The influence of prey consumption and demographic stochasticity on population growth rate of Isle Royale wolves *Canis lupus*

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Vucetich, J. A. and 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.

The relationship between the rates of prey capture and predator population growth is a fundamental aspect of predation, yet it is rarely measured for vertebrate predators. For the isolated wolf population on Isle Royale, annual variation in kill rate explains 22% of the variation in wolf population growth rate. From the slope of this relationship, we estimate that the production efficiency (ratio of production to respiration) of wolves is between 0.5% and 1.5%. More generally, we assess the relative extent to which wolf population growth rate is affected by density dependence, prey availability (moose, *Alces alces*), winter weather, and demographic stochasticity. Prey availability explains the most variation in wolf growth rate (42%), but this is only recognized after accounting for the influence of a disease-induced population crash and age structure of the prey population (i.e. number of vulnerable moose, >9 years of age). Demographic stochasticity accounts for approximately 30% of the variation in wolf growth rate. This recognition is important, but not surprising, given that the average population size of Isle Royale wolves is 22. Previous work indicates that the effect of winter climate, as mediated through prey vulnerability and kill rates, is substantial. This work indicates that the direct effect of winter climate is weak, and explains only about 4% of the variation in wolf growth rate (P = 0.10).

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The dynamics of consumer (predator) populations are often expressed as functions of per capita rate of consumption (Beddington et al. 1976), availability of food (Bayliss and Choquenot 2002, Sibly and Hone 2002), consumer density (Royama 1992), or abiotic variables (Coulson et al. 2001, Jonzen et al. 2002). To the extent that consumption rate determines growth rate, it is sensible to say that population dynamics are determined by bottom-up processes. Decreases in the explanatory power of consumption rate would likely correspond to the increased influence of other processes, such as territoriality, interspecific competition, klepto-parasitism, disease, climate and other abiotic factors, or demographic stochasticity.

To the extent that per capita consumption and population growth rate of the consumer are linearly related, the slope of the relationship provides an estimate of production efficiency (Ginzburg 1998), which is the ratio of production to respiration (Ricklefs and Miller 2000). Production efficiency is important because it links population ecology and energy flux through ecosystems (Odum 1969, Brown 1991).

Except for two important reviews on predatory and parasitic arthropods (Beddington et al. 1976, Hassell et al. 1976), assessments of the relationship between consumption and the population growth of a predator are rare. We are unaware of any such empirical assessment for a vertebrate predator. In this paper, we assess

the relationship between per capita kill rate (consumption rate) and population growth rate for wolves in Isle Royale National Park, USA. We also assess how the population dynamics of these wolves are influenced by abundance of prey and vulnerable prey, density dependence, climate, and demographic stochasticity. This analysis complements previous papers assessing how the kill rate of Isle Royale wolves is affected by the abundance of wolves and moose (Vucetich et al. 2002) and pack size (Vucetich et al. 2004).

Field methods

Data were collected in Isle Royale National Park, USA, an island (544 km^2) in Lake Superior, where wolves (*Canis lupus*) and moose (*Alces alces*) interact essentially as an isolated single-predator-single-prey system (Peterson and Page 1988). Immigration and emigration are likely zero, or at worst negligible, for both wolves and moose on Isle Royale. Moose comprise more than 90% of the biomass in wolf diet (Peterson and Page 1988). Other species capable of preying upon moose are absent and hunting is prohibited on the island.

The wolf population was censused annually (1959 to 2003) in January and February using fixed-wing aircraft (Fig. 1A). Our confidence in census accuracy is high because entire wolf packs are often visible at a single location and time and we make several complete counts during each winter. From the numbers of wolves, we calculated the annual log-transformed growth rate of the wolf population ($=\ln[N_{t+1}] - \ln[N_t]$). Moose abundance was estimated annually from 1979 to 2003 by aerial survey (Fig. 1B), using fixed-wing aircraft (Peterson and Page 1993). During 1958–1991, moose abundance was estimated by cohort analysis. Our method of cohort analysis is similar to that described by Solberg et al. (1999). Between 1979 and 1991, estimates of moose abundance are available for both aerial surveys and cohort analysis. The results presented below are derived from cohort analysis derived estimates during 1959–1991 and aerial survey estimates during 1991–2001. Nevertheless, the results are qualitatively identical when cohort analysis estimates are replaced with aerial survey estimates during the period of overlap.

Calves and moose greater than nine years of age (hereafter old moose) may represent especially vulnerable segments of the wolf population (Peterson 1977). Because the age structure of the moose population is quite dynamic, total moose abundance may not be a good indicator of the abundance of vulnerable moose. Thus, we will examine the influence of the abundance of calves and old moose on wolf growth rate (Fig. 1B).
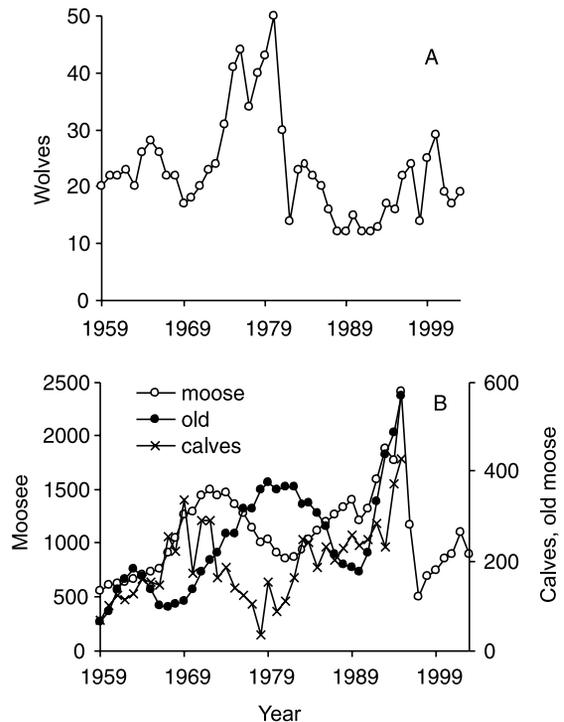

Fig. 1. The abundance of wolves (A) and moose (B) in Isle Royale National Park between 1959 and 2003. The lower panel also shows abundance of calves and old moose (i.e. ≥9 years of age).

These data were derived from cohort analysis and originally described in Peterson et al. (1998, 2004).

During 1971–2001, kill rates were calculated for each wolf pack during each winter session. Each kill rate was based on approximately 44 days of observation (median =44, interquartile range =[38, 47]), during which daily travel and location of kills for wolf packs were determined from aerial observations of tracks in snow (Mech 1966, Peterson 1977). (During winter wolves hunt and travel in family groups called packs, Murie 1944, Olson 1938.) Per capita kill rates were calculated for each pack as the number of kills made by a pack divided by the number of wolves in that pack divided by the number of days during which that pack was observed. The per capita annual kill rate for the population was estimated as the average kill rate for all existing packs, weighted by pack size. Additional details on these field methods are reported elsewhere (Thurber and Peterson 1993, Peterson et al. 1998).

Previous assessments indicate that wolf–prey interactions are affected by snow conditions (Peterson and Allen 1974, Peterson 1977, DelGiudice 1998) and the north Atlantic oscillation (Post et al. 1999). The north Atlantic oscillation (NAO) is a large scale fluctuation in air pressure between the sub-tropical and sub-polar regions of the north Atlantic that affects winter climate

in portions of northeastern North America and elsewhere (Hurrell 1995). To assess the influence of these factors on wolf population growth rate, we obtained annual measures of cumulative snow fall (Nov.–Apr.) in nearby by Thunder Bay, Ontario (approximately 25 km NW of Isle Royale) from Environment Canada (www.ec.gc.ca); and values of the winter (Dec.–Mar.) NAO index from www.cgd.ucar.edu/ ∼jhurrell/nao.stat. winter.html#winter.

Analysis and results

The influence of kill rate on population growth

During 1971–2001, the per capita kill rate varied nearly four-fold, from 0.44 to 1.69 kills per wolf per month (one month is $365 \div 12$ days), and per capita annual growth rate (dP/Pdt) varied from -0.53 to 0.76.

We began by assessing which of several plausible forms best represented the relationship between population growth rate and kill rate (Table 1). We selected the best model on the basis of AIC_C (Akaike's information criterion, corrected for small sample size) and Δ (Burnham and Anderson 1998, Anderson et al. 2000). Δ equals the AIC_C for the model of interest minus the smallest AIC_C for the set of models being considered. By definition, the best model has a Δ of zero, and models with $\Delta < 2$ are generally considered worthy of consideration. Of the models we assessed (Table 1), two performed similarly well – the simple linear model ($\Delta = 0.3$; $R^2 = 0.15$; $P = 0.03$) and the linear model with log-transformed kill rate ($\Delta = 0$; $R^2 = 0.16$; $P = 0.02$; Fig. 2).

We also assessed the direct effects of wolf density, cumulative snowfall, and NAO on population growth
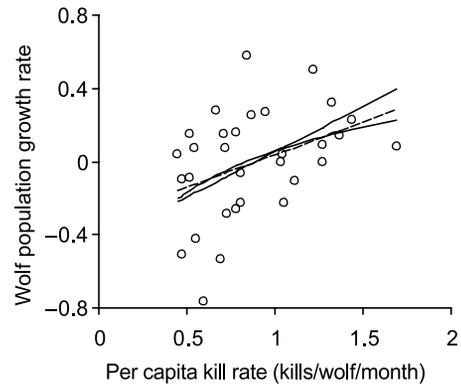

Fig. 2. The relationship between kills/wolf/month and log-transformed growth rate of the wolf population on Isle Royale between 1971 and 2001. The dashed line is the relationship predicted by linear regression analysis and ignores the influence of measurement error, the solid line is the linear relationship that accounts for measurement error in the independent variable (Eq. 2, 3), and the dotted line is the linear relationship between the natural logarithm of kill rate and growth rate (Table 1).

rate. For perspective, snowfall and wolf density indirectly affect population growth rate insomuch as they affect per capita kill rate (Vucetich et al. 2002, Vucetich and Peterson 2004b). Accounting for these direct effects did not result in more parsimonious models (i.e. $\Delta > 2.4$; Table 1). For additional context, the partial correlations (r_p, with respect to the best model in Table 1) between wolf growth rate and wolf density ($r_p = -0.09$, $P = 0.65$), snowfall ($r_p = -0.04$, $P = 0.86$), and NAO ($r_p = -0.01$, $P = 0.94$) were low and not statistically significant.

Next, we assessed models representing the hypothesis that wolf population dynamics after the 1980 population crash have been different than those prior to the crash (Fig. 1A). The population crash was due in part to a disease, canine parvovirus, which may have affected the population until about 1990 (Peterson et al. 1998). The population crash may also have exacerbated possible negative consequences of already high rates of inbreeding (Peterson et al. 1998). To assess changes in population dynamics after 1980, we fit models with indicator variables. For example, to model changes in the intercept and slope associated with a simple linear relationship between kill rate and growth rate, we constructed the following model:

$$dP/Pdt = (b_0 + a_0 I_t) + (b_1 + a_1 I_t)k_t \qquad (1)$$

where I_t is an indicator variable that equals 1 for $t \leq 1980$ and 0 for $t > 1980$. Models such as these may be interpreted by letting b_i represent the coefficient for $t > 1980$, and by letting $b_i + a_i$ represent the coefficient for $t \leq 1980$. Models with various combinations of indicator variables performed less well than simpler models without the indicator variables. Specifically, $R^2 = 20.0$ and $\Delta = 4.1$ for Eq. 1, $R^2 = 19.5$ and $\Delta = 1.5$ for the model in which only the intercept changes after

Table 1. Performance of models predicting wolf population growth rate (1971–2001) from the per capita kill rate. The bs and θ are coefficients estimated by least squares; k is the per capita kill rate. w is the natural logarithm of wolf abundance; s is cumulative annual snowfall; NAO is the north Atlantic oscillation; R^2 is the proportion of total variation explained by the model; Δ equals the Akaike's information criterion (AIC_C) for the model of interest minus the smallest AIC_C for the set of models being considered. The best model has a Δ of zero. W_{AIC} is the AIC_C weight. The ratio $W_{AIC,i}$: $W_{AIC,j}$ estimates how much more support (i.e. likelihood ratio) the data offer to model i than to model j.

Expressions for dP/Pdt	R^2	Δ	W_{AIC}
$b_0 + b_1 k$	0.15	0.3	0.24
$b_0 + b_1 k^\theta$	0.16	2.7	0.08
$b_0 + b_1 k + b_2 k^2$	0.17	2.4	0.09
$b_0 + b_1 k + b_2 k^2 + b_3 k^3$	0.18	5.0	0.03
$b_0 + b_1 \ln(k)$	0.16	0	0.29
$b_0 + b_1 \ln(k) + b_2 w$	0.17	2.4	0.09
$b_0 + b_1 \ln(k) + b_2 w + b_3 s$	0.17	5.3	0.02
$b_0 + b_1 \ln(k) + b_2 w + b_3 NAO$	0.17	5.2	0.02
$b_0 + b_1 \ln(k) + b_2 NAO$	0.16	2.6	0.08
$b_0 + b_1 \ln(k) + b_2 s$	0.17	2.6	0.08

1980, and $R^2 = 18.2$ and $\Delta = 2.0$ for the model in which only the slope changes after 1980 (Table 1). Because our estimates of kill rate only extend back to 1971, the poor performance of these models may only reflect a lack of data prior to the population crash of 1980. In the next section, we will show that differences in dynamics before and after 1980 are well supported.

Virtually all regression models employed in ecological research require the assumption that the independent variable (kill rate) is measured without error. However, measurement (sampling error) in the independent variable tends to yield underestimates of the magnitude of the slope and coefficient of determination – the larger the measurement error is, the greater the bias (Fuller 1987). Although statistical theories about how best to perform regression in the presence of measurement error are recent and in relatively early stages of development, we consider a method of moments approach which likely represents an improvement over ignoring measurement error completely. More specifically, the measurement error model that we used (Fuller 1987) is based on the assumptions that the measurement error of each ob-servation of the independent variable (i.e. kill rate) is distributed: 1) normally with mean value of zero and a variance of σ_{uu}, and 2) independently with respect to the dependent variable, magnitude of the independent vari-able, and other measurement errors. As with traditional regression models, this model requires no special ac-counting for measurement error in the dependent variable. For this model, the slope (b_1), intercept (b_0), standard errors (s_{XX}, s_{ee}), and coefficient of determina-tion (R^2) are related to the sample variances (m_{XX}, m_{YY}) and covariance (m_{XY}), and variance of the measurement (sampling) error (σ_{uu}) as follows:

$$
\begin{aligned}
b_1 &= m_{XY}/(m_{XX} - \sigma_{uu}) \\
s_{XX} &= m_{XX} - \sigma_{uu} \\
s_{ee} &= m_{YY} - b_1 m_{XY} \\
b_0 &= Y - b_1 X \\
R^2 &= (m_{XY})^2/(s_{XX} m_{YY})
\end{aligned}
\tag{2}
$$

Details on this model are given by Fuller (1987).

Because the performance of the linear model ($\Delta = 0.3$ for dP/Pdt = $b_0 + b_1 k$; Table 1; Fig. 2) was nearly identical to that of the best fitting model ($\Delta = 0$ for dP/Pdt = $b_0 + b_1 \ln(k)$), and because the parameters of the linear model are associated with useful biological inter-pretations, we conducted an assessment of measurement error with respect to the linear model. Because the per capita kill rate was estimated several times each year (i.e. once for each pack), we used variation in kill rate among packs each year as an estimate of sampling error. As assumed by the regression model, the standard error of each year's kill rate and average of each year's kill rate was uncorrelated (P = 0.27). The interpack standard error, averaged across all years, was 0.17.

The square of this value (0.03) was used to replace σ_{uu} in Eq. 2.

Using the regression method represented by Eq. 2 and the observed data, the per capita growth rate is predicted to be (Fig. 2):

$$
dP/Pdt = 0.50(\text{kills/wolf/month}) - 0.44. \tag{3}
$$

The model represented by Eq. 3 is statistically significant (P = 0.04) and explains 22% ($= R^2$) of the variation in growth rate. Using the Fisher z transformation, we estimated confidence intervals (CI) for R^2 (Neter et al. 1989:531): the 50% CI is [0.12, 0.32], the 80% CI is [0.05, 0.42], and the 95% CI is [0.01, 0.53]. Had measure-ment error been ignored, the predicted values of the slope and R^2 would have been biased downward. In this case, the estimated slope would have been 0.36 (rather than 0.50, Eq. 3), and the estimated R^2 would have been 0.15, rather than 0.22.

The slope of Eq. 3 is important because an estimate of the net production efficiency of the wolf population can be derived from the slope when it is expressed in terms of kilograms of wolf produced annually per kilogram of moose assimilated annually (Ginzburg 1998, Ricklefs and Miller 2000). The average mass of an Isle Royale wolf is 35 kg, the average mass of edible material is 295 kg per adult moose and 114 kg per calf, and approxi-mately one third of all wolf kills during winter are calves (Peterson 1977). Thus, assuming an assimilation rate of 90% (Golley 1960), the average mass of assimilatible (digestible) material per moose killed is 211 kg. Based on these values the estimated net efficiency is 0.69% ± 0.20% (95%CI). However, due to losses to scavengers and (Vucetich et al. 2004) and depressed kill rates during summer (Messier and Crete 1985), average annual rates of assimilation could be much less than the rate estimated during winter. If the annual consumption rate was three quarters of the estimated kill rate, the gross efficiency would be 0.92% ± 0.26%. If consumption was half the estimated kill rate, then the gross efficiency would be 1.38% ± 0.39%.

The influence of predator and prey density on population growth

We consider several expressions for per capita growth rate of the wolf population that include terms for wolf abundance (W), moose abundance (M), and both W and M (Table 2). Except where noted otherwise, the models are expressed as functions of the natural logarithm of wolf (w) and moose (m) abundance. We considered (linear and non-linear) models including the influence of only wolf abundance. Our non-linear representation (i.e. dP/Pdt = $b_0 + b_1 W^\theta$) is equivalent to the theta-logistic model Gilpin and Ayala (1973): dP/Pdt = r $(1 - (P/K)^\theta)$, where r is the maximum growth rate of

Table 2. Performance of models predicting wolf population growth rate (1959–2001) from the densities of wolves and moose. W is wolf abundance, w is the natural logarithm of W, M is moose abundance, and m is the natural logarithm of M. See Table 1 for definitions of other symbols.

Expressions for dP/dt	R^2	Δ	W_{AIC}
$b_0 + b_1 w_\theta$	0.12	1.0	0.194
$b_0 + b_1 w^\theta$	0.12	4.1	0.041
$b_0 + b_1 m_\theta$	0.05	4.3	0.038
$b_0 + b_1 m^\theta$	0.05	6.7	0.011
$b_0 + b_1 (M/W)$	0.10	1.9	0.127
$b_0 + b_1 w + b_2 m + b_3 (M/W)$	0.15	1.9	0.125
$b_0 + b_1 \exp(Mb_2)$	0.06	6.9	0.015
$b_0 + b_1 \exp(Mb_2) - b_3 W$	0.14	5.0	0.027
$b_0 + b_1 w + b_2 m$	0.14	2.4	0.096
$b_1 w + b_2 m$	0.14	0	0.325

the wolf population, K is the carrying capacity, and θ describes the degree of non-linearity between P and dP/dt. We also considered (linear and non-linear) models including the influence of moose abundance, but not wolf abundance. Excluding wolf abundance from some models permits one to distinguish mechanistic explanation from phenomenological prediction. We also considered models based on the ratio of moose to wolves: $dP/dt = b_0 + b_1(M/W)$. This equation is equivalent to an equation first proposed by Leslie (1948): $dP/dt = r(1 - M/aW)$, where a is the ratio of moose to wolves at equilibrium (Eberhardt 1997, 1998 for previous application of this equation to wolf dynamics). We considered two models that include the expression, $b_0 + b_1\exp(Mb_2)$, which is equivalent to an expression previously considered by May (1973:84): $-a + c(1 - e^{-dM})$, where a is the rate of population decline in the absence of food, c describes the difference between the maximum growth rate and a, and d describes the change in growth with respect to the change in prey abundance (Bayliss and Choquenot 2002). Of the models described above, the most parsimonious model included only a linear term for wolf density (Table 2). However, because the intercept was not significant ($P = 0.94$), we also considered a model with linear terms for wolves and moose, but no intercept. This model was

most parsimonious (i.e. $\Delta = 0$). Despite its relative performance, this model explained only 14% of the variation in wolf population growth rate. We also considered models with wolf and moose densities in previous years (i.e. time lagged models). These did not outperform the best model reported in Table 2 (data not shown).

We extended this analysis of dP/Pdt by assessing the influence of abiotic variables (i.e. cumulative snowfall and NAO), and the possibility that wolf population dynamics after the population crash of 1980 differ from those prior to the crash of 1980. Because there are many models of this type to consider, we began by considering a model that is fully saturated, with respect to the two time periods:

$$dP/Pdt = (b_0 + a_0 I_t) + (b_1 + a_1 I_t)w_t + (b_2 + a_2 I_t)m_t$$
$$+ (b_3 + a_3 I_t)s_t + (b_4 + a_4 I_t)nao_t \qquad (4)$$

where I_t is an indicator variable that equals 1 for $t \leq 1980$ and 0 for $t > 1980$. Terms with I_t represent hypotheses that population dynamics prior to 1980 differ from those after 1980. We also considered models that include: 1) all the terms of Eq. 4 except for the terms describing abiotic factors, 2) all the terms of Eq. 4 except those with indicator variables affecting abiotic factors, and 3) several models that result from the stepwise regression algorithm (Table 3). The best of these models included separate intercepts for the two time periods, separate slopes for the influence of wolf density during the two time periods, and no terms at all for moose, snow, or NAO. This model explained 30% of the variation in wolf growth rate. However, because kill rate is affected by prey density (Vucetich et al. 2002), and because expressions for predator growth should include the variables that affect kill rate (Ginzburg 1998), preference should be given to another model that performed reasonably well ($\Delta = 2.3$; $R^2 = 0.31$) and includes a term for moose (Fig. 3, 4):

$$dP/Pdt = 1.21 - 0.96 I_t + (-0.59 + 0.38 I_t)w_t$$
$$+ 6.69 \times 10^{-2} m_t \qquad (5)$$

Table 3. Performance of models predicting wolf population growth rate (1959–2001) from the densities of wolves and moose and abiotic variables. I_t is an indicator variable that equals 1 for $t \leq 1980$ and 0 for $t > 1980$. Terms with I_t represent hypotheses that population dynamics prior to 1980 differ from those after 1980. See Table 1 for definitions of other symbols.

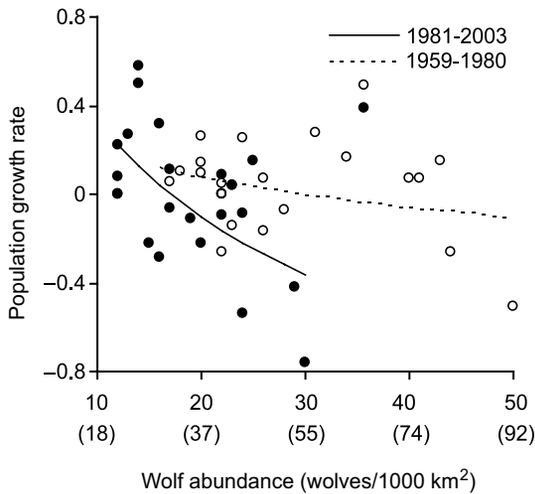| Expressions for dP/dt	R^2	Δ	W_{AIC}
$b_1 w + b_2 m$	0.14	3.7	0.048
$b_0 + a_0 I_t + (b_1 + a_1 I_t)w_t + (b_2 + a_2 I_t)m_t + (b_2 + a_2 I_t)s_t + (b_2 + a_2 I_t)NAO_t$	0.36	15.0	<0.001
$b_0 + a_0 I_t + (b_1 + a_1 I_t)w_t + (b_2 + a_2 I_t)m_t + b_2 s_t + b_2 NAO_t$	0.32	4.3	0.035
$b_0 + a_0 I_t + (b_1 + a_1 I_t)w_t + (b_2 + a_2 I_t)m_t$	0.32	10.5	0.002
$b_0 + (b_1 + a_1 I_t)w_t$	0.25	0.2	0.273
$b_0 + a_0 I_t + (b_1 + a_1 I_t)w_t$	0.30	0	0.304
$b_0 + a_0 I_t + (b_1 + a_1 I_t)w_t + b_2 m_t$	0.31	2.3	0.142
$b_0 + a_0 I_t + (b_1 + a_1 I_t)w_t + (a_2 I_t)m_t + (a_2 I_t)s_t$	0.33	3.8	0.045

Fig. 3. The influence of wolf abundance on population growth rate prior to the wolf population crash (1959–1980; open circles, dotted line) and after the population crash (1981–2001; filled circles, solid line). Lines are predictions from the best model (i.e. $\Delta = 0$) in Table 3.
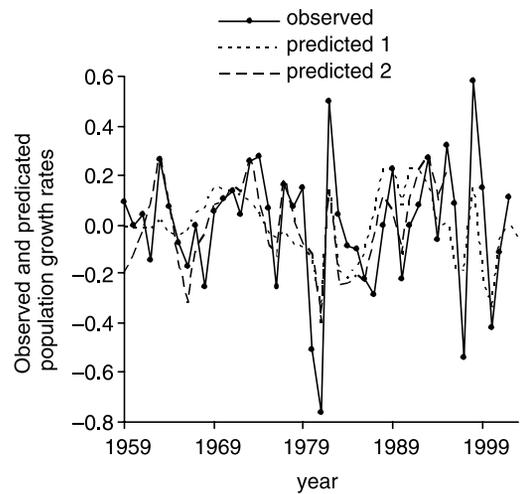
Fig. 4. Observed (solid line with circles) and predicted population growth rates for Isle Royale wolves. The dotted line represents predictions from Eq. 5, which is based on wolf and moose densities. The dashed line represents predictions from Eq. 7, which is based on the abundance of old moose.

Since the canine parvovirus outbreak in 1980, wolf dynamics appear more density dependent and the predicted equilibrium size has been lower. Fluctuations in moose abundance account for only $\sim 1\%$ of the variation in growth rate, and wolf population growth rate increased by only 0.03 as moose abundance is increased from its lower quartile (815) to its upper quartile (1313). Using Eq. 5 as a reference, the partial correlations (r_p) associated with cumulative snowfall ($r_p = 0.05$, P = 0.76), and NAO ($r_p = -0.02$, P = 0.90) were very weak.

The influence of vulnerable prey on population growth

We considered several forms of dP/Pdt expressed in terms of the log-transformed abundances of wolves (w), old moose (o), and calves (c). Again, because there are many models of this type to consider, we began by

considering a model that is fully saturated with respect to the time periods before and after the 1980 population crash:

$$dP/Pdt = b_0 + a_0I_t + (b_1 + a_1I_t)w_t + (b_2 + a_2I_t)o_t$$
$$+ (b_3 + a_3I_t)c_t + (b_4 + a_4I_t)s_t$$
$$+ (b_5 + a_5I_t)nao_t \qquad (6)$$

We also considered models that include: 1) all the terms of Eq. 6 except for the terms describing abiotic factors, 2) all the terms of Eq. 6 except for the terms with indicator variables that describing abiotic factors, and 3) several models that result from the stepwise regression algorithm (Table 4). Of these models, the best was:

$$dP/Pdt = 0.23 - 0.75w_t + (0.36 + 0.12I_t)o_t$$
$$- 9.9 \times 10^{-4}s_t \qquad (7)$$

This model also explained 56% of the variation in wolf growth rate (Fig. 4, 5). More wolves were supported by a given number of old moose prior to the population crash

Table 4. Performance of models predicting wolf population growth rate (1959–1995) from the densities of wolves and vulnerable prey (calves and old moose) and abiotic variables. o_t is the natural logarithm of old moose (>9 years of age) abundance, and c_t is the natural logarithm of calf abundance. See notes in Tables 1 and 3 for definitions of other symbols.

| Expressions for dP/dt	R^2	Δ	W_{AIC}
$b_0 + a_0I_t + (b_1 + a_1I_t)w_t + (b_2 + a_2I_t)o_t + (b_3 + a_3I_t)c_t + (b_4 + a_4I_t)s_t + (b_5 + a_5I_t)nao_t$	0.594	24.3	<0.001
$b_0 + a_0I_t + (b_1 + a_1I_t)w_t + (b_2 + a_2I_t)o_t + (b_3 + a_3I_t)c_t$	0.551	10.3	0.002
$b_0 + a_0I_t + (b_1 + a_1I_t)w_t + (b_2 + a_2I_t)o_t + (b_3 + a_3I_t)c_t + b_4s_t + b_5nao_t$	0.585	15.6	<0.001
$b_0 + b_1w_t$	0.094	17.5	<0.001
$b_0 + b_1w_t + (a_2I_t)o_t$	0.254	13.0	0.001
$b_0 + b_1w_t + (b_2 + a_2I_t)o_t$	0.515	0.2	0.368
$b_0 + b_1w_t + (b_2 + a_2I_t)o_t + b_4s_t$	0.555	0	0.408
$b_0 + b_1w_t + (b_2 + a_2I_t)o_t + b_3c_t + b_4s_t$	0.566	2.2	0.135
$b_0 + b_1w_t + (b_2 + a_2I_t)o_t + b_3c_t$	0.516	3.1	0.085
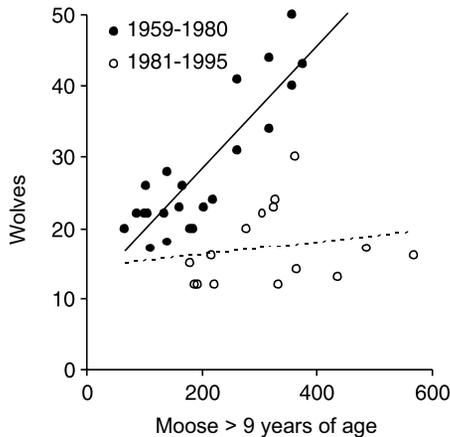
Fig. 5. The influence of abundance of vulnerable prey (i.e. old moose, >9 years old) on wolf population growth rate prior to the wolf population crash (1959–1980; filled circles, solid line) and after the population crash (1981–2001; open circles, dotted line). Lines represent best fit regressions. This model corresponds to Eq. 7 and the best model (i.e. $\Delta = 0$) in Table 3.

(1959–1980), than after (1981–1995; Fig. 5). Wolf abundance accounts for 10% of the variance in wolf population growth rate, and the abundance of old moose account for 42% of the variance in wolf population growth rate. Although Eq. 7 suggests the direct influence of snow on wolves is negative, it accounts for only about 4% ($P = 0.10$) of the variation in wolf population growth rate. Using Eq. 7 as a reference, the partial correlations with calves ($r_p = -0.16$, $P = 0.39$) and NAO ($r_p = 0.01$, $P = 0.97$) were weak.

The influence of demographic stochasticity on predator growth

Demographic stochasticity arises from chance realizations of individual probabilities of survival and reproduction, and its importance tends to increase with decreasing population size (Lande 1993). Here, we assess the portion of the variation in wolf population growth rate that is attributable to demographic stochasticity. The variance in population growth rate can be decomposed into several components (Saether et al. 2000, Bjørnstad and Grenfell 2001): $Var[r_t] = (\sigma_d^2)N^{-1} + \sigma_e^2$, where, $r_t = \ln(N_{t+1}) - \ln(N_t)$, N is population size, $(\sigma_d^2)N^{-1}$ is the variance attributable to demographic stochasticity, and σ_e^2 is the variance attributable to environmental stochasticity (e.g. abundance of prey, climate). The demographic variance can be further decomposed, to yield:

$$Var[r_t] = Var_{demo}[s] + Var_{demo}[m] + \sigma_e^2 \qquad (8)$$

where $Var_{demo}[s]$ and $Var_{demo}[m]$ are the variances attributable to demographic stochasticity in survival and reproduction, respectively.

We obtained annual estimates of $Var_{demo}[s]$ and $Var_{demo}[m]$ for most years between 1971 and 2003 from field data on the number of pups (that survive to their first winter) that were produced by each wolf in each year, and from data on the number of wolves that died each year. These data were presented in Peterson and Page (1988) and Peterson et al. (1998). Estimates of demographic variance were also based on analytical procedures developed by Fox and Kendall (2002).

Demographic stochasticity in survival

The demographic variance associated with survival is (Fox and Kendall 2002):

$$Var_{demo}[s_t] = (V_{s,t} - Var[s_t])/N_t \qquad (9)$$

where N_t is population size in year t, $V_{s,t}$ is the sampling demographic variance in survival in year t, and $Var[s_t]$ is the variance in survival probabilities among individuals within the population. We estimated $Var_{demo}[s_t]$ for each of 30 years between 1971 and 2002 (our field data were inadequate for estimating Eq. 9 for two years). Each estimate was made by first replacing $V_{s,t}$ in Eq. 9 with an estimate of the binomial sampling variability associated the estimated average survival rate. Specifically, we replaced $V_{s,t}$ with $(S_t/N_t)(1 - (S_t/N_t))$, where S_t is the number of wolves that survived year t, and N_t is the number of wolves at the beginning of year t.

To estimate $Var[s_t]$ we need to account for systematic differences in survival probability for different types of wolves. For a wolf population in a homogenous environment, the most important source of variance in survival probability is its social status. The survival probability of dominants (p_{dom}) is greatest, the survival probability of non-territorial wolves (p_{nonter}) is least, and survival probability of subordinant wolves (p_{nonter}) is intermediate. We can estimate $Var[s]$ as:

$$Var[s] = [N_{dom}(p_{dom} - p)^2 + N_{sub}(p_{sub} - p)^2$$
$$+ N_{nonter}(p_{nonter} - p)^2](N - 1)^{-1} \qquad (10)$$

where p is the survival rate averaged across all individuals, and the subscripts, t, have been suppressed for ease of reading. At one extreme, we could assume that $Var[s] = 0$. This is to assume that $p_{dom} = p_{sub} = p_{nonter}$, or that there is no variance reduction (sensu Fox and Kendall 2002). If were we to make such an assumption, then the proportion of variance that is attributable to demographic stochasticity in survival (i.e. $Var_{demo}[s_t]/Var[r_t]$), averaged across years, is 0.093 (interquartile range = [0.06, 0.12]). At the other extreme, we could assume that: 1) p_{sub} is equal to the overall average survival rate, p ($= S_t/N_t$), 2) p_{dom} is equal to $p_{sub} + 0.25$,

but constrained to be no greater than one, and 3) p_{nonter} is equal to $p_{nonter}*$, where $p_{nonter}*$ is the value of p_{nonter} required to balance $p = (p_{dom}N_{dom}/N) + (p_{sub}N_{sub}/N) + (p_{nonter}N_{nonter}/N)$, which is the equation representing the overall survival rate in year t. We also constrain p_{nonter} to be greater than 0.1. For example, consider a representative year (i.e. 1985) during which the overall survival rate was 0.73 ($= p = S_t/N_t = 16/22$). Thus, we set p_{sub} equal to 0.73, and p_{dom} equal to 0.98 ($= 0.73 + 0.25$). Given these values for p_{sub} and p_{dom}, and given that in 1985 there were 6 dominant wolves, 13 sub-ordinate wolves, 3 non-territorial wolves, 0.30 is the value of p_{nonter} that yields an overall survival rate of 0.73. For 1985, we applied these values to Eq. 10 and obtain $Var[s] = 0.044$. Using Eq. 9, we obtain $Var_{demo}[s_t] = ((0.73) \times (1 - 0.73) - 0.044)/22 = 6.96 \times 10^{-3}$ for the year 1985. To obtain an estimate of the proportion of variation in annual growth rate that may be attributable to demographic stochasticity in survival we calculated $Var_{demo}[s_t]/Var[r_t]$ ($= 6.96 \times 10^{-3}/0.086 = 0.081$), where $Var[r_t]$ is the sample variance of wolf population growth rate during the period 1971–2002.

Averaged across years, the assumptions described above yield $p_{dom} = 0.98$, $p_{nonter} = 0.73$, and $p_{sub} = 0.53$. Survival differences in real a wolf population (that are not harvested or expanding) are not likely to exceed this. Also for this set of assumptions, the value of $Var_{demo}[s_t]/Var[r_t]$, averaged across years, is 0.081 (interquartile range $= [0.06, 0.11]$). Conveniently, $Var_{demo}[s_t]/Var[r_t]$ does not appear to be overly sensitive to $Var[s]$. That is, the value of $Var_{demo}[s_t]/Var[r_t]$ which ignores the variance reduction effect (0.093) does not differ much, in this case, from the value (i.e. 0.081) which reflects an anticipated upper limit for the variance reduction effect. Nevertheless, because we want to minimize the risk of overestimating the influence of demographic stochasticity in survival, we take 0.081 to be a useful estimate for the average proportion of variance in annual population growth rate that is attributable to demographic stochasticity in survival.

Demographic stochasticity in reproduction

The variance in annual population growth rate that is attributable to demographic stochasticity in reproduction is (Fox and Kendall 2002):

$$Var_{demo}[m_t] = (V_m(E[m_t]) + 1/2V_m(E[m_t])''Var[m_t])/N_t \qquad (11)$$

where N_t is population size in year t, $V_m(E[m_t])$ is the sampling variance in reproduction for an individual with average reproduction (i.e. $E[m_t]$) for year t, $V_m(E[m_t])''$ is the second derivative of the mean-variance relationship, and $Var[m_t]$ is the variance in reproduction among individuals in the population in year t. Ideally, one

would estimate $Var_{demo}[m_t]$ for the entire population; however, doing so would require accounting for the covariance in reproduction between males and females. Because a means for calculating this covariance is not possible, $Var_{demo}[m_t]$ might usefully be calculated for females only (Saether et al. 2000), where the contribution of female pups that survive to winter by each adult female is the number of pups they produce which survive to their first winter, divided by two (we assume half the pups are females). Though useful, this approach likely underestimates $Var_{demo[m]}$ (Lande et al. 2003: 11).

We estimated $Var_{demo}[m_t]$ for the females of the population for each of 26 years between 1971 and 2002 (For 6 years, our field data were inadequate for estimating $Var_{demo}[m_t]$). We estimated $E[m_t]$ and $Var[m_t]$ as the sample mean and sample variance of the number of pups (divided by 2) produced by each female in the population in year t (that survive to nine months of age). We divide by 2 as a means of separating the reproductive contribution of females from males. We estimate the mean–variance relationship by first assuming that dominant wolves in year t have the same expected reproduction, and then by plotting the series of observed population means values of m_t for these dominants against V_m, the series of among-individual variances in m_t. The best-fitting function to this data was $V_m = 0.456m^{0.0173}$ and the second derivative of this expression is $V_m'' = -0.00775m^{-1.983}$.

Using Eq. 11 and the estimating procedures describe above, the estimated proportion of variance that is attributable to demographic stochasticity in reproduction (i.e. $Var_{demo}[m_t]/Var[r_t]$), averaged across years, is 0.259. The interquartile range was [0.21, 0.30].

Because our individual estimates of V_m are based on relatively small sample sizes, we also estimated V_m based on plausible theoretical considerations. Specifically, we assumed that litter size is distributed according to a Poisson distribution truncated at $m = 6$, the largest litter size for Isle Royale wolves, and that the number of females in the litter follows a binomial distribution with an expected value of 0.5. For this assumption, we estimated V_m by repeatedly sampling from this truncated Poisson distribution for different mean values of m ($= 1, 2, \ldots, 6$). For this approach, the mean value of $Var_{demo}[m_t]/Var[r_t]$ was 0.153 for the theoretical approach, the interquartile range was [0.10, 0.19].

To estimate the overall contribution of demographic stochasiticy to the variance in population growth, we added the contribution of survival (Eq. 9) and reproduction (Eq. 11). Although there are reasons to prefer the empirical approach for estimating the contribution of demographic stochasticity in reproduction (i.e. $Var_{demo}[m_t]/Var[r_t] = 0.259$), the theoretical approach (i.e. $Var_{demo}[m_t]/Var[r_t] = 0.153$) also has merit. Moreover, we wish to minimize the risk of overestimating the overall influence of demographic stochasticity.

Therefore, we simply suggest that demographic stochasticity contributes between 23% (=0.153+0.081) and 34% (=0.259+0.081) of the observed variation in population growth rate.

Discussion

The most important predictor of wolf growth rate is the abundance of old moose (i.e. >9 years). Provided that one accounts for the disease-induced population crash of 1980, the number of old moose explains ∼42% of the variation in wolf growth rate (Fig. 5, 6). Age-dependent predation is likely more complex than previous analyses suggest (Hastings 1983, 1984). Moreover, our work suggest that age-dependent predation is likely more important than is generally recognized. Nevertheless, virtually all management-oriented predictions about wolf–ungulate systems ignore age structure in the prey population (Messier 1994, NRC 1997, Bergerud and Elliott 1998, Eberhardt et al. 2003).

Calf abundance, which reflects another important aspect of prey age structure, does not appear to importantly influence wolf population growth rate (Table 4). From this finding arises the need for several considerations. First, we estimate calf abundance in January when calves are about nine months old. It may be that wolf population growth rate is dependent on calf abundance during summer (i.e. June through Sept), but calf abundance in summer and winter may be unrelated because of summer predation and mortality. Alternatively, as our results suggest, predation may not, in fact, be an important influencer of wolf population dynamics, because the caloric value of a calf carcass is substantially less than for an adult carcass. Thus, it may be that the consequences of calf predation are relatively unimportant to wolf population dynamics, but quite important to moose population dynamics.

The second most important source of variation in population growth rate is demographic stochasticity, which accounts for approximately 30% of the variation in wolf growth rate (Fig. 6). For emphasis, the fluctuations caused by demographic stochasticity are inherently unpredictable (in some sense like the influence of climate), but it cannot be said that this variation is unexplained. It is explained by demographic stochasticity (Goodman 1987). Of the variation that may be attributable to biotic or abiotic processes (but not demographic stochasticity), 60% may be attributable to the abundance of old moose (0.60 =0.42/(1 −0.30)). For additional context, the perturbations caused by demographic stochasticity in wolves may have little influence on moose dynamics, because moose growth rate is only modestly affected by the variation in wolf abundance (Vucetich and Peterson 2004).

Much of the variation in wolf growth can be explained only if the population crash of 1980 is taken into account (Table 3, 4). After the population crash, carrying capacity decreased, the strength of density dependence increased, and the influence of old moose decreased (Eq. 5, 7; Fig. 3, 5). Mechanistically, these changes could result from reduced attack rate (Holling 1959) and (or) decrease efficiency of conversion. Insomuch as the population crash was precipitated by disease (i.e. canine parvovirus, CPV-2), our analysis joins a growing list of examples illustrating the general importance of disease impact on vertebrate population dynamics (Packer et al. 1999, Galvani 2003, Male 2003). However, some observations could indicate that disease alone cannot account for the observed dynamics. First, because the number of wolves per moose was very high in 1980; nutritional stress and intraspecific, interference competition may have accounted for some of the decline population. Second, the population crash included substantial adult mortality (Peterson et al. 1998). Although CPV-2 substantially reduces pup survival, it is uncertain whether CPV-2 could have accounted for all the adult mortality that was observed (Kreeger 2003), Third, wolf exposure to CPV-2 ended by 1990 (Peterson et al. 1998). Finally, the Isle Royale wolf population is highly inbred (Peterson et al. 1998). It is plausible that the observed dynamics reflect a strong interaction between disease and inbreeding (Acevodo-Whitehouse et al. 2003).

Fig. 6. Comparisons among several models (Eq. 3, 5, 7) of the proportion of annual variation in wolf population growth rate attributable to different factors. Each bar represents a different model. The kill rate model corresponds to Eq. 3 and Fig. 2. The wolf, moose model corresponds to Eq. 5 and Fig. 3. The wolf, old moose model corresponds to Eq. 7 and Fig. 5. The contribution of demographic stochasticity is equal for all models and based on the calculations described in the text. The amount of variation attributed to unidentified sources is the unexplained variation (i.e. $1 - R^2$) minus contribution of demographic stochasticity.

The indirect influence of winter climate on wolf population growth rate is important, insomuch as winter climate is an important predictor of kill rate (Vucetich and Peterson 2004b) and prey abundance (Mech et al. 1987, Vucetich and Peterson 2004a). However, after accounting for these indirect effects, the direct effect of winter climate on wolf population growth rate appears to be of little or no importance (Fig. 6). In fact, because deep snow can sometimes inhibit the mobility of wolves, it is sensible that increased snowfall, per se, may actually have a slight negative impact on wolf growth rate (Eq. 7). This clarifies a previous analysis suggesting that wolves are more influenced than moose by the combination of direct and indirect influence of winter weather (Post et al. 1999, Post and Forchhammer 2001). Moreover, the direct and indirect influence of winter climate on moose growth is probably more important (Post and Forchhammer 2001, Vucetich and Peterson 2004). Recent studies suggest that, relative to biological factors, climate may commonly have a substantial influence on population dynamics (Ottersen et al. 2001, Stenseth et al. 2002). New insights are likely to arise from focusing more on the discernment between direct and indirect manifestations of climate, and between statistical patterns and mechanisms through which climate operates.

Many conventional theories of predation assume that predator growth rate depends on consumption rate. For many wolf–prey systems, winter kill rate represents the only means of estimating consumption rate. For the population growth rate of Isle Royale wolves, winter kill rate explains only about half of the variation that is explained by the abundance of old moose (i.e. 0.22 vs 0.42). The rate of consumption may be more important than recognized if winter and summer kill rates are poorly correlated (Jedrzejewski et al. 2002), and (or) kill rates are poorly correlated with consumption rates because of losses to scavengers (Vucetich et al. 2004). Applying population models based primarily on density-dependent kill rates for the management and prediction of wolf–prey dynamics (Messier 1994, Boyce 1995, Eberhardt and Peterson 1999) seems of limited value to the extent that wolf growth is poorly predicted by kill rate (Fig. 2), and to the extent that kill rate is poorly predicted by densities of predator and prey (Vucetich et al. 2002).

Because wolves are highly territorial, it is noteworthy that growth rate does not depend directly on wolf density (Eq. 3). Although direct density-dependent predator growth may be an important stabilizing mechanism for predator–prey systems (Rosenzweig and MacArthur 1963), ratio-dependent kill rate (i.e. kill rate depends on the ratio of prey to predator) may be the important stabilizing force of the predator–prey dynamics on Isle Royale (Vucetich et al. 2002).

Per capita growth rate of the Isle Royale wolf population appears to increase linearly with the rate at which wolves kill moose (Fig. 2). The slope of the consumption-growth relationship, suggests that the gross production efficiency of wolves is likely between 0.5% and 1.5%. To our knowledge, the only estimate for production efficiency of a large carnivore is also for Isle Royale wolves but is based on crude estimates of biomass and vital rates of the Isle Royale wolf and moose population (Colinvaux and Barnett 1979). This estimate was 4.9% (precision was not calculated). In contrast with this earlier value, our revised value is consistent with the previously observed inverse relationship between production efficiency with trophic position (Grodzinski and French 1983), and not inconsistent with the notion that efficiency is independent of body size (Hendriks 1999). For context, among small mammals populations, average efficiencies are: 0.7% for insectivores, 2.3% for granivores, 2.6% for omnivores, and 3.4% for herbivores (Grodzinski and French 1983). To our knowledge, the only other estimate for a carnivorous mammal is the least weasel (*Mustela rixosua*, 2.34%, Humphreys 1979).

We conclude with a methodological note. Linear and non-linear regression is a fundamental aspect of ecological research. Regression coefficient estimates may be biased by measurement error, which is pervasive in ecological data. Nevertheless, most ecological studies ignore the influence of measurement error in independent variables (two exceptions include Ludwig and Walters 1981 and Carpenter et al. 1994). Our work illustrates a moderate effect of measurement error on regression parameter estimates. Because theories that include measurement error are beginning to become accessible to ecologists (Fuller 1987, Ruppert et al. 1995, Cheng and Van Ness 1999), study plans for ecological research should routinely include estimates of measurement error. Because these theories have not yet reached maturity, we recommend that results of measurement error models be considered tentative, and presented along with results of traditional regression models.

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