

THE EFFECT OF PREY AND PREDATOR DENSITIES ON WOLF PREDATION

JOHN A. VUCETICH,¹ ROLF O. PETERSON, AND CARRIE L. SCHAEFER

School of Forestry, Michigan Technological University, Houghton, Michigan 49931 USA

Abstract. Predator kills rate (i.e., kills per predator per time) is routinely presupposed to depend exclusively on prey density. However, per capita rates of killing may typically depend on the density of both prey and predator. Unfortunately, our perception of many ecological phenomena may be limited by the inappropriate assumption that kill rates do not depend on predator density. One of many ways to represent the influence of predator density is ratio-dependent predation, where kill rate depends on the ratio of prey to predator rather than the actual numbers of prey and predator. Determining the role of ratio dependency in predation theory has been contentious. Assessments of the influence of predator density on kill rate have been primarily limited to theoretical considerations, indirect evidence, and simplified laboratory demonstrations. We directly observed the influence of both prey and predator density on kill rates in an unmanipulated terrestrial system of large mammals—wolves (*Canis lupus*) and moose (*Alces alces*). Predator density explained more variation in kill rate than did prey density ($R^2 = 0.36$ vs. $R^2 = 0.17$, respectively). Moreover, the ratio-dependent model greatly outperformed the prey-dependent model. Nevertheless, the ratio-dependent model failed to explain most of the variation in kill rate (i.e., $R^2 = 0.34$). The ratio-dependent–prey-dependent controversy may dissipate with greater appreciation and acknowledgment that both models may be overly simplistic, both have value, and neither deserves primacy.

Key words: *Alces alces*; *Canis lupus*; functional response; Isle Royale National Park (Michigan, USA); kill ratio, per capita; moose–wolf system; predation, prey-dependent vs. ratio-dependent; predator kill rates; predator–prey dynamics.

INTRODUCTION

Fundamental conceptions of predation evolved slowly during the 20th century. In the 1920s, predation was modeled according to the chemical law of mass action, where per capita kill rate increases linearly with prey density (Lotka 1925, Volterra 1926). Although this theory may capture essential dynamics of some populations (e.g., Elton and Nicholson 1942, Huffaker 1958), inadequacies were quickly noted (e.g., Thompson 1937, Smith 1952). In the 1950s, theoretical considerations and behavioral experiments gave rise to other chemical models where per capita kill rate increases asymptotically with prey density (prey-dependent predation; Holling 1966). This theory forms the foundation of five decades of predation research (Taylor 1984, Kerfoot and Sih 1987, Boyce 2000) and underlies paradigms of population regulation (Hairston et al. 1960, Fretwell 1977, Oksanen et al. 1981). However, prey-dependent models have been criticized for being characterized by several allegedly unusual properties (Arditi and Ginzburg 1989, Ginzburg and Akçakaya 1992, Akçakaya et al. 1995): (1) overexploitation of prey and destabilization of predator–prey interactions in response to increased prey carrying capacity (i.e., the paradox of enrichment, Rosenzweig 1971); (2) inde-

pendence between prey equilibrium density and prey growth rate (Oksanen et al. 1981); (3) the impossibility of prey equilibria that are both low and stable, i.e., the paradox of biological control (Arditi and Berryman 1991); and (4) the indirect positive effect of increased primary productivity on predators prevents herbivores from increasing in food chains with even numbers of trophic levels, but not in food chains with odd numbers of trophic levels (Hairston et al. 1960; Arditi and Ginzburg 1989, the situation is more complex for food webs [Polis and Strong 1996]).

Whether these properties are really all that unusual can be rightly contested (Abrams 1994, 1997). For example, the paradox of enrichment has been reported to occur in microcosm experiments (Holyoak 2000). Moreover, prey density is an important determinant of per capita kill rate, and prey-dependent models have been and continue to be useful. However, like all simple models, prey-dependent models are limited, and these limitations have motivated assessments of the notion that additional factor(s) are also generally important determinants of the per capita kill rate.

During the past 25 yr, models have been developed to account for the manner in which both predator density and prey density affect kill rate (Beddington 1975, DeAngelis et al. 1975, Arditi and Ginzburg 1989, Akçakaya et al. 1995). Factors that may lead to predator-dependent kill rates include: (1) various types of be-

Manuscript received 12 July 2001; revised 9 April 2002; accepted 12 April 2002.

¹ E-mail: javuceti@mtu.edu

havior by prey and predator, such as predator avoidance (Abrams 1993), group hunting (Cosner et al. 1999), and interference among predators (Beddington 1975); (2) the limitation of the predator population by resources other than prey (Abrams 1994); and (3) the allocation of prey among predators (Arditi and Ginzburg 1989). Predator dependence via prey allocation is thought to arise from processes that generate variation in vulnerability among individual prey, such as prey refugia, age- or size-structured prey populations, or spatial heterogeneity (Abrams and Walters 1996). Moreover, spatial heterogeneity may represent a generic generator of predator dependence (Keeling et al. 2000). Because many natural systems may be characterized by one or more such factors, predator-dependent models accommodate what would seem to be a common phenomenon in nature (Abrams and Ginzburg 2000). Predator-dependent models also lead to the resolution of many of the purported problems that characterize prey-dependent models, and are consistent with numerous observed patterns of community structure (Hassell 1978, Abrams 1992, 1993, Akçakaya et al. 1995). Although many of purported inadequacies of prey-dependent models can also be rectified within the framework of prey-dependent theory (Abrams 1994), predator dependency remains an important topic for investigation.

Aside from the issue of whether predator density is generally important is debate concerning how predator dependence should be incorporated into existing theory. One view seems to be that because predator dependence arises from a variety of factors, prey-dependent models should be tailored for specific situations according to the specific factors thought to cause predator dependence (see Abrams 1994, Abrams and Ginzburg 2000). Another view seems to be that ecological thinking would be advanced by blanket replacement of prey-dependent models with some generic form of predator dependency, except when specific situations dictate the need for more specific formulation (Akçakaya et al. 1995, Abrams and Ginzburg 2000). A generic form that has been suggested is ratio dependency, where kill rate depends on the ratio of prey to predator rather than the actual numbers of prey and predator (Arditi and Ginzburg 1989). Mechanistically, ratio dependency arises by replacing the constant prey detection rate (a) of the prey-dependent formulation with a rate that decreases monotonically with predator density (i.e., a/P ; see Table 1).

These alternative views underlie a decade-long debate over the value of ratio dependency, and antipathetic assertions that establishment of ratio dependency would represent a “major clarifying step for the future of ecology (Slobodkin 1992:1566)”, and that “widespread acceptance of this idea would set predator-prey theory back by decades (Abrams 1994:1842)”. Although important philosophical issues underlie these unresolved differences (Abrams and Ginzburg 2000),

conceptual progress is hobbled by the relative paucity of direct empirical data. Since 1989, when ratio dependency was first formalized, as far as we know there has been only a single direct assessment of the influence of predator density and prey density on kill rate (i.e., Reeve 1997, see also Arditi and Akçakaya 1990, Abrams and Ginzburg 2000). Ratio dependency has been supported largely on the basis that such models predict positive correlations in abundance among trophic levels—a pattern consistent with observation and experimentation (Arditi and Ginzburg 1989, Arditi et al. 1991a, b, Arditi and Saiah 1992, Ginzburg and Akçakaya 1992, Abrams 1994, Akçakaya et al. 1995). However, such patterns represent indirect evidence of ratio dependency and may be explained by other processes (Abrams 1994). The lack of direct evidence has also led to theoretical considerations playing an important role in evaluating the appropriateness of ratio dependency (Arditi and Ginzburg 1989, Freedman and Mathsen 1993, Abrams 1994, Yodzis 1994, Akçakaya et al. 1995, Abrams 1997). For example, the plausibility of ratio dependence may be doubted because only a limited set of plausible parameter values appear to be associated with persistence in ratio-dependent systems (Freedman and Mathsen 1993, Abrams 1994).

Advancement in this theory-laden topic requires direct empirical assessments of the factors that may affect per capita kill rates. However, direct assessments of per capita kill rates can be limited by bias associated with prey depletion (Abrams 1994), the artificial setting of laboratory experiments, and short time scales that reveal behavioral, but not population dynamical, aspects of predation (Abrams 1994, Akçakaya et al. 1995). While avoiding these pitfalls, we present a direct assessment of the influence of predator density and prey density on the per capita kill rate for an unmanipulated system on a time scale relevant for population dynamics. In doing so, we provide evidence required for assessing the influence and nature of prey density and predator density on per capita kill rates.

METHODS AND ANALYSIS

Data Collection

Our observations consist of predator (wolves, *Canis lupus*) abundance, estimates of prey (moose, *Alces alces*) abundance, and the number of kills made by predators during winter observation sessions conducted each January and February from 1971 to 2001. Data were collected in Isle Royale National Park, (Michigan, USA), an island (544 km²) in Lake Superior where wolves and moose interact essentially as an isolated single-predator–single-prey system (Peterson and Page 1988). Immigration and emigration is likely zero, or at worst negligible, for wolves and moose. Moose comprise >90% of the biomass in wolf diet (Peterson and Page 1988); other species capable of preying upon

TABLE 1. The relative performance of instantaneous-kill-rate models fit to empirical data from the wolf (P) and moose (N) populations in Isle Royale National Park, USA (1971–2001).

Model†	Form	$\Delta‡$	Rank§	$w $	R^2
Constant	a	36.4	12	4.21×10^{-9}	0.0
Prey dependent					
Linear (Lotke 1925, Volterra 1926)	aN	36.5	13	4.00×10^{-9}	0.0
Asymptotic (Holling 1959)	$aN/(1 + ahN)$	20.9	9	9.91×10^{-6}	17.1
Sigmoid (Holling 1959)	$aN^2/(1 + ahN^2)$	21.6	10	6.69×10^{-6}	16.4
Exponential (Rosenzweig 1971)	$a(1 - \exp[-bN])$	20.7	8	1.09×10^{-5}	17.3
Ratio dependent					
Linear	$a(N/P)$	56.8	14	4.75×10^{-13}	0.0
Linear	$a + b(N/P)$	3.7	6	0.052	30.7
Asymptotic (Arditi and Ginzburg 1989)	$aN/(P + ahN)$	0	1	0.335	33.6
Sigmoid	$aN^2/(P + ahN^2)$	6.1	7	0.015	29.1
Exponential (Gutierrez 1992)	$a(1 - \exp[-bN/P])$	0.8	2	0.221	33.1
Predator dependent					
Nonlinear, zero intercept (Hassell and Varley 1969)	aN/P^m	33.6	11	1.68×10^{-8}	5.0
Nonlinear, zero intercept (Hassell and Varley 1969)	$aN/[P^m + ahN]$	2.2	4	0.112	33.6
Linear, non-zero intercept (Beddington 1975, DeAngelis et al. 1975)	$aN/(bN + P - c)$	1.3	3	0.177	34.3
Nonlinear, non-zero (Yodzis 1994)	$aN^n/[b(c + P)^m + N^n]$	¶	¶	¶	0
Nonlinear, zero intercept	$a(1 - \exp[-bN/P^m])$	2.7	5	0.086	33.2

Note: N is prey abundance, P is predator abundance, and a , b , c , h , m , and n are parameters to be estimated from the data.

† Prey- and ratio-dependent models are described according to their shape in relation to kill rate. Predator-dependent models are described by the shape of the corresponding predator isocline, assuming the numerical response is linearly related to the functional response (see Yodzis 1994). Some of the ratio-dependent models are expressed in simplified terms, rather than in terms of the ratio, N/P . Sources are in parentheses.

‡ Δ = the AIC_c (Akaike's information criterion, corrected for small sample size) for the model of interest minus the smallest AIC_c for the set of models being considered.

§ The rank order of the model on the basis of Δ .

|| The AIC_c weight.

¶ The model could not be estimated. Four of the five parameters were unstable and not significantly different from zero for all sets of initial conditions (see *Results*).

moose are absent, and hunting is prohibited on the island.

The wolf population was censused annually from 1971 to 2001 by use of fixed-wing aircraft. Confidence in census accuracy is increased by: (1) the frequent visibility of entire wolf packs at a single location and time and (2) making several complete counts during each winter survey. Moose abundance was estimated annually from 1988 to 2001 by aerial survey using fixed-wing aircraft (Peterson and Page 1993). From 1971 to 1991 moose abundance was estimated by cohort analysis. The method of cohort analysis used here is similar to that described by Solberg et al. (1999). For complete details see J. A. Vucetich and R. O. Peterson, *unpublished manuscript*. Between 1988 and 1991 estimates of moose abundance are available for both aerial surveys and cohort analysis. The results presented below are based on estimates derived from cohort analysis. However, the results are qualitatively identical and quantitatively nearly identical when cohort analysis estimates are replaced with aerial survey estimates during the period of overlap.

During winter wolves hunt and travel in groups called "packs" (Olson 1938, Murie 1944). Kill rates were calculated for each wolf pack during each winter session from 1971 to 2001. Each kill rate was based

on ~44 d of observation (median = 44 d, interquartile range = [38–47 d]), during which travels and kills of wolf packs were determined by aerial observations of tracks in snow (Mech 1966, Peterson 1977). Per capita kill rates were calculated 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. With 31 yr of winter observations and typically three packs in the population at a time (range = 2–5 packs), we obtained 94 measures of kill rate. Additional details on these field methods are reported elsewhere (i.e., Thurber and Peterson 1993, Peterson et al. 1998).

Analysis

We compared our kill-rate data to several models each belonging to one of three classes of *instantaneous* kill-rate models (Table 1): (1) dependent exclusively on prey, (2) dependent on both prey and predator (hereafter, predator–prey dependent), and (3) dependent on prey and predator, but only through the ratio. This set of kill-rate models can produce a predator isocline with any shape (i.e., linear, concave up, or concave down) or y-intercept (i.e., no intercept, zero intercept, and nonzero intercept) (see Yodzis 1994).

Estimation of model parameters was based on min-

imizing the (Gaussian) error sum of squares (i.e., $\Sigma(X_{\text{observed}} - X_{\text{predicted}})^2$; see Zar 1984:263). Parameter estimates were calculated by the nonlinear regression routine of the software S-PLUS 2000 (MathSoft, Seattle, Washington, USA). Results were also confirmed with the software SigmaStat Version 1.0 (Jandel Corporation, San Rafael, California, USA). Selection of the most parsimonious model was based on the information-theoretic approach (Burnham and Anderson 1998, Anderson et al. 2000). Suitable models with the smallest AIC_c (Akaike's information criterion, corrected for small sample size) and Δ were selected as the best model; Δ equals the AIC_c for the model of interest minus the smallest AIC_c for the set of models being considered. AIC_c relies on principles of parsimony and information theory to estimate the relative distance between a model and the underlying process that created the observed data. Models with $\Delta < 2$ are considered worthy of consideration (Burnham and Anderson 1998). From AIC_c values we also calculated AIC_c weight of each model i (w_i). The ratio $w_i:w_j$ estimates how many times more support the data provide for model i than model j .

We also conducted four follow-up analyses designed to increase confidence in the initial assessment. First, we examined models that are exclusively predator dependent (Table 2). Second, we addressed the possibility that adequate descriptions of kill rate require accounting for a dramatic decline in wolf abundance that occurred in the early 1980s. Between 1980 and 1982, the wolf population declined from 50 to 12 individuals. Canine parvovirus was the probable proximate cause of the crash, and genetic deterioration may have been contributing to what may be altered dynamics between wolves and moose since 1980 (Peterson et al. 1998, Peterson 1999). To test for this potential change in dynamics, we estimated and assessed models where indicator variables were used to model differences in parameter values before and after the 1980 population crash. For example, to modify a type II prey-dependent functional response to account for time-dependent predator handling time (h) we used the expression: $aN/(1 + a(h + (Ih'))N)$, where N is prey density, a is attack rate, $I = 0$ for years prior to 1980, $I = 1$ for years after 1980, and the term Ih' represents the change in handling time for years after 1980. We also estimated and compared models where kill rates were assumed to be prey dependent during one time period and ratio dependent during the other time period.

Third, we compared models (Table 3) where the dependent variable was kills per month rather than kills per predator per month (Table 1). This analysis alleviates statistical concerns regarding regression where the dependent and independent variables are both functions of predator density.

Fourth, we compared instantaneous kill-rate models (Table 3), which account for prey depletion that occurs during each season's period of observation as predators

TABLE 2. The relative performance of models that isolate the influence of predator density on kill rate.

Form [†]	Δ [‡]	w [§]	R^2
$c + aP^{-1}$	0	0.63	35.5
$c + a(b + P)^{-1}$	2.18	0.21	35.5
$a(b + P)^{-1}$	3.29	0.12	33.2
aP^{-1}	5.72	0.04	30.0

[†] P is predator density; a , b , and c are parameters estimated from the data.

[‡] Δ = the AIC_c (Akaike's information criterion, corrected for small sample size) for the model of interest minus the smallest AIC_c for the set of models being considered.

[§] The AIC_c weight.

consume prey (Rogers 1972, Abrams and Ginzburg 2000). In any event, prey depletion was minimal (i.e., median = 1.6%; interquartile range = [1.1%, 2.3%]). For the integrated models, parameter estimates were calculated by a program written in the programming language C++ that considered the error sum of squares for the entire plausible parameter space. Standard software packages cannot estimate the integrated models because the dependent variable (i.e., number of kills) cannot be isolated to a single side of the equality (Table 3; Reeve 1997). Standard errors and P values for parameters of the instantaneous models were estimated by observing the distribution of parameter estimates for 1000 bootstrapped realizations of the original data set (Efron and Tibshirani 1993).

RESULTS

Each of the prey-dependent models performed dismally compared to the other models (Δ 's > 20 ; Table 1). The asymptotic form of a ratio-dependent model performed best ($\Delta = 0$). It had 30,700 times more support than the best (i.e., asymptotic) prey-dependent model. The asymptotic ratio-dependent model also explained approximately twice as much variation in kill rates as did the asymptotic prey-dependent model (34% vs. 17%; Fig. 1; Table 4). The similar performance of the exponential and asymptotic ratio-dependent models ($\Delta = 0.8$ and 0.0) may be attributable to similarities in their form.

The predator-prey-dependent model derived by Beddington (1975) ranked third, and its Δ (=1.3) suggests further consideration of this model is warranted. However, this model may be over-parameterized. In this model, c , which corresponds to the intercept of the predator isocline, did not differ significantly from zero ($c = 6.75 \pm 5.62$ [mean ± 1 SE]; $P = 0.23$). Moreover, the estimate for c was positive, indicating predator persistence in the absence of prey. The imprecise and, most certainly, biased estimate of c indicates that the estimate is an unrealistic extrapolation arising from a dearth of observations for prey at low densities. Although the underlying process may be well represented by a model with a nonzero intercept like that of Beddington (1975), 31 years of data from Isle Royale

TABLE 3. The relative performance among models expressed in terms of kill rate, kills per month (rather than per capita kill rate) and the relative performance among models of integrated kill rate (dependent variable = kills).

Description	Form [†]	Δ [‡]	w [§]	R^2
Dependent variable: kills/mo				
Prey dependent	$aNP/(1 + ahN)$	14.4	0.001	12.4
Ratio dependent	$aNP/(P + ahN)$	0	0.729	24.9
Predator and prey	$aNP/(bN + P - c)$	2.0	0.271	25.1
Dependent variable: kills				
Asymptotic ratio dependent	$N[1 - \exp(-aT + bKP^{-1})]$	0	0.737	36.1
Predator dependent	$N[1 - \exp(-aTP^{1-m} + bKP^{-m})]$	2.1	0.262	27.1
Asymptotic prey dependent [¶]	$N[1 - \exp(-aTP + bK)]$	12.5	0.001	25.9

Notes: Models were fit to empirical data from the wolf and moose populations in Isle Royale National Park, Michigan, USA (1971–2001). Comparisons based on AIC_c between, for example, the instantaneous and integrated forms of the ratio-dependent model are not possible because: (1) AIC_c can only be compared among models with exactly the same set of observations for the dependent variable, and (2) the dependent variable is “kills per wolf per month” for the instantaneous models and “kills” for the integrated models.

[†] N = prey (moose) density, P = predator (wolf) density, K = the number of kills observed in T , and lowercase letters are model parameters.

[‡] Δ = the AIC_c (Akaike’s information criterion, corrected for small sample size) for the model of interest minus the smallest AIC_c for the set of models being considered (in this table).

[§] The AIC_c weight.

^{||} Derived from Hassell-Varley model of Table 1 (see Reeve 1997).

[¶] See Rogers (1972).

(Michigan, USA) are inadequate for such an assessment.

Similarly, two of the predator–prey-dependent models corresponding to nonlinear predator isoclines performed reasonably well (i.e., $\Delta = 2.2$ and 2.7 ; Table 1). However, these models were characterized by non-significant parameter estimates ($a = 0.67 \pm 0.86$ [mean ± 1 SE] for the model with $\Delta = 2.2$; $b = -7.2 \pm 6.8$ for the model with $\Delta = 2.9$). The apparent over-parameterization of these models suggests that either the underlying relationship is well approximated by a linear predator isocline, or the Isle Royale data are inadequate for discerning such nonlinearity (see Carpenter et al. 1994). Finally, the predator–prey-dependent model presented by Yodzis (1994), which corresponds to a nonlinear predator isocline and nonzero intercept is apparently so over-parameterized that for any set of initial conditions four of the five model parameters were unstable and not significantly different from zero (i.e., all P ’s > 0.50).

Not surprisingly, the constant model (i.e., a), and the models that are linear with respect to a (i.e., aN , aN/P^m , $a(N/P)$) performed poorly overall and within each of their respective classes (Δ ’s > 33). Also not surprisingly, the sigmoidal models of each class performed less well than did the asymptotic models of the corresponding class (Table 1). Again, because of the dearth of observations for prey at low density, it is unclear whether the underlying process is well represented by an asymptotic model or whether available data are inadequate for assessing a sigmoidal relationship (see Marshal and Boutin 1999).

The high performance of the ratio-dependent (and predator–prey-dependent) model(s) suggest that in-

creased predator density tends to reduce kill rates. The basic structure for expressions relating the effect of predator density to kill rate is $1/P$ (e.g., the Beddington model). Thus, to assess the role of predator density, we examined four models based on this structure (Table 2). The best of these models received ~ 3 times more support than the second-ranked model (Table 2). Moreover, on the basis of proportion of total variation explained, kill rates are more sensitive to changes in predator density ($R^2 = 0.36$; Table 2) than prey density ($R^2 = 0.17$; Table 1).

Per capita kill rates appear to be well described without explicitly accounting for potential changes in dynamics associated with the population crash of 1980. More specifically, prey-dependent and ratio-dependent models including indicator variables to account for time-dependent constants (see *Methods and analysis: Analysis*, above) were less parsimonious (i.e., $\Delta > 16.4$ for all prey-dependent models with indicator variables, and > 1.6 for all ratio-dependent models with indicator variables). Models where dynamics were assumed to be prey dependent during one time period and ratio dependent during the other time period were also less parsimonious (i.e., $\Delta > 7.7$) than the simple asymptotic ratio-dependent model.

The comparisons depicted in Table 1 are similar to comparisons among models where the dependent variable was kills per month (Table 3) and to comparisons among integrated models that account for prey depletion (also Table 3). In both sets of comparisons, the ratio-dependent model greatly outperformed the prey-dependent model (Table 3). Among models depending on kills per month, and among integrated kill-rate models, the ratio-dependent model received more than 700

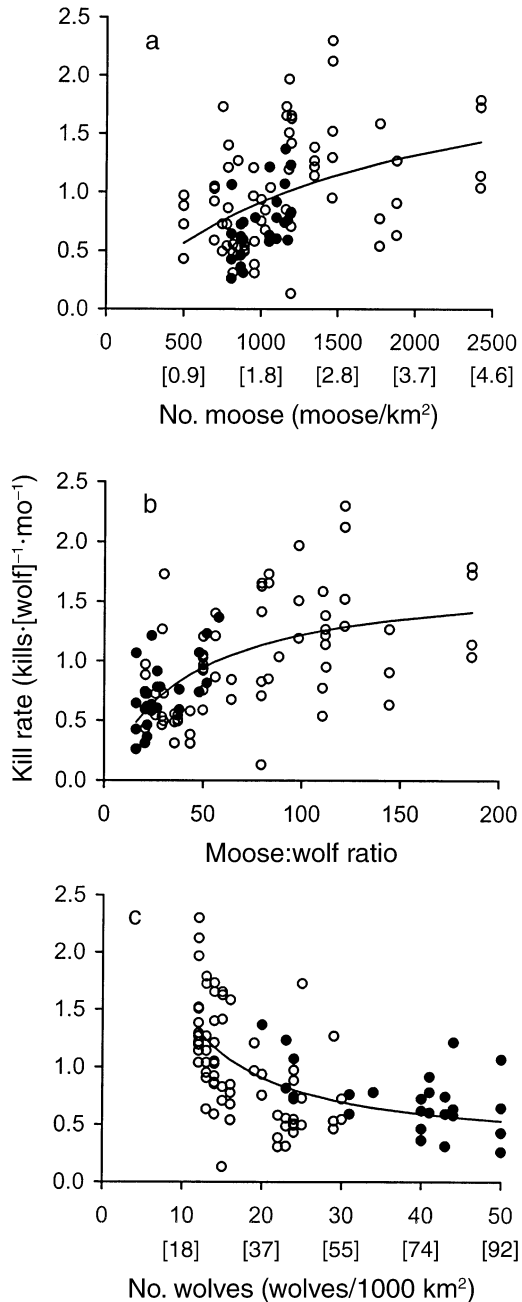


FIG. 1. The effect of (a) prey density, (b) prey to predator ratio, and (c) predator density on the kill rate (i.e., kills per wolf per month). Each data point represents an estimate for each pack present in Isle Royale National Park (Lake Superior, Michigan, USA) during each year from 1971 to 2001. The solid lines represent the best-fitting models (see Tables 1 and 2). Solid symbols represent observation prior to 1980, and open symbols represent data after 1980, when the population crashed from 50 to 12 wolves.

times more support than the prey-dependent model. The predator-prey-dependent models also performed well, but were over-parameterized similar to the Yodzis model (Table 1) and Beddington model (Table 4). The

proportions of total variation explained by the instantaneous ($R^2 = 0.34$; Table 1) and integrated ($R^2 = 0.36$; Table 3) ratio-dependent models were similar. However, the proportion of total variation explained by the ratio-dependent model with kills per month as a dependent variable was somewhat lower (i.e., $R^2 = 0.25$).

DISCUSSION

Implications for understanding wolf predation

The per capita rates at which Isle Royale (Michigan, USA) wolves kill moose is poorly described by prey-dependent models, and much better described by the asymptotic ratio-dependent model (Table 1, Fig. 1). To this extent, our results are consistent with the hypothesis that correlations in wolf and prey density across ecosystems (Arditi et al. 1991a, see also Fuller 1989) arise from per capita kill rates that are approximated by the ratio-dependent models.

Moreover, wolf density was a better predictor of kill rate than was moose density (Fig. 1, Table 2). The importance of wolf density is consistent with the observation that wolf-prey interactions are characterized by many of the factors expected to generate predator interference and promote predator-dependent kill rates (see Abrams and Ginzburg 2000). Wolves exhibit group hunting, aggressive interactions among groups, and social interactions that are time consuming and density dependent. Predator dependence may also be promoted by the limited number of sites where prey can be captured easily (e.g., winter yarding areas). In moose populations, the proportion of prey vulnerable to predation varies greatly with age structure, because juvenile and senescent moose are more vulnerable to wolf predation (Peterson et al. 1984, see also Murie 1944). Finally, wolves and their prey interact in a spatially heterogeneous environment (see Keeling et al. 2000). Despite intensive study of these populations, it would be nearly impossible to build a useful mechanistic model capable of disentangling how each of these factors give rise to predator dependence. The phenomenological nature of the ratio-dependent model represents a critical first step for better understanding the dynamics of wolf-prey systems. This complexity probably typifies many or most natural systems.

The inadequacy of prey-dependent kill-rate models does not, by itself, imply that moose predation by wolves is well described by ratio-dependent models. On the contrary, the ratio-dependent model explained only 34% of the variation. The rate at which wolves prey on moose appears to be substantially more complex than: $aN/(P + ahN)$ (Table 4). Frustratingly, more complex models depending on prey and predator density do not explain enough additional variation to be justified on the basis of parsimony (Table 1). Nevertheless, it is significant that a single variable (the ratio of prey to predators) explains as much variation as it does when one considers the many factors that could

TABLE 4. Parameter estimates for the best model within each of the four model classes (i.e., prey, ratio, predator-prey, and integrated; see Tables 1 and 3).

Model [†]	Parameter \pm 1 SE	<i>P</i>
$aN/(1 + ahN)$	$a = 1.48 \times 10^{-3} \pm 3.35 \times 10^{-4}$	<0.01
	$h = 0.42 \pm 0.13$	<0.01
$aN/(P + ahN)$	$a = 4.19 \times 10^{-2} \pm 7.51 \times 10^{-3}$	<0.01
	$h = 0.58 \pm 6.42 \times 10^{-2}$	<0.01
$aN/(bN + P - c)$	$a = 3.39 \times 10^{-2} \pm 8.18 \times 10^{-3}$	<0.01
	$b = 2.25 \times 10^{-2} \pm 5.63 \times 10^{-3}$	<0.01
	$c = 6.75 \pm 5.62$	0.23
$N[1 - \exp(-at + aKP^{-1})]$	$a = 3.1 \times 10^{-4} \pm 4.7 \times 10^{-5}$	<0.01
	$b = 64 \pm 7.9$	<0.01
$aNP/(P + ahN)$	$a = 1.06 \times 10^{-2} \pm 1.77 \times 10^{-3}$	<0.01
	$h = 2.30 \pm 0.38$	<0.01

[†] In the models, N = prey (moose) abundance, P = predator (wolf) abundance, K = number of kills observed, and lowercase letters are model parameters.

plausibly have important influences on kill rate (e.g., climate, social structure, age structure of prey and predator, and spatial heterogeneity in prey and predator habitat quality). For example, even though disease has been an important component of the dynamics of the Isle Royale system, wolf and moose density are nevertheless useful predictors of kill rate.

Although the lack of stability observed in the Isle Royale wolf-moose system is at odds with the tendency for deterministic models of ratio-dependent predation to produce highly stable point equilibria, highly variable population abundances might be explained if a substantial portion of the temporal variation in kill rate was inherently stochastic. In fact, interannual variability in winter climate may explain an additional 10–15% of the total variation in kill rates for Isle Royale wolves and moose (J. A. Vucetich and R. O. Peterson,

unpublished data). Also, stochasticity may arise if chance predation events lead to substantial deviations from expected rates. Such stochasticity may be important for predation in locally small populations (e.g., rare or endangered predators or prey, predator-prey systems in fragmented landscapes). In any event, stochasticity associated with kill rates may have important and potentially nonintuitive implications for the dynamics of predator-prey systems (May 1976, Markus et al. 1987, Boyce 2000), and warrants further study.

The application of models to management and conservation

Our study highlights a dilemma for the interpretation and application of empirically based studies of predation (see also Yodzis 1994, Abrams and Ginzburg 2000):

1) The ratio-dependent model predicts a linear predator isocline with a positive slope that is determined by empirical observation, but is restricted to having a zero intercept. A predator isocline that passes through the origin is problematic because it predicts predator persistence at vanishingly small numbers of prey (Fig. 2; Abrams 1994), and has been the basis for justifying misguided management (Yodzis 1994).

2) The prey-dependent model relies on empirical observation to predict the value at which the predator isocline crosses the prey axis, but restricts the isocline to being vertical. A vertical predator isocline excludes the possibility of potentially important dynamical properties (e.g., in a simple prey-dependent model the prey equilibrium is independent of increased prey growth rate and carrying capacity; Arditi and Ginzburg 1989, but see Abrams 1997).

3) The predator-prey-dependent model predicts a linear isocline with a positive slope and (nonzero) intercept that are both determined by the data, but the intercept cannot be estimated accurately or precisely due to a dearth of observations at low prey density (Fig. 2).

Although the ratio-dependent model solves the prey-dependent model's greatest weakness, and vice versa,

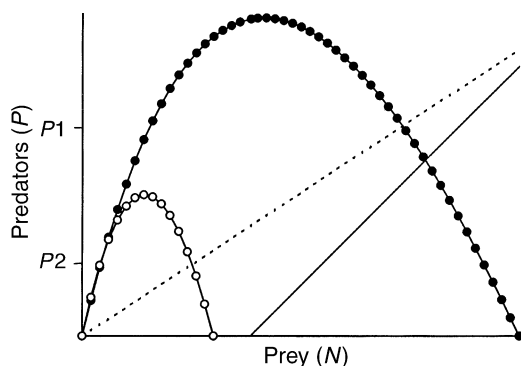


FIG. 2. The effect of prey reduction on predators with ratio-dependent and predator-dependent kill rates. Equilibria occur wherever prey isoclines (lines with circles) intersect predator isoclines (lines without circles). Dramatic reduction in the prey carrying capacity (shifting from line with solid circles to line with hollow circles) causes dramatic population decline for ratio-dependent predators (dashed line) and extinction for predator-prey-dependent predators (solid line). For example, as prey carrying capacity shifts from high to low, equilibrium abundance for ratio-dependent predators shifts from P_1 to P_2 . Contrary to common sense, ratio-dependent predators persist even when prey are extremely rare (see Yodzis 1994).

neither model has a completely satisfying structure. In contrast, the predator–prey-dependent model possesses a satisfying model structure; however, it depends on parameters that often will not be reliably estimatable from field data (Tables 1 and 4). A useful model would seem to require both appropriate model structure and reasonable parameter estimates. Empirically based models may also require the flexibility to retain what is assumed to be appropriate structure even if the data are unavailable to support such complexity (see Boyce [2000] for a comparable philosophy; cf. Burnham and Anderson 1998). If common sense is used to veto the model structure supported by available data, then the properties of the model not explicitly favored by the data should be clearly identified and isolated.

Fortunately, the ratio-dependent model is easily adjusted to accommodate this approach. Specifically, a predator isocline with a negative intercept can be achieved by subtracting from N (prey abundance) the threshold number of prey (τ) below which a predator population cannot be supported:

$$\text{kill rate} = a(N - \tau) / [P + ah(N - \tau)] \quad (1)$$

where P = predator abundance. If the numerical response is a linear function of the kill rate (Yodzis 1994, Ginzburg 1998), this model predicts a linear predator isocline with a slope of $a(q - h)$ and an intercept of $\tau a(h - q)$, where q is trophic efficiency (e) divided by mortality (m). In a mechanistic manner, this modification transforms the ratio-dependent model into a predator–prey-dependent model that can be expressed in terms of Beddington's (1975) model. This modification would be especially pertinent for analyzing how human harvest might impact persistence. Most importantly, if available data were too sparse to support any value other than zero for τ , other bases might allow one to judge some other value of τ , and the effect of such subjective modification would be isolated and could be easily assessed.

To illustrate the application of this modification, we used the data from Isle Royale. First, we fit the model to the data with τ as a free parameter. The data suggest that τ is $5.3 \times 10^{-6} \pm 405.8$ (mean ± 1 SE; $P = 1.00$). This result is analogous to the nonsignificant estimate of c in the predator–prey-dependent model (Table 4). Because wolf predation was not observed for small values of N , these estimates represent an extrapolation. The estimate of τ can also be judged unreliable because $\tau = 0$ corresponds to a model structure that predicts wolf persistence for extremely low moose abundances (i.e., predator isocline with zero intercept). Thus, we may be justified, or at least aboveboard, in selecting a value for τ based on more reliable information. Information about τ is contained in a correlative study of wolf and moose abundances across North American study sites (Messier 1994). The correlation produced by Messier (1994) predicts that four wolves could be supported by 82 ± 81 (95% CI) moose. (Because of

generational overlap, four is a reasonable value for the smallest number that can be considered a wolf population.) Under some circumstances (e.g., Yodzis 1994), a conservative estimate might be appropriate and thus justify a value as high as $82 + 81 = 163$ for τ (Fig. 3). In the absence on this sort of information, even a well-reasoned value of τ might be more appropriate than assuming its value to be zero, as in the ratio-dependent model. For example, because a pack of four wolves needs to kill a moose approximately every 15 d to survive (Thurber and Peterson 1993), and because a typical recruitment rate for a moose population is $\sim 13\%$ (Peterson and Vucetich 2001), τ should be ~ 190 ($= 365 \text{ d} \div 15 \text{ d per moose} \div 0.13$) moose (Fig. 3). Although assigning a value to τ may be reasonable if appropriate data are unavailable, assigning a value of τ that conflicts with the data may be less appropriate. To assess this possibility, we calculated Δ for models with assumed values of τ ($\Delta = 0.0$ for $\tau = 0$ [see Table 1]; $\Delta = 0.6$ for $\tau = 82$; $\Delta = 2.0$ for $\tau = 190$).

This illustration highlights the challenge for science-based management to carefully balance empirical observation, theoretically derived knowledge, and common sense. In some cases, it may be “well worthwhile to add one or two parameters to get results that make sense” (Abrams 1997:170). Unfortunately, it can be easy to underestimate the difficulty of clearly identifying and isolating portions of a model more supported by “common-sense” than by empirical observation. Although these considerations are critical for better management and conservation, they may be less useful for advancing scientific understanding.

Implications for resolving the controversy

A great deal of theoretical weight supports the notion that predator density can affect per capita kill rates (Abrams and Ginzburg 2000; but see Rosenzweig and MacArthur 1963). Theory also suggests that the mechanisms underlying this influence are diverse, and that these mechanisms, collectively, may occur commonly in nature (Abrams and Ginzburg 2000). Although direct measurement of the influence of predator density and prey density on kill rate is rare, the only experimental assessment (Reeve 1997) and the only observational assessment (this study) support the claim that predator density can be an important influence on per capita kill rate. Nevertheless, an assessment of the generality of predator dependence currently eludes empirical confirmation. The prevalence of various mechanisms that might lead to predator dependence is even less certain. Future studies should aim for a better empirical understanding of the conditions (e.g., behavioral, life-history, and environmental characteristics) for which an accounting of predator dependence is essential. Although additional direct measurements will likely increase our understanding, the notions that predator dependence is frequently important and that the causal

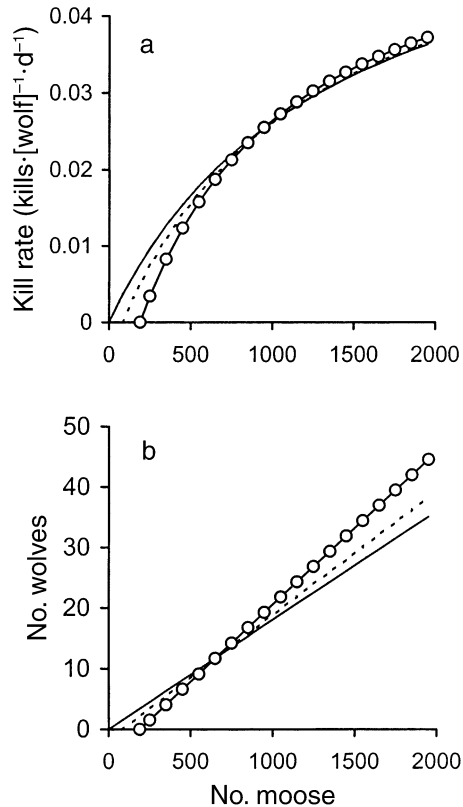


FIG. 3. The effect of imposing a minimum threshold number (τ) of prey (moose) below which predators (wolves) cannot persist on the predicted (a) per capita kill rate and (b) predator isocline. The values for τ are 0 moose (solid line), 82 moose (dashed line), and 190 moose (circles); see Discussion for justification. The curves in (a) were generated from Eq. 1, and parameters were estimated from the data (see Fig. 1). The curves in (b) are obtained by assuming that the numerical response is linearly related to the functional response and that q , the ratio of trophic efficiency to predator mortality rate, is 0.20 (see text below Eq. 1). The curves depicted in (a) occur when the number of predators (P) is 20 (see Eq. 1).

mechanisms are likely to be varied do not seem to elicit much controversy (see Abrams and Ginzburg 2000).

Controversy seems to arise over the relative value of ratio-dependent and prey-dependent models. Some aspects of the controversy seem to have been resolved. It is no longer generally accepted that primacy should be given to a process (e.g., ratio dependence) on the basis of observing a pattern (e.g., correlated abundances among trophic levels) that can be predicted by many processes.

The controversy may persist, in part, from attempts to reject prey-dependent models as a means of gaining primacy for ratio-dependent models (and vice versa) on the basis of purportedly anomalous predictions (e.g., Abrams 1994, 1997, Akçakaya et al. 1995). Our study highlights the limitations of this approach. For the Isle Royale system, one could reject the prey-dependent model for poor relative performance ($\Delta = 20.7$, Table

1), the ratio-dependent model for poor explanatory power ($R^2 = 0.34$, table 1), and the predator-dependent models for over-parameterization (Tables 1 and 4). Although each rejection is logically justified, rejecting one overly simplistic model as a means of gaining primacy for another overly simplistic model may not be very useful. Controversy may dissipate with less focus on declarations that one model or the other is wrong, and more focus on appreciating the circumstances for which each model is wrong, how wrong, and which neglected factors contribute most to each model's wrongness.

Another source of controversy seems to be differing views on the value of simple models of predation (Abrams and Ginzburg 2000:341). One view appears to be based on the premise that simple predation models are most appropriately used as conceptual tools for the development of theory. Thus, prey-dependent models, with their solid theoretical underpinnings, should be the foundation to which mathematical terms can be added to account for specific mechanisms of predator dependence. The other view is based on the premise that simple predation models can be useful tools for prediction and management. Under such circumstances, the influence of predator dependence may be suspected or detected, but information may be too limited to support models based on detailed mechanisms of predator dependence. In such cases ratio dependence may typically be a useful and parsimonious approximation. Although our study exemplifies the second point of view, this aspect of controversy is resolved by recognizing that simple predation models are used both for the development of conceptual theory (Rosenzweig 1971, Abrams and Walters 1996, Keeling et al. 2000) and as tools for prediction and management (Rosenzweig 1971, May et al. 1979, Boyce 1993, Flaaten and Stollery 1994, Yodzis 1994, 2001, Spencer 1997).

Ratio-dependent predation deserves increased attention from theorists, empiricists, and educators (Ricklefs and Miller 2000), because at times it will be the best approximation of nature, and because the proper interpretation of simple models is so challenging. The more general influence of predator density on kill rate deserves increased attention from empiricists to better understand its causes, frequency, and importance in natural systems. The primacy of exclusive prey dependence may be an artifact of historical development, not its superior depiction of nature. Neither prey dependency nor ratio dependency deserves primacy. Both are sufficiently useful and limited and to serve as co-null models.

ACKNOWLEDGMENTS

We are grateful to P. Abrams, R. Arditi, J. Fryxell, and L. Ginzburg for valuable discussion, and two anonymous reviewers for helpful comments. We thank the U.S. National Science Foundation (DEB-9317401, DEB-9903671), EarthWatch, National Geographic Society, and U.S. National Park Service for financial support.

LITERATURE CITED

- Abrams, P. A. 1992. Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptations. *American Naturalist* **140**:573–600.
- Abrams, P. A. 1993. Why predation rate should not be proportional to predator density. *Ecology* **74**:726–733.
- Abrams, P. A. 1994. The fallacies of “ratio-dependent” predation. *Ecology* **75**:1842–1850.
- Abrams, P. A. 1997. Anomalous predictions of ratio-dependent models of predation. *Oikos* **80**:163–171.
- Abrams, P. A., and L. R. Ginzburg. 2000. The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology and Evolution* **15**:337–341.
- Abrams, P. A., and C. I. Walters. 1996. Invulnerable prey and the paradox of enrichment. *Ecology* **77**:1125–1133.
- Akçakaya, H. R., R. Arditi, and L. R. Ginzburg. 1995. Ratio-dependent predation: an abstraction that works. *Ecology* **76**:995–1004.
- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* **64**:912–923.
- Arditi, R., and H. R. Akçakaya. 1990. Underestimation of mutual interference of predators. *Oecologia* **83**:358–361.
- Arditi, R., and A. A. Berryman. 1991. The biological control paradox. *Trends in Ecology and Evolution* **6**:32.
- Arditi, R., and L. R. Ginzburg. 1989. Coupling in predator-prey dynamics: ratio dependence. *Journal of Theoretical Biology* **139**:311–326.
- Arditi, R., L. R. Ginzburg, and H. R. Akçakaya. 1991a. Variation in plankton densities among lakes: a case for ratio-dependent predation models. *American Naturalist* **138**:1287–1296.
- Arditi, R., N. Perrin, and H. Saïah. 1991b. Functional response and heterogeneities: an experimental test with cladocerans. *Oikos* **60**:69–75.
- Arditi, R., and H. Saïah. 1992. Empirical evidence of the role of heterogeneity in ratio-dependent consumption. *Ecology* **73**:1544–1551.
- Beddington, J. R. 1975. Mutual interference between parasites or predators and its effect on searching efficiency. *Journal of Animal Ecology* **44**:331–340.
- Boyce, M. S. 1993. Predicting the consequences of wolf recovery to ungulates in Yellowstone National Park. Pages 234–269 in R. S. Cook, editor. *Ecological issues on reintroducing wolves into Yellowstone National Park*. United States Department of Interior, National Park Service, Nature Resource Publications office, Denver, Colorado, USA.
- Boyce, M. S. 2000. Modeling predator-prey dynamics. Pages 253–287 in L. Boitani and T. Fuller, editors. *Research techniques in animal ecology*. Columbia University Press, New York, New York, USA.
- Burnham, K. P., and D. R. Anderson. 1998. *Model selection and inference*. Springer-Verlag, New York, New York, USA.
- Carpenter, S. R., K. L. Cottingham, and C. A. Stow. 1994. Fitting predator-prey models to time series with observation errors. *Ecology* **75**:1254–1264.
- Cosner, C., D. L. DeAngelis, J. A. Ault, and D. B. Olson. 1999. Effects of spatial grouping on the functional response of predators. *Theoretical Population Biology* **56**:65–75.
- DeAngelis, D. L., R. A. Goldstein, and R. V. O'Neill. 1975. A model for trophic interaction. *Ecology* **56**:881–892.
- Efron, B., and R. J. Tibshirani. 1993. *An introduction to the bootstrap*. Chapman and Hall, New York, New York, USA.
- Elton, C., and M. Nicholson. 1942. The ten year cycle in numbers of the lynx in Canada. *Journal of Animal Ecology* **11**:215–244.
- Flaaten, O., and K. Stollery. 1994. The economic effects of biological predation: theory and application to the case of the North-east Atlantic minke whale's (*Balaenoptera acutorostrata*) consumption of fish. *Cemare Research Papers* number **67**.
- Freedman, H. I., and R. M. Mathsen. 1993. Persistence in predator-prey systems with ratio-dependent predator influence. *Bulletin of Mathematical Biology* **55**:817–827.
- Fretwell, S. D. 1977. The regulation of plant communities by food chains exploiting them. *Perspectives in Biology and Medicine* **20**:169–185.
- Fuller, T. K. 1989. *Population dynamics of wolves in Northern Minnesota*. Wildlife Monographs Number **105**.
- 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.
- Ginzburg, L. R., and H. R. Akçakaya. 1992. Consequences of ratio-dependent predation for steady-state properties of ecosystems. *Ecology* **73**:1536–1543.
- Gutierrez, A. P. 1992. Physiological basis of ratio-dependent predator-prey theory: the metabolic pool model as a paradigm. *Ecology* **73**:1552–1563.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* **94**:421–425.
- Hassell, M. P. 1978. *The dynamics of arthropod predator-prey systems*. Princeton University Press, Princeton, New Jersey, USA.
- Hassell, M. P., and G. C. Varley. 1969. New inductive population model for insect parasites and its bearing on biological control. *Nature* **223**:1133–1136.
- Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Canadian Entomologist* **91**:293–320.
- Holling, C. S. 1966. The functional response of invertebrate predators to prey density. *Memoirs of the Entomological Society of Canada* **48**:1–60.
- Holyoak, M. 2000. Effects of nutrient enrichment on predator-prey metapopulation dynamics. *Journal of Animal Ecology* **69**:985–997.
- Huffaker, C. B. 1958. Experimental studies on predation. II. Dispersion factors and predator-prey oscillations. *Hilgardia* **27**:343–383.
- Keeling, M. J., H. B. Wilson, and S. W. Pacala. 2000. Reinterpreting space, time lags, and functional responses in ecological models. *Science* **290**:1758–1760.
- Kerfoot, W. C., and A. Sih, editors. 1987. *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, New Hampshire, USA.
- Lotka, A. J. 1925. *Elements of physical biology*. Williams and Wilkins, Baltimore, Maryland, USA.
- Markus, M., B. Hess, J. Rossler, and K. Kiwi. 1987. Populations under periodically and randomly varying growth conditions. Pages 267–277 in H. Degn, A. V. Holden, and L. F. Olsen, editors. *Chaos in biological systems*. NATO ASI Series 138. Plenum, New York, New York, USA.
- Marshal, J. P., and S. Boutin. 1999. Power analysis of wolf-moose functional responses. *Journal of Wildlife Management* **63**:396–402.
- May, R. M. 1976. Models for single populations. Pages 4–25 in R. M. May, editor. *Theoretical ecology: principles and applications*. Blackwell Scientific, Oxford, UK.
- May, R. M., J. R. Beddington, C. W. Clark, S. J. Holt, and R. M. Laws. 1979. *Management of multispecies fisheries*. *Science* **205**:267–277.
- Mech, L. D. 1966. *The wolves of Isle Royale*. National Park Service Scientific Monograph Series Number 7. U.S. Government Printing Office, Washington, D.C., USA.
- Messier, F. 1994. Ungulate population models with predation: a case study with North American moose. *Ecology* **75**:478–488.
- Murie, A. 1944. *The wolves of Mount McKinley*. National

- Park Service Scientific Monograph Series Number 5. U.S. Government Printing Office, Washington, D.C., USA.
- Oksanen, L. S., S. D. Farewell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* **118**:240–261.
- Olson, S. F. 1938. Organization and range of the pack. *Ecology* **19**:168–170.
- Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. National Park Service Scientific Monograph Series Number 11. U.S. Government Printing Office, Washington, D.C., USA.
- Peterson, R. O. 1999. Wolf–moose interaction on Isle Royale: the end of natural regulation? *Ecological Applications* **9**:10–16.
- Peterson, R. O., and R. E. Page. 1988. The rise and fall of Isle Royale wolves, 1975–1986. *Journal of Mammalogy* **69**:89–99.
- Peterson, R. O., and R. E. Page. 1993. Detection of moose in midwinter from fixed-wing aircraft over dense forest cover. *Wildlife Society Bulletin* **21**:80–86.
- Peterson, R. O., N. J. Thomas, J. M. Thurber, J. A. Vucetich, and T. A. Waite. 1998. Population limitation and the wolves of Isle Royale. *Journal of Mammalogy* **79**:828–841.
- Peterson, R. O., and J. A. Vucetich. 2001. Ecological studies of wolves on Isle Royale. Annual report. Michigan Technological University, Houghton, Michigan, USA.
- Peterson, R. O., J. D. Woolington, and T. N. Bailey. 1984. Wolves of Kenai Peninsula, Alaska. *Wildlife Monograph* **88**:1–52.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* **147**:813–842.
- Reeve, J. D. 1997. Predation and bark beetle dynamics. *Oecologia* **112**:48–54.
- Ricklefs, R. E., and G. L. Miller. 2000. *Ecology*. Fourth edition. W. H. Freeman and Company, New York, New York, USA.
- Rogers, D. J. 1972. Random search and insect population models. *Journal of Animal Ecology* **41**:369–383.
- Rosenzweig, M. L. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. *Science* **171**:385–387.
- Rosenzweig, M., and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator–prey interaction. *American Naturalist* **97**:217–223.
- Slobodkin, L. B. 1992. A summary of the special feature and comments on its theoretical context and importance. *Ecology* **73**:1564–1566.
- Smith, F. E. 1952. Experimental methods in population dynamics: a critique. *Ecology* **33**:441–450.
- Solberg, E. J., B.-E. Saether, O. Strand, and A. Loison. 1999. Dynamics of a harvested moose population in a variable environment. *Journal of Animal Ecology* **68**:186–204.
- Spencer, P. D. 1997. Optimal harvesting of fish populations with nonlinear rates of predation and autocorrelated environmental variability. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:59–74.
- Taylor, R. J. 1984. *Predation*. Chapman and Hall, New York, New York, USA.
- Thompson, W. R. 1937. *Science and common sense: an Aristotelian excursion*. Longmans, Green, London, UK.
- Thurber, J. M., and R. O. Peterson. 1993. Effects of population density and pack size on the foraging ecology of gray wolves. *Journal of Mammalogy* **74**:879–889.
- Volterra, V. 1991. Fluctuations in the abundance of a species considered mathematically. [Reprint of the translation (*Nature* **118**:558–560) from the 1926 original (in Italian.)] *In* L. A. Real and J. H. Brown, editors. *Foundations of ecology*. University of Chicago Press, Chicago, Illinois, USA.
- Yodzis, P. 1994. Predator–prey theory and management of multispecies fisheries. *Ecological Applications* **4**:51–58.
- Yodzis, P. 2001. Must predators be culled for the sake of fisheries? *Trends in Ecology and Evolution* **16**:78–84.
- Zar, J. H. 1984. *Biostatistical analysis*. Second edition. Prentice Hall, Engelwood Cliffs, New Jersey, USA.