Hidden layers of density dependence in consumer feeding rates

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Abstract

Functional responses relate a consumer's feeding rates to variation in its abiotic and biotic environment, providing insight into consumer behavior and fitness, and underpinning population and food-web dynamics. Despite their broad relevance and long-standing history, we show here that the types of density dependence found in classic resource- and consumer-dependent functional-response models equate to strong and often untenable assumptions about the independence of processes underlying feeding rates. We first demonstrate mathematically how to quantify non-independence between feeding and consumer interference and between feeding on multiple resources. We then analyze two large collections of functional-response datasets to show that non-independence is pervasive and borne out in previously-hidden forms of density dependence. Our results provide a new lens through which to view variation in consumer feeding rates and disentangle the biological underpinnings of species interactions in multi-species contexts.

Keywords: *Mutual predator effects, interaction modifications, indirect effects, non-additive effects, higher-order interactions, generalist–specialist continuum*

Introduction

Functional responses are a critical component in our understanding of consumer-resource interactions. Since the pioneering work of Holling (1959a;b; 1965), numerous researchers have used manipulative and observational experiments to elucidate the empirical ways in which varied biotic and abiotic factors alter consumer feeding rates in diverse biological contexts (e.g., DeLong, 2014; Preston *et al.*, 2018; Uiterwaal & DeLong, 2020). In parallel, researchers have proposed a large suite of models to characterize functional responses mathematically (Abrams & Ginzburg, 2000; Jeschke *et al.*, 2002; Gentleman *et al.*, 2003; Koen-Alonso, 2007; Arditi & Ginzburg, 2012), with emphasis increasingly being placed on the evaluation of their statistical performance and empirical relevance (Skalski & Gilliam, 2001; Jeschke *et al.*, 2004; Novak *et al.*, 2017; Uiterwaal & DeLong, 2020).

Though they differ in their finer details, one assumption that is common to virtually all functional-response models is that feeding rates will exhibit density-dependent variation. The agents of this density dependence provide a convenient classification scheme: on one hand, we have "resource-dependent" or "consumer-dependent" models (whereby a focal consumer's feeding rate is either determined by resource abundance alone, or by the abundances of resources and consumers together; Abrams & Ginzburg, 2000); on the other, we have "single-resource" versus "multi-resource" models (whereby focal consumers are assumed to be specialists feeding on a single resource, or generalists whose feeding rates on non-focal resources could influence their feeding rate on the focal resource; Murdoch, 1973). For example, the well-

known Holling Type II functional-response model, $F(N) = aN/(1+ahN)$, is a single-resource dependent model since the per capita feeding rate F saturates only as a function of increasing resource density N (Holling, 1959b). In this model, the rate of saturation is determined by the "attack rate" a and the "handling time" h, the latter of which imposes an ever greater cost to the consumer as the rate with which it encounters (and captures) resources increases with resource density.

Despite the ubiquity of density dependence in functional-response models, the parameters that control how species densities affect variation in feeding rates are rarely themselves considered to be explicit functions of species' densities (Abrams, 1982; Kéfi *et al.*, 2012). For example, although the Holling Type III model (Holling, 1959b) may be interpreted as assuming that the attack rate is a linearly increasing function of resource density N, it is far less common to allow handling time to also depend on N (but see Abrams, 1990; Okuyama, 2010). And yet, while almost all resource-dependent and consumer-dependent models consider feeding rate saturation to be a function of (i) increasing resource density via handling times and (ii) increasing consumer density via conspecific interference, neither handling times nor interference rates are themselves considered to depend on consumer or resource densities, respectively.

Broadly-speaking, density dependence of interaction-rate parameters leads to interaction modifications (Wootton, 1993; Adler & Morris, 1994; Goudard & Loreau, 2008) reflecting indirect effects (Wootton, 1994; Okuyama & Bolker, 2007; Abrams & Cortez, 2015), trait- and behavior-mediated effects (Beckerman *et al.*, 1997; Peacor & Werner, 2001; Werner & Pea-

cor, 2003; Toscano & Griffen, 2014), and other forms of non-additivity or higher-order effects (Mayfield & Stouffer, 2017; Letten & Stouffer, 2019; Kleinhesselink *et al.*, 2019). Though these phenomena have long been recognized as being biologically widespread (Abrams, 1983; Strauss, 1991; Levine *et al.*, 2017), there are multiple explanations for why they remain under-represented in the functional-response literature and why their potential importance for consumer feeding rates has not been empirically addressed. Among these reasons are the high logistical costs associated with even the simplest of functional-response experiments, with statistical insight into additionally-assumed parameters requiring ever more treatment levels and greater amounts of replication (Beck & Arnold, 1977; Bolker, 2008). Researchers are also well-justified in wishing to avoid unnecessary increases in model complexity that complicate mathematical analyses and can lead to over-fit statistical models (Rissanen, 1996; Myung *et al.*, 2000; Burnham & Anderson, 2002). A more fundamental challenge, however, is that it is far easier to add potentially unnecessary new terms to a model than it is to provide a biological rationale for why they should be included (Abrams, 1997; Ginzburg & Jensen, 2004; Otto & Day, 2007; Guimerà *et al.*, 2020). This represents a general problem for the functional-response literature because it lacks a general perspective from which to biologically motivate such terms.

To address this challenge, we provide a mathematical analysis to demonstrate how these under-studied density-dependent terms can emerge from classic consumer functional-response models. We focus our analysis on two broadly-studied scenarios: First, we consider the case of multiple conspecific consumer individuals foraging on a single resource species. In this con-

text, we derive new models that generate a spectrum of emergent consumer-interference effects that have not been described previously. Second, we consider the case of a single consumer individual foraging on two different resource species. In this context, we derive new models that generate a spectrum of emergent effects between resource species that have also not been previously recognized. To assess the empirical relevance of these new functional-response models and thereby motivate targeted experimental designs in the future, we then fit them to two large collections of published functional-response data pertaining to each scenario. Our analysis provides evidence for the widespread prevalence of unrecognized density-dependent effects in many existing functional-response experiments.

Mathematical analysis

We first show how links between the various processes that underlie feeding rates can create novel functional forms for feeding rate variation; specifically when the rates of consumer interference and/or consumption of different resources are, or are not, independent of each other. Our analysis demonstrates why non-independence leads directly to new functional-response models containing "density dependence of interaction-rate parameters" (e.g., handling times that are explicit functions of consumer densities). For simplicity and to better link to the prevailing literature, we will generally refer to consumers as predators and resources as prey. However, we will subsequently use our data analysis to show that the scenarios described apply to consumer–resource interactions more broadly.

Single-resource consumer dependence

We first consider how interactions between conspecific predators act to change their own per capita feeding rate. One of the simplest models that includes such interactions by allowing for both resource and consumer density dependence is the single-resource consumer-dependent Beddington–DeAngelis functional response (Beddington, 1975; DeAngelis *et al.*, 1975). This model takes the form

$$F_{ki}\left(N_i, P_k\right) = \frac{a_{ki} N_i}{1 + a_{ki} h_{ki} N_i + c_k P_k}\,, \tag{1}$$

where F_{ki} is the feeding rate of predators k consuming prey i (with dimensions of [(prey consumed per predator) per time available]), N_i is the number of prey i available, P_k is the number of predators k, a_{ki} is the attack rate (with dimensions of [(prey consumed per prey available) per time available]), h_{ki} is the handling time (with dimensions [time handling per prey consumed]), and c_k is the strength of interference between predators (with dimensions [(time interfering per time available) per predator interfering]). When P_k represents a count rather than a density of predators, as is common in experimental settings, P_k is replaced by $(P_k - 1)$ because a predator individual cannot interfere with itself. Note that the 1 in the denominator is dimensionless for the same reason that time cancels out in the dimensions of interference strength c_k. We have also refrained from including dimensions of area or volume in a_{ki} or c_k because they have no impact on our subsequent data analysis (but see Uiterwaal & DeLong, 2020).

A related model, the Crowley–Martin functional response (Crowley & Martin, 1989), takes

the form

$$F_{ki}\left(N_i, P_k\right) = \frac{a_{ki} N_i}{\left(1 + a_{ki} h_{ki} N_i\right)\left(1 + c_k P_k\right)}\,, \tag{2}$$

where all parameters are defined precisely as above. Whereas the Beddington–DeAngelis model is interpreted as characterizing predators that only interfere when searching for resources, the Crowley–Martin model is interpreted as characterizing predators that interfere both when searching for and when handling prey.

Focusing on the denominators of Eqs. (1-2), the key mathematical difference between the Beddington–DeAngelis and Crowley–Martin models is an additional term in the latter that varies with the product of N_i and P_k. Without loss of generality, we could instead rewrite both models as

$$F_{ki}\left(N_i, P_k\right) = \frac{a_{ki} N_i}{1 + a_{ki} h_{ki} N_i + c_k P_k + \left(1 - \phi\right) a_{ki} h_{ki} c_k N_i P_k}\,, \tag{3}$$

where ϕ is a dimensionless parameter that controls the strength of this $N_i P_k$ term. Written in this way, we immediately recover the Beddington–DeAngelis model when $\phi = 1$ and the Crowley–Martin model when $\phi = 0$.

Understanding the parameter ϕ

We can conceptualize the role of ϕ in creating density-dependent functional-response parameters in various ways. For example, we could rearrange the denominator of Eq. (3) to instead give

$$F_{ki}\left(N_i, P_k\right) = \frac{a_{ki} N_i}{1 + a_{ki} h_{ki}\left[1 + \left(1 - \phi\right) c_k P_k\right] N_i + c_k P_k}\,, \tag{4}$$

in which case the implied interpretation is that ϕ influences the extent to which handling time h_{ki} is a function of the abundance of interfering predators P_k; h_{ki} is only independent of interfering predators when $\phi = 1$. One could equivalently rearrange Eq. (3) to give

$$F_{ki}\left(N_i, P_k\right) = \frac{a_{ki} N_i}{1 + a_{ki} h_{ki} N_i + c_k \left[1 + \left(1 - \phi\right) a_{ki} h_{ki} N_i\right] P_k}\,, \tag{5}$$

in which case the implied interpretation is that ϕ influences the extent to which interference strength c_k is a function of the abundance of available prey N_i; c_k is only independent of available prey when $\phi = 1$. From a phenomenological perspective, it is important to recognize that both viewpoints are equally correct—as are combinations of them—as they are mathematically identical. Stepping back a bit, this implies that the most parsimonious role of ϕ is as an indicator that neither prey dependence—as captured with handling time h_{ki}—nor predator dependence—as captured with interference strength c_k—can be properly measured independent of the other.

To clarify the origin of this dependence of h_{ki} and c_k on species densities, we extend a derivation previously presented by Crowley & Martin (1989). Rather than describe predator–prey functional responses phenomenologically, as formulated above, those authors described how the observed feeding rate F_{ki} relates to an implicit, unmeasured interference rate I_k:

$$F_{ki}\left(N_i, P_k\right) = a_{ki} N_i \left(1 - h_{ki} F_{ki} - \beta_k I_{ki}\right) \tag{6}$$

$$I_k\left(N_i, P_k\right) = \alpha_k P_k \left(1 - \phi h_{ki} F_{ki} - \beta_k I_k\right)\,. \tag{7}$$

Upon algebraically solving Eqs. (6-7) for F_{ki}, we immediately obtain Eq. (3) with interference

strength $c_k = \alpha_k \beta_k$. The two new parameters are an "interference rate" α_k (akin to the attack rate and with dimensions [(predator interfered per predator interfering) per time available]), and an "interference time" β_k (akin to handling time and with dimensions [time interfering per predator interfered]). The parenthetical term of each equation therefore corresponds to the proportion of total time available for attacking and the proportion of total time available for interfering, respectively. That is, consistent with the definitions of h_{ki} and β_k, time for searching in Eq. (6) is reduced by time spent handling and time spent interfering. Similarly, time available for interfering in Eq. (7) is also reduced by interfering. In contrast, whether and how time spent handling influences the realized rate of interference is explicitly determined by the value of ϕ.

Expressed in this way, we can shift from a generic parameter ϕ and formally define $\phi_{I_k F_{ki}}$ as the parameter capturing how the predator's feeding rate F_{ki} alters its realized conspecific interference rate I_k. As described verbally above, predators can interfere while searching but cannot interfere while feeding in the Beddington–DeAngelis model (Eq.1), implying $\phi_{I_k F_{ki}} = 1$. In the Crowley–Martin model (Eq.2), predators interfere both while searching and while feeding, implying $\phi_{I_k F_{ki}} = 0$. Crowley & Martin (1989) referred to these as distraction and distraction-free models, respectively. Beyond these two cases, note that *any* value of $\phi_{I_k F_{ki}} \neq 1$ leads to the appearance of a "higher-order" term in the denominator that involves the product of both prey and predator densities, $N_i P_k$. Parameter $\phi_{I_k F_{ki}}$ causes feeding rates to *decrease* with increasing $N_i P_k$ whenever $\phi_{I_k F_{ki}} < 1$, and causes feeding rates to *increase* with increasing $N_i P_k$ whenever $\phi_{I_k F_{ki}} > 1$ (Fig. 1a).

Multi-resource dependence

We follow a similar methodology for multi-resource dependence—as occurs when a single predator is feeding on two different prey species—to measure the effect that feeding on one prey species has on the predator's rate of feeding on the second prey species (and vice versa). Similar to Eqs. (6-7), we define the feeding rates on prey i and prey j as

$$F_{ki}\left(N_i, N_j\right) = a_{ki} N_i \left(1 - h_{ki} F_{ki} - \phi_{F_{ki}F_{kj}} h_{kj} F_{kj}\right) \tag{8}$$

$$F_{kj}\left(N_i, N_j\right) = a_{kj} N_j \left(1 - \phi_{F_{kj}F_{ki}} h_{ki} F_{ki} - h_{kj} F_{kj}\right), \tag{9}$$

where $\phi_{F_{ki}F_{kj}}$ represents the extent to which feeding on j impacts feeding on i, $\phi_{F_{kj}F_{ki}}$ represents the extent to which feeding on i impacts feeding on j, and all other parameters are interaction-specific versions of the quantities already defined above (e.g., a_{ki} and a_{kj} vs. only a_{ki}). Hence the parenthetical term of each equation corresponds to the proportion of total time available for attacking i (respectively j) after accounting for time spent handling both prey.

With algebraic manipulation of Eqs. (8-9), we can solve for each of the two feeding rates to give

$$F_{ki}\left(N_i, N_j\right) = \frac{a_{ki} N_i \left[1 + \left(1 - \phi_{F_{ki}F_{kj}}\right) a_{kj} h_{kj} N_j\right]}{\left(1 + a_{ki} h_{ki} N_i\right)\left(1 + a_{kj} h_{kj} N_j\right) - \phi_{F_{ki}F_{kj}} \phi_{F_{kj}F_{ki}} a_{ki} h_{ki} a_{kj} h_{kj} N_i N_j} \tag{10}$$

for the predator's feeding rate on i. (An equivalent expression for the predator's feeding rate on prey j can be obtained by swapping all i's for j's and vice versa.) As was the case for predator interference, note that *any* values of $\phi_{F_{ki}F_{kj}}$ and $\phi_{F_{kj}F_{ki}}$ such that their product $\phi_{F_{ki}F_{kj}}\phi_{F_{kj}F_{ki}} \neq$

1 lead to the appearance of the additional "higher-order" term in the denominator involving the product of both prey densities, $N_i N_j$.

In order to better elucidate the behavior of these expressions for feeding rates, it is useful to explore three limiting cases and the resulting forms for F_{ki}. First, consider a scenario in which $\phi_{F_{ki}F_{kj}} = 1$ and $\phi_{F_{kj}F_{ki}} = 1$, implying that predators cannot search for any prey while handling either. Here the dependence on the "other" prey vanishes from the numerators of both feeding-rate expressions and the higher-order term cancels within both denominators. As a result, we are left with the standard "multi-resource Holling Type II functional response" (Murdoch, 1973; Koen-Alonso, 2007) given by

$$F_{ki}\left(N_i, N_j\right) \quad = \quad \frac{a_{ki} N_i}{1 + a_{ki} h_{ki} N_i + a_{kj} h_{kj} N_j} \,. \tag{11}$$

Second, consider the scenario where $\phi_{F_{ki}F_{kj}} = 0$, implying that feeding on j has no impact on feeding on i. In this case, the higher-order term vanishes from the denominator in F_{ki} irrespective of the value of $\phi_{F_{kj}F_{ki}}$. Moreover, the potential dependence on N_j can be factored out since identical expressions of the form $1 + a_{kj} h_{kj} N_j$ appear in both the numerator and denominator. Reassuringly, we are left with a single-resource Holling Type II functional response for F_{ki} that is independent of the abundance of prey j (Holling, 1959a;b); namely we obtain

$$F_{ki}\left(N_i\right) = \frac{a_{ki} N_i}{1 + a_{ki} h_{ki} N_i} \,. \tag{12}$$

Third, consider what happens when $\phi_{F_{ki}F_{kj}} = 1$ and $\phi_{F_{kj}F_{ki}} = 0$, implying that a predator handling j cannot attack i but a predator handling i could still attack j. Under these conditions,

feeding on i behaves as

$$F_{ki}\left(N_i, N_j\right) = \frac{a_{ki}N_i}{1 + a_{ki}h_{ki}N_i + a_{kj}h_{kj}N_j + a_{ki}h_{ki}a_{kj}h_{kj}N_iN_j}\,, \tag{13}$$

which shows systematic variation for any abundance of j and includes the higher-order term in the denominator. Compared to first two limiting cases, feeding F_{ki} is lowest in this third scenario (for equivalent values of the attack rates and handling times). This is because increased feeding F_{kj} on j acts to decrease the time available for feeding on i. Delineating values of $\phi_{F_{ki}F_{kj}}$ and $\phi_{F_{kj}F_{ki}}$ that always lead to increased or decreased feeding rates is more complicated than for single-resource consumer dependence since both rates are a combination of both parameters. Moreover, two given values of $\phi_{F_{ki}F_{kj}}$ and $\phi_{F_{kj}F_{ki}}$ could hypothetically lead to a decrease in F_{ki} while still increasing the *total* feeding rate $F_k = F_{ki} + F_{kj}$ (Fig. 1b).

Methods

Data compilation

Our mathematical analysis indicates that *any* non-independence between processes such as feeding and interference can induce higher-order, non-additive terms in the denominator of common functional-response models. We therefore next aimed to determine whether there is empirical support for such non-independence and the inclusion of the parameters $\phi_{I_kF_{ki}}$, $\phi_{F_{ki}F_{kj}}$, and $\phi_{F_{kj}F_{ki}}$ when modeling observed feeding rates. Focusing on the two specific scenarios discussed above, we searched the literature to obtain two different types of empirical datasets. First, single-resource consumer-dependence datasets designed specifically to assess consumer

interference; these consisted of feeding rates as a function of variation in prey and predator abundances, or parasitism rates as a function of variation in host and parasitoid abundances (Table S1). Second, multi-resource dependence datasets designed to assess the dependence of consumer feeding rates on the availability of two alternative resources; these universally consisted of feeding rates for single predator individuals as a function of variation in the abundances of two prey (Table S2). When possible, we obtained the original data from the authors. Otherwise, we extracted (i) data points or (ii) means and their associated uncertainties from the publication in tables by hand or figures using GraphClick (2010).

Single-resource consumer-dependent models

We considered five different functional-response models when examining the consumer-interference datasets (Table 1): the resource-dependent, consumer-independent Holling Type I and Holling Type II models (Holling, 1959a;b), the resource- and consumer-dependent Beddington–DeAngelis (Beddington, 1975; DeAngelis *et al.*, 1975) and Crowley–Martin (Crowley & Martin, 1989) models, and our new resource- and consumer-dependent model with the additional parameter $\phi_{I_k F_{ki}}$ (Eq. 3).

Multi-resource dependent models

We considered four different functional-response models when examining the multiple-resource datasets (Table 2): the Holling Type I functional responses that arise when $h_{ki} = h_{kj} = 0$, the Holling Type II functional responses that arise when $\phi_{F_{ki}F_{kj}} = \phi_{F_{kj}F_{ki}} = 0$ (Holling, 1959a;b),

the multi-resource Type II functional responses that arise when $\phi_{F_{ki}F_{kj}} = \phi_{F_{kj}F_{ki}} = 1$ (Murdoch, 1973), and our generalized multi-resource Type II functional responses that emerge when both $\phi_{F_{ki}F_{kj}}$ and $\phi_{F_{kj}F_{ki}}$ are free parameters (Eq. 10).

Biological and statistical constraints to the parameters

There is one more particularly important detail to consider when fitting Eqs.(3) & (10) to data. In the preceding mathematical descriptions, we primarily focused on examples in which the various parameters $\phi_{I_kF_{ki}}$, $\phi_{F_{ki}F_{kj}}$, and $\phi_{F_{kj}F_{ki}}$ took values of 0 or 1. We did so to build on the intuition behind the distraction and distraction-free interpretations of predator behavior (Crowley & Martin, 1989), and to relate our generalized models to pre-existing functional-response models. This notwithstanding, the values these parameters may take on are not restricted to this 0 to 1 region. Instead, their values depend on the extent to which they generate biologically plausible (or implausible) feeding rate behavior. This may be understood as follows.

When considering the processes involved, the most fundamental constraints are that the rate of predator k feeding on prey i (F_{ki}), the rate of predator k feeding on prey j (F_{kj}), and interference rate of predator k (I_k) in Eqs. (7-9) must each remain greater than or equal to zero. This means, for example, that the statistical best-fit value of $\phi_{I_kF_{ki}}$ for a given single-resource consumer-dependence dataset could be (i) $\phi_{I_kF_{ki}} < 0$ if β_k were sufficiently large or (ii) $\phi_{I_kF_{ki}} > 0$ if h_{ki} were sufficiently small. This contrasts to parameters such as handling time that are directly constrained by their explicit interpretation (e.g., the time associated with handling a prey cannot be negative). Similar arguments hold for $\phi_{F_{ki}F_{kj}}$ and $\phi_{F_{kj}F_{ki}}$ in the

context of multiple prey. While an absence of constraints on $\phi_{I_k F_{ki}}$, $\phi_{F_{ki} F_{kj}}$, and $\phi_{F_{kj} F_{ki}}$ does not impact the mathematical derivation performed above, it does influence their statistical inference as outlined below. It also impacts a model's ability to generate biologically plausible "out-of-sample" predictions. That is, a large positive value of $\phi_{I_k F_{ki}}$ may be consistent with a given dataset while also predicting implausible, negative interference rates for larger-than-observed consumer or resource abundances (Novak & Stouffer, 2020).

Parameter inference

Given each empirical dataset, we determined the best-fit parameter values for each functional-response model using a two-step procedure. In the first step, we used the global-optimization algorithm *sbplx* from the *nloptr* package (Johnson, 2020) in R (R Core Team, 2020) to obtain an estimate of the maximum-likelihood parameter values. In the second step, we passed the optimal parameter values identified by *sbplx* to the *mle2* function from the *bbmle* package (Bolker & R Development Core Team, 2020) to search for local improvements and assess model convergence. The likelihood being optimized was determined by the dataset's experimental design (Supplementary Material), and all handling times, attack rates, and interference rates were constrained to be positive. We allowed the values of $\phi_{I_k F_{ki}}$, $\phi_{F_{ki} F_{kj}}$, and $\phi_{F_{kj} F_{ki}}$ to vary freely as long as predicted mean feeding rates remained greater than or equal to zero.

When a fit converged (i.e., when the maximum-likelihood parameter values were identified), we first attempted to estimate parameter uncertainty via their 68% profile confidence intervals—which roughly correspond to standard error—using the *confint* function from *bbmle*.

On occasion, this approach failed because, although the optimization converged, the likelihood surface was nearly flat around the optimum. This is usually indicative of the model being over-parameterized (Gill & King, 2004), the occurrence of which was not altogether surprising in our context since none of the experiments were designed for the purpose of fitting our most complex functional-response models. In these instances, we used the quadratic approximation of the parameter standard errors provided directly by *mle2*.

When we could only obtain a dataset as means and associated uncertainties, we simulated 250 bootstrapped datasets with a sample size equivalent to that of the original dataset and then inferred the best-fit parameter values to each of these (Supplementary Material). We then performed the same two-step parameter fitting process separately for each of these bootstrapped datasets. Given these 250 separate fits, we treated the median of the bootstrapped parameter values as the parameter's point estimate and used the central 68% interval of the bootstrap distribution as its uncertainty.

Model assessment and model comparison

After fitting the parameters of the various functional-response models, we focused on two primary ways in which the data could lend support to the processes captured by the parameters $\phi_{I_k F_{ki}}$, $\phi_{F_{ki} F_{kj}}$, and/or $\phi_{F_{kj} F_{ki}}$. The first came from comparing AIC (Akaike Information Criterion) across the various candidate models. Since AIC incorporates a penalty for additional parameters, smaller values of AIC provide an indication of a better out-of-sample prediction error conditional on model complexity. The second was provided by our aforementioned abil-

ity to infer maximum-likelihood values for these parameters that differed from values of 0 or 1 with well-defined, and relatively small, estimates of uncertainty. Even when a model is not the most parsimonious among a set of alternative models, well-defined estimates of parameter uncertainty are still a good indication that it provides a robust description of the data-generating process (Beck & Arnold, 1977; Gill & King, 2004).

Results

Consumer interference

We obtained a total of 77 single-resource consumer-dependence datasets with which to infer the effect of feeding on consumer interference (Table S1). This included 44 datasets in the form of raw data and 33 datasets in the form of means and associated uncertainties. On average, the datasets consisted of 120 replicate feeding observations (min: 10, max: 528, median: 80).

As judged by AIC, our generalized consumer-dependent model including $\phi_{I_k F_{ki}}$ (Eq. 3) was ranked first for 42 (55%) datasets and tied for first (i.e., was within 2 AIC units) for an additional 24 (31%) datasets (Fig. 2). Maximum-likelihood point estimates of $\phi_{I_k F_{ki}}$ (i.e., the effect of feeding on interference) varied considerably across the datasets (Fig. 2). Well over half (47 out of 77) of the datasets provided point estimates that were less than or equal to one, implying that handling times and/or consumer interference *increased* as the product of resource and consumer abundances increased. The uncertainties of these $\phi_{I_k F_{ki}}$ point estimates overlapped only the Beddington–DeAngelis model ($\phi_{I_k F_{ki}} = 1$) for 15 datasets, overlapped

only the Crowley–Martin model ($\phi_{I_k F_{ki}} = 0$) for 11 datasets, and overlapped both models for 23 datasets. This overlap was largely consistent with instances where the generalized model was judged equivalent to simpler models based on AIC. A full 28 datasets had uncertainties that were not consistent with *any* pre-existing model: 4 datasets fell entirely in the region $\phi_{I_k F_{ki}} < 0$, 10 datasets fell exclusively between the two models (e.g., consistent with "partial" distraction of consumers), and 14 datasets fell entirely in the region $\phi_{I_k F_{ki}} > 1$. Overall, the uncertainties of only 34 datasets (43%) were consistent with the idea that interference and feeding were independent of each other (i.e., $\phi_{I_k F_{ki}} \approx 0$).

Multiple resources

We obtained a total of 30 multi-resource dependence datasets with which to infer the effect that feeding on one prey has on feeding on another and vice versa (Table S2). This included 15 datasets in the form of raw data and 15 datasets in the form of means and associated uncertainties. On average, the datasets consisted of 135 replicate pairs of feeding observations (min: 37, max: 290, median: 116).

As judged by AIC, our generalized multi-resource Holling Type II model including both $\phi_{F_{ki} F_{kj}}$ and $\phi_{F_{kj} F_{ki}}$ (Eq.10) was ranked first for 20 (67%) multiple-resource datasets and tied for first for an additional 1 (3%) dataset (Fig. 3). Maximum-likelihood point estimates of $\phi_{F_{ki} F_{kj}}$ and $\phi_{F_{kj} F_{ki}}$ varied considerably across the different datasets (Fig. 3), including estimates indicative of (i) feeding rates being unaffected by the non-focal resource ($\phi_{F_{ki} F_{kj}} \approx 0$ and $\phi_{F_{kj} F_{ki}} \approx 0$), (ii) feeding on one resource completely precluding feeding on the other

($\phi_{F_{ki}F_{kj}} \approx 1$ and/or $\phi_{F_{kj}F_{ki}} \approx 1$), (iii) feeding on one resource only partially precluding feeding on the other ($0 < \phi_{F_{ki}F_{kj}} < 1$ and $0 < \phi_{F_{kj}F_{ki}} < 1$), and (iv) almost all combinations of these.

Discussion

Our analyses provide compelling evidence that the processes affecting resource- and consumer dependence in feeding rates are frequently density dependent themselves. Across a large proportion of the single-resource consumer-dependence datasets, we observed that feeding impacts interference rates different than how interference impacts foraging rates. This contrasts to many models that implicitly assume a symmetry among these processes. Likewise, we observed that a consumer's behavior when feeding on one resource can appear very different to its behavior when feeding on another. That we were able to obtain these inferences despite the fact that, to our knowledge, the experimental design of none of the analyzed datasets was developed to measure our additional parameters, lends further credibility to our conclusions. We thus predict that evidence in support of functional-response models containing higher-order model terms will increase as datasets with larger sample sizes and targeted experimental designs are generated in the future.

Across the single-resource consumer-dependence datasets, the vast majority had $\phi_{I_k F_{ki}} > 1$, indicating that per capita feeding rates saturate at ever decreasing levels as the number of consumers increases. Phenomenologically, this arises either because the total time spent handling resources increases in higher consumer-density situations, or because consumers spend more

and more time interfering with conspecifics that they would have otherwise spent feeding. In some datasets (e.g., Chong & Oetting, 2006; Crowley & Martin, 1989), feeding in the presence of just over 3 additional conspecific consumers led to an effective doubling of each consumer's handling time per resource consumed, relative to that of an isolated consumer individual. In contrast, a smaller subset of consumer-interference datasets suggest that consumers spent less and less time handling resources when feeding in the presence of more and more conspecifics (e.g., Long *et al.*, 2012b; Kratina *et al.*, 2009).

Across the multi-resource dependence datasets, we found that most were inconsistent with the assumptions implied by either the single-resource or multi-resource Holling Type II functional responses. Intriguingly, the multi-resource Holling Type II is widely used in simulations of food webs and other complex communities (Brose *et al.*, 2006; Williams *et al.*, 2007; Berlow *et al.*, 2009; Iles & Novak, 2016; Delmas *et al.*, 2017). Our results therefore challenge this basic assumption of theory, suggesting that ecological communities are most likely composed of a much broader array of consumer types. What dynamical properties these varied consumer types may impart to their populations and food webs remains unknown. Recent analyses of existing functional-response models suggest their effects could be quite strong (Adamson & Morozov, 2013; 2014; Aldebert & Stouffer, 2018; Coblentz & DeLong, 2020). In both the empirical and theoretical literatures, it is common for researchers to decide a priori which model is most appropriate given their focal consumer and to analyze their data accordingly. In contrast, our results indicate that one would almost always need to know the characteristics of the

consumers *and* resources before being able to adequately describe feeding rates. Moreover, a given consumer's feeding rate could just as easily appear consistent with one model for a first resource and with a different model with regard to another (e.g., Long *et al.*, 2012a) or, worse yet, somewhere in between (e.g., Lester & Harmsen, 2002). Clearly, more empirical work is needed to understand the biology that determines why any given consumer–resource–resource combination lands in one particular location along the spectra of process inter-dependencies, particularly in the context of predators that feed on more than just two prey species.

Functional responses emerge from independent and non-independent processes

Our analyses emphasize the fact that even the simplest functional responses are impacted by more than static attack rates, handling times, and interference rates. We argue it is more instructive to think about feeding as but one of multiple *processes* in which a predator could be engaging at any given moment of time (see also Koen-Alonso, 2007; Kéfi *et al.*, 2012; Lafferty *et al.*, 2015). The parameters $\phi_{I_k F_{ki}}$, $\phi_{F_{ki} F_{kj}}$, and/or $\phi_{F_{kj} F_{ki}}$ introduced here then allow us to quantify the first-order dependencies that exist between these processes. Importantly, while Crowley & Martin (1989) considered these dependencies to determine the extent to which a predator can or cannot interfere and feed simultaneously, we show here that viewing this as a dichotomy is vastly oversimplified. Instead, it is more appropriate to consider the various ϕ's as capturing two key features of biological relevance: First, they allow us to infer whether or not the rates of two processes proceed independently of each other. Second, when those rates do not

proceed independently, they capture whether one process can be said to accelerate or decelerate the other. Within a functional-response context, we hope that this ontology will come rather naturally. After all, the Holling Type II functional response emerges precisely from the separation and assumed mutual exclusion of time spent searching and time spent handling (Holling, 1959b).

The lessons learned here likely apply to many other areas of ecology and biology as well. For example, the widespread use of Holling Type II functional responses and models like it in the study of plant–pollinator interactions (Holland *et al.*, 2002; Morris *et al.*, 2010) contrasts sharply with evidence that plant-neighborhood effects on pollinator behavior can be complex (Underwood *et al.*, 2020). Models of such mutualisms often assume a priori that no interference occurs between pollinators (Okuyama & Holland, 2008; Vázquez *et al.*, 2015; Valdovinos, 2019). Based on our analyses, we expect there to be many more under-estimated processes at play in these systems, extending well beyond the densities of any focal interacting pair. Beyond consumer-resource interactions, standard growth-response curves (Tilman, 1977; 1982; Rothhaupt, 1988; Dybzinski & Tilman, 2007; Letten *et al.*, 2018) and models of enzyme kinetics (Michaelis & Menten, 1913) applied to plant and microbial systems are both mathematical equivalents to the single-resource Holling Type II functional response, yet are routinely adopted in multi-resource contexts (Descamps-Julien & Gonzalez, 2005; Kleinhesselink & Adler, 2015; Letten *et al.*, 2018). This occurs despite the tremendous utility that exists in identifying scenarios in which access to multiple resources synergistically promotes or retards growth (Sperfeld

et al., 2012; Jeyasingh *et al.*, 2020). Indeed, from trophic interactions and growth models to epistasis (Poelwijk *et al.*, 2016; Sailer & Harms, 2017a;b) and drug-drug interactions (Tekin *et al.*, 2018; Katzir *et al.*, 2019), there are countless areas of biology in which researchers are interested in ways to quantify similar forms of non-independence and non-additivity. Our mathematical framework provides a general basis with which to explore each of these and others, following a tradition of embracing biological complexity rather than shying away from it (Evans *et al.*, 2013).

As useful as this shift in perspective might appear, we nevertheless admit that it is not without practical limitations. As the numbers of processes and species under consideration increase, so too does the maximum number of potential parameters at a disproportionately high rate. In our "simple" scenario of a single consumer feeding on two resources, there were just two new parameters linking the two feeding rates; with three resources there are six new parameters, with four there are 12, and so on. The situation with multiple consumers *and* multiple resources is even more extreme. Even when a model could potentially be simplified below the maximum possible number of parameters, the proper inference of additional parameters will always necessitate increased replication and more creative study designs for manipulative experiments and observational studies alike. Some progress is possible by recognizing that many processes of relevance to feeding rates—such as consumer interference and even prey handling—can only be measured indirectly in terms of their impact on feeding rates, and that only one such implicit process can be measured per species density (Supplementary Material). Greater statistical

power must therefore be achieved by obtaining information on response variables in addition to feeding rates, as each such variable will contribute to the statistical likelihood of a given experimental replicate (Arditi & Glaizot, 1995). That said, the correct interpretation of such measured response variables is often not as cut and dry as it is with feeding (where prey are either consumed or not consumed), with even observable "handling times" not necessarily reflecting a rate-limiting process (Jeschke *et al.*, 2002) and observable antagonistic encounters among individuals not necessarily reflecting rate-altering behavioral effects (Sheriff *et al.*, 2020). The development of new and innovative empirical and statistical approaches will thus remain key for exploring the relevance of the diverse processes that could be at play (Dell *et al.*, 2014; Novak *et al.*, 2017; Ovaskainen *et al.*, 2017; Martin *et al.*, 2018; Maynard *et al.*, 2020).

Conclusions

The study of biological models serves a variety of purposes (Evans *et al.*, 2013; Otto & Rosales, 2020). We have focused here on the ability of generalizable mathematical models to explain observed variation in feeding rates across a large collection of empirical datasets. Rather than just introduce additional, phenomenological parameters in the way that can occur with statistical methods like multiple regression (e.g., the inclusion of m-way interaction terms in addition to main effects; Cox, 1984), we provide a mathematical demonstration of where such interaction terms come from: the inter-dependence of multiple biological processes. In doing so, we echo the notion that much dynamically-relevant biology encoded within functional responses still remains to be uncovered (Abrams, 2015; Novak *et al.*, 2017; Uszko *et al.*, 2017).

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Author contributions

DBS and MN conceived of the project, the modelling framework, and contributed to the writing of analysis code; MN compiled the empirical data; DBS led the writing of the manuscript.

Code and data availability

Code for all analyses, as well as most datasets, are available at `https://github.com/stoufferlab/general-functional-responses`. These and additional data sets

have also been posted to online repositories per agreement with data contributors (see Tables S1 & S2), or were obtained from repositories to which they had previously been posted by the original authors.

References

Abrams, P. (1997). Anomalous predictions of ratio-dependent models of predation. *Oikos*, 80, 163–171.

Abrams, P.A. (1982). Functional responses of optimal foragers. *Am. Nat.*, 120, 382–390.

Abrams, P.A. (1983). Arguments in favor of higher order interactions. *Am. Nat.*, 121, 887–891.

Abrams, P.A. (1990). The effects of adaptive behavior on the Type-2 functional response. *Ecology*, 71, 877–885.

Abrams, P.A. (2015). Why ratio dependence is (still) a bad model of predation. *Biol. Rev.*, 90, 794–814.

Abrams, P.A. & Cortez, M.H. (2015). The many potential indirect interactions between predators that share competing prey. *Ecol. Monogr.*, 85, 625–641.

Abrams, P.A. & Ginzburg, L.R. (2000). The nature of predation: prey dependent, ratio dependent or neither? *Trends Ecol. Evol.*, 15, 337–341.

Adamson, M.W. & Morozov, A.Y. (2013). When can we trust our model predictions? Unearthing structural sensitivity in biological systems. *Proc. R. Soc. Lond. A*, 469, 20120500.

Adamson, M.W. & Morozov, A.Y. (2014). Bifurcation analysis of models with uncertain function specification: How should we proceed? *Bull. Math. Biol.*, 76, 1218–1240.

Adler, F.R. & Morris, W.F. (1994). A general test for interaction modification. *Ecology*, 75, 1552–1559.

Aldebert, C. & Stouffer, D.B. (2018). Community dynamics and sensitivity to model structure: towards a probabilistic view of process-based model predictions. *J. R. Soc. Interface*, 15, 20180741.

Arditi, R. & Ginzburg, L.R. (2012). *How Species Interact: Altering the Standard View on Trophic Ecology*. Oxford University Press, Oxford, UK.

Arditi, R. & Glaizot, O. (1995). Assessing superparasitism with a model combining the functional response and the egg distribution of parasitoids. *Entomophaga*, 40, 235–262.

Beck, J.V. & Arnold, K.J. (1977). *Parameter Estimation in Engineering and Science*. John Wiley & Sons, Inc., New York, NY, USA.

Beckerman, A.P., Uriarte, M. & Schmitz, O.J. (1997). Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proc. Natl. Acad. Sci. USA*, 94, 10735–10738.

Beddington, J.R. (1975). Mutual interference between parasites or predators and its effect on searching efficiency. *J. Anim. Ecol.*, 44, 331–340.

Berlow, E.L., Dunne, J.A., Martinez, N.D., Stark, P.B., Williams, R.J. & Brose, U. (2009). Simple prediction of interaction strengths in complex food webs. *Proc. Natl. Acad. Sci. USA*, 106, 187–191.

Bolker, B. & R Development Core Team (2020). *bbmle: Tools for General Maximum Likelihood Estimation*. R package version 1.0.23.1.

Bolker, B.M. (2008). *Ecological Models and Data in R*. Princeton University Press, Princeton, NJ, USA.

Brose, U., Williams, R.J. & Martinez, N.D. (2006). Allometric scaling enhances stability in complex food webs. *Ecol. Lett.*, 9, 1128–1236.

Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multimodel Inference*. Springer-Verlag, New York, NY, USA.

Chong, J.H. & Oetting, R.D. (2006). Functional response and progeny production of the Madeira mealybug parasitoid, *Anagyrus sp. nov. nr. sinope*: the effects of host and parasitoid densities. *Biological Control*, 39, 320–328.

Coblentz, K.E. & DeLong, J.P. (2020). Predator-dependent functional responses alter the coexistence and indirect effects among prey that share a predator. *Oikos*. doi: 10.1111/oik.07309.

Cox, D.R. (1984). Interaction. *Int. Stat. Rev.*, 52, 1–24.

Crowley, P.H. & Martin, E.K. (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., Goldstein, R.A. & O'Neill, R.V. (1975). A model for tropic interaction. *Ecology*, 56, 881–892.

Dell, A.I., Bender, J.A., Branson, K., Couzin, I.D., de Polavieja, G.G., Noldus, L.P., Pérez-Escudero, A., Perona, P., Straw, A.D., Wikelski, M. & Brose, U. (2014). Automated image-based tracking and its application in ecology. *Trends Ecol. Evol.*, 29, 417–428.

Delmas, E., Brose, U., Gravel, D., Stouffer, D.B. & Poisot, T. (2017). Simulations of biomass dynamics in community food webs. *Methods Ecol. Evol.*, 8, 881–886.

DeLong, J.P. (2014). The body-size dependence of mutual interference. *Biol. Lett.*, 10, 20140261.

Descamps-Julien, B. & Gonzalez, A. (2005). Stable coexistence in a fluctuating environment: An experimental demonstration. *Ecology*, 86, 2815–2824.

Dybzinski, R. & Tilman, D. (2007). Resource use patterns predict long-term outcomes of plant competition for nutrients and light. *Am. Nat.*, 170, 305–318.

Evans, M.R., Grimm, V., Johst, K., Knuuttila, T., de Langhe, R., Lessells, C.M., Merz, M., O'Malley, M.A., Orzack, S.H., Weisberg, M., Wilkinson, D.J., Wolkenhauer, O. & Benton, T.G. (2013). Do simple models lead to generality in ecology? *Trends Ecol. Evol.*, 28, 578–583.

Gentleman, W., Leising, A., Frost, B., Strom, S. & Murray, J. (2003). Functional responses for zooplankton feeding on multiple resources: a review of assumptions and biological dynamics. *The US JGOFS Synthesis and Modeling Project: Phase II*, 50, 2847–2875.

Gill, J. & King, G. (2004). What to do when your hessian is not invertible: Alternatives to model respecification in nonlinear estimation. *Sociol. Method. Res.*, 33, 54–87.

Ginzburg, L.R. & Jensen, C.X.J. (2004). Rules of thumb for judging ecological theories. *Trends Ecol. Evol.*, 19, 121–126.

Goudard, A. & Loreau, M. (2008). Nontrophic interactions, biodiversity, and ecosystem functioning: An interaction web model. *Am. Nat.*, 171, 91–106.

GraphClick (2010). *Graph and movie digitizer for Mac OS X.* Arizona Software.

Guimerà, R., Reichardt, I., Aguilar-Mogas, A., Massucci, F.A., Miranda, M., Pallarès, J. & Sales-Pardo, M. (2020). A Bayesian machine scientist to aid in the solution of challenging scientific problems. *Sci. Adv.*, 6, eaav6971.

Holland, J.N., DeAngelis, D.L. & Bronstein, J.L. (2002). Population dynamics and mutualism: Functional responses of benefits and costs. *Am. Nat.*, 159, 231–244.

Holling, C.S. (1959a). The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can. Entomol.*, 91, 293–320.

Holling, C.S. (1959b). Some characteristics of simple types of predation and parasitism. *Can. Entomol.*, 91, 385–398.

Holling, C.S. (1965). The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.*, 97, 5–60.

Iles, A.C. & Novak, M. (2016). Complexity increases predictability in allometrically constrained food webs. *Am. Nat.*, 188, 87–98.

Jeschke, J.M., Kopp, M. & Tollrian, R. (2002). Predator functional responses: Discriminating between handling and digesting prey. *Ecol. Monogr.*, 72, 95–112.

Jeschke, J.M., Kopp, M. & Tollrian, R. (2004). Consumer-food systems: why type i functional responses are exclusive to filter feeders. *Biological Reviews*, 79, 337–349.

Jeyasingh, P.D., Goos, J.M., Lind, P.R., Roy Chowdhury, P. & Sherman, R.E. (2020). Phosphorus supply shifts the quotas of multiple elements in algae and daphnia: ionomic basis of stoichiometric constraints. *Ecol. Lett.*, 23, 1064–1072.

Johnson, S.G. (2020). *The NLopt nonlinear-optimization package*.

Katzir, I., Cokol, M., Aldridge, B.B. & Alon, U. (2019). Prediction of ultra-high-order antibiotic combinations based on pairwise interactions. *PLoS Comput. Biol.*, 15, 1–15.

Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., Boit, A., Joppa, L.N., Lafferty, K.D., Williams, R.J., Martinez, N.D., Menge, B.A., Blanchette, C.A., Iles, A.C. & Brose, U. (2012). More than a meal... integrating non-feeding interactions into food webs. *Ecology Letters*, 15, 291–300.

Kleinhesselink, A.R. & Adler, P.B. (2015). Indirect effects of environmental change in resource competition models. *Am. Nat.*, 186, 766–776.

Kleinhesselink, A.R., Kraft, N.J. & Levine, J.M. (2019). Mechanisms underlying higher order interactions: from quantitative definitions to ecological processes. *bioRxiv*. doi: 10.1101/857920.

Koen-Alonso, M. (2007). A process-oriented approach to the multispecies functional response. In: *From Energetics to Ecosystems: The Dynamics and Structure of Ecological Systems* (eds. Rooney, N., McCann, K.S. & Noakes, D.L.G.). Springer Netherlands, Dordrecht, pp. 1–36.

Kratina, P., Vos, M., Bateman, A. & Anholt, B.R. (2009). Functional responses modified by predator density. *Oecologia*, 159, 425–433.

Lafferty, K.D., DeLeo, G., Briggs, C.J., Dobson, A.P., Gross, T. & Kuris, A.M. (2015). A general consumer-resource population model. *Science*, 349, 854–857.

Lester, P.J. & Harmsen, R. (2002). Functional and numerical responses do not always indicate the most effective predator for biological control: an analysis of two predators in a two-prey system. *Journal of Applied Ecology*, 39, 455–468.

Letten, A.D., Dhami, M.K., Ke, P.J. & Fukami, T. (2018). Species coexistence through simultaneous fluctuation-dependent mechanisms. *Proc. Natl. Acad. Sci. USA*, 115, 6745–6750.

Letten, A.D. & Stouffer, D.B. (2019). The mechanistic basis for higher-order interactions and non-additivity in competitive communities. *Ecol. Lett.*, 22, 423–436.

Levine, J.M., Bascompte, J., Adler, P.B. & Allesina, S. (2017). Beyond pairwise mechanisms of species coexistence in complex communities. *Nature*, 546, 56–64.

Long, W.C., Gamelin, E.F., Johnson, E.G. & Hines, A.H. (2012a). Density-dependent indirect effects: apparent mutualism and apparent competition coexist in a two-prey system. *Marine Ecology Progress Series*, 456, 139–148.

Long, W.C., Popp, J., Swiney, K.M. & Van Sant, S.B. (2012b). Cannibalism in red king crab, *Paralithodes camtschaticus* (Tilesius, 1815): Effects of habitat type and predator density on predator functional response. *Journal of Experimental Marine Biology and Ecology*, 422, 101–106.

Martin, B., Munch, S. & Hein, A. (2018). Reverse-engineering ecological theory from data. *Proceedings of the Royal Society B: Biological Sciences*, 285, 20180422.

Mayfield, M.M. & Stouffer, D.B. (2017). Higher-order interactions capture unexplained complexity in diverse communities. *Nature Ecol. Evol.*, 1, 0062.

Maynard, D.S., Miller, Z.R. & Allesina, S. (2020). Predicting coexistence in experimental ecological communities. *Nature Eco. Evol.*, 4, 91–100.

Michaelis, L. & Menten, M.L. (1913). Die Kinetik der Invertinwirkung. *Biochem. Z*, pp. 333–369.

Morris, W.F., Vázquez, D.P. & Chacoff, N.P. (2010). Benefit and cost curves for typical pollination mutualisms. *Ecology*, 91, 1276–1285.

Murdoch, W.W. (1973). The functional response of predators. *J. Appl. Ecol.*, 41710, 335–342.

Myung, I.J., Balasubramanian, V. & Pitt, M.A. (2000). Counting probability distributions: Differential geometry and model selection. *Proc. Natl. Acad. Sci. USA*, 97, 11170–11175.

Novak, M. & Stouffer, D.B. (2020). Systematic bias in studies of consumer functional responses. *Unpublished*.

Novak, M., Wolf, C., Coblentz, K.E. & Shepard, I.D. (2017). Quantifying predator dependence in the functional response of generalist predators. *Ecol. Lett.*, 20, 761–769.

Okuyama, T. (2010). Prey density-dependent handling time in a predator-prey model. *Community Ecol.*, 11, 91–96.

Okuyama, T. & Bolker, B.M. (2007). On quantitative measures of indirect interactions. *Ecol. Lett.*, 10, 264–271.

Okuyama, T. & Holland, J.N. (2008). Network structural properties mediate the stability of mutualistic communities. *Ecol. Lett.*, 11, 208–216.

Otto, S.P. & Day, T. (2007). *A Biologist's Guide to Mathematical Modeling in Ecology and Evolution*. Princeton University Press, Princeton, NJ, USA.

Otto, S.P. & Rosales, A. (2020). Theory in service of narratives in evolution and ecology. *Am. Nat.*, 195, 290–299.

Ovaskainen, O., Tikhonov, G., Dunson, D., Grøtan, V., Engen, S., Sæther, B.E. & Abrego, N. (2017). How are species interactions structured in species-rich communities? A new method for analysing time-series data. *Proc. R. Soc. Lond. B*, 284, 20170768.

Peacor, S.D. & Werner, E.E. (2001). The contribution of trait-mediated indirect effects to the net effects of a predator. *Proc. Natl. Acad. Sci. USA*, 98, 3904–3908.

Poelwijk, F.J., Krishna, V. & Ranganathan, R. (2016). The context-dependence of mutations: A linkage of formalisms. *PLoS Comput. Biol.*, 12, 1–19.

Preston, D.L., Henderson, J.S., Falke, L.P., Segui, L.M., Layden, T.J. & Novak, M. (2018). What drives interaction strengths in complex food webs? A test with feeding rates of a generalist stream predator. *Ecology*, 99, 1591–1601.

R Core Team (2020). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rissanen, J.J. (1996). Fisher information and stochastic complexity. *IEEE Trans. Inform. Theory*, 42, 40–47.

Rothhaupt, K.O. (1988). Mechanistic resource competition theory applied to laboratory experiments with zooplankton. *Nature*, 333, 660–662.

Sailer, Z.R. & Harms, M.J. (2017a). Detecting high-order epistasis in nonlinear genotype-phenotype maps. *Genetics*, 205, 1079–1088.

Sailer, Z.R. & Harms, M.J. (2017b). High-order epistasis shapes evolutionary trajectories. *PLoS Comput. Biol.*, 13, 1–16.

Sheriff, M.J., Peacor, S.D., Hawlena, D. & Thaker, M. (2020). Non-consumptive predator effects on prey population size: A dearth of evidence. *Journal of Animal Ecology*.

Skalski, G.T. & Gilliam, J.F. (2001). Functional responses with predator interference: Viable alternatives to the Holling Type II model. *Ecology*, 82, 3083–3092.

Sperfeld, E., Martin-Creuzburg, D. & Wacker, A. (2012). Multiple resource limitation theory applied to herbivorous consumers: Liebig's minimum rule vs. interactive co-limitation. *Ecol. Lett.*, 15, 142–150.

Strauss, S.Y. (1991). Indirect effects in community ecology: Their definition, study and importance. *Trends Ecol. Evol.*, 6, 206–210.

Tekin, E., Yeh, P.J. & Savage, V.M. (2018). General form for interaction measures and framework for deriving higher-order emergent effects. *Front. Ecol. Evol.*, 6, 166.

Tilman, D. (1977). Resource competition between plankton algae: An experimental and theoretical approach. *Ecology*, 58, 338–348.

Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ, USA.

Toscano, B.J. & Griffen, B.D. (2014). Trait-mediated functional responses: predator behavioural type mediates prey consumption. *J. Anim. Ecol.*, 83, 1469–1477.

Uiterwaal, S.F. & DeLong, J.P. (2020). Functional responses are maximized at intermediate temperatures. *Ecology*. doi: 10.1002/ecy.2975.

Underwood, N., Hambäck, P.A. & Inouye, B.D. (2020). Pollinators, herbivores, and plant neighborhood effects. *Q. Rev. Biol.*, 95, 37–57.

Uszko, W., Diehl, S., Englund, G. & Amarasekare, P. (2017). Effects of warming on predator–prey interactions – a resource-based approach and a theoretical synthesis. *Ecol. Lett.*, 20, 513–523.

Valdovinos, F.S. (2019). Mutualistic networks: moving closer to a predictive theory. *Ecology Letters*, 22, 1517–1534.

Vázquez, D.P., Ramos-Jiliberto, R., Urbani, P. & Valdovinos, F.S. (2015). A conceptual framework for studying the strength of plant–animal mutualistic interactions. *Ecol. Lett.*, 18, 385–400.

Werner, E.E. & Peacor, S.D. (2003). A review of trait-mediated indirect interactions in ecological communities. *Ecology*, 84, 1083–1100.

Williams, R.J., Brose, U. & Martinez, N.D. (2007). Homage to Yodzis and Innes 1992: Scaling up feeding-based population dynamics to complex ecological networks. In: *From Energetics to Ecosystems: The Dynamics and Structure of Ecological Systems* (eds. Rooney, N., McCann, K.S. & Noakes, D.L.G.). Springer Netherlands, Dordrecht.

Wootton, J.T. (1993). Indirect effects and habitat use in an intertidal community: Interaction chains and interaction modifications. *Am. Nat.*, 141, 71–89.

Wootton, J.T. (1994). The nature and consequences of indirect effects in ecological communities. *Annu. Rev. Ecol. Syst.*, 25, 443–466.

Tables

Table 1: The five models we considered describing single-resource consumer-dependent consumption. These expressions for consumer per capita consumption rates correspond to the instantaneous consumption rate for both replacement and non-replacement studies.

Name	Abbreviation	Per capita consumption rate, F_{ki}	Parameters
Holling Type I	H1	$a_{ki}N_i$	1
Holling Type II	H2	$\frac{a_{ki}N_i}{1+a_{ki}h_{ki}N_i}$	2
Beddington–DeAngelis	BD	$\frac{a_{ki}N_i}{1+a_{ki}h_{ki}N_i+c_kP_k}$	3
Crowley–Martin	CM	$\frac{a_{ki}N_i}{(1+a_{ki}h_{ki}N_i)(1+c_kP_k)}$	3
Generalized consumer dependence	G	$\frac{a_{ki}N_i}{(1+a_{ki}h_{ki}N_i)(1+c_kP_k)-\phi_{I_kF_{ki}}a_{ki}h_{ki}c_kN_iP_k}$	4

Table 2: The four models we considered describing multi-resource dependent consumption. These expressions for consumer per capita consumption rates correspond to the instantaneous consumption rate for both replacement and non-replacement studies. As there are two resources under consideration, the number of parameters corresponds to the total number across *both* resources.

Name	Abbreviation	Per capita consumption rate, F_{ki}	Parameters
Holling Type I	H1	$a_{ki}N_i$	2
Holling Type II	H2	$\frac{a_{ki}N_i}{1+a_{ki}h_{ki}N_i}$	4
Multi-resource Holling Type II	H2-m	$\frac{a_{ki}N_i}{1+a_{ki}h_{ki}N_i+a_{kj}h_{kj}N_j}$	4
Generalized multi-resource Holling Type II	H2-g	$\frac{a_{ki}N_i\left[1+\left(1-\phi_{F_{ki}F_{kj}}\right)a_{kj}h_{kj}N_j\right]}{(1+a_{ki}h_{ki}N_i)\left(1+a_{kj}h_{kj}N_j\right)-\phi_{F_{ki}F_{kj}}\phi_{F_{kj}F_{ki}}a_{ki}h_{ki}a_{kj}h_{kj}N_iN_j}$	6

Figures and figure legends

Figure 1: **a**, The effect of the parameter $\phi_{I_k F_{ki}}$ on feeding rate F_{ki}. We show isoclines of constant consumption for the Holling Type II model (H2) and the generalized resource- and consumer-dependent model introduced here (Eq. 3). Each line corresponds to $P_k F_{ki} \equiv 1$ with the values of $\phi_{I_k F_{ki}}$ specified in the legend, and fixed values of attack rate $a_{ki} = 0.2$, handling time $h_{ki} = 0.5$, and interference $c_k = 0.25$. As $\phi_{I_k F_{ki}}$ shifts from 1.5 (short-dashed line) to -0.5 (dot-dashed line), more and more consumers are required to achieve equivalent consumption. Note that G(1) and G(0) correspond to the Beddington–DeAngelis and Crowley–Martin models, respectively. **b**, The effect of the parameters $\phi_{F_{ki} F_{kj}}$ and $\phi_{F_{kj} F_{ki}}$ on total feeding rate $F_k = F_{ki} + F_{kj}$. We show isoclines of constant consumption for the generalized multi-resource dependent model introduced here (Eq. 10). Each line corresponds to $P_k F_k \equiv 1$ with the values of $\phi_{F_{ki} F_{kj}}$ and $\phi_{F_{kj} F_{ki}}$ specified in the legend and $P_k = 1$. Both resources are otherwise equivalent (i.e., $a_{ki} = a_{kj} = 0.5$ and $h_{ki} = h_{kj} = 0.5$). When $\phi_{F_{ki} F_{kj}} = \phi_{F_{kj} F_{ki}} = 1$ (solid line), resources are perfectly substitutable; when $\phi_{F_{ki} F_{kj}} = \phi_{F_{kj} F_{ki}} = 0$, consumers require fewer resources to achieve equivalent feeding rates (short-dashed line); and when $\phi_{F_{ki} F_{kj}} = 1$ and $\phi_{F_{kj} F_{ki}} = 1.3$, consumers require more resources to achieve equivalent feeding rates (dot-dashed line). Note that H2-g$(1, 1)$ corresponds to the multi-resource Holling Type II functional response (H2-m).

Figure 2: The effect of feeding on consumer interference as estimated across 77 single-resource consumer-dependence datasets. One the left, we show the rank-order performance of functional-response models as judged by AIC, with rank 1 indicating the best model and rank 5 indicating the worst. The gray region indicates models with statistically equivalent support (i.e., $\Delta AIC < 2$). The red square is the generalized consumer-dependent model introduced here (G). (See Table 1 for all model abbreviations.) On the right, we show the estimated mean and uncertainty for the effect of feeding on interference (i.e., $\phi_{I_k F_{ki}}$). The vertical line at 0 corresponds to the Crowley–Martin model (CM), and the vertical line at 1 corresponds to the Beddington–DeAngelis model (BD). We use black dots for datasets for which the generalized model introduced here (G; Eq. 3) performs best or is statistically equivalent to the best as judged by AIC; blue dots indicate datasets for which this is not the case Line types indicate the method for estimating uncertainty: solid for profile confidence intervals, dot-dashed for quadratic approximation, and dotted for bootstrapped data. Uncertainty estimates that are fully or partially beyond the plot region are indicated by arrows. Point estimates outside the plot region are indicated with circles on the plot border.

Figure 3: The effect that feeding on one prey species has on feeding on another as estimated across 30 multi-resource dependence datasets. One the left, we show the rank-order performance of functional-response models as judged by AIC, with rank 1 indicating the best model and rank 4 indicating the worst. The gray region indicates models with statistically equivalent support (i.e., $\Delta AIC < 2$). The red square is the generalized multi-resource Holling Type II model introduced here (H2-g; Eq. 10). (See Table 2 for all model abbreviations.) On the right, we show the estimated mean and uncertainty for the effect feeding on one prey has on feeding on another (i.e., $\phi_{F_{ki}F_{kj}}$ and $\phi_{F_{kj}F_{ki}}$ in Eq. 10). The vertical line at 0 corresponds to the single-resource Holling Type II model (H2), and the vertical line at 1 corresponds to the multi-resource Holling Type II model (H2-m). All colors and line types are as in Fig. 2.

Figure 1

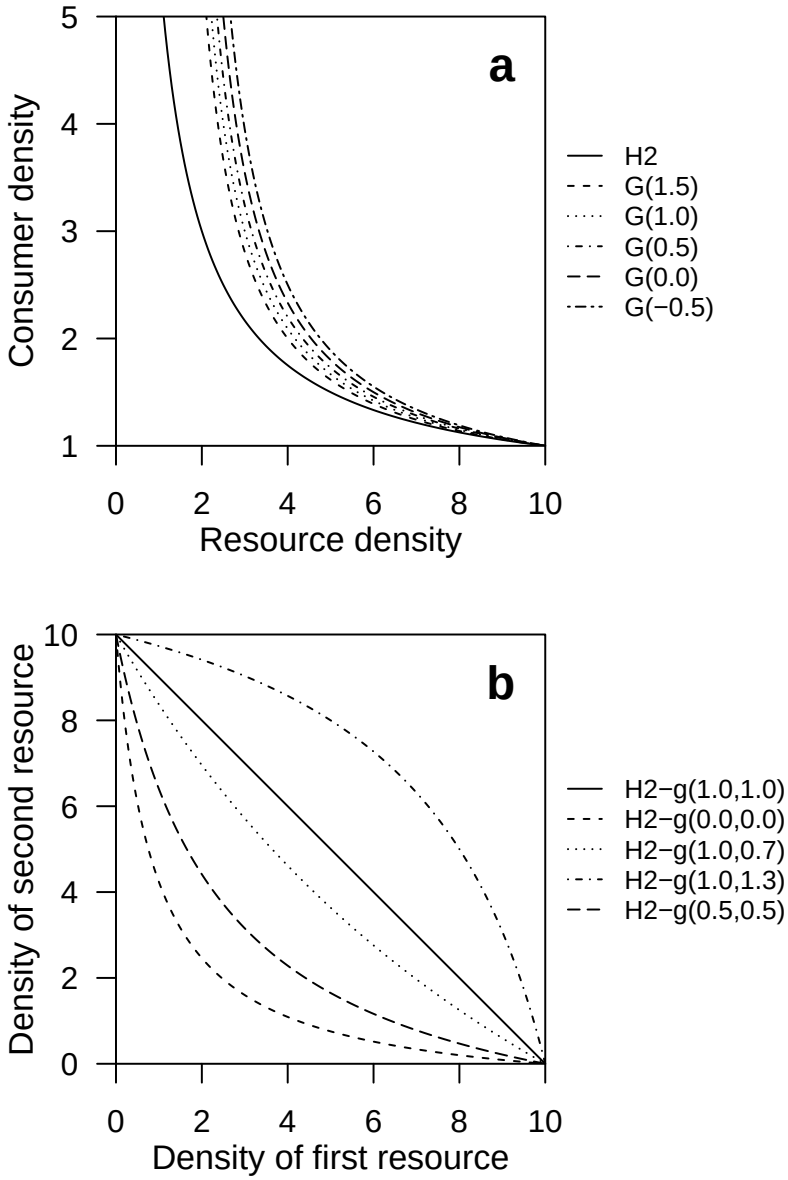

a
Consumer density
Resource density
H2
G(1.5)
G(1.0)
G(0.5)
G(0.0)
G(−0.5)
b
Density of second resource
Density of first resource
H2−g(1.0,1.0)
H2−g(0.0,0.0)
H2−g(1.0,0.7)
H2−g(1.0,1.3)
H2−g(0.5,0.5)

Figure 2

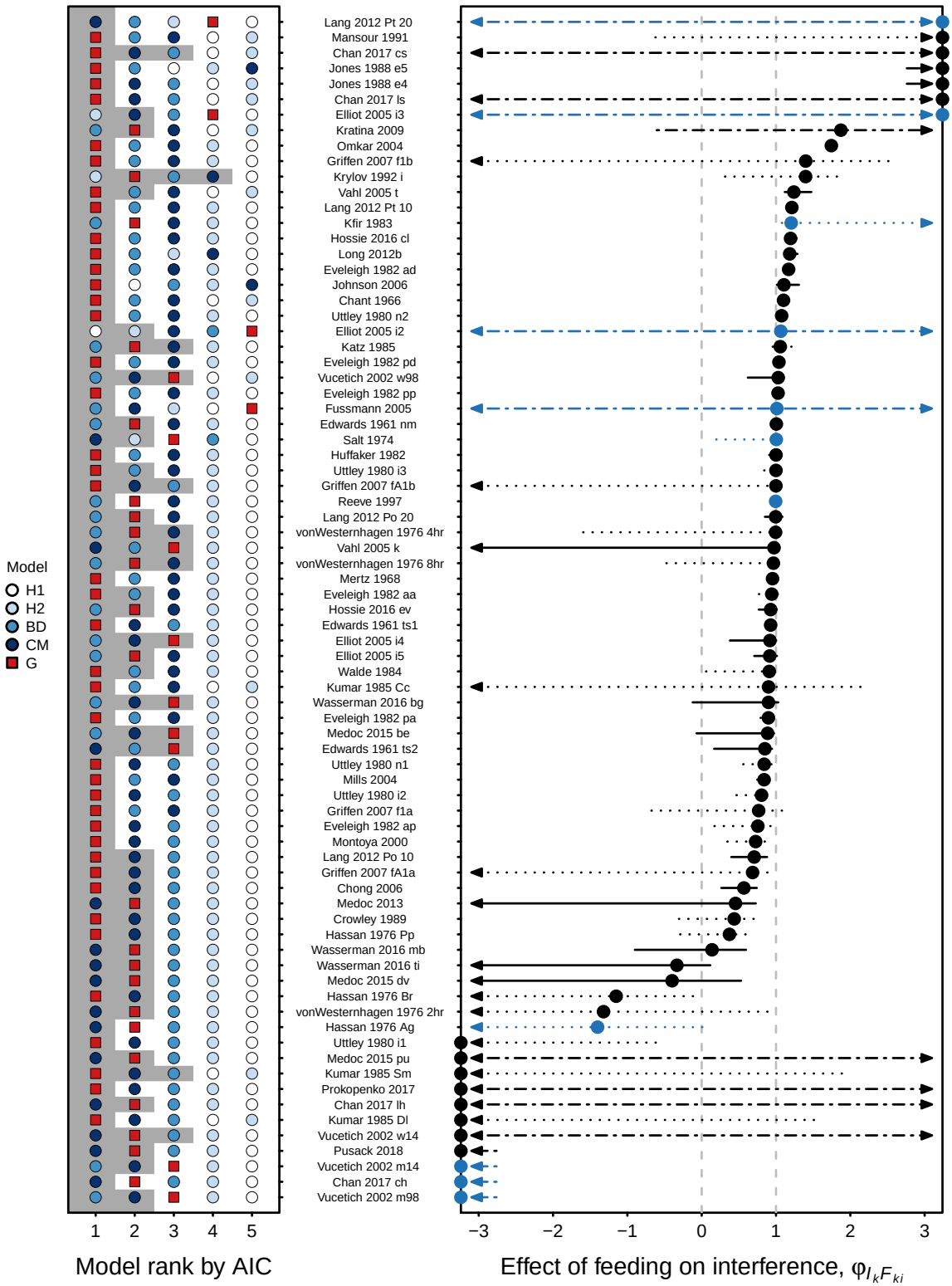
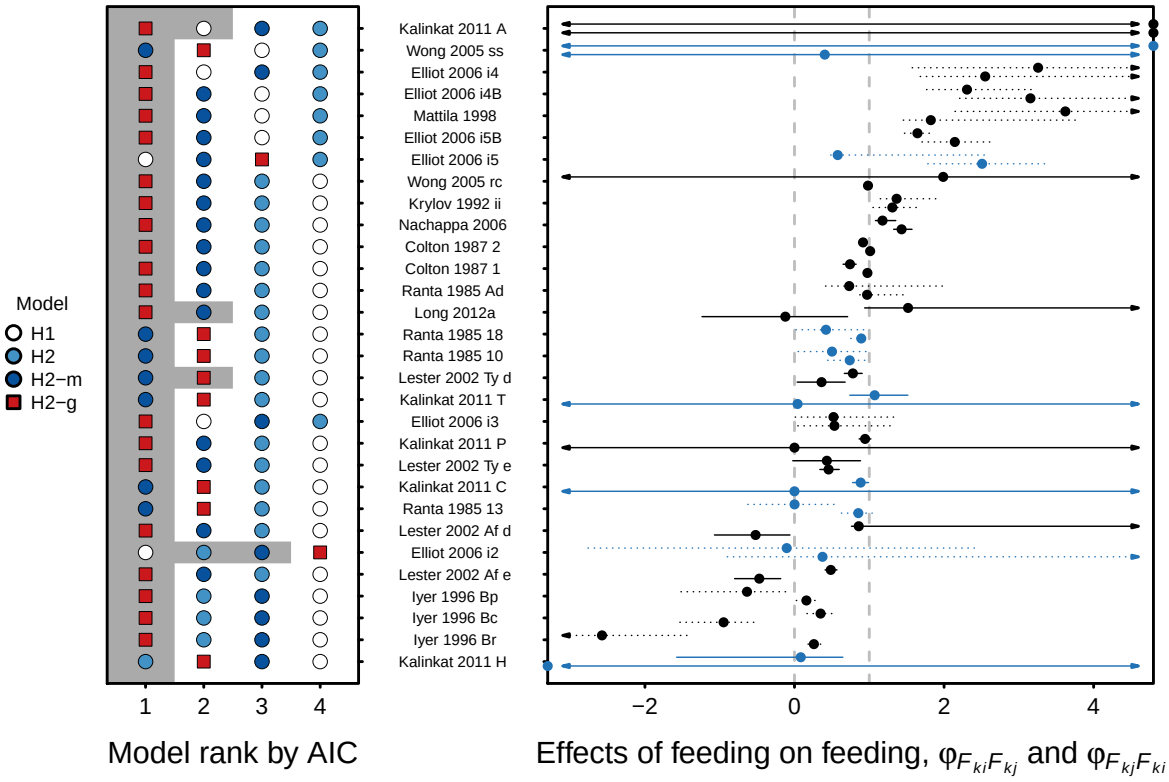

Model
H1
H2
BD
CM
G
Lang 2012 Pt 20
Mansour 1991
Chan 2017 cs
Jones 1988 e5
Jones 1988 e4
Chan 2017 ls
Elliot 2005 i3
Kratina 2009
Omkar 2004
Griffen 2007 f1b
Krylov 1992 i
Vahl 2005 t
Lang 2012 Pt 10
Kfir 1983
Hossie 2016 cl
Long 2012b
Eveleigh 1982 ad
Johnson 2006
Chant 1966
Uttley 1980 n2
Elliot 2005 i2
Katz 1985
Eveleigh 1982 pd
Vucetich 2002 w98
Eveleigh 1982 pp
Fussmann 2005
Edwards 1961 nm
Salt 1974
Huffaker 1982
Uttley 1980 i3
Griffen 2007 fA1b
Reeve 1997
Lang 2012 Po 20
vonWesternhagen 1976 4hr
Vahl 2005 k
vonWesternhagen 1976 8hr
Mertz 1968
Eveleigh 1982 aa
Hossie 2016 ev
Edwards 1961 ts1
Elliot 2005 i4
Elliot 2005 i5
Walde 1984
Kumar 1985 Cc
Wasserman 2016 bg
Eveleigh 1982 pa
Medoc 2015 be
Edwards 1961 ts2
Uttley 1980 n1
Mills 2004
Uttley 1980 i2
Griffen 2007 f1a
Eveleigh 1982 ap
Montoya 2000
Lang 2012 Po 10
Griffen 2007 fA1a
Chong 2006
Medoc 2013
Crowley 1989
Hassan 1976 Pp
Wasserman 2016 mb
Wasserman 2016 ti
Medoc 2015 dv
Hassan 1976 Br
vonWesternhagen 1976 2hr
Hassan 1976 Ag
Uttley 1980 i1
Medoc 2015 pu
Kumar 1985 Sm
Prokopenko 2017
Chan 2017 lh
Kumar 1985 Dl
Vucetich 2002 w14
Pusack 2018
Vucetich 2002 m14
Chan 2017 ch
Vucetich 2002 m98
1
2
3
4
5
Model rank by AIC
−3
−2
−1
0
1
2
3
Effect of feeding on interference, $\varphi_{I_k F_{ki}}$

Figure 3


Model
H1
H2
H2−m
H2−g
Kalinkat 2011 A
Wong 2005 ss
Elliot 2006 i4
Elliot 2006 i4B
Mattila 1998
Elliot 2006 i5B
Elliot 2006 i5
Wong 2005 rc
Krylov 1992 ii
Nachappa 2006
Colton 1987 2
Colton 1987 1
Ranta 1985 Ad
Long 2012a
Ranta 1985 18
Ranta 1985 10
Lester 2002 Ty d
Kalinkat 2011 T
Elliot 2006 i3
Kalinkat 2011 P
Lester 2002 Ty e
Kalinkat 2011 C
Ranta 1985 13
Lester 2002 Af d
Elliot 2006 i2
Lester 2002 Af e
Iyer 1996 Bp
Iyer 1996 Bc
Iyer 1996 Br
Kalinkat 2011 H
1
2
3
4
Model rank by AIC
−2
0
2
4
Effects of feeding on feeding, $\varphi_{F_{ki}F_{kj}}$ and $\varphi_{F_{kj}F_{ki}}$