Hidden layers of density dependence in consumer feeding rates

Abstract

Functional responses relate a consumer’s feeding rates to variation in its abiotic and biotic environment, providing insight into consumer behaviour 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 analyse two large collections of functional-response data sets 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

Generalist–specialist continuum, higher-order interactions, indirect effects, interaction modifications, mutual predator effects, non-additive effects.

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 characterise 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). 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 (1) increasing resource density via handling times and (2) 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; Gouard & Loreau, 2008) reflecting indirect effects (Wootton, 1994; Okuyama & Bolker, 2007; Abrams & Cortez, 2015), trait- and behaviour-mediated effects (Beckerman et al., 1997; Peacor & Werner, 2001; Werner & Peacor, 2003; Toscano & Griffen, 2014), and other forms of non-additivity or higher-order effects (Mayfield & Stouffer, 2017; Letten & Stouffer, 2019; Kleinheselink et al., 2020).
2019). Though these phenomena have long been recognised 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 context, we derive new models that generate a spectrum of emergent consumer-interference effects that have not been previously described. 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 recognised. 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 representing consumer identities that range from wolves to ciliates. Our analysis provides evidence for the widespread prevalence of unrecognised 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 relate 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

\[
F_{ki}(N_i, P_k) = \frac{a_{ki}N_i}{1 + a_{ki}h_{ki}N_i + c_kP_k},
\]

where \(F_{ki}\) is the feeding rate of predators \(k\) consuming prey \(i\) (with dimensions of \([\text{prey consumed per predator per time available}]\)), \(N_i\) is the density of prey \(i\) available, \(P_k\) is the density of predators \(k\), \(a_{ki}\) is the attack rate (with dimensions of \([\text{prey consumed per prey available per time available}]\)) and \(h_{ki}\) is the handling time (with dimensions \([\text{time handling per prey consumed}]\)). \(c_k\) is the strength of interference between predators (with dimensions \([\text{time interfering per time available per predator interfering}]\)). 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

\[
F_{ki}(N_i, P_k) = \frac{a_{ki}N_i}{(1 + a_{ki}h_{ki}N_i)(1 + c_kP_k)},
\]

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

Focusing on the denominators of eqns (1) and (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 \(P_k\). We could therefore instead rewrite both models as

\[
F_{ki}(N_i, P_k) = \frac{a_{ki}N_i}{1 + a_{ki}h_{ki}N_i + c_kP_k + (1 - \phi)h_{ki}c_kN_iP_k},
\]

where \(\phi\) 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 \(\phi\)**

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

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\[ F_k(N_i, P_k) = \frac{a_{ki} N_i}{1 + a_{ki} h_{ki} [1 + (1 - \phi) c_k P_k] N_i + c_k P_k}, \]  

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

\[ F_k(N_i, P_k) = \frac{a_{ki} N_i}{1 + a_{ki} h_{ki} N_i + c_k [1 + (1 - \phi) a_{ki} h_{ki} N_i] P_k}, \]  

in which case the implied interpretation is that \( \phi \) influences the extent to which interference strength \( c_k \) is a function of the abundance of available prey \( N_i \). That is, \( c_k \) is only independent of available prey when \( \phi = 1 \). From a phenomenological perspective, it is important to recognise 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 \( \phi \) 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 \( F_k \) relates to an implicit, unmeasured interference rate \( I_k \):

\[ F_k(N_i, P_k) = a_{ki} N_i (1 - h_{ki} F_k - \beta_k I_k) \]  

\[ I_k(N_i, P_k) = a_k P_k (1 - \phi h_{ki} F_k - \beta_k I_k). \]  

Upon algebraically solving eqns (6) and (7) for \( F_k \), we immediately obtain eqn (3) with interference strength \( c_k = a_k \beta_k \). The two new parameters are an ‘interference rate’ \( \alpha_k \) (akin to the attack rate and with dimensions [predator interfered per predator interfering per time available]) and an ‘interference time’ \( \beta_k \) (akin to handling time and with dimensions [time interfering per predator interfered]). The parenthetical term of each equation 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 \( \beta_k \), time for searching in eqn (6) is reduced by time spent handling and time spent interfering. Similarly, time available for interfering in eqn (7) is also reduced by interfering. In contrast, whether and how time spent handling influences the realised rate of interference is explicitly determined by the value of \( \phi \). [Correction added on 20 January 2021, after first online publication: equation 6 has been modified.]

Expressed in this way, we can shift from a generic parameter \( \phi \) and formally define \( \phi_{F_k,F_k} \) as the parameter capturing how the predator’s feeding rate \( F_k \) alters its realised conspecific interference rate \( I_k \). As described verbally above, predators can interfere while searching but cannot interfere while feeding in the Beddington–DeAngelis model (eqn 1), implying \( \phi_{F_k,F_k} = 1 \). In the Crowley–Martin model (eqn 2), predators interfere both while searching and while feeding, implying \( \phi_{F_k,F_k} = 0 \). Crowley & Martin (1989) referred to these as distraction and distraction-free models respectively. Beyond these two cases, note that any value of \( \phi_{F_k,F_k} \neq 1 \) 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 \( \phi_{F_k,F_k} \) causes feeding rates to decrease with increasing \( N_i P_k \) whenever \( \phi_{F_k,F_k} < 1 \), and causes feeding rates to increase with increasing \( N_i P_k \) whenever \( \phi_{F_k,F_k} > 1 \) (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 eqns (6) and (7), we define the feeding rates on prey \( i \) and prey \( j \) as

\[ F_k(N_i, N_j) = a_{ki} N_i \left( 1 - h_{ki} F_{ki} - \phi_{F_k,F_i} h_{kj} F_{kj} \right) \]  

\[ F_k(N_i, N_j) = a_{kj} N_j \left( 1 - \phi_{F_k,F_j} h_{ki} F_{ki} - h_{kj} F_{kj} \right), \]  

where \( \phi_{F_k,F_i} \) represents the extent to which feeding on \( j \) impacts feeding on \( i \) and \( \phi_{F_k,F_j} \) represents the extent to which feeding on \( i \) impacts feeding on \( j \). The attack rates \( a_{ki} \) and \( a_{kj} \) are prey-specific versions of the attack rate defined above. The parenthesis 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. As such, the interpretation of the handling times \( h_{ki} \) and \( h_{kj} \) is slightly different than above because they only directly equate to ‘time lost to handling’ for the prey in question; that is, time available to search for prey \( i \) decreases by \( h_{ki} \) for each prey \( i \) consumed, but it decreases by \( \phi_{F_k,F_j} h_{kj} \) for each prey \( j \) consumed (with similar behaviour when focusing on time available to search for prey \( j \)). The 1 in the parentheses implies that the predator is potentially searching for either prey; we adopt this assumption in order to avoid adding even more parameters to the resulting model (Supplementary Material).

With algebraic manipulation of eqns (8) and (9), we can solve for each of the two feeding rates and obtain

\[ F_k(N_i, N_j) = \frac{a_{ki} N_i \left[ 1 + (1 - \phi_{F_k,F_i}) a_{ki} h_{ki} N_j \right]}{(1 + a_{ki} h_{ki} N_j) \left( 1 + a_{ki} h_{kj} N_i \right) - \phi_{F_k,F_i} \phi_{F_k,F_j} a_{ki} h_{ki} a_{kj} N_i N_j}, \]  

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, *any* values of \( \phi_{F_k,F_i} \) and \( \phi_{F_k,F_j} \) such that their product \( \phi_{F_k,F_i} \phi_{F_k,F_j} \neq 1 \) lead to the appearance of the additional ‘higher-order’ term in the denominator of eqn (10) involving the product of both prey densities, \( N_i N_j \). For the multi-resource-dependence case, the density of the second prey also appears in the numerator of eqn (10). As a direct consequence, non-independence between feeding on both prey species as captured by the parameters \( \phi_{F_k,F_i} \) and \( \phi_{F_k,F_j} \) can lead to density-dependent changes in feeding of the sort expected when predators exhibit prey-switching behaviour (Supplementary Material).

In order to better elucidate the behaviour of these expressions for feeding rates, it is useful to explore three limiting cases and the resulting forms for \( F_k \). First, consider a scenario
Type II functional response’ (Murdoch, 1973; Koen-Alonso, 2007) given by

\[
F_{kj}(N_i, N_j) = \frac{a_{ki}N_i}{1 + a_{kj}h_{ki}N_i + a_{kj}h_{kj}N_j}.
\]  

(11)

Second, consider the scenario where \(\phi_{Fki,Fkj} = 0\), implying that the feeding rate on \(j\) has no impact on the feeding rate on \(i\) as might occur for drift-feeding fish that are unlikely to pass up an opportunistic encounter with \(i\) even shortly after ingesting \(j\) (e.g. Neuwanger et al., 2014). Alternatively, this could arise whenever \(F_{kj}\) is effectively Type I over the range of experienced abundances (Novak, 2010). In this scenario, the higher-order term vanishes from the denominator in \(F_{kj}\) irrespective of the value of \(\phi_{Fki,Fkj}\). Moreover, the potential dependence on \(N_j\) can be factored out since identical expressions of the form \(1 + a_{kj}h_{ki}N_j\) appear in both the numerator and denominator. Reassuringly, we are left with a single-resource Holling Type II functional response for \(F_{kj}\) that is completely independent of the abundance of prey \(j\) (Holling, 1959a;b); namely we obtain

\[
F_{kj}(N_i, N_j) = \frac{a_{ki}N_i}{1 + a_{kj}h_{ki}N_j}.
\]  

(12)

Third, consider what happens when \(\phi_{Fki,Fkj} = 1\) and \(\phi_{Fki,Fkj} = 0\), implying that a predator handling \(j\) cannot attack \(i\) but a predator handling \(i\) could still attack \(j\). This scenario could arise when prey differ dramatically in size (e.g. Kalinkat et al., 2011). Under these conditions, feeding on \(i\) behaves as

\[
F_{kj}(N_i, N_j) = \frac{a_{ki}N_i}{1 + a_{kj}h_{ki}N_i + a_{kj}h_{kj}N_j + a_{kj}h_{ki}a_{kj}h_{kj}N_iN_j},
\]  

(13)

which shows systematic variation for any abundance of \(j\) and includes the higher-order term in the denominator. Compared to the first two limiting cases, feeding \(F_{kj}\) 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 \(\phi_{Fki,Fkj}\) and \(\phi_{Fki,Fkj}\) 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 \(\phi_{Fki,Fkj}\) and \(\phi_{Fki,Fkj}\) could hypothetically lead to a decrease in \(F_{kj}\) 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 aimed to determine whether there is empirical support for such non-independence and the inclusion of the parameters \(\phi_{Fki,Fkj}\), \(\phi_{Fki,Fkj}\) when modelling observed feeding rates. Focusing on the two specific scenarios discussed above, we searched the literature to obtain two different types of empirical data sets. First, single-resource consumer-dependence data sets 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 data sets 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 (1) data points or (2) means and their associated uncertainties from the publication in tables by hand or figures using Graph Click (2010).

Single-resource consumer-dependent models

We considered five different functional-response models when examining the consumer-interference data sets (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 $\phi_{F_{ki}F_{kj}}$ (eqn 3).

Multi-resource-dependent models

We considered four different functional-response models when examining the multiple-resource data sets (Table 2): the Holling Type I functional responses that arise when $h_{ik} = h_{kj} = 0$, 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 generalised multi-resource Type II functional responses that emerge when both $\phi_{F_{ki}F_{kj}}$ and $\phi_{F_{kj}F_{ki}}$ are free parameters (eqn 10).

Biological and statistical constraints to the parameters

There is a particularly important detail to consider when fitting eqns (3) and (10) to data. In the preceding mathematical descriptions, we primarily focused on examples in which the various parameters $\phi_{F_{ki}F_{kj}}, \phi_{F_{kj}F_{ki}}$ and $\phi_{F_{ki}F_{kj}}$ took values of 0 or 1. We did so to build on the intuition behind the distraction and distraction-free interpretations of predator behaviour (Crowley & Martin, 1989), and to relate our generalised 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 behaviour. 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 eqns (6–9) must each remain greater than or equal to 0. This means, for example, that the statistically best-fit value of $\phi_{F_{ki}F_{kj}}$ for a given single-resource consumer-dependence data set could be $\phi_{F_{ki}F_{kj}} < 0$ if $h_{ki}$ were sufficiently large, or could be $\phi_{F_{ki}F_{kj}} > 0$ 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 resources. While an absence of constraints on $\phi_{F_{ki}F_{kj}}$, $\phi_{F_{kj}F_{ki}}$ and $\phi_{F_{ki}F_{kj}}$ 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 $\phi_{F_{ki}F_{kj}}$ may be consistent with a given data set while also predicting implausible, negative interference rates for larger-than-observed consumer or resource abundances (see also Novak & Stouffer, 2020).

Parameter inference

Given each empirical data set, 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-optimisation algorithm $shp1x$ from the $nlmrt$ 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 $shp1x$ to the $mle$ function from the $bbmle$ package (Bolker & R Development Core Team, 2020) to search for local improvements and assess model convergence. The likelihood being optimised was determined by the data set’s experimental design (Supplementary Material), and all handling times, attack rates and interference strengths were constrained to be positive. We allowed the values of $\phi_{F_{ki}F_{kj}}, \phi_{F_{kj}F_{ki}}$ and $\phi_{F_{ki}F_{kj}}$ to vary freely as long as predicted mean feeding rates remained greater than or equal to 0.

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 ±1 standard error—using the $confint$ function from $bbmle$. On occasion, this approach failed because, although the optimisation converged, the likelihood surface was nearly flat around the optimum. This is usually indicative of the model being over-parameterised (Gill & King, 2004), the occurrence of which was not

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Table 1 The five models we considered describing single-resource consumer-dependent consumption.

<table>
<thead>
<tr>
<th>Name</th>
<th>Abbreviation</th>
<th>Per capita consumption rate, $F_{ki}$</th>
<th>Parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Holling Type I</td>
<td>H1</td>
<td>$a_{ki}/N_i$</td>
<td>1</td>
</tr>
<tr>
<td>Holling Type II</td>
<td>H2</td>
<td>$\frac{a_{ki}}{1 + a_{ki}h_{kj}}$</td>
<td>2</td>
</tr>
<tr>
<td>Beddington–DeAngelis</td>
<td>BD</td>
<td>$\frac{a_{ki}/h_{ki}}{1 + a_{ki}/h_{ki} + a_{kj}/h_{kj}}$</td>
<td>3</td>
</tr>
<tr>
<td>Crowley–Martin</td>
<td>CM</td>
<td>$\frac{a_{ki}}{1 + a_{ki}/h_{ki} + a_{kj}/h_{kj}}$</td>
<td>3</td>
</tr>
<tr>
<td>Generalised consumer</td>
<td>G</td>
<td>$\frac{a_{ki}}{1 + a_{ki}/h_{ki} + a_{kj}/h_{kj} + \phi_{F_{ki}F_{kj}}h_{ki}h_{kj}}$</td>
<td>4</td>
</tr>
</tbody>
</table>

These expressions for consumer per capita consumption rates correspond to the instantaneous consumption rate for both replacement and non-replacement studies.
Table 2 The four models we considered describing multi-resource-dependent consumption.

<table>
<thead>
<tr>
<th>Name</th>
<th>Abbreviation</th>
<th>Per capita consumption rate, ( F_{uk} )</th>
<th>Parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Holling Type I</td>
<td>H1</td>
<td>( a_1 N_1 )</td>
<td>2</td>
</tr>
<tr>
<td>Holling Type II</td>
<td>H2</td>
<td>( a_1 N_1 / (1 + a_1 N_1) )</td>
<td>4</td>
</tr>
<tr>
<td>Multi-resource Holling Type II</td>
<td>H2-m</td>
<td>( a_1 N_1 / (1 + a_1 N_1 + a_2 N_2) )</td>
<td>4</td>
</tr>
<tr>
<td>Generalised multi-resource Holling Type II</td>
<td>H2-g</td>
<td>( a_1 N_1 / (1 + a_1 N_1 + a_1 a_2 N_2) )</td>
<td>6</td>
</tr>
</tbody>
</table>

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.

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 as our estimate of parameter uncertainty.

When we could only obtain a data set as means and associated uncertainties, we simulated 250 parametrically bootstrapped data sets with a sample size equivalent to that of the original data set and then inferred the best-fit parameter values of each of these (Supplementary Material). We then performed the same two-step parameter fitting process separately for each of these simulated data sets. We treated each parameter’s median value across these 250 separate fits as its point estimate. As an estimate of its uncertainty, we used the central 68% interval of the 250 values as this corresponds to ±1 standard deviation for a normal distribution.

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 \( \phi_{ij,F_{uk}} \) and/or \( \phi_{F_{uk}} \). The first came from comparing AIC (Akaike information criterion) across the various candidate models. 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 ability 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; Reichert & Omlin, 1997; Gill & King, 2004).

RESULTS

Consumer interference

We obtained 77 single-resource consumer-dependence data sets with which to infer the effect of feeding on consumer interference (Table S1). This included 61 data sets with predator consumers and 17 data sets with parasitoid consumers. In total, we obtained 44 data sets in the form of raw data and 33 data sets in the form of means and associated uncertainties. On average, the data sets consisted of 120 replicate feeding observations (min: 10, max: 528, median: 80).

As judged by AIC, our generalised consumer-dependent model including \( \phi_{ij,F_{uk}} \) (eqn 3) was ranked first for 42 (55%) data sets and tied for first (i.e. was within 2 AIC units) for an additional 24 (31%) data sets (Fig. 2). We obtained qualitatively similar results using the alternative information criteria AICc and BIC (Fig. S1). Maximum-likelihood point estimates of \( \phi_{ij,F_{uk}} \) (i.e. the effect of feeding on interference) varied considerably across the data sets (Fig. 2). Well over half (47 out of 77) of the data sets provided point estimates that were less than or equal to 1, implying that handling times and/or consumer interference increased as the product of resource and consumer abundances increased. The uncertainties of these point estimates overlapped only the Beddington–DeAngelis model (\( \phi_{ij,F_{uk}} = 1 \)) for 15 data sets, overlapped only the Crowley–Martin model (\( \phi_{ij,F_{uk}} = 0 \)) for 11 data sets, and overlapped both models for 23 data sets. This overlap was largely consistent with instances where the generalised model was judged equivalent to simpler models based on AIC. There were 28 data sets with uncertainties that were not consistent with any pre-existing model: four data sets fell entirely in the region \( \phi_{ij,F_{uk}} < 0 \), 10 data sets fell exclusively between the two models (e.g. consistent with ‘partial’ distraction of consumers) and 14 data sets fell entirely in the region \( \phi_{ij,F_{uk}} > 1 \). Overall, the uncertainties of only 34 data sets (43%) were consistent with the idea that interference and feeding were independent of each other (i.e. \( \phi_{ij,F_{uk}} \approx 0 \)).

Multiple resources

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

As judged by AIC, our generalised multi-resource Holling Type II model including both \( \phi_{F_{uk}} \) (eqn 10) was ranked first for 20 (67%) multiple-resource data sets and tied for first for an additional one (3%) data set (Fig. 3). We obtained qualitatively similar results using the alternative information criteria AICc and BIC (Fig. S2). Maximum-likelihood point estimates of \( \phi_{F_{uk}} \) and \( \phi_{F_{uk}} \) varied considerably across the different data sets (Fig. 3), including estimates...
indicative of (1) feeding rates being unaffected by the non-fo-
cal resource ($\phi_{FkiFkj} \approx 0$ and/or $\phi_{FkjFki} \approx 0$), (2) feeding on one resource completely precluding feeding on the other ($\phi_{FkiFkj} \approx 1$ and/or $\phi_{FkjFki} \approx 1$), (3) feeding on one resource only partially precluding feeding on the other ($0 < \phi_{FkiFkj} < 1$ and/or $0 < \phi_{FkjFki} < 1$) and (4) 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 data sets, we observed that feeding and interference are rarely mutually exclusive. Likewise, we observed that a consumer’s behaviour when feeding on one resource can appear very dif-
ferent to its behaviour 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 analysed data sets 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 data sets with larger sample sizes and targeted experimental designs are generated in the future.

Across the single-resource consumer-dependence data sets, the Beddington–DeAngelis model provided a reasonably good approximation to a rather large number of the single-resource consumer-interference data sets, even when that model was not statistically ‘best’ (Fig. 2). In terms of their point estimates, the vast majority of these data sets had $\phi_{F_i,F_i} \leq 1$, 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 data sets (e.g. ‘Chong 2006’ and ‘Crowley 1989’), feeding in the presence of just over three 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. Dynamically, such ‘self-limitation’ would lead to larger equilibrium resource densities and smaller equilibrium consumer densities. In contrast, a smaller subset of consumer-interference data sets suggest that consumers spent less and less time handling resources when feeding in the presence of more and more conspecifics (e.g. ‘Long 2012b’ and ‘Kratina 2009’), which may be indicative of cooperative foraging.

Across the multi-resource-dependence data sets, we found that most were inconsistent with the assumptions implied by either the single-resource or multi-resource Holling Type II functional responses, and hence neither classical model obtained widespread support. In both the empirical and theoretical literatures, it is common for researchers to decide a priori which model is most appropriate given known biology of their focal consumer and to analyse their data accordingly. Our results indicate that this may be an unwise path to follow since 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 for another (e.g. ‘Long 2012a’ where $\phi_{F_i,F_i} \approx 0$ and $\phi_{F_i,F_i} \approx 1$), or somewhere in between (e.g. ‘Lester 2002 Ty d’ where $\phi_{F_i,F_i} = 0.36$ and $\phi_{F_i,F_i} = 0.78$). Clearly, more empirical research is needed to understand the biology that determines why each consumer–resource combination lands in one particular location along the spectra of process interdependencies. The multi-resource Holling Type II is also widely used in the 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 assumption of theory as well, suggesting that ecological communities are most likely composed of a much broader array of consumer types. The exact dynamical properties that these varied consumer types may impart to their populations and food webs remain unknown. However, research on apparent competition (Holt, 1977; Abrams & Matsuda, 1996) and analyses of other functional-response models suggest their effects could be quite strong (Adamson & Morozov, 2013, 2014; Aldebert & Stouffer, 2018; Coblentz & DeLong, 2020).

Functional responses emerge from independent and non-independent processes

Our analyses emphasise the fact that even the simplest functional responses are impacted by more than static attack rates, handling times and interference strengths. Instead, we argue it is more instructive to think about feeding as just 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 $\phi_{F_i,F_j}$, $\phi_{F_i,F_j}$ and/or $\phi_{F_i,F_j}$ 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 $\phi$’s as capturing two key features of biological relevance. First, they allow us to statistically infer whether 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 expect 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. 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 behaviour 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 underestimated processes at play in these systems, extending well beyond the densities of any focal interacting pair. Beyond consumer–resource interactions, standard growth-response (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; Kleinhesslein & 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 becomes even more extreme. On the plus side, the data themselves can impose limits on model complexity since 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 only one such implicit process can be measured per species density (Supplementary Material). Greater statistical power can therefore be achieved by obtaining information on additional response variables beyond 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 resources 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 behavioural effects (Sheriff et al., 2020).

Given these practical limitations, a major challenge is to find model simplifications that can be supported, and to determine robust strategies for doing so. One option is to adopt a descriptive approach as proposed by Arditi & Michalski (1996); its phenomenological nature lends itself to a quick reduction in the number of parameters needing to be inferred. Alternatively, one can follow a statistical approach to the problem. For example, our fits to the multi-resource-dependent data sets always treated both resources as functionally distinct (i.e. \( a_i \neq a_j \) and \( h_i \neq h_j \)). Given a many-resource data set, it may instead be advantageous to assess whether two or more resources are functionally equivalent in terms of model fit (Carrara et al., 2015; Ovaskainen et al., 2017). The statistical approach could also treat variation between resources as a statistical random effect (Ovaskainen & Soininen, 2011; Ovaskainen et al., 2016) or allow parameter variation to mirror phylogenetic or trait distances (Kalinkat et al., 2013). Clearly, proper inference of any such models will benefit from increased replication (Novak & Stouffer, 2020), as well as more robust and creative study designs (e.g. Dell et al., 2014; Novak et al., 2017; Uszko et al., 2017). Even so, not all phenomenological or statistical approaches are guaranteed to be logically consistent (Arditi & Michalski, 1996; Morozov & Petrovskii, 2013). All models should therefore be tested against criteria beyond fit and parsimony before they are applied, for example in population models (Malard et al., 2020; Moisset de Espanés et al., 2020).

CONCLUSIONS

The study of biological models serves a wide variety of purposes (Evans et al., 2013; Otto & Rosales, 2020). We have focused here on the ability of generalisable models to fit observed variation in feeding rates across a large collection of empirical data sets. Rather than 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; Cox, 1984), our mathematical approach demonstrates how and why such interaction terms emerge: the interdependence of biological processes. Biological explanations for the large variation we observed across data sets remain to be determined. We therefore hope our study will also provide a fruitful starting point for a more mechanistic synthesis in the not too distant future.

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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.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13670.

OPEN RESEARCH BADGES

This article has earned Open Data and Open Materials badges. Data and materials are available at https://github.com/stoufferlab/general-functional-responses.
DATA AVAILABILITY STATEMENT

Code for all analyses, as well as most data sets, 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 and S2), or were obtained from repositories to which they had previously been posted by the original authors. Readers should get in contact with the journal if they discover issues with data.

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