

1 Quantifying predator dependence in the functional
2 response of generalist predators.

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7 CW contributed to method development, KC and IS performed the caging experi-
8 ment, and MN conceived of the study, carried out the fieldwork and analyses, and
9 wrote the manuscript.

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17 - *Intuition for the observational approach*

18 - *Derivation of the observational approach*

19 - *Functional response parameter point estimates*

20 - *Supplementary figures*

21 - *Data tables*

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25 <https://github.com/marknovak/PredDep>

26

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Abstract

A longstanding debate concerns whether functional responses are best described by prey-dependent versus ratio-dependent models. Theory suggests that ratio dependence can explain many food web patterns left unexplained by simple 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 rates of predators interacting with arbitrary numbers of prey and predator species. We apply the approach to field surveys and two field experiments involving two intertidal whelks and their full suite of potential prey. Our study provides strong evidence for the presence of weak predator dependence that is closer to being prey dependent than ratio dependent 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: Interaction strengths, consumer dependence, Beddington-DeAngelis functional response, multiple predator effects, per capita attack rates, prey preference, interaction modification, *Nucella* whelks.

Introduction

How predator feeding rates respond to changes in prey abundance underlies the dynamics of all predator-prey interactions (Murdoch & Oaten, 1975). A longstanding and still vigorous debate in the predator-prey literature concerns whether these functional responses are best described by prey-dependent models, such as the classical Holling type forms, or by ratio-dependent models (Abrams, 2015; Abrams & Ginzburg, 2000; Arditi & Ginzburg, 2012; Barraquand, 2014). 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 responses more generally encapsulate the hypothesis that predator individuals alter each others feeding rate and include ratio dependence as a special case. Models including predator dependence indicate that the effective refuge that prey experience at high predator-to-prey ratios can explain many of nature's patterns left unexplained by simple prey-dependent models, including the apparent stability of food webs and the response of successive trophic levels to ecosystem enrichment (Arditi & Ginzburg, 2012).

Unfortunately the debate remains largely philosophical and based on indirect tests of generic theoretical predictions. Direct empirical evaluations are still limited. These have primarily taken the form of experiments manipulating the abundances of both a predator and a prey (e.g., Fussmann *et al.*, 2005), analyses of predator-prey population dynamics in microcosms (e.g., Jost & Arditi, 2001), and, in rare cases, long-term studies of cooperatively foraging top predator populations (e.g., Vucetich *et al.*, 2002). The majority of these studies have evidenced functional responses that are closer to ratio dependence than to prey dependence (Arditi & Ginzburg, 2012; DeLong & Vasseur, 2011; Skalski & Gilliam, 2001).

Although direct evaluations of predator dependence are increasing in frequency, the logistical and statistical constraints imposed by considering both prey and predator abundances has limited 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, both in manipulative experiments and time-series analyses. Evaluations of the functional forms of interspecific effects between multiple predator species

74 have similarly been inaccessible. Given that most predators in nature are generalists and
75 can alter each others feeding rates in many ways (Kéfi *et al.*, 2012; Peacor & Werner, 2004;
76 Sih *et al.*, 1998) extrapolations regarding the prevalence, strength, and hence importance
77 of predator dependence in species-rich food webs may be premature.

78 Here we introduce a new approach for characterizing and quantifying the functional
79 responses of generalist predators. By avoiding the logistical constraints imposed by a
80 generalist's many prey species, the approach may even be used in contexts involving an
81 arbitrary number of interacting predator species. We apply the approach in one set of non-
82 manipulative field surveys and two manipulative field experiments involving two predatory
83 whelks of the Oregon rocky intertidal, *Nuccella ostrina* and *N. canaliculata*. Our study of
84 these two predators exposed to their full suite of potential prey provides strong evidence
85 for weak intraspecific predator dependence in *N. ostrina*'s functional response. In the
86 field, over both experimentally-extended and naturally-occurring ranges of predator and
87 prey abundances, this generalist predator is thereby shown to exhibit a functional response
88 that is closer to being prey dependent than ratio dependent. Our study further indicates
89 that *N. ostrina*'s predator dependence is itself prey-specific, with variation in community
90 structure controlling even its qualitative nature. This implies that new functional response
91 models are needed to adequately describe predator-prey interactions in species-rich food
92 webs.

93 **Methods**

94 We first provide a brief description of the observational approach in order to build intuition
95 for its success. Further details are provided in the *Supplementary Online Materials* (SOM),
96 which also includes descriptions of the functional response models we evaluated in three
97 different contexts. These context (henceforth 'cases') were (i) a set of non-manipulative
98 field surveys, (ii) a caging experiment that manipulated predator densities, and (iii) a
99 larger-scale combination of field surveys and predator manipulations, each of which was
100 used to detect or elicit an *in situ* signal of predator dependence.

101 **The observational approach**

102 Novak & Wootton (2008) introduced a method for inferring the prey-specific per capita
103 attack rates of a generalist predator presumed to exhibit a prey-dependent multispecies
104 type II functional response. Their method is observational in that it uses only data on prey
105 abundances (N_i), handling times (h_i), and counts of the number of feeding (n_i) and non-
106 feeding (n_0) individuals observed during a snapshot survey of a focal predator population.
107 Wolf *et al.* (2015) subsequently showed this method's analytical estimator for the attack
108 rate on the i^{th} prey to be equivalent to

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

109 We provide a new and simpler derivation in the SOM.

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

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

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

118 Here we place the Novak & Wootton (2008) method within a general statistical frame-
119 work, showing eqn. 1 to be the maximum likelihood estimator for the attack rates. This
120 framework enables us to extend the observational approach to situations where ratio-
121 dependent or other, more general, predator-dependent functional response forms are ex-
122 pected, including the Hassell-Varley model (Arditi & Akçakaya, 1990; Hassell & Varley,
123 1969) and both single- and multi-predator versions of the Beddington-DeAngelis model
124 (Beddington, 1975; DeAngelis *et al.*, 1975). Intuitively, this is possible by considering that
125 the more interference among predators there is, the larger the per capita attack rates must
126 be to maintain the same proportion of feeding individuals. For example, for a specialist
127 predator exhibiting a Beddington-DeAngelis response, the fraction of individuals expected
128 to be feeding at any point in time (Fig. 1B) is described by a binomial likelihood with a
129 probability of ‘success’ equaling

$$\frac{n_1}{n_0 + n_1} = \frac{\hat{a}_1 h_1 N_1}{1 + \hat{a}_1 h_1 N_1 + \sum_p \hat{\gamma}_{jp} P_p}. \quad (3)$$

130 Here γ_{jp} reflects the per capita strength of the effect of predator species p on the focal
131 predator j ’s feeding rate, and P_p reflects its density. Note that predators can exhibit
132 facilitative effects when $\gamma < 0$. Correspondingly, the fraction of feeding and non-feeding
133 individuals of a generalist predator population are described by a multinomial likelihood.

134 Fitting more complex models like the Beddington-DeAngelis model to estimate both
135 the attack rates and mutual predator effects is not possible with only one feeding survey.
136 Rather, doing so requires replicate surveys that vary in predator densities. Specifically,
137 we require at least one more survey than the number of considered predator species. An
138 additional benefit of the statistical framework is that it permits us to evaluate the relative
139 performance of different models in describing empirical data using information theoretics
140 (e.g., AIC). Comparisons can thereby also be made to a simpler (non-functional) density-
141 independent ‘null’ model in which survey-to-survey variation in prey-specific feeding rates
142 is determined not by variation in prey or predator abundances but rather by differences in
143 handling times associated with variation in predator and prey body sizes (see SOM).

144 Study system

145 Our study focused on the species interactions of two intertidal whelks, *Nucella ostrina*
146 and *N. canaliculata*, in midshore ‘mussel-bed patches’. While *N. ostrina* tends to occur
147 higher on the shore than *N. canaliculata*, their tidal range overlaps considerably in the
148 midshore mussel zone where both species often exhibit their highest densities (Connell,
149 1970; Navarrete, 1996; Spight, 1981). Both species consume the same variety of prey
150 taxa, including mussels, barnacles, limpets, and littorine snails (Palmer, 1984; Spight,
151 1981). Intertidal whelks like these two species are particularly interesting in the context
152 of functional responses because a key experiment by Katz (1985) involving the Atlantic
153 whelk, *N. lapillus*, has been interpreted by both sides of the debate in support of their
154 arguments (Abrams, 1994; Akçakaya *et al.*, 1995).

155 Whelk densities are typically highest in patches within the mussel bed where mussels
156 have been removed by wave-induced disturbance (Plate 1; Navarrete, 1996). Patches large
157 enough not to be encroached by the surrounding mussel bed undergo a semi-deterministic

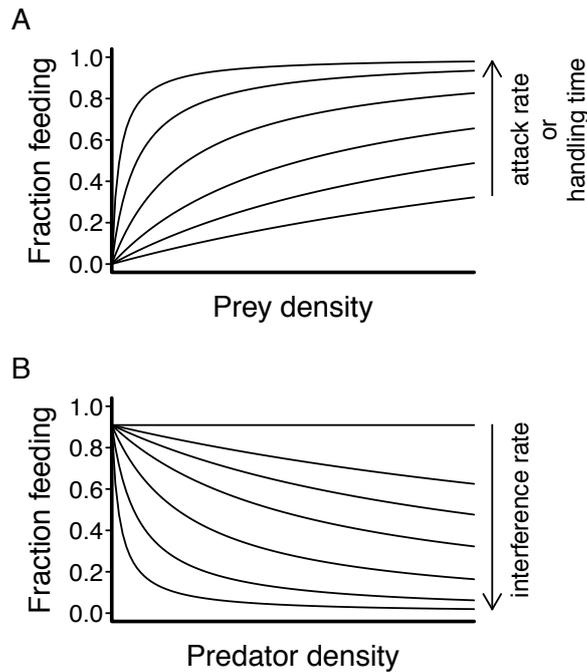


Figure 1: The probability that an individual predator feeding with a type II or Beddington-DeAngelis functional response will be observed in the process of feeding at any point in time (A) increases the higher its attack rate, the longer its handling time, and the more abundant its prey species is (eqn. 2), and (B) decreases with stronger intra- or inter-specific interference among predator individuals (eqn. 3). 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.

158 trajectory of recovery (Berlow, 1997; Levin & Paine, 1974; Wootton, 2002), being first colo-
159 nized by diatoms and algae, then acorn barnacles (*Balanus glandula* and some *Chthamalus*
160 *dalli*), then *Mytilus trossulus* mussels, then *Pollicipes polymerus* gooseneck barnacles, be-
161 fore eventually returning to being dominated by the larger, mussel-bed forming species
162 *Mytilus californianus*. Slow-growing *Semibalanus cariosus* barnacles initiate recruitment
163 in low numbers with the other acorn barnacles but achieve notable densities only at the
164 later stages of succession. At our study site (Yachats, Oregon, 44.3°N, -124.1°W), whelks,
165 limpets (*Lottia asmi*, *L. digitalis* and *L. pelta*) and littorines (*Littorina sitkana*) are present
166 throughout succession but their abundances vary considerably from patch-to-patch and
167 over time.

168 Unmanipulated patches

169 To quantify attack rates and predator dependence over the natural range of variation in
170 predator and prey densities, we first applied the observational approach to 10 naturally-
171 formed unmanipulated patches. Patches were chosen haphazardly and varied in size (0.8 –
172 5.8 m², $\bar{x} = 2.4 \pm 1.4$ sd) and successional age and thus in species composition, both in terms
173 of absolute and relative species abundances. Species abundances were estimated in each
174 patch using three randomly placed quadrats (25 x 35 cm). Low tide feeding surveys were
175 performed in each patch by systematically inspecting and measuring all whelks (± 1 mm)
176 and noting prey identity and prey size when individuals were feeding (i.e. in the process

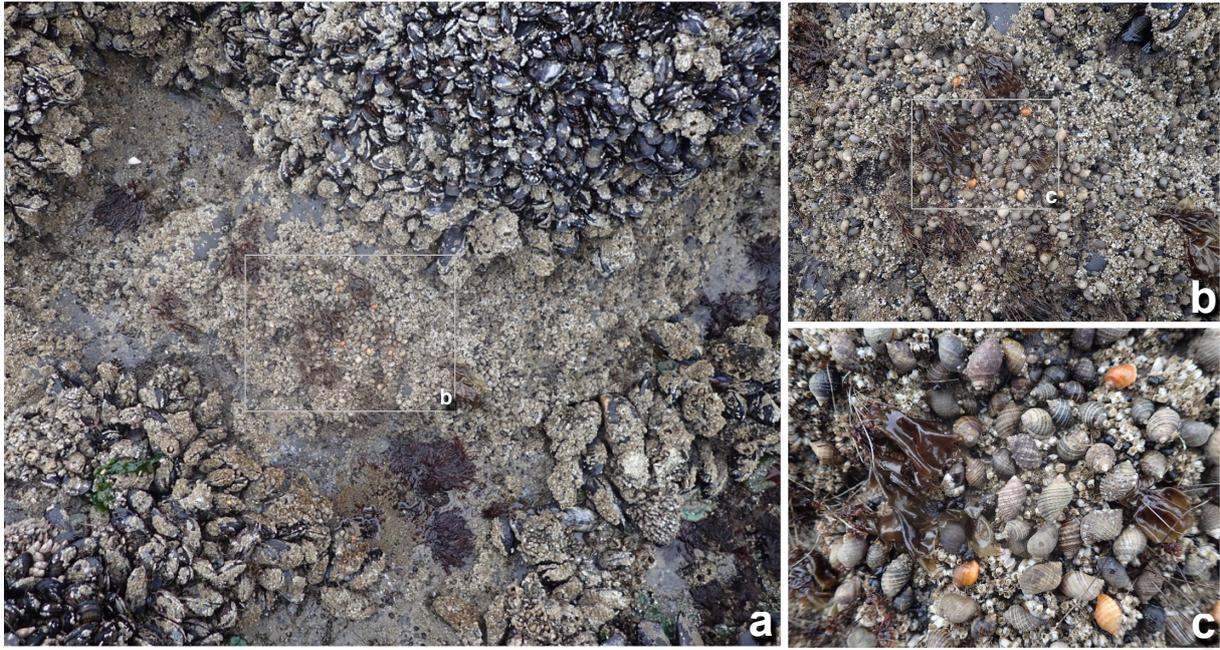


Plate 1: The predatory whelks *Nucella ostrina* and *N. canaliculata* co-occur and can reach extremely high densities in the wave-disturbed patches of a mussel bed.

177 of drilling, prying or consuming a prey item).

178 **Caging experiment**

179 We used a manipulative caging experiment to assess predator dependence over a range
180 of predator densities exceeding that observed in the natural patches, as is typically done
181 in manipulative functional response experiments. Fifteen stainless steel cages (25 x 35
182 cm) were placed in a single large patch of a low-diversity successional age dominated
183 by a homogeneous cover of *Balanus glandula* barnacles. Each cage was photographed to
184 determine prey abundances, then received between 5 and 160 *Nucella ostrina* (11 - 16 mm
185 shell length). Feeding surveys of each cage were performed on two subsequent occasions,
186 2 and 4 weeks later.

187 **Manipulated patches**

188 Finally, to determine whether predator dependence could be experimentally altered at the
189 patch scale, we combined surveys of naturally-formed patches with a manipulation of their
190 whelk densities. The experiment was performed in 9 haphazardly chosen patches of variable
191 successional age and consisted of five steps: (i) an estimation of species abundances using
192 three haphazardly located quadrats (25 x 35 cm); (ii) a first systematic feeding survey
193 of the whelks, (iii) a manipulation of whelk densities, and, after four subsequent high
194 tides, (iv) a re-estimation of whelk densities using three quadrats placed in the same
195 approximate locations as before, and (v) a second systematic feeding survey of the whelks.
196 The manipulation of whelk densities entailed either a decrease or increase (0.07 to 3.3
197 times their pre-manipulation density), or a control treatment in which all whelks were
198 returned (Fig. S2). Three patches were haphazardly assigned to each treatment. The
199 whelks in all treatments were picked up either during or immediately after the first feeding

200 survey to avoid confounding treatments by the potential effects of whelk handling. Prior
201 observations indicated that a two-day recovery period was ample time for whelks to regain
202 normal activity but insufficient for whelks to have an appreciable effect on prey densities.

203 Model-fitting and comparison

204 Focusing on the feeding observations of *Nucella ostrina*, we estimated the parameters and
205 evaluated the relative performance of five types of multispecies functional response models:
206 type II, ratio-dependent, Beddington-DeAngelis, Hassell-Varley, and the non-functional
207 ‘null’ model. We considered two Beddington-DeAngelis models for the unmanipulated and
208 the manipulated patches in which both *Nucella ostrina* and *N. canaliculata* occurred, one
209 including only an intraspecific predator effect and one including both intra- and inter-
210 specific predator effects; only *N. ostrina* was present in the caging experiment.

211 Our fitting of the models treated the surveys of each case (i.e. the caging experiment,
212 the unmanipulated patches, and the manipulated patches) as independent and identically-
213 distributed, describing feeding rates for each case by one set of attack- and interference
214 rate estimates across all surveys. We also relaxed this assumption for the manipulated
215 patches where two surveys of the same patch had been performed by additionally fitting
216 all models with patch-specific parameters.

217 Model-fitting involved describing the observed feeding counts by a multinomial dis-
218 tribution whose probabilities were determined by species densities and handling times
219 according to a given functional response model. For the patches, a species’ density was
220 estimated by its mean abundance (m^{-2}), averaged over replicate quadrats. A species’ han-
221 dling time was estimated by its mean expected handling time (in hours), averaged over
222 the expected handling times of its feeding observations. The expected handling time of a
223 given feeding observation was estimated from its measurements of whelk- and prey size and
224 ambient temperature (the average of water and air over the month in which surveys were
225 performed) using regression coefficients derived from laboratory experiments manipulating
226 these variables for *Haustrum scobina*, a New Zealand whelk species with ecologically equiv-
227 alent characteristics and prey (Novak, 2010, 2013). In fitting the models we constrained
228 all attack rates as well as the interference rate parameter of the Hassell-Varley model to
229 be positive. The interference rates of the Beddington-DeAngelis models remained uncon-
230 strained. Convergence was reached in all cases by setting the attack rate starting values
231 to reflect the appropriate analytical solutions of the type II or ratio-dependent functional
232 response models (eqns. 1 and S5). Model performance was evaluated by AIC_c that con-
233 verges on the AIC goodness-of-fit statistic as sample size increases (Burnham & Anderson,
234 2004).

235 Results

236 Variation in diet and species abundances

237 We observed *Nucella ostrina* feeding on 11 and 10 species, including itself, in the unmanip-
238 ulated and manipulated patches, respectively. Only 5 of these species were observed being
239 fed upon in the cages, despite the presence of all potential prey and sufficient sampling
240 effort to detect them (Fig. S1). The total number of feeding observations per prey species
241 varied from 2 (*Lotta digitalis*) to 1,089 (*Balanus glandula*), with 14.8% of the 13,131 to-
242 tal examined *N. ostrina* whelks found to be feeding. Six whelks were observed drilling a

243 conspecific individual. *N. ostrina*'s densities ranged between 133 - 1143 m^{-2} in the un-
244 manipulated patches, 57 - 1,829 m^{-2} in the cages, and 80 - 1,939 m^{-2} in the manipulated
245 patches prior to manipulation; post-manipulation densities ranged from 80 - 2,518 m^{-2}
246 (Fig. S2). *N. canaliculata*'s densities were consistently and considerably lower (Fig. S2),
247 with only a 128 total feeding observations (14.2% of all examined individuals) being made
248 in the subset of patches in which they were present.

249 Patches represented early to late successional ages and thus varied considerably in
250 their prey abundances. In particular, the mean densities of *Mytilus trossulus* mussels and
251 *Balanus glandula* barnacles, representing *Nucella ostrina*'s primary prey (both in terms of
252 diet frequency and subsequently estimated feeding rates), respectively varied between 3.8-
253 7,295 m^{-2} and 240 - 114,987 m^{-2} . There was no discernible relationship between whelk
254 and prey abundances in the unmanipulated patches (Fig. S3). A positive relationship
255 between *N. ostrina* and *Balanus glandula* densities observed in the manipulated patches
256 prior to manipulation was broken by the manipulation of *N. ostrina* densities (Fig. S3).
257 Patches consequently varied substantially both in the relative ratio of mussels to barnacles
258 and in the relative ratio of whelks to prey (Fig. 2A,C). In contrast, the experimental cages,
259 which were located within a single early successional age barnacle-dominated patch, varied
260 little in their absolute and relative prey abundances (Figs. 2B and S4). The larger-than-
261 natural range of whelk to prey ratios in the cages was therefore due to the manipulation
262 of *N. ostrina* densities. In fitting the alternative functional response models to the data,
263 one prey species, the burrowing mussel *Adula californiensis*, on which two whelks were
264 observed feeding in the unmanipulated patches, was excluded prior to analysis because it
265 was not detected in any abundance survey.

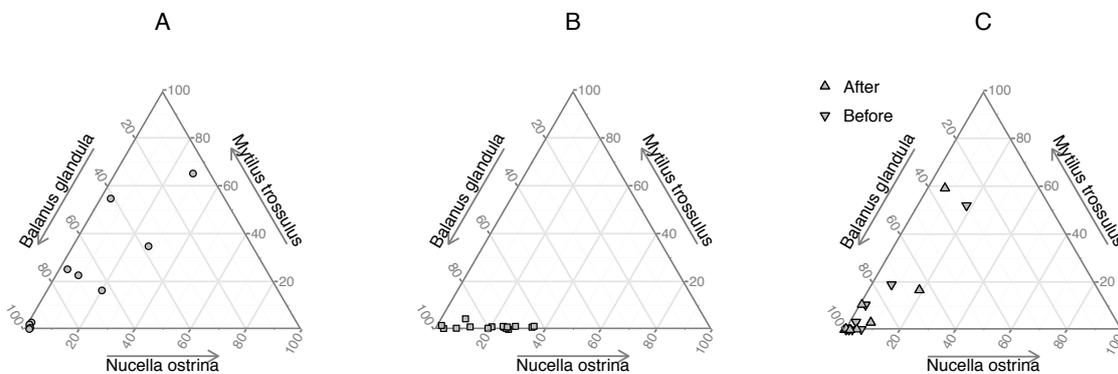


Figure 2: The relative abundance of *Nucella ostrina* and its two primary prey species, *Mytilus trossulus* mussels and *Balanus glandula* acorn barnacles, as illustrated by their proportional densities in the (A) unmanipulated patches, (B) experimental cages, and (C) manipulated patches before and after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

266 Model-performance and parameter estimates

267 The Beddington-DeAngelis functional response entailing only intraspecific predator depen-
268 dence was unambiguously the best-performing model for the unmanipulated patches; its
269 AIC_c-weight, reflecting the conditional probability of it being the best-performing model,

Table 1: Comparison by AICc of all 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). 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	AICc	Δ AICc	df	weight
A. Unmanipulated Patches				
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
Dens. indep.	978.4	248.1	10	<0.001
Ratio	1088.0	357.7	10	<0.001
B. Caging Experiment				
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
Dens. indep.	174.5	27.1	5	<0.001
Ratio	178.6	31.2	5	<0.001
C. Manipulated Patches				
BD (intra)*	124.4	0	44	>0.999
HV*	154.7	30.3	44	<0.001
Dens indep.*	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
Dens. indep.	912.4	788	10	<0.001

270 exceeded 0.999 (Table 1A). The patch-specific version of the same model outperformed all
 271 others with equally unambiguous evidence for the manipulated patches (Table 1C). Only
 272 for the caging experiment did model comparisons fail to provide clear support for a partic-
 273 ular model, with the Type II, the Beddington-DeAngelis, and the Hassell-Varley models all
 274 exhibiting AICc values within 4 units of each other (Table 1B). Nevertheless, in all three
 275 cases the ratio-dependent and density-independent models performed substantially worse
 276 than all other models.

277 As estimated assuming the Beddington-DeAngelis model, *Nucella ostrina*'s prey-specific
 278 per capita attack rates varied by up to 3 orders-of-magnitude within each of the three cases
 279 (Fig. 3A). Attack rates varied over almost 5 orders-of-magnitude across the three cases
 280 overall. The range of variation in attack rates was similar in the two sets of patches where

281 *N. ostrina* was observed consuming 10 to 11 species. In the cages, by contrast, the subset
 282 of five prey species on which *N. ostrina* was observed feeding evidenced attack rates that
 283 were 4 to 1004 times higher than in either set of patches. There was no rank-order corre-
 284 lation between the attack rates of the three cases (Table S10), with a similar number of
 285 prey evidencing attack rates that were relatively higher versus lower in one case compared
 286 to another. In contrast, although *Nucella ostrina*'s prey-specific feeding rates also varied
 287 over 3 orders-of-magnitude, these were of similar magnitude and positively rank-correlated
 288 across the three cases (Fig. 3B, Spearman's $\rho \geq 0.7$, Table S10).

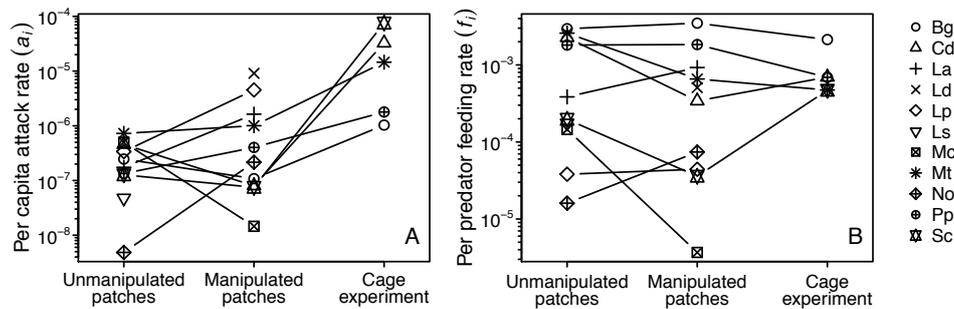


Figure 3: *Nucella ostrina*'s prey-specific per capita attack rates and per predator feeding rates. (A) Per capita attack rate estimates assume a Beddington-DeAngelis functional response with only intraspecific predator effects, and evidence no rank-order correlation between the three cases (Table S10). (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.

289 Estimates for the per capita magnitude of intraspecific predator dependence in *Nucella*
 290 *ostrina* were larger for the two sets of patches than for the cages (Fig. 4A), consistent
 291 with the poorer discrimination among models by AIC_c for the cages (Table 1). However,
 292 while γ estimates were positive for both the cages and the manipulated patches (indicating
 293 interference effects), the estimate in the unmanipulated patches was negative (indicating a
 294 facilitative effect). The patch-specific γ estimates for the manipulated patches also exhib-
 295 ited both positive and negative values, with four of the five positive (interference) estimates
 296 exhibiting considerably higher magnitudes than the other estimates (Fig. 4B).

297 Discussion

298 Two fundamental yet often conflated questions have contributed to sustaining the debate
 299 over predator functional responses: How to best represent predator-prey interactions in
 300 models of population dynamics? And, what are the mechanistic relationships between
 301 predator feeding rates and species abundances? The importance of these questions tran-
 302 scends predator-prey interactions (Abrams, 2015; Perretti *et al.*, 2013). Indeed, all methods
 303 for quantifying the strengths and hence importance of species interactions make assump-
 304 tions regarding their functional form (Novak *et al.*, 2016; Vázquez *et al.*, 2015; Wootton
 305 & Emmerson, 2005). Recognizing that the answers to these two questions may not be the
 306 same will be key to future progress. For example, predator dependence may be sufficiently
 307 weak that it has no appreciable effect over the range of species abundances that actu-

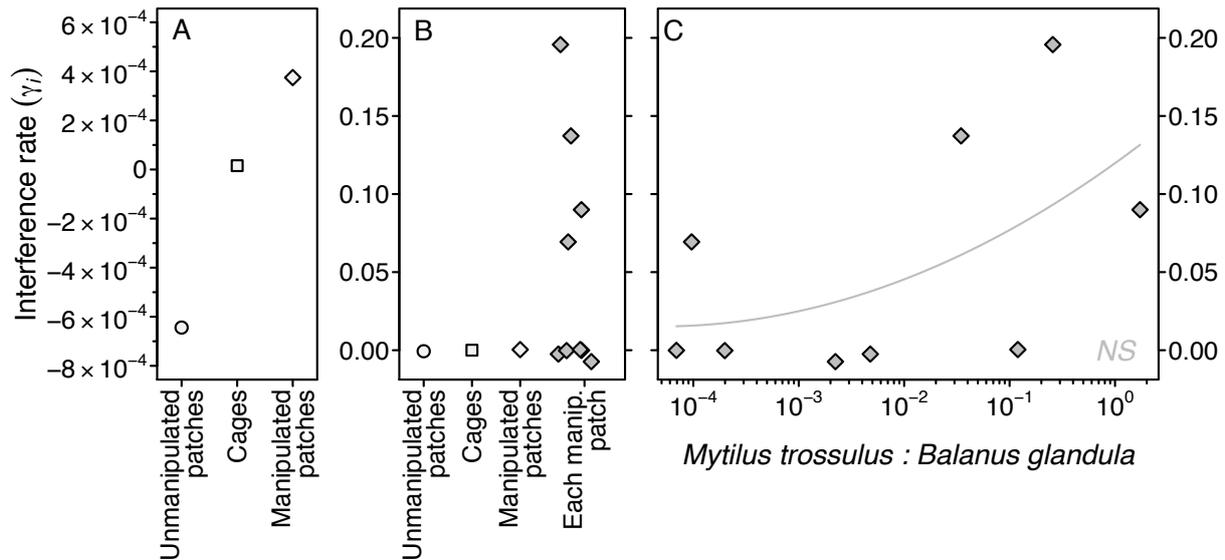


Figure 4: *Nucella ostrina*'s intraspecific predator effects as estimated assuming a Beddington-DeAngelis functional response in (A) each of the three cases (i.e. the unmanipulated patches, caging experiment, and manipulated patches) and (B) each case compared to at the patch-specific scale in the manipulated patches. Positive values indicate interference effects while negative values indicate mutualistic effects. (C) Patch-specific predator effect estimates versus 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 different y-axis scales in A versus B and C.

308 ally occur in nature's species-rich communities, despite being discernible in manipulative
 309 experiments (Fussmann *et al.*, 2005).

310 Strong evidence for weak predator dependence

311 Our study indicates that predator dependence as encapsulated by Beddington-DeAngelis
 312 model characterizes *Nucella ostrina*'s functional response the best, and that its effects are
 313 discernible over the species abundances and diversity of prey that this generalist predator
 314 experiences in the field. The per capita strength of predator dependence was nonetheless
 315 weak. This was most clearly evidenced by the relative performance of the next-best prey-
 316 dependent type II model (Table 1), and by the point estimates for the interference-strength
 317 parameter of the Hassell-Varley model ($m \leq 3.28 \cdot 10^{-5}$ in all three cases, where $m =$
 318 0 reflects complete prey dependence, Tables S2 - S4). In contrast, the ratio-dependent
 319 model, which has seen more theoretical treatment than any other predator-dependent
 320 model (Arditi & Ginzburg, 2012), was consistently among the worst-performing models.
 321 In two of three cases it performed even more poorly than the model which assumed feeding
 322 rates to be independent of species abundances altogether (Table 1). Our study thereby
 323 distinguishes itself in that most previous studies have dichotomously concluded functional
 324 responses to be best described by either a prey-dependent or the ratio-dependent model,
 325 despite general recognition that the truth is somewhere in between (Abrams, 2015; Abrams
 326 & Ginzburg, 2000; Arditi & Ginzburg, 2012).

327 Surprisingly, our analysis inferred no effect of *Nucella canaliculata* on *N. ostrina*'s

328 feeding rates, despite their seeming ecological similarities. This may have been due to
329 insufficient statistical power associated with low replication ($n \leq 10$ patches) and the
330 relatively low variation seen in *N. canaliculata*'s abundances (Fig. S2); the Beddington-
331 DeAngelis model including both inter- and intraspecific predator effects did perform best
332 in the two sets of patches when model performance was evaluated by AIC rather than AIC_c
333 (Table S11). However, an implicit benefit of the observational framework is that its focus
334 on the fraction of feeding individuals makes it most sensitive to the effects of predator
335 dependence at low predator densities, where a doubling of predator numbers has a larger
336 effect on per individual feeding rates than it does at high predator densities (Fig. 1B).
337 This differs from the approach of traditional functional response experiments where the
338 largest and thus most easily estimated rates of overall prey removal occur at high predator
339 densities. Therefore, *N. canaliculata*'s low densities should not have been an issue. Our
340 results therefore suggest that the interaction between the two whelk species is primarily
341 one of indirect effects mediated by prey exploitation, rather than representing a significant
342 interaction modification of feeding rates (Kéfi *et al.*, 2012; Spight, 1981).

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

350 One explanation for the experiment's inability to discriminate among models more
351 clearly was that the fraction of feeding individuals will not have been estimated as reliably
352 in the low predator density cages. Given the dimensions of a cage, the number of whelks
353 in the lowest density cage was only five, for example. Thus the probability of observing
354 all or none of the individuals feeding at any given time was high regardless of their true
355 mean feeding rate. This issue will have been alleviated by our use of repeated cage surveys
356 ($n = 30$ surveys), and was altogether avoided for the much larger natural patches that each
357 contained many more whelks in total.

358 A more likely explanation for the weak expression of predator dependence in the caging
359 experiment is that the cages, or their placement within an early successional age patch
360 that was dominated by a single barnacle species, altered whelk foraging behavior from that
361 exhibited across the sets of surveyed patches more generally. This interpretation challenges
362 the concern that such more traditional functional response experiments involving isolated
363 predator-prey pairs could be favoring the detection of predator dependence by selecting for
364 and magnifying the strength of strong predator-prey interactions (Abrams, 2015). However,
365 the results of our analysis are also consistent with this concern in that *Nucella ostrina*'s
366 per capita attack rates were substantially higher in the cages (Fig. 3A). Indeed, the
367 observation that the highest prey-specific feeding rates decreased while the lowest prey-
368 specific feeding rates increased in the cages relative to the patches, even as their overall
369 rank-order remained relatively consistent across the three cases (Fig. 3B), suggests that
370 the caged whelks altered their foraging strategy to compensate for the reduced breadth of
371 their diet.

372 **Prey-specific predator dependence**

373 While further experiments involving generalist predators will be needed to determine how
374 diet breadth itself can affect the strength of predator dependence, a likely feature dis-

375 tinguishing the functional responses of generalist and specialist predators is the variable
376 propensity of a generalist's different prey species to elicit predator dependence. For whelks
377 in particular, predator dependence will have been driven by a number of mechanisms that
378 vary by prey identity and differ in their qualitative nature.

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

395 Much less considered in the debate over functional responses is that predator density
396 can also have positive facilitative effects on feeding rates, even in the absence of cooperative
397 group hunting. This omission persists despite the longstanding awareness of the synergistic
398 effects between predator species (Sih *et al.*, 1998). For whelks, a potentially common
399 mechanism for facilitative effects is the feeding-induced release of prey chemical cues. That
400 this mechanism can be prey-specific has recently been demonstrated by the characterization
401 of a cuticular glycoprotein in *Balanus glandula* that acts as a potent stimulant for whelk
402 feeding, the nature of which is specific to acorn barnacles (Zimmer *et al.*, 2016).

403 If both facilitative and interference-based mechanisms of predator dependence exist
404 and are dependent upon prey identity, then, for generalists, both the strength and net
405 qualitative nature of predator dependence should depend on community structure. This
406 appears to have been the case in our study, with γ estimates for the Beddington-DeAngelis
407 model indicating (1) net interference in the manipulated patches where *Mytilus trossulus*
408 mussels tended to be more common, (2) weaker interference in the cages where *Balanus*
409 *glandula* barnacles were dominant, and (3) net facilitation in the unmanipulated patches
410 where a second barnacle species tended to be more common (Table 1, Figs. 2 and S4).
411 Further support is suggested by our patch-specific analysis of the manipulated patches, with
412 γ estimates tending to increase with the ratio of available mussels and barnacles (Fig. 4C).
413 Future experiments manipulating community structure directly will be needed to determine
414 whether such prey-specific influences of community structure tend to be idiosyncratic or
415 conform to useful categorizations.

416 Conclusions

417 That many prey-specific mechanisms of predator dependence are likely to occur in the
418 functional responses of generalist predators indicates that additional, more complex mod-
419 els will be useful in characterizing the species interactions of nature's species-rich food
420 webs. Many more such models, including those that relax the assumptions of predator ho-
421 mogeneity and the constancy of per capita rates (e.g., Baudrot *et al.*, 2016; Chesson, 1984;

422 Murdoch & Oaten, 1975), should become empirically accessible with the observational
423 framework, particularly when applied in combination with experimental manipulations.
424 Additional matters of ‘instantism’ in the parameterization of dynamical population mod-
425 els that have plagued the interpretation of traditional functional response and interaction
426 strength experiments (see Fussmann *et al.*, 2007; Jensen *et al.*, 2007; Novak & Wootton,
427 2010) should also be assuaged by the now logistically feasible repeated application of the
428 observational approach over the biologically appropriate time-scales of a focal predator’s
429 numerical response.

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