

## ESTIMATING NONLINEAR INTERACTION STRENGTHS: AN OBSERVATION-BASED METHOD FOR SPECIES-RICH FOOD WEBS

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**Abstract.** Efforts to estimate the strength of species interactions in species-rich, reticulate food webs have been hampered by the multitude of direct and indirect interactions such systems exhibit and have been limited by an assumption that pairwise interactions display linear functional forms. Here we present a new method for directly measuring, on a per capita basis, the nonlinear strength of trophic species interactions within such food webs. This is an observation-based method, requiring three pieces of information: (1) species abundances, (2) predator and prey-specific handling times, and (3) data from predator-specific feeding surveys in which the number of individuals observed feeding on each of the predator's prey species has been tallied. The method offers a straightforward way to assess the completeness of one's sampling effort in accurately estimating interaction strengths through the construction of predator-specific prey accumulation curves. The method should be applicable to a variety of systems in which empirical estimates of direct interaction strengths have thus far remained elusive.

**Key words:** consumption rates; functional response; handling time; indirect effects; omnivory; parameter estimation; predator–prey interactions; species interaction strengths.

### INTRODUCTION

Food webs are fundamental components of ecological communities, characterizing who eats whom within the complex network of species interactions. Natural communities often exhibit species-rich, reticulate food webs that make measuring species interaction strengths difficult. Nevertheless, empirical estimates of interaction strengths represent an important step toward parameterizing mechanistic models of species interactions, understanding the forces that regulate community structure, and making quantitative predictions to inform conservation and resource-use strategies (Berlow et al. 2004, Ebenman and Jonsson 2005, Agrawal et al. 2007).

Many approaches have been employed to quantify the strength of trophic species interactions (reviewed in Berlow et al. 2004, Wootton and Emmerson 2005). Approaches producing estimates on a per capita (or per biomass) basis have the advantage of allowing straightforward comparisons to be made across populations and taxa because they scale out species-effect differences caused by differences in abundance (i.e., species-impacts; Wootton 1997). Per capita interaction strengths underlay all other metrics of species interaction strengths (Laska and Wootton 1998). Approaches capable of producing per capita estimates have used manipulative field experiments (e.g., Bender et al. 1984, Paine 1992), short-term laboratory experiments (e.g., Levitan 1987), time-series dynamics (e.g., Seifert and Seifert 1976, Ives

et al. 2003), energetic perspectives (e.g., Moore et al. 1993, Hall et al. 2000, Libralato et al. 2006), allometric relationships (e.g., Emmerson and Raffaelli 2004), and direct observation-based methods (e.g., Wootton 1997, Woodward et al. 2005). Inherent problems associated with many of these approaches, however, include logistically impractical time, treatment, or replication requirements, or the loss of species-specific properties by the application of generalized relationships (Berlow et al. 2004). Manipulative field experiments also suffer in particular from the indeterminacy of direct and indirect effects of reticulate food webs and cannot, for example, be applied easily to systems exhibiting trophic omnivory (Yodzis 1988, Menge 1997).

A further shortcoming associated with most current approaches is their assumption that predator–prey interactions exhibit a linear functional form (Abrams 2001). Thus they assume that a predator's feeding rate exhibits an unbounded Type I functional response to changes in its prey's abundance. There are some theoretical arguments and empirical evidence to support this assumption (Wootton and Emmerson 2005), but there is also ample indication from laboratory experiments, survey data, and theory that predator–prey interactions can be strongly nonlinear (Ruesink 1998, Abrams 2001, Sarnelle 2003). In fact, at high enough prey densities, predators with nontrivial handling times must exhibit the saturated feeding rate exemplified by the Type II functional response, which is the most often observed response, especially in single-prey studies (Murdoch and Oaten 1975, Jeschke et al. 2002, 2004). Obtaining adequate empirical information on the nonlinear form of interactions in natural multispecies

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communities therefore represents a major challenge to food web ecologists (Abrams and Ginzburg 2000).

We propose a step toward rectifying these issues by introducing a new method for estimating the per capita strength of trophic species interactions. The observation-based approach of our method enables it to be applied in species-rich systems while avoiding the obscurity of indirect trophic effects. With knowledge of prey abundances, prey-specific handling times, and feeding surveys of focal predator populations, the method estimates species-specific attack rates of predators expected to exhibit Type II functional responses. We present the derivation of our method, assess its success using simulations, and show how the information used in calculating attack rates may be used to gauge the accuracy of one's estimates through the construction of predator-specific prey accumulation curves. We conclude by noting the method's own assumptions and suggest systems in which it is likely to be most suitably applied.

## METHODS

### *Derivation of Type II observation-based method*

Our goal was an equation that uses data of an observational type to estimate the attack rate constant  $c$  of a Holling Type II functional response, written as

$$f(N) = \frac{cN}{1 + chN} \quad (1)$$

where  $f(N)$  is a function describing an individual predator's feeding rate in response to changes in the abundance of its prey,  $N$ , and  $h$  is the prey's handling time (Holling 1959). This equation remains the most frequently employed representation of saturating feeding rates by both empiricists and theoreticians alike. We define a prey's handling time as the time required for a predator individual to consume a single prey individual, ignoring chase and post-ingestion digestion times (cf. Jeschke et al. 2002). Thus handling time denotes the time that a predator could be observed in contact with its prey, as it is commonly used in empirical studies (e.g., Menge 1972, Fairweather and Underwood 1983, Yamamoto 2004). The attack rate constant (also known as the instantaneous rate of discovery [Holling 1959]) describes the rate at which a predator approaches the saturation point of its functional response ( $1/h$ ) as the abundance of its prey increases. Parameter  $c$ , therefore, has units of feeding events per predator per prey per unit time. When evaluated at a given prey abundance,  $f(N)/N$  is equivalent to the per capita interaction strength of most previous approaches.

Eq. 1 can be extended to the multispecies functional response with  $S$  prey species as

$$f(N_i) = \frac{c_i N_i}{1 + \sum_{k=1}^S c_k h_k N_k} \quad (2)$$

(e.g., Murdoch 1973). This equation assumes no prey switching (i.e., constant  $c_i$ ). In Appendix A we show that with empirical knowledge of (1) prey abundances,  $N_i$ , (2) prey-specific handling times,  $h_i$ , and (3) data from surveys of a given predator population that tally the number of individuals observed feeding on different prey species, prey-specific  $c_i$  can be calculated as

$$c_i = \frac{F_i A_x}{(F_x - A_x) h_i N_i} \quad (3)$$

In Eq. 3,  $F_i$  is the fraction of feeding individuals that were observed in the process of feeding on prey species  $i$ , and  $A_x$  denotes the fraction of all predator individuals surveyed (feeding and not feeding) that were observed in the process of feeding on prey species  $x$ . Species  $x$  is an arbitrarily chosen species used throughout the calculation of all prey-specific attack rates (see Appendix A).

### *Assessment of observation-based method using simulations*

We used stochastic nonspatial individual-based simulations of feeding predator populations to assess the observation error of our method in estimating prey-specific attack rates. Specifically, we were interested in determining how sampling effort (the number of predator individuals that are surveyed), prey richness (the number of prey species in the predator's diet), and a predator population's level of feeding activity (the proportion of the population observed actively feeding) affected the method's accuracy.

To do so we simulated populations of 50 to 7500 predator individuals feeding on a prey pool of four to 40 species at a range of feeding activity levels where between 3% and 60% of the population, on average, was feeding at any given time (see Appendix B for simulation algorithm). All combinations of sampling effort (= simulated population size) and diet richness, and all combinations of sampling effort and feeding activity level, were simulated independently, with species-specific prey attributes of abundance, handling times, and attack rates selected anew each time. Simulations used to assess the influence of sampling effort and diet richness were run at a feeding activity level such that, on average, ~10% of individuals were feeding at any given time. Simulations used to assess how sampling effort and feeding activity affected the method's accuracy were run with predators having a diet richness of 10 prey species.

We parameterized our simulations to capture several general empirical properties of communities (Appendix B: Table B1). We drew prey abundances from lognormal distributions to reproduce abundance structures commonly observed in nature (Halley and Inchausti 2002). We then made the handling time of each prey species inversely proportional to its abundance, modified with a random term that introduced abundance-dependent amounts of variation. Our rationale was that handling time is probably proportional to prey body size, coupled

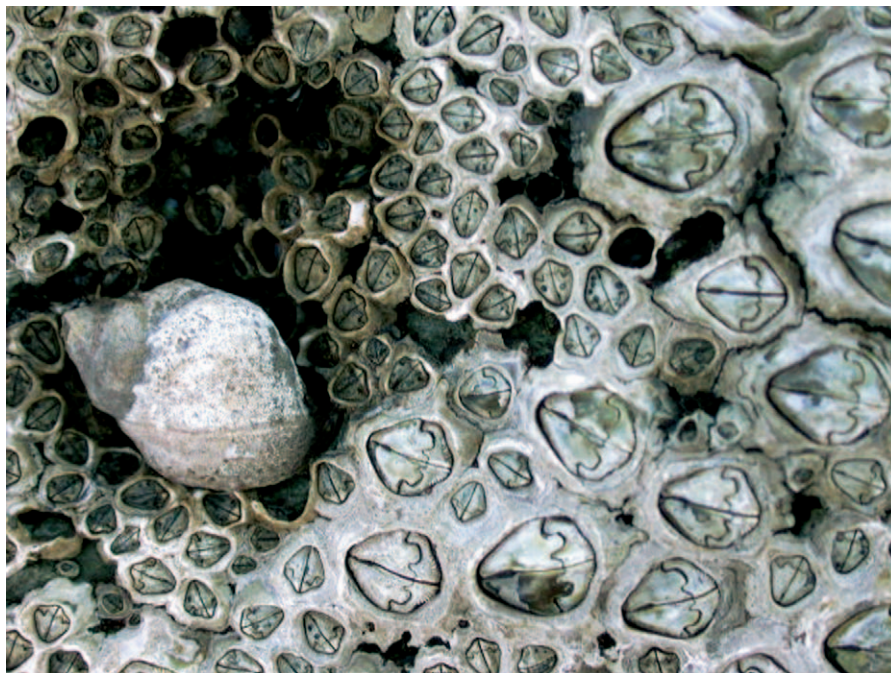


PLATE 1. *Haustrum* (=Lepsiella) *scobina* feeding on *Chamaesiphon* *columna* and *Ch. brunnea* barnacles near Kaikoura, New Zealand. Photo credit: M. Novak.

with the empirically well-documented inverse relationship of both the mean and range of body sizes with abundance (Blackburn and Lawton 1994). Thus, prey species with high abundance were presumed to be small and to require short handling times, while prey species with low abundance could be small or large with correspondingly small or large handling times. Parameter values were chosen to produce prey abundances (per  $m^2$ ) typical of intertidal invertebrates and handling times (hours) typical of whelks feeding upon them (M. Novak, unpublished data; see Plate 1). We drew species-specific attack rates from uniform distributions to avoid bias in this parameter across prey attributes. To obtain a target fraction of feeding predators in a given simulation, the distribution from which attack rates were drawn was limited to a maximum value that was inversely related to the richness of the predator's diet. This resulted in prey-specific feeding rates that ranged from being unsaturated when predators fed at low levels, to relatively saturated when a large proportion of the population was feeding at any given time (Appendix B: Fig. B2).

After sampling effort, prey richness, and feeding level had been set, and the attributes and attack rates of each prey species had been drawn, a simulation proceeded through time with the expected probability that an individual predator encountered a specific prey species in a given time step being equal to the product of the prey's abundance and its attack rate. If an encounter occurred, the predator fed upon that prey species for a number of time steps equal to the handling time of the species. When this time period was over, the predator

individual returned to the original status of not feeding and could encounter additional prey. To explore the effects of specific parameters on the method's performance, encounter probabilities between nonfeeding individuals and each prey species were set to remain constant through time; prey abundance was not affected by feeding events. It is straightforward to apply the method to situations with changing prey populations by measuring abundance at the same time a feeding survey is performed.

For each simulation we tabulated the number of predators in the process of consuming each prey species after a burn-in time of 500 time steps. This survey was then combined with prey-specific abundances and handling times to calculate estimated prey-specific attack rates using Eq. 3. We then correlated these estimates (including estimates of zero for prey species not actually observed being fed upon in the survey) with the "true" attack rates initially drawn for the simulation using Pearson product-moment coefficients to calculate the proportion of variation explained. All simulations were performed in R (R Development Core Team 2006).

## RESULTS

Our ability to accurately recover true input attack rates given prey abundances, handling times, and feeding surveys of the simulated predator populations increased asymptotically as the number of predators surveyed was increased (Fig. 1a). With a diet of four prey species and 10% of the predator population feeding at any given time,  $R^2$  values  $>0.85$  (0.89 with nonobserved prey removed) were achieved when as few as 80 feeding

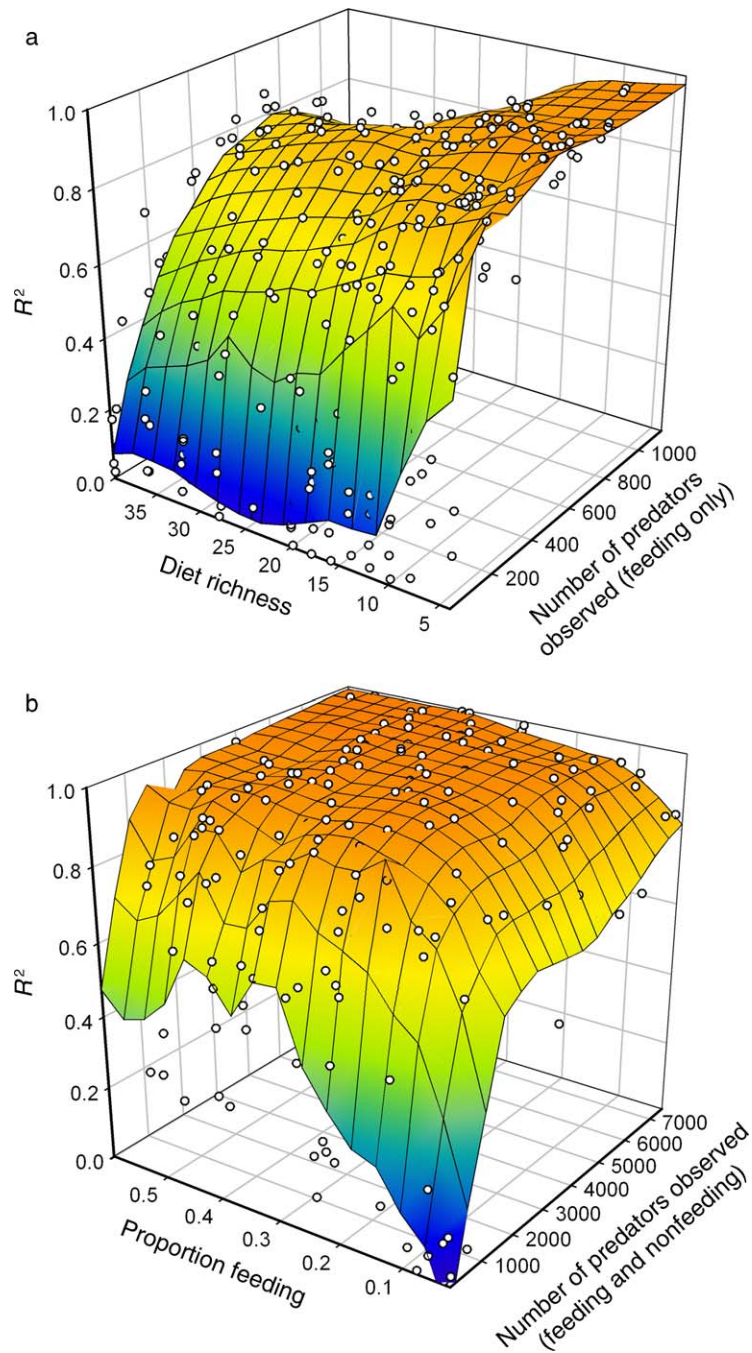


FIG. 1. Correspondence between estimated and true attack rates assessed as the proportion of variation in true attack rates explained by the estimates (with unobserved prey included). The plots show simulated predator populations varying in (a) diet richness, with  $\sim 10\%$  of the individuals feeding at any given time, and (b) feeding activity level, with populations feeding on a potential diet of 10 prey species. Surfaces were produced by Loess smoothing (locally weighted polynomial regression with degree 1 and sampling proportion 0.1) in SigmaPlot (SPSS 2002). Colors reflect the interpolated  $R^2$  values, from low (violet) to high (red-orange).

individuals were observed.  $R^2$  values  $>0.98$  were achieved for six of the seven surveys that observed  $>300$  predators feeding on a diet of four prey species. An increased diet richness led to less accurate estimates at a given sampling effort. When the diet consisted of 40 prey

species, observing 600 feeding individuals was sufficient to produce estimated attack rates that explained  $>75\%$  of the variation in true attack rates (76% with non-observed prey removed). Such survey sizes are regularly obtained in detailed studies of predator diets (e.g., Paine

1966, 1969, Menge 1972, Estes et al. 1982, Irons et al. 1986, West 1986, 1988, Wootton 1997), though are perhaps unlikely to be necessary for most predators given that the most fully resolved food webs suggest that the average number of trophic interactions per species is typically <10 (Dunne et al. 2002).

Increasing the predator population's level of feeding activity increased the accuracy of attack rate estimates for a given sampling effort (Fig. 1b). Thus an increase in the predator population's feeding level from 7% to 15% increased  $R^2$  values from 0.75 to 0.9 for a total population of 1750 individuals feeding on 10 prey species. Equivalently, situations with higher proportions of feeding predators required fewer predator observations to achieve the same level of accuracy. Species-specific estimation accuracies were not affected by prey handling time or abundance, but tended to be higher for larger attack rates (see Appendix C).

#### DISCUSSION

The results of the simulations suggest that our new observation-based method can perform remarkably well at estimating the attack rate constants needed to assess the per capita strength and functional form of species-specific top-down trophic interactions. Of course, the accuracy of applying the method to empirical data will also depend on the variation measured in prey handling times and abundances, which will differ among studies. Nevertheless, given a sufficient amount of survey effort our method can be successfully applied to predators with a diet richness high enough to otherwise make them empirically intractable. Our conclusions were unchanged by using the mean absolute deviation of estimated and true attack rates as a measure of the method's success. Furthermore, no systematic biases were observed when plotting prey-specific deviations between estimated and true attack rates against prey abundances, handling times, or the true strength of the attack rates themselves (Appendix C).

Moreover, the mean absolute deviation of estimated and true attack rates was related negatively to the proportion of the diet richness that sampled predators were actually observed feeding upon; estimation accuracy increases with the completeness of one's sampling of a predator's diet (Fig. 2). This suggests that one's accuracy, or conversely, the remaining sampling effort needed for generating estimates of attack rates at a specified level of accuracy, can be gauged with knowledge of the complete prey pool available to a given predator. Such information can often be obtained directly by comparison of literature compilations of a predator's diet to site-specific prey lists (resulting, for example, from the species abundance surveys performed for the purpose of applying our method). It may also be obtained by constructing species accumulation curves of a predator's observed diet to make extrapolated estimates of the predator's total diet (methods reviewed by Colwell and Coddington [1994]). Such estimates will

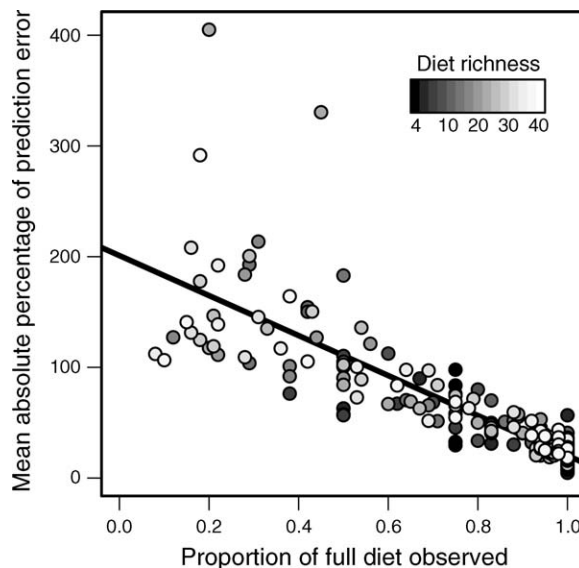


FIG. 2. Relationship between estimation accuracy of predator attack rates and the proportion of the diet observed. Points represent mean absolute percentage differences between "true" and estimated attack rates of all prey (including unobserved species) in each simulated combination of sampling effort and diet richness. The linear regression line is plotted across all sampling efforts for all independently simulated combinations together.

also be informative for assessing the number of rarely occurring, though not necessarily weak, interactions that remain unobserved and, therefore, unestimated.

Our method is not, of course, without its own assumptions. These include: (1) that an individual predator's feeding rate is adequately described by a multispecies Type II functional response (Eq. 2); (2) that predator individuals feed upon only one prey item at a time; (3) that predators have sufficiently large handling times that the probability of observing feeding events is nonzero; (4) that post-handling digestion times do not preclude a predator's ability to search for further prey; (5) that there is no bias toward observing either feeding or nonfeeding predator individuals; (6) that patchy prey abundances are measured at a spatial scale appropriate to the feeding biology of the predator and are not significantly reduced by feeding over the time period of a survey; and finally (7) that surveys are performed at a temporal scale appropriate to the scale at which inferences of interaction strengths are to be made. Thus, if predators feed in a periodic fashion at the temporal scale at which feeding surveys are performed (e.g., day/night), extrapolating attack rates to larger temporal scales (e.g., seasonal rates) is unwarranted unless repeated surveys are performed across this temporal scale or nonfeeding times are accounted for (e.g., Wootton 1997). Additionally, if handling times are measured in hourly units, these must be rescaled appropriately if inferences about the strength of interactions are to be made at a different temporal

scale. Given these assumptions, our method may be suitably applied to a wide range of species, including invertebrates (e.g., whelks and seastars; Menge 1972, Yamamoto 2004), arthropods (e.g., wolf spiders; Samu 1993), birds (e.g., gulls; Wootton 1997), and mammals (e.g., sea otters, Estes et al. 1982), for many of which a sufficient amount of the necessary pieces of information can already be found in the literature.

The observation-based nature of the approach provides a broadly applicable method that circumvents many of the logistical problems associated with other approaches. The method may easily be applied to size-structured interactions by treating predator or prey cohorts as separate species. Feeding surveys may entail repeated samples of a predator population or of focal individuals, as long as observations are separated by time intervals sufficiently large to ensure independence. Handling times may be derived from several sources that include: (1) detailed observations of focal individuals (e.g., Laidre and Jameson 2006); (2) direct observation in laboratory studies (handling times being both less sensitive than attack rates to differences between laboratory and field conditions, and logistically more feasible to obtain than the treatment permutations needed to characterize all multispecies functional responses experimentally); and (3) application of Eq. 3 to empirical situations with differing prey abundances to solve for  $c_i$  and  $h_i$  simultaneously.

The method's strength lies in its applicability to predators that feed on diverse suites of prey species. The ubiquity of such generalist predators has made the estimation of direct interaction strengths in natural food webs especially difficult, particularly when they engage in omnivorous interactions. Nevertheless, our method may also be applied to the relatively simple systems typically used in experimental approaches and may, in fact, be preferably employed given the confounding factors often involved in manipulating species abundances (Chalcraft et al. 2005, Skelly 2005, Miller and Gaylord 2007, Yoshida et al. 2007). Its suitability to natural field settings, furthermore, allows this observation-based method to estimate the realized strength of trophic species interactions within the empirical context of the multispecies web of density-mediated effects and interaction modifications (Wootton 1994, Peacor and Werner 2004). Species interactions with functional forms more complicated than Holling Type II responses are clearly present in nature (Skalski and Gilliam 2001). By employing derivation techniques similar to those used here or, for example, by repeated application of our method across gradients of community structure, it may nevertheless be possible to assess and quantify the form by which even these modifications affect the strength of trophic species interactions.

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#### APPENDIX A

Derivation of Type II observation-based method (*Ecological Archives* E089-120-A1).

#### APPENDIX B

Simulation algorithm, parameters, and resultant feeding rates (*Ecological Archives* E089-120-A2).

#### APPENDIX C

The bias and accuracy of the observation-based method (*Ecological Archives* E089-120-A3).