FUNCTIONAL RESPONSES WITH PREDATOR INTERFERENCE: VIABLE ALTERNATIVES TO THE HOLLING TYPE II MODEL

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Abstract. A predator's per capita feeding rate on prey, or its functional response, provides a foundation for predator–prey theory. Since 1959, Holling's prey-dependent Type II functional response, a model that is a function of prey abundance only, has served as the basis for a large literature on predator–prey theory. We present statistical evidence from 19 predator–prey systems that three predator-dependent functional responses (Beddington-DeAngelis, Crowley-Martin, and Hassell-Varley), i.e., models that are functions of both prey and predator abundance because of predator interference, can provide better descriptions of predator feeding over a range of predator–prey abundances. No single functional response best describes all of the data sets. Given these functional forms, we suggest use of the Beddington-DeAngelis or Hassell-Varley model when predator feeding rate becomes independent of predator density at high prey density and use of the Crowley-Martin model when predator feeding rate is decreased by higher predator density even when prey density is high.

Key words: Beddington-DeAngelis model; Crowley-Martin model; foraging; functional response; Hassell-Varley model; Holling Type II model; interference; predator; prey.

INTRODUCTION

Understanding the relationship between predator and prey is a central goal in ecology, and one significant component of the predator–prey relationship is the predator's rate of feeding upon prey. The feeding rate describes the transfer of biomass between trophic levels and, in the simplest models, completely describes the dynamic coupling between predator abundance and prey abundance (e.g., Lotka 1925). Since the early development of predator–prey theory, ecologists have recognized the theoretical importance of understanding the details of a predator's feeding rate (Nicholson and Bailey 1935, Holling 1959*a*). More recent theoretical work has demonstrated that the mathematical form of the feeding rate can influence the distribution of predators through space (van der Meer and Ens 1997), the stability of enriched predator–prey systems (DeAngelis et al. 1975, Huisman and De Boer 1997), correlations between nutrient enrichment and the biomass of higher trophic levels (DeAngelis et al. 1975), and the length of food chains (Schmitz 1992).

The description of a predator's instantaneous, per capita feeding rate, *f,* as a function of prey abundance, *N,* is the classic definition of a predator's "functional response" (Holling 1959*a*). One type of functional response derived by Holling (1959*b*), the "Type II," describes the average feeding rate of a predator when the predator spends some time searching for prey and some time, exclusive of searching, processing each captured

prey item (i.e., handling time). In this case the instantaneous, per capita feeding rate of the predator is given by a function of the form

$$f_1(N, P) = \frac{aN}{1 + bN} \tag{1}$$

where parameters *a* (units: 1/time) and *b* (units: 1/prey) are positive constants that describe the effects of capture rate and handling time, respectively, on the feeding rate (handling time = *b/a*). Note that the feeding rate given by Eq. 1 is unaffected by predator abundance, *P.* Eq. 1, known as the Holling Type II functional response (hereafter the H2 model), is widely used and has stood as the "null model" upon which much predator–prey theory has been constructed (Brown 1991).

Eq. 1, as suggested by Holling's (1959*a*) empirical results, assumes that predators do not interfere with one another's activities; thus competition among predators for food occurs only via the depletion of prey. However, Beddington (1975) derived and DeAngelis et al. (1975) proposed, independently, a functional response that can accommodate interference among predators (see Huisman and De Boer [1997] for a mathematically detailed derivation). In this model, individuals from a population of two or more predators not only allocate time to searching for and processing prey, but also spend some time engaging in encounters with other predators, resulting in a functional response that gives an instantaneous, per capita feeding rate:

$$f_2(N, P) = \frac{aN}{1 + bN + c(P - 1)} \tag{2}$$

where *P* is the predator abundance and *c* (units: 1/

predator) is a positive constant describing the magnitude of interference among predators. When $c = 0$ or $P = 1$, Eq. 2, the Beddington-DeAngelis functional response (hereafter the BD model), reduces to Eq. 1, the H2 functional response. The precise form of the model proposed by DeAngelis et al. (1975) differs slightly from the Beddington (1975) derivation in that DeAngelis et al. use the term P instead of $P - 1$. We retain Beddington's original $P - 1$ form here and also retain the $P - 1$ term in the Crowley-Martin functional response that follows below. The $P - 1$ form was used by Beddington and by Crowley and Martin (below) in building mechanistic models in which predator abundance is expressed as counts (integers), and the mechanism of predator dependence is interference via direct encounters with other predators. Hence the $P - 1$ term is used because a predator does not interfere with itself in those models, and setting $P = 1$ reduces the models exactly to the H2 model. However, when predator abundance is modeled as a continuous variable as in usual models of population dynamics, or when some other mechanism of predator dependence is hypothesized (e.g., prey behavior that depends on predator density), replacement of $P - 1$ by P in predator-dependent functional responses will often be more appropriate.

The BD model assumes that handling and interfering are exclusive activities. Crowley and Martin (1989) removed that assumption in what they called their "preemption" model, allowing for interference among predators regardless of whether a particular individual is currently handling prey or searching for prey. The Crowley-Martin model (hereafter the CM model) thus adds an additional term in the denominator:

$$f_3(N, P) = \frac{aN}{1 + bN + c(P - 1) + bcN(P - 1)}$$

$$= \frac{aN}{(1 + bN)(1 + c(P - 1))}. \qquad (3)$$

The parameters $a, b,$ and c have the same interpretation as in the BD model, and, like the BD model, the CM functional response reduces to the H2 functional response when $c = 0$. An important distinction between the BD and CM models is that the BD model predicts that the effects of predator interference on feeding rate become negligible under conditions of high prey abundance (because predators that are handling prey do not interfere), but the CM model predicts that interference effects on feeding rate remain important, that is, rearranging the BD model by dividing the numerator and denominator by N,

$$\lim_{N \to \infty} f_2(N, P) = \lim_{N \to \infty} \frac{a}{\dfrac{1}{N} + b + \dfrac{c(P - 1)}{N}} = \frac{a}{b}$$

while the CM model yields

$$\lim_{N \to \infty} f_3(N, P) = \lim_{N \to \infty} \frac{a}{\dfrac{1}{N} + b(1 + c(P - 1)) + \dfrac{c(P - 1)}{N}}$$

$$= \frac{a}{b(1 + c(P - 1))}.$$

Hence, as prey abundance becomes large, the functional response asymptotes at a level independent of predator abundance in the BD model, but the asymptote depends on predator abundance in the CM model. In both models, the distance between the functional response and its asymptotic value depends on the relative abundance of predators and prey, specifically the value of $1/N + c(P - 1)/N$ and the parameters a and b.

The H2, BD, and CM models all have mechanistic bases stated by their authors. However, they can also be viewed as phenomenological models with increasing complexity (in the denominator, for the H2, BD, and CM models, respectively, only a linear prey term, the addition of a linear predator term, and the addition of a prey $\times$ predator interaction term). Also, the BD model and the CM model can be derived from other premises. For example (P. Abrams, *personal communication*), the DeAngelis et al. (1975) form of the BD model (use of P instead of $P - 1$) can be derived by assuming no direct interference among predators, but rather that the prey adjust their behavior in the presence of the predators. Writing the H2 model as $CN/(1 + ChN)$, where C is a capture coefficient and h is handling time, and writing $C = C'/(1 + iP)$ where C' and i are parameters, yields an equation identical to Eq. 2 if $P - 1$ is replaced by P. The CM model can also be derived via a different route than the mechanistic approach of Crowley and Martin. Harrison (1995) divided the H2 functional response by a term, $1 + \beta P$, where β is a positive parameter, to produce a predator-dependent functional response as a phenomenological model rather than positing any particular mechanism. This division yields the CM model if $P - 1$ in the CM model is replaced with P.

There is a vast literature of ecological theory resting upon the H2 model. We inspected papers in three leading ecology journals over the past 4 yr (Table 1) and found that 69% of the papers specifying a functional response employ the H2 model. The secondmost specified functional response was the linear Lotka-Volterra model, $f = aN,$ as specified in 27% of the papers. In contrast, 7% and 0% of these studies employ the BD and CM models, respectively (two of the three studies employing the BD model are authored by DeAngelis, who introduced the model in 1975).

Four of the papers (9%) in Table 1 specified predator-dependent forms based on the Hassell-Varley model (Hassell and Varley 1969) and similar ratio-dependent forms (forms dependent on N/P rather than N) that have been the subject of many criticisms over the past 10 yr (e.g., Abrams 1994, 1997). Because the BD and CM

TABLE 1. The numbers and percentages of papers specifying different types of functional responses in papers during 1996–1999 in three major ecology journals.

Functional response	Ecology (14 papers)	American Naturalist (17 papers)	Theoretical Population Biology (14 papers)	Total (45 papers)	Percentage of papers
Holling Type II	10	11	10	31	68.8
Lotka-Volterra (linear)	3	6	3	12	26.6
Hassell-Varley†	1	2	1	4	8.8
Beddington-DeAngelis	1	0	2	3	6.7
Crowley-Martin	0	0	0	0	0
Other	1	1	0	2	4.4

† Here Hassell-Varley refers to both ratio-dependent models using prey abundance/predator abundance and forms based on the model given in Hassell and Varley (1969).

models are mechanistic extensions of the H2 model, we prefer them to the Hassell-Varley model, which was written without a stated mechanistic basis subject to test. However, because of its relatively high profile in the functional response literature, we also include a version of the Hassell-Varley model in our analyses. Also, recently Cosner et al. (1999) have shown that special cases of the Hassell-Varley model ($m = 1/3$, $1/2$, or 1 in Eq. 4, below) can arise from mechanistic assumptions about foraging by spatially grouped predators, and Abrams and Ginzburg (2000) discuss possible mechanistic bases leading to ratio dependence ($m = 1$).

Specifically, we analyze a version of the Hassell-Varley model, modified to include handling time following Sutherland (1983):

$$f_4(N, P) = \frac{aN}{bN + P^m}. \tag{4}$$

Hereafter, we call Eq. 4 the HV model. When $m = 0$ or $P = 1$ the HV model reduces to the H2 model. Arditi and Akçakaya (1990) compared this same model to the H2 model and found $m > 0$ in each of the 10 predator–prey systems they analyzed, hence concluding that the HV model was a better descriptor of the data than the H2 model. They also concluded that ratio-dependent functional responses are likely because most of their confidence intervals for m contain one. When $m = 1$ the HV model depends on N and P only through the ratio N/P, because Eq. 4 can then be rewritten as $f = a(N/P)/(1 + b(N/P))$.

However, the H2 model's relative monopoly of the theoretical literature and the debate over ratio dependence (including Arditi and Akçakaya's results) linger while empirically it remains unclear as to what form the functional response should take (Abrams and Walters 1996, Murdoch and Briggs 1996, Abrams and Ginzburg 2000). Indeed, Abrams and Walters (1996: 1131) conclude, ''Although the idea of predator density dependence is very plausible, it is something that has not received much empirical investigation. The literature on ratio-dependent functional responses has yet to produce any conclusive evidence for density dependence of any kind affecting the functional response.''

Given that large numbers of experiments and observations suggest that predators do indeed interfere with one another's activities so as to result in competitive effects (reviews in Schoener 1983, MacIsaac and Gilbert 1991) and that prey alter their behavior under increased predator threat (reviewed by Lima 1998), the BD, CM, and HV models stand as reasonable alternatives to the H2 model. Therefore, in this paper we expand on Arditi and Akçakaya's (1990) work by presenting the results of statistical tests that can discriminate among these four alternative functional response models using data sets from 19 simple predator–prey systems.

METHODS

We searched the literature via electronic database and literature citations for any study from which we could extract measured instantaneous or integrated feeding rates (defined below) for at least two prey abundances and two predator abundances. We located 19 data sets (Table 2) from 15 sources (14 from the peer-reviewed literature, one Ph.D. dissertation). We did not consider any study that measured a feeding rate but failed to report both predator abundance and prey abundance (e.g., many studies of predator feeding with continuous input of prey; Kennedy and Gray 1993). Some papers reported several similar data sets for the same predator, and in this case we randomly selected one of these data sets so as to include a maximum of one data set per predator–prey system in our analysis. We tested among the four functional response models by first testing each of the three predator-dependent forms against the H2 model and then testing the alternative predator-dependent models against one another. In keeping with the assumptions of each model, the parameters *a, b, c,* and *m* are assumed to be nonnegative. We distinguish between two types of data sets: those that attempted to measure instantaneous feeding rates by assuming a relatively constant prey abundance over the duration of the study and those that measured integrated feeding

TABLE 2. Characteristics of the 19 data sets used in the analysis. Data sets are sorted into two groups: those measuring instantaneous feeding rates and those measuring integrated feeding rates.

Data set	Predator–Prey	Reference	Data source
Instantaneous feeding rates			
1	protozoan–protozoan	Salt (1974)	Fig. 3, Table 1
2	stonefly–mayfly	Walde and Davies (1984)	Figs. 2, 4
3	dragonfly–dragonfly	Crowley and Martin (1989)	Fig. 2
4	coyote–hare	O'Donoghue et al. (1998)	Figs. 1, 5
5	lynx–hare	O'Donoghue et al. (1998)	Figs. 1, 5
Integrated feeding rates			
6	parasitoid–house fly	Edwards (1961)	Table 1
7	parasitoid–moth eggs	Edwards (1961)	Table 2
8	fish–cladoceran	Chant and Turnbull (1966)	Table 1
9	beetle–beetle	Mertz and Davies (1968)	Table 1
10	amphipod–fish	von Westernhagen and Rosenthal (1976)	Fig. 3
11	damselfly–cladoceran	Uttley (1980)	Fig. 4.3.1
12	back swimmer–cladoceran	Uttley (1980)	Fig. 8.3.2
13	mite–mite	Eveleigh and Chant (1982)	Tables 3, 5
14	mite–mite	Eveleigh and Chant (1982)	Tables 7, 8
15	parasitoid–caterpillar	Huffaker and Matsumoto (1982)	Table 1
16	parasitoid–moth eggs	Kfir (1983)	Table 1
17	parasitoid–aphid	Kumar and Tripathi (1985)	Table 1
18	snail–barnacle	Katz (1985)	Figs. 4, 8
19	parasitoid–caterpillar	Taylor (1988)	Fig. 1a

rates because prey abundance was depleted by predator feeding over the duration of the study (Table 2). These two types of data sets require slightly different mathematical approaches.

We analyzed five data sets as representing direct estimates of instantaneous feeding rates, because the author(s) either (1) regularly replaced prey that had been consumed by predators (data sets 2 and 3) or (2) directly measured the number of prey killed along with predator and prey densities (data sets 1, 4, and 5).

When prey are depleted over the course of the study by predator feeding then integrated feeding rates are measured, and the computations become more cumbersome. In this case, to compare model predictions with the observed data we must integrate the predators' instantaneous feeding rate over the duration of the empirical study, accounting for prey depletion, resulting in an integrated feeding rate, F_i, i.e.,

$$F_i(N(0), P) = \frac{N(0) - N(t)}{P}$$

where $N(0)$ is the initial number of prey and $N(t)$ is the number of prey remaining after time t. The prey remaining after time t, $N(t)$, is the solution to the appropriate differential equation, in which the rate of prey depletion by P predators is

$$\frac{dN}{dt} = -f_i(N, P)P \qquad i = 1, 2, 3, 4 \qquad (5)$$

for the H2, BD, CM, and HV functional responses, respectively. Predator abundance, P, and initial prey abundance, $N(0)$, are given as the treatment combinations and Eqs. 5 must be solved for the final prey abundance after time t, $N(t)$. These equations can be solved analytically, resulting in an implicit function that must then be solved numerically to find $N(t)$ (Beddington 1975). Alternatively, Eqs. 5 can be numerically integrated to obtain $N(t)$.

Using the method of maximum likelihood we fit model predictions of integrated feeding rates ($N(t)$ obtained by numerical integration of Eqs. 5 via a second-order Runge-Kutta algorithm; Kincaid and Cheney 1996) to the experimental observations of integrated feeding rates for different levels of initial prey abundance, $N(0)$, and predator abundance, P, to estimate the parameters a, b, c and m. We assumed the statistical models for instantaneous and integrated measurements of predator feeding rates, respectively (Hilborn and Walters 1992, Carpenter et al. 1994, Pascual and Kareiva 1996, Jost and Arditi 2000):

$$W_j \sim \text{lognormal}(\log(f_i(N_j, P_j)), \sigma^2_{w,i})$$

$$Y_j \sim \text{lognormal}(\log(F_i(N_j(0), P_j)), \sigma^2_{y,i})$$

Here the sets $\{W_j, N_j, P_j\}^n_{j=1}$ and $\{Y_j, N_j(0), P_j\}^n_{j=1}$ are the observed feeding rates, prey abundances, and predator abundances from experiments measuring instantaneous and integrated feeding rates, respectively. The parameter n is the sample size, and the parameters $\log(f_i(N_j, P_j))$ and $\log(F_i(N_j(0), P_j))$, and $\sigma^2_{w,i}$ and $\sigma^2_{y,i}$ are the expectations and variances of $\log(W_j)$ and $\log(Y_j)$, respectively. We estimated the parameters a, b, c, and m by maximum likelihood, minimizing the sums of squares,

$$\text{ss}_{w,i} = \sum_{j=1}^{n} [\log(W_j) - \log(f_i(N_j, P_j))]^2,$$

for instantaneous feeding rates. The sums of squares

for integrated feeding rates is analogous. We estimated the variances using

$$\hat{\sigma}^2_{w,i} = \frac{\widehat{SS}_{w,i}}{n - p}$$

where p is the number of parameters in the functional response and $\widehat{SS}_{w,i}$ is the maximum likelihood estimate of $ss_{w,i}$ (Seber and Wild 1989; the variance estimator for integrated feeding rates is analogous).

To test the BD and CM models against the H2 model we tested whether $c = 0$, because each of the three predator-dependent models reduces to the H2 model when $c = 0$, by computing 95% confidence intervals for c for each of the predator-dependent forms. Similarly, for the HV model, we computed 95% confidence intervals for m, because the HV model reduces to the H2 model for $m = 0$. We computed the 95% confidence intervals by computer simulation (i.e., we employed a parametric bootstrap with 500 bootstrap replicates per model per data set; Efron and Tibshirani 1993, Dennis and Taper 1994).

To test among the alternative predator-dependent forms we used the likelihood-ratio test statistic, defined, for instantaneous feeding rates, for example, as

$$T_{i,j} = n(\log[\widehat{SS}_{w,j}] - \log[\widehat{SS}_{w,i}])$$

(the test statistic for integrated feeding rates is analogous). If model i fits the data better than model j, then $T_{i,j}$ will be positive. Conversely, if model j fits the data better than model i, then $T_{i,j}$ will be negative. This test statistic is identical to the difference between two Akaike information criterion (AIC) values for the case of comparing two models with the same number of parameters (Hilborn and Mangel 1997), as is the case here.

Our tests of each of the predator-dependent models vs. the H2 model treat the H2 model as a null hypothesis in the classic sense in that our test manages Type I errors (i.e., incorrectly rejecting the H2 model), but does not control for Type II errors (i.e., incorrectly accepting the H2 model). This approach gives the H2 model the ''benefit of the doubt'' in a statistical sense when compared to the three-parameter models we consider here. However, for testing among the three predator-dependent models we do not have justification for specifying any model as the null hypothesis and therefore we employ a test that puts the BD, CM, and HV models on ''equal footing'' by managing for errors in either direction. Accordingly, we defined the critical values for the test statistic $T_{i,j}$ as

$$L_{i,j} = \min(k^1_{i,j}, k^2_{i,j}) \text{ and } U_{i,j} = \max(k^1_{i,j}, k^2_{i,j})$$

where $k^1_{i,j}$ and $k^2_{i,j}$ satisfy

$$\Pr\{T_{i,j} < k^1_{i,j} | H_i\} = 0.05$$

$$\Pr\{T_{i,j} > k^2_{i,j} | H_j\} = 0.05$$

where H_i and H_j represent the hypothesized functional responses f_i and f_j, respectively. The resulting test is: reject H_i if $T_{i,j} < L_{i,j}$, reject H_j if $U_{i,j} < T_{i,j}$, or reject neither H_i nor H_j if $L_{i,j} \leq T_{i,j} \leq U_{i,j}$.

We parameterized the models with 95% confidence intervals for a, b, c, and m and computed $L_{i,j}$ and $U_{i,j}$ by computer simulation (i.e., we used parametric bootstrap to compute confidence intervals and the distributions of the test statistics using 500 bootstrap replicates per model per data set). We report the outcomes of our hypothesis tests using the observed values of the test statistic $T^{obs}_{i,j}$, the P values $\Pr\{T_{i,j} < T^{obs}_{i,j} | H_i\}$ and $\Pr\{T_{i,j} > T^{obs}_{i,j} | H_j\}$ for each pairwise test of the alternative predator-dependent models and the confidence intervals for c or m for the best-fitting (i.e., greatest likelihood) model for each data set.

RESULTS

When compared with the Holling Type II (H2) model as the null hypothesis, all three alternatives show statistically significant improvement over the Holling model by the criterion that the 95% confidence interval for the interference parameter (c or m) does not contain zero (Fig. 1a–c). Treating the H2 model as the null hypothesis, comparison with the Beddington-De-Angelis (BD) model results in rejection of the H2 model in favor of the BD model in 18 of the 19 data sets (Fig. 1a). The Crowley-Martin (CM) comparison results in rejection of the H2 model in 15 of the 19 cases (Fig. 1b), and the Hassell-Varley (HV) comparison is essentially identical to the result of the BD vs. H2 comparison: rejection of the H2 model in all but one case (data set 5, as in the BD comparison; Fig. 1c). Appendix A gives 95% confidence intervals for the interference parameters (c and m) and the other parameters for the best-fit model for each data set. Only for data set 5 is the H2 null hypothesis accepted.

To illustrate the fits of the three alternative predator-dependent models, in Fig. 2 we show the model fits for three cases, one for each of the three models. As explained in the introduction, the CM model accommodates different asymptotic feeding rates for different predator levels as prey increase in density. Data set 11 (Fig. 2b) shows that phenomenon, and the CM model provides the best fit to that data set (Appendix A); the asymptotic feeding levels for low predator abundances ($P = 1, 2$) appear not to be reached over the range of prey abundances studied, but exceed the asymptotic feeding levels inferred for high predator abundances ($P = 6, 8$). In contrast, the BD and HV models provide better fits (Appendix A) to data sets without evidence for different asymptotes, such as data set 6 (Fig. 2a) and data set 12 (Fig. 2c). However, we note that for some data sets, e.g., Fig. 2a, the prey abundances studied were not sufficiently high to make a convincing case regarding the existence of an asymptotic feeding rate common to all predator abundances vs. asymptotes that depend on predator abundance.
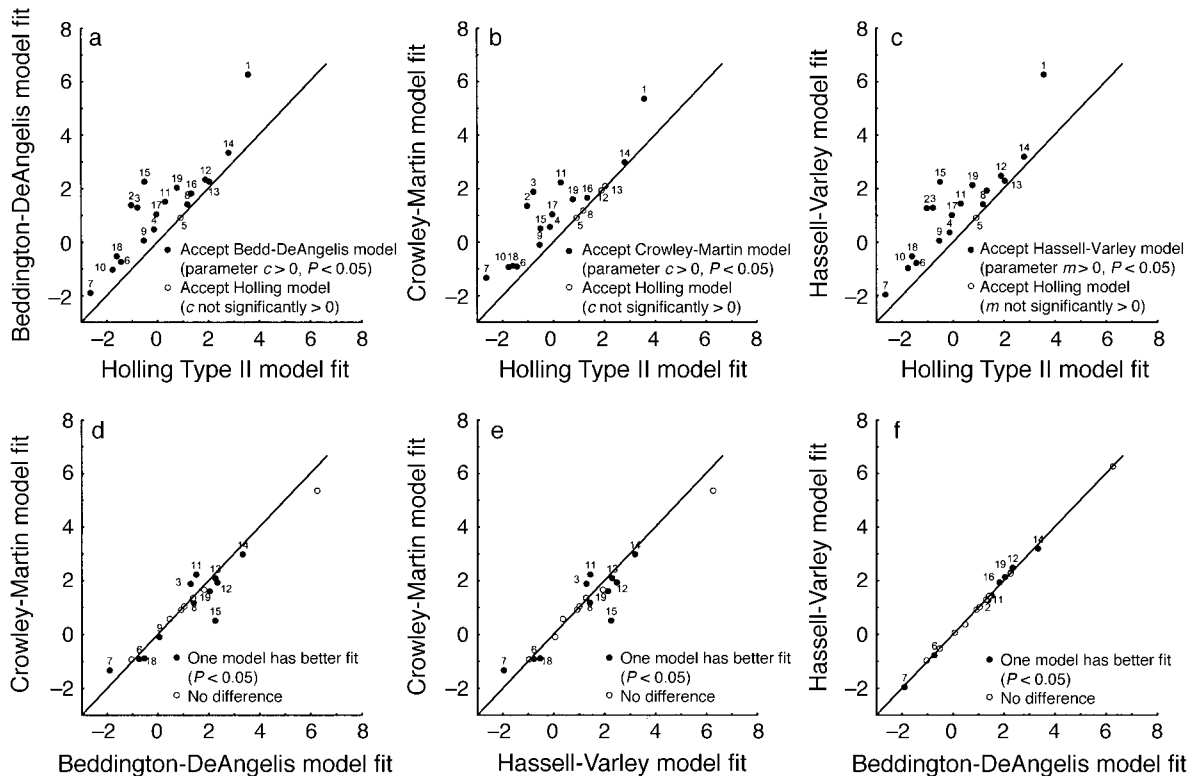
FIG. 1. The fits of the four alternative functional response models to the 19 data sets by the log-likelihood criterion. The 45° line indicates equal fits, so points lying above that line indicate a better fit by the model on the vertical axis. Cases in which one model provides a statistically better fit are indicated by filled circles. In some cases statistically significant differences occur despite similar fits (i.e., points very close to the 45° line) because of large sample sizes and/or small variances. (a–c) Comparisons of the predator-dependent models with the Holling Type II model. (d–f) Comparisons among the three predator-dependent models.

Comparison of the BD, CM, and HV models (Fig. 1 and Appendix B) shows that the CM model fits are often significantly different from the BD model fits (Fig. 1d) and the HV model fits (Fig. 1e), but that the BD and HV models are usually not distinguishable from one another (Fig. 1f). When compared to the BD model (Fig. 1d and Appendix B), the CM model yields significantly better fits in three cases (data sets 3, 7, and 11), and inspection of those fits confirmed that those data sets indicate asymptotes that differ across predator level. Similarly, nine data sets favor the BD model over the CM model (Fig. 1d and Appendix B), and in these data sets a common asymptote within each data set, across predator levels, is indicated. Comparison of the CM model with the HV model (Fig. 1e, Appendix B) yields the identical result, except that eight data sets rather than nine data sets support the HV model over the CM model.

In contrast, the statistical distinction between the BD and HV models is quite subtle; their respective best-fitting predator-dependent terms in the denominator, $1 + \hat{c}(P - 1)$ and $P^{\hat{m}}$ (where $\hat{c}$ and $\hat{m}$ are the maximum likelihood estimates of c and m), are nearly identical over the relevant set of predator abundances for all of

the data sets, including those data sets that statistically distinguish one form as superior to the other (e.g., data sets 6 and 12 in Fig. 2a and 2c). In 11 of the 19 cases, the data do not support one model over the other (Appendix B, Fig. 1f). In the eight cases that reveal a difference, five support the BD model and three support the HV model. However, even in those cases in which the models have significantly different statistical fits, the fits are qualitatively quite similar (Fig. 1f).

DISCUSSION

Our most salient finding is that predator dependence in the functional response is a nearly ubiquitous property of the published data sets. In 18 of the 19 studies, the classical Holling Type II model, which assumes only prey dependence, was rejected in favor of at least one of the three predator-dependent models.

While the result of predator dependence in all but one of the data sets is clear, we do not attempt to infer the mechanism(s) that produced the predator dependence in these studies. Several mechanisms can produce declining per capita intake with increasing predator abundance (e.g., Abrams and Ginzburg 2000). One mechanism is "direct" interactions among predators,
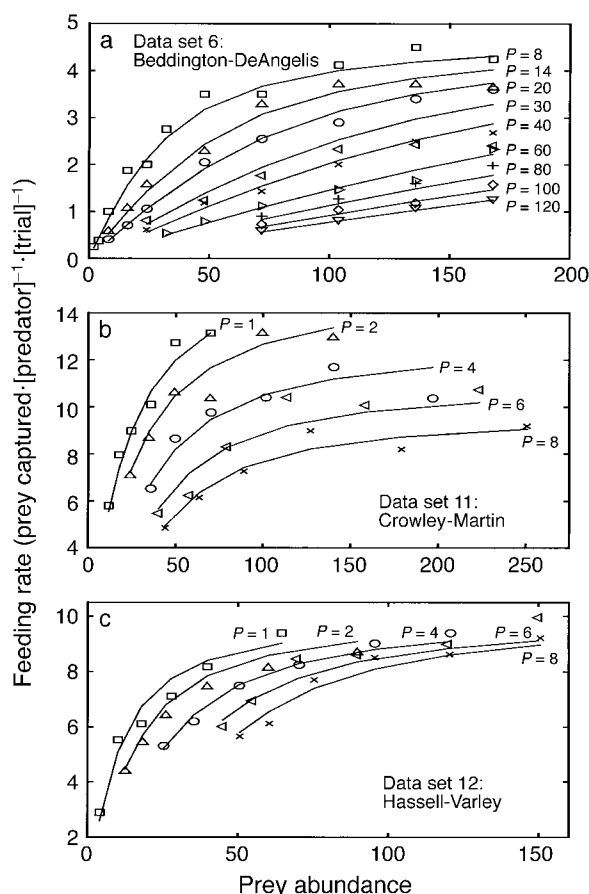
FIG. 2. The measured and predicted integrated feeding rates plotted against prey abundance for each predator abundance treatment for data sets 6, 11, and 12 (P = predator abundance). The best-fitting model is indicated for each data set. Some predator levels are omitted from data set 6 to improve clarity. Data set 11 (b) indicates different asymptotes for different predator levels, in agreement with the Crowley-Martin model, while the other data sets are consistent with a common asymptote, in agreement with the Beddington-DeAngelis (a) or Hassell-Varley model (c).

such as those embodied in the Beddington-DeAngelis and the Crowley-Martin models, in which encounters between predator individuals is modeled as time lost from hunting for prey. A second mechanism is changes in prey behavior that result in less vulnerable prey under higher predator densities (Charnov et al. 1976), and a third mechanism, applicable when prey are depleted, is heterogeneity in vulnerability within the prey population, e.g., that there is a subset of the total prey population that is more vulnerable than others, with that subset depleted more rapidly at higher predator abundances (Abrams 1994). In some of the 19 studies, additional information was given that pointed to specific mechanisms. For example, Walde and Davies (1984) observed predator and prey behavior directly and reported that the first two mechanisms appeared to play roles in producing the predator dependence. In

other cases the experimental settings rule out some mechanism. For example, in data set 7 the parasitoid *Trichogamma* parasitizes the eggs of the host *Sitotroga* in a laboratory setting, and we can presumably rule out altered prey (egg) behavior as the mechanism in that case. The same argument applies to data sets 6 and 16 where the parasitoids lay eggs on fly pupae and moth eggs, respectively. However, given a large empirical and theoretical literature addressing changes in prey behavior across predator abundances (Lima 1998, Houston and McNamara 1999), prey behavior almost surely contributes to the phenomenon of predator dependence in some of the 19 data sets and in many other predator–prey systems in nature.

The degree to which our results from 19 data sets can be extrapolated to some larger set of predator–prey systems is not known. The data sets measuring feeding rate across both prey abundance and predator abundance tend to be laboratory studies, and we agree with Osenberg et al. (1999) that the sample is likely to be biased towards systems in which the researchers suspected predator dependence in the first place, hence motivating their commitment of effort to measuring the functional response across multiple predator abundances. Our study analyzes available data, but we caution against overgeneralization and point to the usefulness of an effort to randomly sample predator–prey systems from some population of systems.

Nonetheless, our statistical results suggest that the three predator-dependent models that we consider deserve more attention in the literature than they have received to date (Table 1). No single model best describes all of the 18 data sets that exhibit predator dependence. However, some patterns in the results are evident. Based on their different asymptotic properties as prey density becomes high, the CM model can be quite different from the BD and HV models, and some of the data sets strongly support the CM model whereas the remaining data sets support the BD and HV models over the CM model. Among the data sets that do not support the CM model, choosing between the BD and HV models based on our statistical results is difficult. As we note in the results, the BD and HV models are very similar because their forms of predator dependence are very similar for any given data set. Moreover, 5 of the 10 data sets that prefer the BD and/or HV models over the CM and H2 models do not distinguish between the BD and HV models.

Our overall suggestion for choosing among these three predator-dependent functional responses is that the CM model be used for data sets that indicate an asymptotic feeding rate that is affected by predator density and otherwise the BD or HV model be used. Statistically the BD and HV models are effectively equivalent in our study, and we recognize that the choice between the BD model and the HV model will largely be a matter of preference for either mechanistic or phenomenological models, respectively. We tend to

prefer the mechanistic alternative, but Sutherland (1983) stated the opposite view, preferring the HV model specifically because it assumes no mechanistic basis. The special case of $m = 1$ in the HV model, which corresponds to ratio dependence, appears to have little general support in the data sets we examined. In the HV model fits, 13 of the 19 95% confidence intervals for m do not contain the value one, and many of the confidence intervals that do contain the value one are rather wide, indicating uncertainty in the estimate of m (examples in Appendix A). Still, our analyses do not exclude ratio dependence as a simple two-parameter descriptor of some data sets.

We have limited our analysis to the four models considered here. However, Jost (1998), (see also Jost 2000) catalogued 12 models of purely prey-dependent functional responses in the literature and 15 models of predator-dependent functional responses. Four of the predator-dependent models listed by Jost (1998) have the property exhibited by the CM model, that is, the feeding rate at high prey abundance asymptotes at a level that is dependent on predator abundance (Aiba et al. 1968, Hassell and Rogers 1972, Rogers and Hassell 1974, Harrison 1995). One simple phenomenological approach to producing that effect is to divide the H2 prey-dependent model or any other prey-dependent model by some term that depends on predator abundance, e.g., to divide the H2 model by P^m (Hassell and Rogers 1972), $1 + \beta P$ (Harrison 1995), or e^{kP} (Aiba et al. 1968), where m, β, and k are parameters, hence producing simple three-parameter predator-dependent models. The other 11 predator-dependent models catalogued by Jost (1998) show either no saturation at high prey abundance or a saturation level independent of predator abundance, as in the BD and HV models considered here. There is also a large literature on models of foraging behavior when under threat from predators, providing additional models of predator-dependent functional responses or a path to writing such functional responses (e.g., Abrams 1982, 1992, Gilliam and Fraser 1987, Abrahams and Dill 1989, Gilliam 1990, Werner and Anholt 1993, Hugie and Dill 1994, Sih 1998, Brown et al. 1999, Houston and MacNamara 1999). These models of adaptive prey behavior are often written in general forms with the number of parameters depending on the choice of functional forms and level of detail included, but some of the models have the capability of dealing with complexities such as spatial structure and alternative prey, albeit at the cost of requiring substantially more parameters in the model. The predator-dependent models that we considered here fit the data reasonably well and have the additional advantage of being simple three-parameter models, but they cannot be expected to describe all cases accurately.

In conclusion, our results suggest that predator-dependent functional responses, including the forms based on interference that we consider here, should be more widely studied in the literature. Because some predator-dependent models of the functional response predict asymptotic feeding rates at high prey abundance that are independent of predator abundance (e.g., the BD and HV models), but others predict asymptotes that depend on predator abundance (e.g., the CM model), we recommend that measurements be taken for the limiting cases of low and high prey and predator abundance. Also, because there are multiple possible mechanisms for predator dependence, we advocate careful observations and measurements of predator and prey behavior in such experiments; while some of the papers containing the data analyzed here had such observations, reports of behavioral observations and measurements were usually cursory or absent. Finally, while phenomenological models can suffice for many purposes, we feel that models derived from mechanistic principles will lead to clearer science because the resulting hypothesis tests provide a direct route for making inferences about the relationship between process and pattern.

Literature Cited

Abrahams, M. V., and L. M. Dill. 1989. A determination of the energetic equivalence of predation. Ecology **70**:999–1007.

Abrams, P. A. 1982. Functional responses of optimal foragers. American Naturalist **120**:382–390.

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. 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. J. Walters. 1996. Invulnerable prey and the paradox of enrichment. Ecology **77**:1125–1133.

Aiba, S., M. Shoda, and M. Nagatani. 1968. Kinetics of product inhibition in alcohol fermentation. Biotechnology and Bioengineering **10**:845–864.

Arditi, R., and H. R. Akçakaya. 1990. Underestimation of the mutual interference of predators. Oecologia **83**:358–361.

Beddington, J. R. 1975. Mutual interference between parasites or predators and its effect on searching efficiency. Journal of Animal Ecology **51**:331–340.

Brown, J. H. 1991. Methodological advances: new approaches and methods in ecology. Pages 445–455 *in* L. A. Real and J. H. Brown, editors. Foundations of ecology: classic papers with commentaries. University of Chicago Press, Chicago, Illinois, USA.

Brown, J. S., J. W. Laundré, and M. Gurung. 1999. The

ecology of fear: optimal foraging, game theory, and trophic interactions. Journal of Mammalogy **80**:385–399.

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.

Chant, D. A., and A. L. Turnbull. 1966. Effects of predator and prey densities on interactions between goldfish and *Daphnia pulex* (De Geer). Canadian Journal of Zoology **4**: 285–289.

Charnov, E. L., G. H. Orians, and K. Hyatt. 1976. Ecological implications of resource depression. American Naturalist **110**:247–259.

Cosner, C., D. L. DeAngelis, J. S. Ault, and D. B. Olson. 1999. Effects of spatial grouping on the functional response of predators. Theoretical Population Biology **56**: 65–75.

Crowley, P. H., and E. K. Martin. 1989. Functional responses and interference within and between year classes of a dragonfly population. Journal of the North American Benthological Society **8**:211–221.

DeAngelis, D. L., R. A. Goldstein, and R. V. O'Neill. 1975. A model for trophic interaction. Ecology **56**:881–892.

Dennis, B., and M. L. Taper. 1994. Density dependence in time series observations of natural populations: estimation and testing. Ecological Monographs **64**:205–224.

Edwards, R. L. 1961. The area of discovery of two insect parasites, *Nasonia vitripennis* (Walker) and *Trichogamma evanescens* Westwood, in an artificial environment. Canadian Entomologist **93**:475–481.

Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall, New York, New York, USA.

Eveleigh, E. S., and D. A. Chant. 1982. Experimental studies on acarine predator–prey interactions: the effects of predator density on prey consumption, predator searching efficiency, and the functional response to prey density (Acarina: Phytoseiidae). Canadian Journal of Zoology **60**:611–629.

Gilliam, J. F. 1990. Hunting by the hunted: optimal prey selection by foragers under predation hazard. Pages 797–818 *in* R. N. Hughes, editor. Behavioural mechanisms of food selection. Springer-Verlag, Berlin, Germany.

Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology **68**:1856–1862.

Harrison, G. W. 1995. Comparing predator–prey models to Luckinbill's experiment with *Didinium* and *Paramecium.* Ecology **76**:357–374.

Hassell, M. P., and D. J. Rogers. 1972. Insect parasite responses in the development of population models. Journal of Animal Ecology **41**:661–676.

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.

Hilborn, R., and M. Mangel. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, New Jersey, USA.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York, New York, USA.

Holling, C. S. 1959a. 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. 1959b. Some characteristics of simple types of predation and parasitism. Canadian Entomologist **91**: 385–398.

Houston, A. I., and J. M. McNamara. 1999. Models of adaptive behaviour: an approach based on state. Cambridge University Press, Cambridge, UK.

Huffaker, C. B., and B. M. Matsumoto. 1982. Group versus individual functional responses of *Venturia* [=*Nemeritis*]

canescens (Grav.). Researches on Population Ecology **24**: 250–269.

Hugie, D. M., and L. M. Dill. 1994. Fish and game: a game theoretic approach to habitat selection by predators and prey. Journal of Fish Biology **45**:151–169.

Huisman, G., and R. J. De Boer. 1997. A formal derivation of the ''Beddington'' functional response. Journal of Theoretical Biology **185**:389–400.

Jost, C. 1998. Comparing predator–prey models qualitatively and quantitatively with ecological time-series data. Dissertation. Institut national agronomique, Paris-Grignon, France.

Jost, C. 2000. Predator–prey theory: hidden twins in ecology and microbiology. Oikos **90**:202–208.

Jost, C., and R. Arditi. 2000. Identifying predator–prey processes from time series. Theoretical Population Biology **57**: 325–337.

Katz, C. H. 1985. A nonequilibrium marine predator–prey interaction. Ecology **66**:1426–1438.

Kennedy, M., and R. D. Gray. 1993. Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the ideal free distribution. Oikos **68**:158–166.

Kfir, R. 1983. Functional response to host density by the egg parasite *Trichogramma pretiosum.* Entomophaga **28**:345–353.

Kincaid, D. R., and E. W. Cheney. 1996. Numerical analysis. Brooks/Cole, Pacific Grove, California, USA.

Kumar, A., and C. P. M. Tripathi. 1985. Parasitoid–host relationship between *Trioxys* (*Binodoxys*) *indicus* Subba Rao & Sharma (Hymenoptera: Aphidiidae) and *Aphis craccivora* Koch (Hemiptera: Aphidiidae): effect of host plants on the area of discovery of the parasitoid. Canadian Journal of Zoology **63**:192–195.

Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior **27**:215–290.

Lotka, A. J. 1925. Elements of physical biology. Williams and Wilkins, Baltimore, Maryland, USA.

MacIsaac, H. J., and J. J. Gilbert. 1991. Discrimination between exploitative and interference competition between Cladocera and *Keratella cochlearis.* Ecology **72**:924–937.

Mertz, D. B., and R. B. Davies. 1968. Cannibalism of the pupal stage by adult flour beetles: an experiment and a stochastic model. Biometrics **24**:247–275.

Murdoch, W. M., and C. J. Briggs. 1996. Theory for biological control: recent developments. Ecology **77**:2001–2013.

Nicholson, A. J., and V. A. Bailey. 1935. The balance of animal populations. Proceedings of the Zoological Society of London **3**:551–598.

O'Donoghue, M., S. Boutin, C. J. Krebs, G. Zuleta, D. L. Murray, and E. J. Hofer. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. Ecology **79**: 1193–1208.

Osenberg, C. W., O. Sarnelle, S. D. Cooper, and R. D. Holt. 1999. Resolving ecological questions through meta-analysis: goals, metrics, and models. Ecology **80**:1105–1117.

Pascual, M. A., and P. Kareiva. 1996. Predicting the outcome of competition using experimental data: maximum likelihood and Bayesian approaches. Ecology **77**:337–349.

Rogers, D. J., and M. P. Hassell. 1974. General models for insect parasite and predator searching behaviour: interference. Journal of Animal Ecology **43**:239–253.

Salt, G. W. 1974. Predator and prey densities as controls of the rate of capture by the predator *Didinium nasutum.* Ecology **55**:434–439.

Schmitz, O. J. 1992. Exploitation in model food chains with mechanistic consumer–resource dynamics. Theoretical Population Biology **41**:161–183.

Schoener, T. W. 1983. Field experiments on interspecific competition. American Naturalist **122**:240–285.

Seber, G. A. F., and C. J. Wild. 1989. Nonlinear regression. John Wiley and Sons, New York, New York, USA.

Sih, A. 1998. Game theory and predator–prey response races. Pages 221–238 *in* L. A. Dugatkin and H. K. Reeve, editors. Game theory and animal behavior. Oxford University Press, New York, New York, USA.

Sutherland, W. J. 1983. Aggregation and the 'ideal free' distribution. Journal of Animal Ecology **52**:821–828.

Taylor, A. D. 1988. Host effects on functional and ovipositional responses of *Bracon hebetor*. Journal of Animal Ecology **57**:173–184.

Uttley, M. G. 1980. A laboratory study of mutual interference between freshwater invertebrate predators. Dissertation. University of York, UK.

van der Meer, J., and B. J. Ens. 1997. Models of interference and their consequences for the spatial distribution of ideal and free predators. Journal of Animal Ecology **66**:846–858.

von Westernhagen, H., and H. Rosenthal. 1976. Predator–prey relationships between Pacific herring, *Clupea harengus,* larvae and a predatory amphipod, *Hyperoche medusarum.* Fishery Bulletin **74**:669–674.

Walde, S. J., and R. W. Davies. 1984. The effect of intraspecific interference on *Kogotus nonus* (Plecoptera) foraging behavior. Canadian Journal of Zoology **62**:2221–2226.

Werner, E. E., and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. American Naturalist **142**:242–272.

APPENDIX A

Maximum-likelihood parameter estimates for the 19 data sets are available in ESA's Electronic Data Archive: *Ecological Archives* E082-033-A1.

APPENDIX B

Test statistics, *P* values, and inferences for hypothesis tests involving the three alternative predator-dependent models are available in ESA's Electronic Data Archive: *Ecological Archives* E082-033-A2.