

LETTER

Quantifying predator dependence in the functional response of generalist predators

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Abstract

A long-standing debate concerns how functional responses are best described. Theory suggests that ratio dependence is consistent with many food web patterns left unexplained by the simplest prey-dependent models. However, for logistical reasons, ratio dependence and predator dependence more generally have seen infrequent empirical evaluation and then only so in specialist predators, which are rare in nature. Here we develop an approach to simultaneously estimate the prey-specific attack rates and predator-specific interference (facilitation) rates of predators interacting with arbitrary numbers of prey and predator species in the field. We apply the approach to surveys and experiments involving two intertidal whelks and their full suite of potential prey. Our study provides strong evidence for predator dependence that is poorly described by the ratio dependent model over manipulated and natural ranges of species abundances. It also indicates how, for generalist predators, even the qualitative nature of predator dependence can be prey-specific.

Keywords

Beddington–DeAngelis functional response, consumer dependence, food webs, interaction modification, interaction strengths, mutual predator effects, *Nucella* whelks, *per capita* attack rates, prey preference.

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INTRODUCTION

How predator feeding rates respond to changes in prey abundance underlies the dynamics of all predator–prey interactions (Murdoch & Oaten 1975). A central debate in the predator–prey literature concerns the degree to which these functional responses are better characterized using prey-dependent models, such as the classical Holling type forms, or by ratio-dependent models (Abrams & Ginzburg 2000; Arditi & Ginzburg 2014; Barraquand 2014; Abrams 2015). In the former, feeding rates respond only to changes in prey abundance. In the latter, feeding rates respond to the prey available per predator. Predator-dependent functional response models more generally encapsulate the notion that predator individuals can alter each others feeding rate, and include ratio dependence as a special case. Models including mutual predator interference have been reasoned to explain many of nature's patterns left unexplained by the simplest of prey-dependent models, including the apparent stability of food webs and the response of successive trophic levels to enrichment (Arditi & Ginzburg 2012; but see Abrams 1993).

A growing number of studies has begun to shed light on what has long remained largely a philosophic debate based on indirect tests of generic theoretical predictions. These studies have primarily taken the form of manipulative functional response experiments varying the abundances of both a predator and a prey (e.g. Fussmann *et al.* 2005), analyses of microcosm predator–prey population dynamics (e.g. Jost & Arditi

2001), and, rarely, long-term studies of cooperatively foraging top predator populations (e.g. Vucetich *et al.* 2002). The majority of studies have been interpreted as evidencing functional responses being closer to ratio- than prey dependent (DeLong & Vasseur 2011; Arditi & Ginzburg 2012).

Field-based studies nonetheless remain extremely rare. Moreover, the logistical and statistical constraints imposed by considering both prey and predator abundances has limited almost all studies to species-poor systems of single predator species interacting with only one primary prey species. Even inherently generalist predators have thereby been reduced to effective specialists, whether in manipulative experiments or in time-series analyses. Evaluations of the functional forms of interspecific effects between multiple predator species have similarly been inaccessible. Given that most predators in nature are generalists and can alter each others feeding rates in many ways (Peacor & Werner 2004; Golubski & Abrams 2011; Kéfi *et al.* 2012) extrapolations regarding the prevalence, form, strength, and hence importance of predator dependence in species-rich food webs may be premature.

Here we develop an approach for characterizing and quantifying the functional responses of generalist predators. By avoiding the logistical constraints imposed by a generalist's many prey species, the approach may even be used in field contexts involving an arbitrary number of interacting predator species. We apply the approach in one set of non-manipulative field surveys and two manipulative field experiments involving two predatory whelks of the Oregon rocky

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intertidal, *Nucella ostrina* and *Nucella canaliculata*. Our study of these two predators exposed to their full suite of potential prey provides strong support for intraspecific predator dependence in *N. ostrina*'s functional response that is poorly described by the ratio-dependent model over both experimentally extended and naturally occurring ranges of predator and prey abundances. Our study further suggests that *N. ostrina*'s predator dependence is itself prey-specific, with variation in community structure controlling even its qualitative nature (i.e. interference vs. facilitation). This implies that new functional response models are needed to better characterize predator–prey interactions in species-rich food webs.

METHODS

We first provide a brief description of the observational approach in order to build intuition for its success. Further details are provided in the *Supplementary Online Materials* (SOM), which also includes descriptions of the various functional response models we evaluated in three different empirical contexts. These contexts (henceforth ‘cases’) were (1) a set of non-manipulative field surveys, (2) a caging experiment that manipulated predator densities, and (3) a larger-scale combination of field surveys and predator manipulations. Each of these cases was used to detect or elicit an *in situ* signal of predator dependence.

The observational approach

Novak & Wootton (2008) introduced a method for inferring the prey-specific *per capita* attack rates of a generalist predator presumed to exhibit a prey-dependent multispecies Holling type II functional response. Their method is observational in that it uses only data on prey abundances (N_i), handling times (h_i), and counts of the number of feeding (n_i) and non-feeding (n_0) individuals observed during a single snapshot survey of a focal predator population. Wolf *et al.* (in press) showed this method's analytical estimator for the attack rate on the i th prey to be equivalent to

$$\hat{a}_i = \frac{n_i}{n_0} \frac{1}{h_i N_i}. \quad (1)$$

We provide a statistical derivation that is significantly simpler than the statistics-free ‘first-principles’ argument of Novak & Wootton (2008) and Wolf *et al.* (in press) in the SOM.

Intuition for the method's success may be built by using the attack rate estimator to reformulate the type II model in terms of the fraction of predator individuals that are expected to be observed feeding at any given time. For example, when the predator is a specialist feeding on only one prey species,

$$\frac{n_1}{n_0 + n_1} = \frac{\hat{a}_1 h_1 N_1}{1 + \hat{a}_1 h_1 N_1}, \quad (2)$$

which tends to 1 as a_1 , h_1 , or N_1 increase. The fraction of individuals observed to be feeding on a particular prey species during a snapshot survey will therefore increase the higher the attack rate, the longer the handling time, or the more abundant the prey species is (Fig. 1a). Knowledge of a prey's

handling time, its abundance and the fraction of predator individuals feeding on it during a snapshot survey therefore allows its attack rate to be inferred (Novak & Wootton 2008). (We use a ‘hat’ to indicate an estimated parameter.)

Here we place the Novak & Wootton (2008) method within a general statistical framework, showing eqn 1 to be (1) the maximum likelihood estimator for the attack rates of the type II functional response and (2) a special case of a far more general approach for inferring feeding rates (f_i) from a single snapshot survey:

$$\hat{f}_i = \frac{n_i}{n} \frac{1}{d_i}, \quad (3)$$

where n is the total number of surveyed individuals and d_i is the detection time during which a feeding event on prey i is observable (otherwise assumed to equal h_i , see SOM).

Equation 3 enables the estimation of a predator population's feeding rates without assuming an underlying functional response (Bajkov 1935; Woodward *et al.* 2005). This forms the basis for extending the approach to situations where ratio-dependent or more general predator-dependent functional response forms are expected, including the Hassell–Varley model and both single- and multi-predator versions of the Beddington–DeAngelis model (Hassell & Varley 1969; Beddington 1975; DeAngelis *et al.* 1975; Arditi & Akçakaya 1990). Intuitively, this is possible because the more interference among predators there is, the larger the attack rates must be to maintain the same proportion of feeding individuals

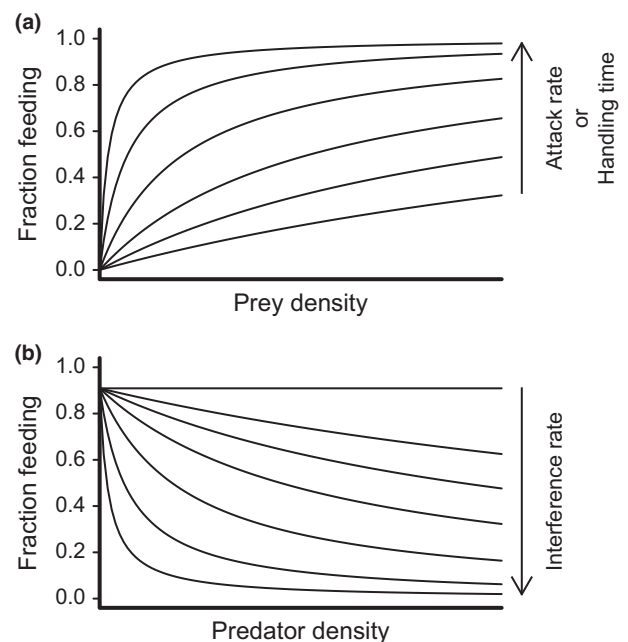


Figure 1 The probability that an individual predator feeding with a type II or Beddington–DeAngelis functional response will be observed in the process of feeding at any point in time (a) increases the higher its attack rate, the longer its handling time, and the more abundant its prey species is (eqn 2), and (b) decreases with stronger intra- or inter-specific interference among predator individuals (eqn 4). Under the assumption that all individuals are independent and equivalent, this probability corresponds to the fraction of individuals that are expected to be observed feeding in a snapshot survey of the population.

when handling times and abundances are fixed. For example, for a specialist predator exhibiting a Beddington–DeAngelis response (Fig. 1b), the fraction of individuals expected to be feeding at any point in time is described by a binomial likelihood with a probability of ‘success’ equaling

$$\frac{n_1}{n_0 + n_1} = \frac{\hat{a}_1 h_1 N_1}{1 + \hat{a}_1 h_1 N_1 + \sum_p \hat{\gamma}_{jp} P_p}. \quad (4)$$

Here P_p reflects predator p 's density and γ_{jp} its *per capita* effect on focal predator j 's available time to search for prey. Correspondingly, the fraction of feeding and non-feeding individuals of a generalist predator are described by a multinomial likelihood. Note that predators exhibit facilitative effects when $\gamma < 0$.

Fitting more complex models like the Beddington–DeAngelis model to estimate both the attack rates and mutual predator effects is not possible with only one feeding survey. Rather, as in any regression, doing so requires multiple surveys that vary in predator densities. Specifically, we require at least one more survey than the number of considered predator species. Models including further unknown parameters and co-variables (e.g. size-structure, environmental conditions, community composition) necessitate additional surveys. That said, a further benefit of the statistical framework is that it permits us to evaluate the relative performance of different models in describing data from surveys using information theoretics. Thus, even the performance of the ‘non-functional’ (density-independent) model of eqn 3 – in which survey-to-survey variation in the fractions of feeding and non-feeding individuals is explained not by variation in prey or predator abundances but solely by differences in detection times associated with survey-to-survey variation in predator and prey body sizes (see below and SOM) – may be compared to the performance of the various density-dependent functional response models.

Study system

Our field study focused on two intertidal whelk species, *N. ostrina* and *N. canaliculata*, in midshore ‘mussel-bed patches’. While *N. ostrina* tends to occur higher on the shore than *N. canaliculata*, their tidal range overlaps considerably in the midshore mussel zone where both species often exhibit their highest densities (Spight 1981; Navarrete 1996). Both species consume the same variety of prey taxa, including sessile mussels and barnacles and mobile limpets and littorine snails (Spight 1981), and are of similar size. Intertidal whelks are particularly interesting in the context of functional responses because an experiment by Katz (1985) involving the Atlantic whelk, *Urosalpinx cinerea*, has been interpreted by both sides of the debate in support of their arguments (Abrams 1994; Akçakaya *et al.* 1995).

Nucella densities are typically highest in patches within the mussel bed where mussels have been removed by wave-induced disturbance (Plate 1; Navarrete 1996). Patches large enough not to be encroached by the surrounding mussel bed undergo a semi-deterministic trajectory of recovery of increasingly larger species (Levin & Paine 1974; Berlow 1997; Wootton 2002), being first colonised by diatoms and algae, then acorn barnacles (*Balanus glandula* and *Chthamalus dalli*),

Mytilus trossulus mussels, then *Pollicipes polymerus* gooseneck barnacles, and eventually the mussel-bed forming species *Mytilus californianus*. Slow-growing *Semibalanus cariosus* barnacles initiate recruitment in low numbers with the other acorn barnacles but achieve notable densities only at the later stages of succession. At our study site (Yachats, Oregon, 44.3° N, –124.1° W), whelks and their mobile prey species, limpets (*Lottia asmi*, *L. digitalis* and *L. pelta*) and littorines (*Littorina sitkana*), are present throughout succession, but their abundances vary considerably from patch-to-patch and over time.

Unmanipulated patches

To quantify attack rates and assess predator dependence over the natural range of variation in predator and prey densities, we first applied the observational approach to 10 naturally formed unmanipulated patches. Patches were chosen haphazardly and varied in size (0.8–5.8 m², $\bar{x} = 2.4 \pm 1.4$ SD) and successional age and thus in species composition, both in terms of absolute and relative species abundances. Species abundances were estimated in each patch using three randomly placed quadrats (25 × 35 cm²). Low tide feeding surveys were performed in each patch by systematically inspecting and measuring all whelks (± 1 mm) and noting prey identity and prey size (± 1 mm) when individuals were feeding (i.e. in the process of drilling, prying or consuming a prey item).

Caging experiment

We used a manipulative caging experiment to assess predator dependence over a range of predator densities exceeding that observed in the natural patches. Fifteen stainless steel cages (25 × 35 cm²) were placed in a single large patch of a low-diversity successional age dominated by a homogeneous cover of *B. glandula* barnacles. Each cage was photographed to determine prey abundances, then received between 5 and 160 *N. ostrina* (11–16 mm shell length) corresponding to densities below and above natural mean densities. Feeding surveys of each cage were performed on two subsequent occasions, 2 and 4 weeks later.

Manipulated patches

Finally, to determine whether a signal of predator dependence could be experimentally elicited at the patch scale, we combined surveys of naturally formed patches with a manipulation of their whelk densities. The experiment was performed in nine haphazardly chosen patches of variable successional age and consisted of five steps: (1) an estimation of species abundances using three haphazardly located quadrats (25 × 35 cm²); (2) a first systematic feeding survey of the whelks, (3) a manipulation of whelk densities, and, after four subsequent high tides, (4) a re-estimation of whelk densities using three quadrats placed in the same approximate locations as before, and (5) a second systematic feeding survey of the whelks. The manipulation of whelk densities entailed either a decrease or increase (0.07 to 3.3 times their pre-manipulation

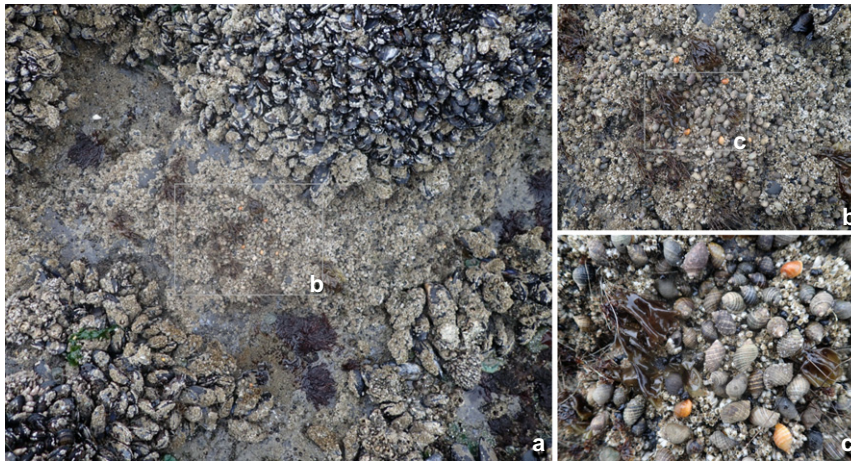


Plate 1 The predatory whelks *Nucella ostrina* and *Nucella canaliculata* co-occur and can reach extremely high densities in the wave-disturbed patches of a mussel bed.

density), or a control treatment in which all whelks were returned (Fig. S2). Three patches were haphazardly assigned to each treatment. The whelks in all treatments were picked up either during or immediately after the first feeding survey to avoid confounding treatments by the potential effects of whelk handling. Prior observations indicated that a 2-day recovery period was ample time for whelks to regain normal activity but insufficient for whelks to have an appreciable effect on prey densities.

Model-fitting and comparison

Focusing on the feeding observations of *N. ostrina*, we estimated the parameters and evaluated the relative performance of four functional response models (Holling type II, ratio-dependent, Beddington–DeAngelis, and Hassell–Varley; see SOM for details) and the ‘non-functional’ model that treated feeding rates as being independent of species densities. We considered two Beddington–DeAngelis models for the unmanipulated and manipulated patches in which both *N. ostrina* and *N. canaliculata* occurred, one including only an intraspecific predator effect and one including intra and inter-specific predator effects; only *N. ostrina* was present in the caging experiment.

Model-fitting treated the surveys of each case as independent and identically distributed, describing feeding rates for each case by one set of attack- and interference rate estimates across all surveys. We also relaxed this assumption for the manipulated patches where two surveys of the same patch had been performed by fitting all models with patch-specific parameters. For each patch, a species’ abundance was estimated by its mean density (m^{-2}), averaged over replicate quadrats. A species’ handling time was estimated by its mean expected handling time (in hours), averaged over the expected handling times of the feeding observations made for that species within the patch. The expected handling time of each feeding observation was estimated from measurements of the whelk’s size, its prey’s identity and size, and the ambient temperature (the average of water and air over the month in which surveys were performed) using regression coefficients

derived from laboratory experiments manipulating these variables for *Haustrum scobina*, a New Zealand whelk species with ecologically equivalent characteristics and prey (Novak 2010, 2013). In fitting the models we constrained all attack rates, as well as the interference rate parameter of the Hassell–Varley model, to be positive. The mutual predator effect parameters of the Beddington–DeAngelis models remained unconstrained. Convergence was reached in all cases by setting the attack rate starting values to reflect the appropriate analytical solutions of the type II or ratio-dependent functional response models (eqns 1 and S5). Model performance and parsimony was evaluated by AIC_c (Burnham & Anderson 2004), thereby focusing on the predictive capacity of the considered models (Aho *et al.* 2014).

RESULTS

Variation in diet and species abundances

We observed *N. ostrina* feeding on 11 and 10 species, including itself, in the unmanipulated and manipulated patches, respectively. Only five of these species were observed being fed upon in the cages, despite the presence of all potential prey and sufficient sampling effort to detect them (Fig. S1). The total number of feeding observations per prey species varied from 2 (*Lotta digitalis*) to 1089 (*B. glandula*), with 14.8% of the 13131 total examined *N. ostrina* whelks found to be feeding. Six whelks were observed drilling a conspecific individual. *N. ostrina*’s densities ranged between 133–1143 m^{-2} in the unmanipulated patches, 57–1829 m^{-2} in the cages, and 80–1939 m^{-2} in the manipulated patches prior to manipulation; post-manipulation densities ranged from 80–2518 m^{-2} (Fig. S2). *N. canaliculata*’s densities were consistently and considerably lower (Fig. S2), with only 128 total feeding observations (14.2% of all examined individuals) being made in the subset of patches in which they were present.

Patches represented early to late successional ages and thus varied considerably in their prey abundances. In particular, the mean densities of *M. trossulus* mussels and *B. glandula* barnacles, representing *N. ostrina*’s primary prey (both in

terms of diet frequency and subsequently estimated feeding rates), respectively varied between 3.8–7295 m⁻² and 240–114987 m⁻². There was no discernible relationship between whelk and prey abundances in the unmanipulated patches (Fig. S3). A positive relationship between *N. ostrina* and *B. glandula* densities observed in the manipulated patches prior to manipulation was broken by the manipulation of whelk densities (Fig. S3). Patches consequently varied substantially both in the relative ratio of mussels to barnacles and in the relative ratio of whelks to prey (Fig. 2a,c). In contrast, the experimental cages, which were located within a single early successional age barnacle-dominated patch, varied little in their absolute and relative prey abundances (Figs 2b and S4). The larger-than-natural range of whelk to prey ratios in the cages was therefore due to the manipulation of *N. ostrina* densities. In fitting the alternative functional response models to the data, one prey species, the burrowing mussel *Adula californiensis*, on which two whelks were observed feeding in the unmanipulated patches, was excluded prior to analysis because it was not detected in any abundance survey.

Model-performance and parameter estimates

The Beddington–DeAngelis functional response entailing only intraspecific predator dependence was unambiguously the best-performing model for the unmanipulated patches; its AIC_c-weight, reflecting the conditional probability of it being the best-performing model, exceeded 0.999 (Table 1a). The patch-specific version of the same model outperformed all others with equally unambiguous evidence for the manipulated patches (Table 1c). Only for the caging experiment did model comparisons fail to provide clear support for a particular model, with the Type II, the Beddington–DeAngelis, and the Hassell–Varley models all exhibiting AIC_c values within four units of each other (Table 1b). Nevertheless, in all three cases the ratio-dependent and density-independent models performed substantially worse than all other models.

As estimated assuming the Beddington–DeAngelis model, *N. ostrina*'s prey-specific *per capita* attack rates varied by up to three orders-of-magnitude within each of the three cases

(Fig. 3a). Attack rates varied over almost five orders-of-magnitude across the three cases overall. The range of variation in attack rates was similar in the two sets of patches where *N. ostrina* was observed consuming 10–11 species. In the cages, by contrast, the subset of five prey species on which *N. ostrina* was observed feeding evidenced attack rates that were 4–1004 times higher than in either set of patches. There was no rank-order correlation between the attack rates of the three cases (Table S10), with a similar number of prey evidencing attack rates that were relatively higher vs. lower in one case compared to another. In contrast, although *N. ostrina*'s prey-specific feeding rates also varied over three orders-of-magnitude, these were of similar magnitude and positively rank-correlated across the three cases (Fig. 3b, Spearman's $\rho \geq 0.7$, Table S10).

Point estimates for the *per capita* magnitude of intraspecific predator dependence in *N. ostrina* were better constrained for the two sets of patches than for the cages (Fig. 4a), consistent with the poorer discrimination among models by AIC_c for the cages (Table 1). However, while γ estimates were positive for both cages and the manipulated patches (indicating interference effects), the estimate in the unmanipulated patches was negative (indicating a facilitative effect). The patch-specific γ estimates for the manipulated patches also exhibited both positive and negative values, with four of the five positive (interference) estimates exhibiting considerably higher magnitudes than the other estimates (Fig. 4b).

DISCUSSION

Two fundamental yet often conflated questions have contributed to sustaining the debate over predator functional responses: How to best represent predator–prey interactions in models of population dynamics? And what functional response models best describe the relationship between predator feeding rates and species abundances? The importance of these questions is immense in applied contexts, such as fisheries management, and transcends the study of predator–prey interactions (Hunsicker *et al.* 2011; Perretti *et al.* 2013; Abrams 2015). Indeed, all methods for quantifying the strengths and hence importance of species interactions make

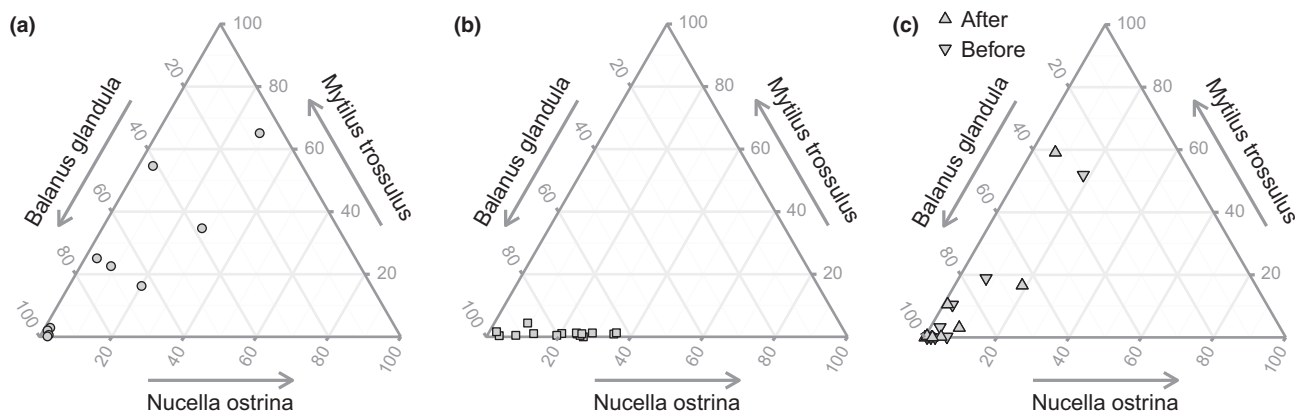


Figure 2 The relative abundance of *Nucella ostrina* and its two primary prey species, *Mytilus trossulus* mussels and *Balanus glandula* acorn barnacles, as illustrated by their proportional densities in the (a) unmanipulated patches, (b) experimental cages, and (c) manipulated patches before and after the manipulation of *N. ostrina*'s densities.

Table 1 Comparison of functional response models applied to (a) the unmanipulated patches, (b) the caging experiment, and (c) the manipulated patches (for which asterisks indicate models with patch-specific parameters) using AIC_c , which converges on the AIC goodness-of-fit statistic as sample size increases. Note that it was not possible to fit the Beddington–DeAngelis model including both intra- and inter-specific effects to the cages or to the manipulated patches on a patch-specific basis

Model	AIC_c	ΔAIC_c	d.f.	Weight
<i>(a) Unmanipulated patches</i>				
BD (intra)	730.3	0.0	11	> 0.999
BD (intra & inter)	746.9	16.6	12	< 0.001
Type II	748.8	18.5	10	< 0.001
HV	838.8	108.5	11	< 0.001
Density independent	978.4	248.1	10	< 0.001
Ratio	1088.0	357.7	10	< 0.001
<i>(b) Caging experiment</i>				
Type II	147.4	0.0	5	0.54
BD (intra)	148.3	0.9	6	0.34
HV	150.6	3.2	6	0.11
Density independent	174.5	27.1	5	< 0.001
Ratio	178.6	31.2	5	< 0.001
<i>(c) Manipulated patches</i>				
BD (intra)*	124.4	0	44	> 0.999
HV*	154.7	30.3	44	< 0.001
Density independent*	193.2	68.8	35	< 0.001
Type II*	195.3	70.9	35	< 0.001
Ratio*	474.9	350.5	35	< 0.001
Type II	502.1	377.7	10	< 0.001
BD (intra)	514.6	390.2	11	< 0.001
HV	514.7	390.3	11	< 0.001
BD (intra & inter)	517.1	392.7	12	< 0.001
Ratio	762.7	638.3	10	< 0.001
Density independent	912.4	788	10	< 0.001

assumptions regarding their functional form (Wootton & Emmerson 2005; Vázquez *et al.* 2015; Novak *et al.* 2016). Recognising that the answers to these two questions will not be the same in all circumstances will be key to future progress. For example, predator dependence may be sufficiently

weak that it has no appreciable effect on population dynamics over the range of species abundances that actually occur in nature's species-rich communities, despite being discernible in manipulative functional response experiments (see also Fussmann *et al.* 2005).

Strong evidence for predator dependence

Our study does not address the presence of predator dependence in *N. ostrina's* population dynamics. It does, however, indicate that predator dependence as encapsulated by Beddington–DeAngelis model characterizes *N. ostrina's* feeding rates the best among the models we considered, and that its effects are discernible over the species abundances and diversity of prey that this generalist predator experiences in the field. The poorer performance of the Hassell–Varley model implies that *Nucella's* mutual predator effects result from individuals altering each other's available prey search time rather than search efficiency (DeLong 2014). More generally, the nature of predator dependence was far from ratio dependent. This was most clearly evidenced by the relative performance of the prey-dependent Holling type II model (Table 1), and by the point estimates for the interference-strength parameter of the Hassell–Varley model ($m \leq 3.28 \times 10^{-5}$ in all three cases, where $m = 0$ reflects complete prey dependence, Tables S2–S4). Indeed, the ratio-dependent model was consistently among the worst-performing models, in two of three cases performing even more poorly than the model which assumed feeding rates to be independent of species abundances altogether (Table 1).

Surprisingly, our analysis inferred no effect of *N. canaliculata* on *N. ostrina's* feeding rates, despite their seeming ecological similarities. This may have been due to insufficient statistical power associated with low replication ($n \leq 10$ patches) and the relatively low variation seen in *N. canaliculata's* abundances (Fig. S2); the Beddington–DeAngelis model including both inter- and intraspecific predator effects did perform best in the two sets of patches when model performance was evaluated by AIC rather than AIC_c (Table S11).

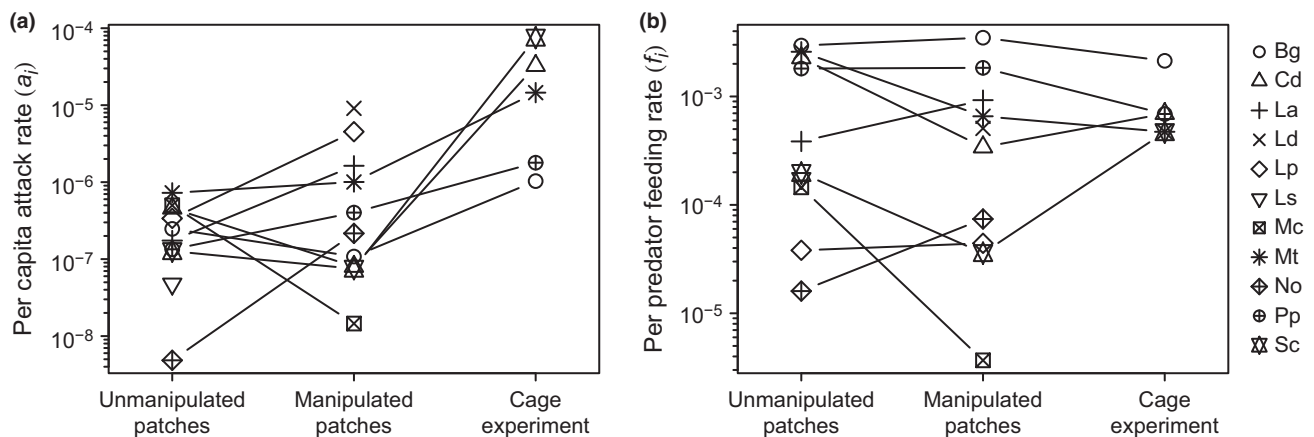


Figure 3 *Nucella ostrina's* prey-specific *per capita* attack rates and per predator feeding rates. (a) *Per capita* attack rate estimates assume the Beddington–DeAngelis functional response with only intraspecific predator effects, and evidence no rank-order correlation between the three cases (Table S10). (b) Feeding rate estimates assume no functional response form and evidence positive rank-order correlations between all pairs of cases (Table S10). Estimates for the manipulated patches are those of the non-patch-specific model. Prey name abbreviations: Bg – *Balanus glandula*, Mt – *Mytilus trossulus*; see Table S1 for others.

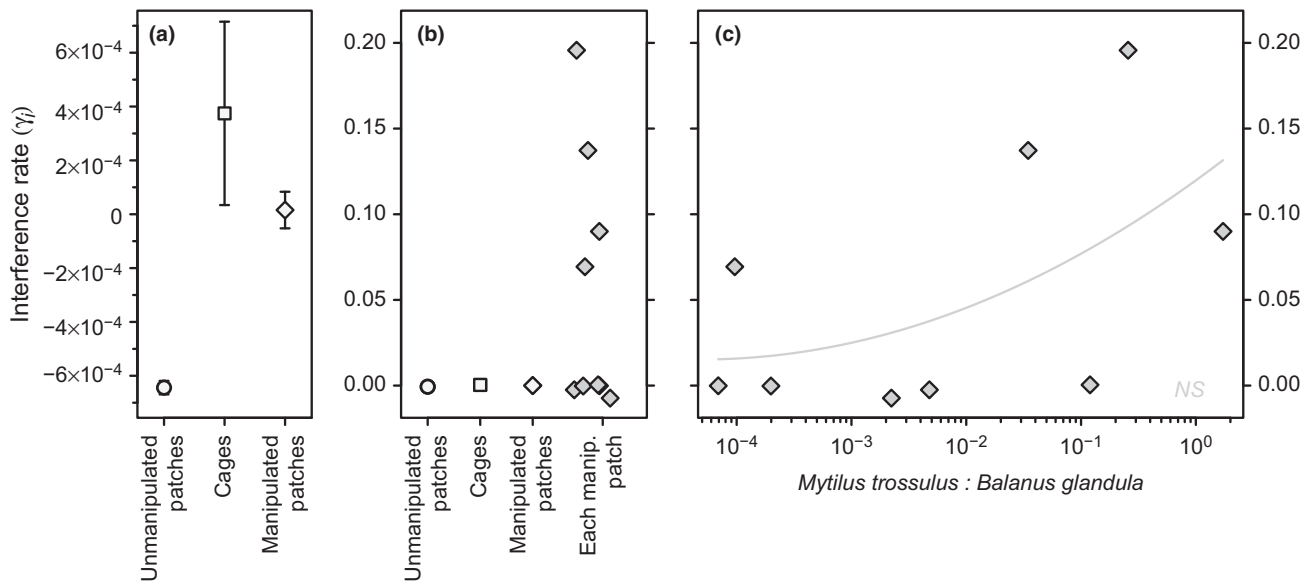


Figure 4 *Nucella ostrina*'s intraspecific predator effects (± 1 SE) as estimated assuming a Beddington–DeAngelis functional response in (a) each of the three cases (i.e. the unmanipulated patches, caging experiment, and manipulated patches) and (b) each case compared to at the patch-specific scale in the manipulated patches. Positive values indicate interference effects while negative values indicate facilitative effects. (c) Patch-specific predator effect estimates vs. the relative density of *N. ostrina*'s two primary prey, *Mytilus trossulus* mussels and *Balanus glandula* barnacles, in the manipulated patches suggests that the *per capita* strength of predator interference may depend on prey abundances. The fitted second-order polynomial trendline is *not* significant ($R^2 = 0.3$, $P = 0.34$). Note the different y-axis scales in (a) vs. (b) and (c), and that standard errors could not be estimated for the patch-specific estimates of (b) and (c) as only two surveys were performed on each manipulated patch.

However, an implicit benefit of the observational framework is that its focus on the fraction of feeding individuals makes it most sensitive to the effects of predator dependence at low predator densities, where a doubling of predator numbers has a larger effect on per individual feeding rates than it does at high predator densities (Fig. 1b). This differs from traditional manipulative functional response experiments on macroscopic organisms where the largest and thus most easily estimated rates of overall prey removal occur at high predator densities where stochasticity associated with variation among predator individuals is minimised. Therefore, *N. canaliculata*'s low densities should not have been an issue. Our results thus suggest that the interaction between the two whelk species is primarily one of indirect effects mediated by prey exploitation, rather than representing a significant interaction modification of feeding rates through wasted time (Spight 1981; Kéfi *et al.* 2012; DeLong & Vasseur 2013).

Similarly unexpected was that the weakest support for predator dependence was seen in the caging experiment where its effects were most expected (Table 1); the experiment manipulated *N. ostrina*'s densities beyond their typical range and affected predator–prey ratios exceeding their natural variation (Figs 2 and S2). Furthermore, the prey depletion that likely occurred between the initiation of the experiment and when the feeding surveys were conducted should have favoured predator-dependent models by reducing feeding rates most in the high density cages.

One explanation for the experiment's inability to discriminate among models more clearly was that the average fraction of feeding individuals will not have been estimated as reliably in the low predator density cages. Given the dimensions of a cage, the number of whelks in the lowest density cage was

only five, for example. Thus the probability of observing all or none of the individuals feeding at any given time was high regardless of their true mean feeding rate. This universal issue for small-scale manipulative experiments with macroscopic organisms will have been alleviated by our use of repeated cage surveys ($n = 30$ surveys), and was altogether avoided for the much larger natural patches that each contained many more whelks in total.

An alternative explanation for the weak support for predator dependence in the caging experiment is that the cages, or their placement within an early successional age patch that was dominated by a single barnacle species, altered whelk foraging behaviour from that exhibited across the sets of surveyed patches more generally. This interpretation may seem to challenge the concern that traditional functional response experiments involving isolated predator–prey pairs could be favoring the detection of predator dependence by selecting for strong predator–prey interactions (Abrams 2015). However, the results of our analysis are also consistent with this concern in that *N. ostrina*'s estimated interference rate (Fig. 4a) and *per capita* attack rates (Fig. 3a) were substantially higher in the cages. Indeed, the observation that the highest prey-specific feeding rates decreased while the lowest prey-specific feeding rates increased in the cages relative to the patches, even as their overall rank-order remained relatively consistent across the three cases (Fig. 3b), suggests that the caged whelks altered their foraging strategy to compensate for the reduced breadth of their diet.

Prey-specific predator dependence

While further studies involving generalist predators will be needed to determine how diet breadth itself can affect the

strength of predator dependence, a likely feature distinguishing the functional responses of generalist and specialist predators is the variable propensity of a generalist's different prey species to elicit predator dependence. For example, rates of predator interference are expected to depend on the relative velocities with which predators and prey move, hence should differ for mobile and sessile prey species (DeLong 2014). For the whelks of our study in particular, predator dependence will have been driven by a number of mechanisms that vary by prey identity and differ in their qualitative nature even for similarly (im)mobile prey.

For example, two mechanisms of interference that we observed directly were the drilling of conspecific individuals and the simultaneous feeding on the same prey item by two individuals. Similar mechanisms are commonly invoked in the literature (Arditi & Ginzburg 2012). Consistent with the mechanism for predator dependence underlying the Beddington–DeAngelis response, conspecific drilling represents time wasted in regards to further foraging opportunities, even when consumption itself does not occur. Its frequency would typically be expected to increase with predator density irrespective of prey identity, but this was not observed in our study (Fig. S5). Extensive surveys at a nearby study site nonetheless show that the shells of least 0.1% of the *N. ostrina* population bear the mark of drilling events ($n > 45000$ total observations, *unpubl. data*). In turn, the simultaneous feeding by two individuals on the same prey item represents reduced energetic payoff, which may also be substantial for whelks given their long handling times. In contrast to conspecific drilling, we observed simultaneous feeding almost exclusively when whelks fed on *M. trossulus* mussels. This was likely a consequence of the large surface area for drilling that a mussel shell represents, the longer handling time of the average mussel relative to other prey species, and the tendency of mussels to form clusters around whose accessible perimeters whelk densities are often locally increased (see also Hossie & Murray 2016).

Much less considered in the debate over functional responses is that predator density can also have facilitative effects on feeding rates, even in the absence of cooperative group hunting. This omission persists despite the longstanding awareness of the synergistic effects between predator species (Sih *et al.* 1998). Mechanisms for facilitative effects include the feeding-induced release of prey chemical cues. That chemical cues can be prey-specific has recently been demonstrated in the intertidal by the characterization of a cuticular glycoprotein in *B. glandula* that acts as a potent stimulant for whelk feeding (Zimmer *et al.* 2016).

If both facilitative and interference-based mechanisms of predator dependence exist and are dependent upon prey identity, then, for generalists, both the strength and net qualitative nature of predator dependence should depend on community structure. This appears to have been the case in our study, with γ estimates for the Beddington–DeAngelis model indicating (1) net interference in the manipulated patches where *M. trossulus* mussels tended to be more common, (2) stronger but more poorly constrained interference in the cages where *B. glandula* barnacles were dominant, and (3) net facilitation in the unmanipulated patches where a second barnacle species tended to be more common (Table 1, Figs 2 and S4). Further support is

provided by our patch-specific analysis of the manipulated patches in which γ estimates tended to increase with the ratio of available mussels to barnacles (Fig. 4c). Future experiments manipulating community structure directly will be needed to determine whether such prey-specific influences of community structure tend to be idiosyncratic or conform to useful categorisations (see also DeLong 2014).

CONCLUSIONS

That many prey-specific mechanisms of predator dependence are likely to occur in the functional responses of generalist predators indicates that additional, more complex models will be useful in characterizing the species interactions of nature's species-rich food webs. Many more such models, including those that consider allometric constraints and those that more generally relax the assumptions of predator homogeneity and the constancy of attack rates and handling times (e.g. Murdoch & Oaten 1975; Abrams 2010; Okuyama 2012; Rall *et al.* 2012; Baudrot *et al.* 2016; Kalinoski & DeLong 2016), should become empirically accessible with the observational framework, particularly when applied in combination with experimental manipulations. Whether the inferences of our study on whelks will conform to generalizable theory or will instead represent insightful outliers will be unknowable until more field-based studies of generalist predators are performed.

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AUTHOR CONTRIBUTIONS

CW contributed to method development, KEC and IS performed the caging experiment, and MN conceived of the study, carried out the fieldwork and analyses, and wrote the manuscript.

DATA ACCESSIBILITY SECTION

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.sj94k>; <https://github.com/marknovak/PredDep>

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