *Ecology*, **83**, 3003–3013.

- Vucetich, J.A., Peterson, R.O. & Waite, T.A. (2004) Raven scavenging favours group foraging in wolves. *Animal Behaviour*, **67**, 1117–1126.
- Vucetich, J.A., Smith, D.W. & Stahler, D.R. (2005) Influence of harvest, climate, and wolf predation on Yellowstone elk, 1961–2004. *Oikos*, **111**, 259–270.

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Supporting Information

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

Appendix S1 Details related to estimation of predation rate, analytical results, and simulations.

Table S1 Model selection results corresponding to Fig. 3.

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