

Consumer functional responses under intra- and inter-specific interference competition

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ABSTRACT

Mechanistic models of population, community and ecosystem dynamics require the mathematical description of trophic interactions in the form of functional response equations. There is a wealth of such equations developed to incorporate the effects of multitude forms of foraging behaviour including intra-specific interference competition. However, there has been no attempt to include inter-specific behaviours beyond the obvious consumer–resource relationship, and thus, mechanistic models of communities and ecosystems remain limited in their incorporation of individual behaviour. In this paper we extend existing functional response models to account for both intra- and inter-specific interference behaviours. Together with response surface experiments, these can be used to investigate the role of both types of interference for a given species' resource acquisition efficiency. We illustrate this with data from foraging trials of guppies *Poecilia reticulata* in the presence and absence of a competitor species, Hart's killifish *Rivulus hartii*. Our results show that in the studied example, intra-specific interference is important and stronger than inter-specific competition.

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1. Introduction

Resource competition plays a central role in the understanding of ecological processes as diverse and important as natural selection, population regulation and community dynamics (Begon et al., 1996; Tilman, 1982). As a consequence, it has been the subject of a large number of field experiments (reviewed by Connell, 1983; Sih et al., 1985) and extensive analyses (e.g. Gurevitch et al., 1992). Historically, the field has been dominated by phenomenological approaches that assess community, population or life-history patterns that result from the addition of inter- or intra-specific competitors (Inouye, 2001). An alternative approach is to explicitly investigate the competitive mechanisms behind the observed patterns, such as resource acquisition or interference, to predict the consequences of competition.

Functional response equations are a key component of any mechanistic model describing interactions between consumers and their resources. They model the rate of resource consumption as a function of resource density (Holling, 1959; Solomon, 1949). They can be broadly classified in two categories: consumer-independent

and consumer-dependent (Abrams and Ginzburg, 2000). The first type of models (reviewed by Jeschke et al., 2002) assumes that, for a given density of resources, their *per capita* consumption by consumers is independent of consumer numbers. It is important to note that this does not mean that they assume no competition. When embedded in a dynamic consumer–resource model, resource density will decrease as consumer numbers increase, decreasing average consumption as they move down the resource gradient of the functional response. Such a scenario represents exploitative competition for resources, where consumers only affect each other through the consumption of a common resource. In contrast, consumer-dependent models (reviewed in Jeschke et al., 2002; Skalski and Gilliam, 2001) incorporate a direct effect of consumer density in the functional response. This scenario mimics interference competition, where individuals directly affect each other's efficiency of resource consumption. The importance of distinguishing between the two sets of models lies in the fact that exploitative and interference competition can lead to very different predictions regarding evolution (Ishii and Shimada, 2008; Toquenaga, 1993), and community dynamics (Lomnicki, 2009; Abrams and Ginzburg, 2000; Kuang, 2002). Moreover, the co-evolution of character displacement among competitor species depends on the relative intensities of exploitative and interference competition, as well as the costs of the latter (Grether et al., 2009).

The importance of intra-specific interference between foraging consumers can be assessed by integrating response-surface exper-

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iments and consumer-dependent functional equations (Kratina et al., 2009). Response surface experiments consist of competition trials where consumer and resource density are manipulated and related to a response variable of interest (Inouye, 2001). In this case, the response in question is the resource intake rate by a focal consumer. The results are then used to parameterize consumer-dependent functional response equations and evaluate the magnitude and significance of the parameters associated with consumer density.

So far, only one-species functional response models exist. These allow for the modeling of inter-specific competition for resources as long as this is a mere result of resource depletion. Inter-specific competitors, however, can also be an important source of interference (Beddington, 1975; Crowley and Martin, 1989). When explaining community composition or ecosystem functioning, the type of competition, again, matters (Ishii and Shimada, 2008). However, there is currently no functional-response equation that incorporates interference between species and allows for a mechanistic modeling of the process.

In this paper, we review current consumer-dependent functional response models (Beddington, 1975; Crowley and Martin, 1989; DeAngelis et al., 1975) and extend them to incorporate inter-specific as well as intra-specific interference. We subsequently illustrate their parameterization with data from a laboratory functional-response experiment on a system of two competing stream fish species: the Trinidadian guppy *Poecilia reticulata* and Hart's killifish *Rivulus hartii*. By fitting a variety of alternative models and parameterizations representing different assumptions on the mode and intensity of competition, we will assess the relative importance of intra- and inter-specific competition as well as make inferences on the nature of the competition.

2. Incorporating interference in the functional response

The rate of consumption of resources (or prey) by an individual consumer (or predator) as a function of resource density has been traditionally modelled according to one of three response curves described by Holling (1959). They are commonly known as type I, II and III functional responses, and follow, respectively, a linear, saturating or sigmoidal shape. With some notable exceptions (e.g. Kempf et al., 2008; Sarnelle and Wilson, 2008), most organisms studied with a density-independent model have been shown to have a type II functional response, instead of a type I or III, which can be written as:

$$f(N) = \frac{aN}{1 + ahN}. \quad (1)$$

Here, N is the density of resources, a is the attack rate and h is the handling time. The attack rate a (or volume-specific encounter rate between consumer and resource) is equivalent to the inverse of the average search time between successful resource captures. The handling time h represents the time spent by a consumer handling the resource before he can continue the search. Different biological factors potentially affecting the handling time include digestion, killing of the prey or simply the time taken to ingest the prey. Holling's equation can be derived by assuming that a predation event consists of two episodes or states: searching for and handling of resources (see Appendix A for details). While searching time diminishes with an increase in resource density, handling time is assumed to be constant, thus limiting the acceleration of intake as resource density increases.

Holling's original equations do not incorporate consumer interference, but type II models have been extended to incorporate it. These can be derived by incorporating a third episode (or state) in the resource consumption process: interference time. During this time, which increases with consumer density, individuals cannot

search for resources. Two main models have been derived depending on whether interference can occur at any time or only during the search phase.

If interference can only be incurred by searching competitors, the result is a Beddington–DeAngelis (BD) functional response (Beddington, 1975; DeAngelis et al., 1975; Huisman and De Boer, 1997), which reads:

$$f(N, F) = \frac{1}{1 + ahN + cF}, \quad (2)$$

where F is the density of consumers (henceforth considered as the focal species) and c is the interference coefficient, which can be decomposed into the product of two parameters: the *per capita* encounter rate between consumers and the duration of interference (respectively called b and d in Appendix A). Since the two parameters are not estimable independently in our empirical example, we do not decompose c in its two components. Using the same notation but assuming that handling competitors can also interfere, we get a Crowley–Martin (CM) model (Crowley and Martin, 1989):

$$f(N, F) = \frac{1}{(1 + ahN) \cdot (1 + cF)} \quad (3)$$

In order to extend either of the two single-consumer models, we need to assume a fourth state representing the time wasted in inter-specific competition. Therefore, the foraging time of a focal consumer can be split in four possible states: searching, handling, intra-specific interference and inter-specific interference. Appendix A contains the formal derivations of the two-consumer BD and CM models. These derivations are made without taking into account any spatial effect for predation (Cosner et al., 1999). The resulting equations are intuitively simple, merely involving the splitting of the interference component of the equation into two additive components representing the two types of competitor. The BD extension can be written as:

$$f(N, F, C) = \frac{aN}{1 + ahN + cF + c'C} \quad (4)$$

Here, C represents the number of the competitor consumer species, while c and c' represent the “time” wasted in intra- and inter-specific competition, respectively.

Similarly, the extension to the CM model can be written as:

$$f(N, F, C) = \frac{aN}{(1 + ahN) \cdot (1 + cF + c'C)} \quad (5)$$

The relative importance of resource competition, intra-specific interference competition and inter-specific interference competition can be evaluated from the estimates of ah , c , and c' respectively. Although the realised strength of either mechanism will depend on the actual ecological conditions (i.e. the relative density of resources, conspecifics and heterospecific competitors) these three indexes indicate the sensitivity of resource acquisition to the three behavioural mechanisms.

3. The guppy-killifish system

We illustrate the ideas and analyses proposed in this paper using a system of two stream fish: the guppy *Poecilia reticulata* and Hart's killifish *Rivulus hartii*, from the Northern Range Mountains of Trinidad, in the Southern Caribbean. Guppies and killifish co-exist in two types of habitat separated by barrier waterfalls and differing in their predation regime. Upstream from the barrier, they represent the only two fish species, while downstream they share habitat with bigger predatory fish such as the pike cichlid (*Crenicichla alta*) or the wolf-fish (*Hoplias malabricus*), which are known to consume adult guppies (Gilliam et al., 1993; Reznick and Endler, 1982). These two types of habitat are commonly referred to as

high predation (HP) and low predation (LP). It has been hypothesized that killifish and guppies may feed on each other's larvae (Reznick, 1982; Reznick and Endler, 1982). The differences between the two habitats in predation regime and other environmental factors have major consequences to the life-history of the guppies (Reznick, 1982; Reznick and Endler, 1982) and killifish (Walsh and Reznick, 2008, 2009). Throughout their colonization, guppies have transitioned multiple times from HP to LP environments, repeatedly evolving lower growth rates, reduced reproductive allocation, delayed maturity and bigger offspring size, among other traits (Reznick, 1989; Reznick and Bryga, 1996). When artificially translocated to a low predation environment, high predation guppies have shown to evolve these traits in a very small number of generations (Reznick et al., 1990, 1997).

Although there is a good accumulation of evidence for the importance of mortality in guppy life-history evolution, the mechanism through which mortality exerts a selection pressure is not yet well understood. It remains unclear whether the evolution from high to low predation phenotype is a direct individual response to lower mortality or a response to increased competition given higher population densities in populations with reduced mortality. The latter hypothesis is known as the indirect effects of mortality hypothesis, and has found support in some laboratory experiments (Bashey, 2008). Low predation streams, indeed, have higher densities of both guppies and Hart's killifish than high predation populations (Gilliam et al., 1993). If competition, whether intra- or inter-specific, is an important selective force in low predation guppies, predictive models of life-history evolution must incorporate the link between individual life-histories, population dynamics and resource availability. Understanding this link relies on the description of the appropriate functional response.

4. Materials and methods

4.1. Functional response experiments

We performed a total of 150 feeding trials on a total of 19 individual focal guppies (9 from HP and 10 from LP) under three competition treatments: (1) no competition, where the focal guppy was alone; (2) intra-specific competition, where a similar-sized guppy was placed in the same feeding tank; and (3) inter-specific competition, where a similar-sized killifish was placed in the feeding tank. These treatments were crossed with fish origin (High Predation or Low Predation). We also performed 30 trials with a total of 10 individual killifish (4 from HP and 6 from LP) in order to estimate their attack rates a' . These trials followed the same protocol as the no-competition trials in guppies (i.e. the fish was left to forage alone) and had the same range of food density treatments.

Feeding trials were performed in a 10L tank with a simulated circular drift of 60L/h. We used mayflies (Family Ephemeroptera) that were dropped on the surface of the water as feeding items. Adult guppies and killifish are known to drift-feed in the wild, with drift invertebrates representing an important percentage of their diet (Zandona et al., in preparation). Wild mayflies between 0.25 and 1 mm were collected with drift-nets from streams in Trinidad and kept frozen, to be thawed before each experiment. To estimate the shape of the functional response, each treatment combination was repeated for five different resources densities: 1, 2, 3, 5 and 10 mayflies per tank (i.e. 0.1, 0.2, 0.3, 0.5 and 1 mayfly per litre). Resources densities were kept constant by immediately dropping a new item after one had been eaten.

We aimed at using each fish was used as focal individual for all the competition treatments and resource-levels in the experiment, allowing to partition the variation within and between individuals.

Due to escape mortality, this was not always possible and hence the design is unbalanced. However, given that we randomized the order of treatments and resource levels, the sample can be considered unbiased. Competitors for the competition treatments were randomly selected from the stock tank. When outside the experimental tank, guppies and killifish were housed together in 40L tanks, to avoid any artefact in the experiments due to the addition of an unfamiliar fish. For each experiment, individuals were placed in the experimental tank and allowed to habituate to observer presence for 10 min before an observation period of 10 min. During this period, mayflies were added to the tank and the number of feeding events were recorded. For each feeding event, a new larva was added in the tank. Repeated trials of same individuals were separated between 12 and 24 h. Standard lengths for all fish were measured after the experiment.

4.2. Model fitting

We assessed the importance of different mechanisms (inter-specific and intra-specific interference at different foraging phases) and variables (size, predation) on the functional response by fitting and comparing a series of alternative functional-response models to the data from the experiment. For all models, the response variable was the number of prey eaten in an interval of 10 min, explained by the functional response model. We fitted two types of models: Beddington–DeAngelis (Eq. (4)) and Crowley–Martin (Eq. (5)), which can be used to infer whether interference occurs only at the searching phase or also at the handling phase, respectively. All models are modifications of the basic BD and CM non-linear equations in which different parameters can be made null (e.g. $c=0$ implies no intra-specific interference), constant or linear combinations of the explanatory variables: size (whether absolute or relative to its competitor) or predation ecotype (HP or LP). To avoid false-positives due to multiple-testing, we reduced the set of models to a total of 26 models (see Table 1) that included biologically relevant combinations of variables (Burnham and Anderson, 2002).

For illustration purposes, we describe below the deterministic component of the complete model for a Beddington–DeAngelis response, with all possible explanatory variables.

$$E(Y|N, F, C) \sim \frac{aN}{1 + ahN + cF + c'C} \quad (6)$$

where coefficients a , h , c and c' are linear combinations of the following explanatory variables:

a , h ~ population (HP/LP) + focal fish size

c , c' ~ population (HP/LP) + focal fish size + size ratio between focal fish and competitor

Note that in the absence of competitors, the functional responses described by both Eqs. (4) (BD) and (5) (CM) reduce to a Holling type II curve (F and C are null) like in Eq. (1). The comparison between the no competition and intra-specific competition treatments allows for the estimation of the intra-specific interference coefficient c ($F=1/\text{volume}$ and $C=0$). The inter-specific competition treatment allows for the calculation of the inter-specific interference coefficient c' (with $F=0$ and $C=1/\text{volume}$).

We considered alternative random structures around the deterministic model described above. First, we considered three distributional assumptions for the residual errors: Poisson, Negative Binomial and Double Poisson. The negative binomial and double Poisson distributions allow for overdispersion (higher variance than mean). While in the negative binomial the variance increases with the mean, the double Poisson – a distribution from the double exponential family – models the variance independently

Table 1
Model selection of fitted functional response models for guppies.

Type ^a	Parameter dependencies ^b				AICc	Log-likelihood	Δ AICc	Weight
	<i>a</i>	<i>h</i>	<i>c</i>	<i>c'</i>				
CM	pop	size	1	1	631.52	308.26	0.00	0.40
CM	1	pop+size	1	1	632.32	308.66	0.80	0.27
CM	1	size	1	1	633.84	310.55	2.32	0.12
CM	size	pop	1	1	634.18	309.59	2.65	0.10
CM	1	pop	1	1	634.20	310.73	2.68	0.10
CM	1	1	1	1	643.06	316.27	11.54	<0.01
CM	1	1	pop	pop	643.86	314.43	12.34	<0.01
CM	1	1	ratio	ratio	647.52	316.26	16.00	<0.01
BD	pop	size	1	1	647.51	316.35	16.19	<0.01
BD	1	pop+size	1	1	645.80	316.45	16.38	<0.01
CM	pop+size	pop+size	pop+ratio+size		648.64	307.01	17.12	<0.01
BD	1	size	1	1	649.08	318.17	17.56	<0.01
BD	1	pop	1	1	649.55	318.40	18.03	<0.01
BD	size	pop	1	1	649.97	317.49	18.45	<0.01
CM	1	pop+size	$c=c'$		656.30	321.78	24.78	<0.01
CM	1	pop+size	1	0	656.52	321.89	24.99	<0.01
BD	1	1	1	1	657.54	323.51	26.02	<0.01
BD	1	1	pop	pop	658.73	321.86	27.21	<0.01
BD	1	pop+size	1	0	661.64	324.45	30.12	<0.01
BD	1	1	ratio	ratio	662.00	323.50	30.48	<0.01
BD	pop+size	pop+size	pop+ratio+size		665.79	315.59	34.27	<0.01
BD	1	pop+size	$c=c'$		670.43	328.85	38.91	<0.01
HII	1	pop+size	0	0	710.49	349.98	78.97	<0.01
CM	1	pop+size	0	1	712.66	349.96	81.14	<0.01
BD	1	pop+size	0	1	712.66	349.96	81.14	<0.01
HII	pop+size	0	0	0	839.89	415.27	207.37	<0.01

^a CM: Crowley–Martin; BD: Beddington–DeAngelis; HII: Holling type II (no interference).

^b pop: dependent on population (HP-LP); size: dependent on fish size; ratio: dependent on the relative size of the competitor and focal fish; 1: independent; 0: parameter omission.

of the mean (Efron, 1986). Second, since the same fish was used for all competition and resource density treatments, we also tested a hierarchical model that included focal individual as a random effect. We tested the random structure of the functional response using the full deterministic model outlined above, with all considered fixed effects included before selecting the fixed effects. These models were fit by Restricted Maximum Likelihood (REML) in order to avoid biases in the variance estimates (Zuur et al., 2009). The appropriate error structure was decided by comparison of their corrected Akaike Information Criteria (AICc, Burnham and Anderson, 2002). Once the error structure was decided with the full model, we fitted several combinations of fixed effects via Maximum Likelihood. Models were also compared by their AICc and the calculation of Akaike weights (Burnham and Anderson, 2002) in order to test for the importance of covariates and interference coefficients and perform model averaging when needed. The reason to follow a two-stage approach is two-fold. First, it is incorrect to compare AIC values calculated with REML with those using ML (Pinheiro and Bates, 2000; Zuur et al., 2009). Second, using a subset of fixed effects to test the error structure can lead to fixed-effect variance being spuriously absorbed by random effects (Zuur et al., 2009). All models were fit with package `gnlm` in program R (R Development Core Team, 2005). To check the robustness of our results to the choice of random effects, we repeated the selection of fixed effects given alternative error structures. Estimates of fixed effects and model weights did not change with the choice of random effects.

To estimate the product ah (for comparison with c and c') accounting for parameter uncertainty, we used Monte Carlo simulation. For that, we used a guppy size of 20 mm and the best model defining a and h (see Section 5, Eq. (6)). Parameter values for the equations were randomly drawn from normal distributions with the means and standard deviations estimated from the model fitting. The distribution for the index estimate is based on 10,000 simulations.

5. Results

AICc comparisons of our full mixed models with all the fixed terms indicate a double Poisson as the most likely error distribution, indicating data over-dispersion (Δ AICc = 13.4 between a double Poisson and a Poisson errors for the complete model) and a very high within-individual variation (i.e. individuals are not self-consistent and hence, individual identity is not predictive of its behaviour) that justifies the exclusion of individual identity as a random effect (Δ AICc = 2.4 between the fit with and without individual random effect for the complete model).

Table 1 shows the results of the model selection analysis for guppies. The first obvious result is that Crowley–Martin-type models are better supported by the data, with no Beddington–DeAngelis-type function receiving more than 0.01% of the information weight (Table 1). This suggests that interference between competitors is possible both during the attack and the handling phases of foraging; BD models only assume interference in the searching phase (i.e. a forager cannot be interfered with once it has captured the prey, see Section 2). A second consistent pattern is that all 14 best models (>99.9% of the AIC weight) include interference competition, both intra- and inter-specific. There is, however, very little support for either type of competition to be size or population dependent. The five most parsimonious models – those with 99.7% of cumulative weight and Δ AICc < 4 (Burnham and Anderson, 2002; Johnson and Omland, 2004) – differ in whether they include or not an effect of size and population on the attack rate and handling time (Table 1). Since no model had a weight superior to 95%, we used model averaging to get robust estimates of the parameters (Burnham and Anderson, 2002). Parameters of the averaged model are shown in Table 2. Data and curves for the average model are shown in Fig. 1.

Results for the *Rivulus*-only functional response (Table 3) are ambiguous with respect to the importance of population or size in attack rate or handling time but clearly support the addition of

Table 2
Model selection for fitted functional response models for killifish with no competitors.

Parameter dependencies		AIC _c	Log-likelihood	AAIC _c	Weight
<i>a</i>	<i>h</i>				
pop	size	178.51	84.45	0.00	0.35
1	pop+size	178.53	84.46	0.02	0.34
pop+size	1	180.07	85.24	1.56	0.16
size	pop	180.38	85.39	1.87	0.14
pop+size	pop+size	184.55	84.45	6.04	0.02
size	0	234.94	115.25	56.43	<0.0001
pop+size	0	236.72	114.90	58.21	<0.0001
pop	0	245.15	120.35	66.65	<0.0001

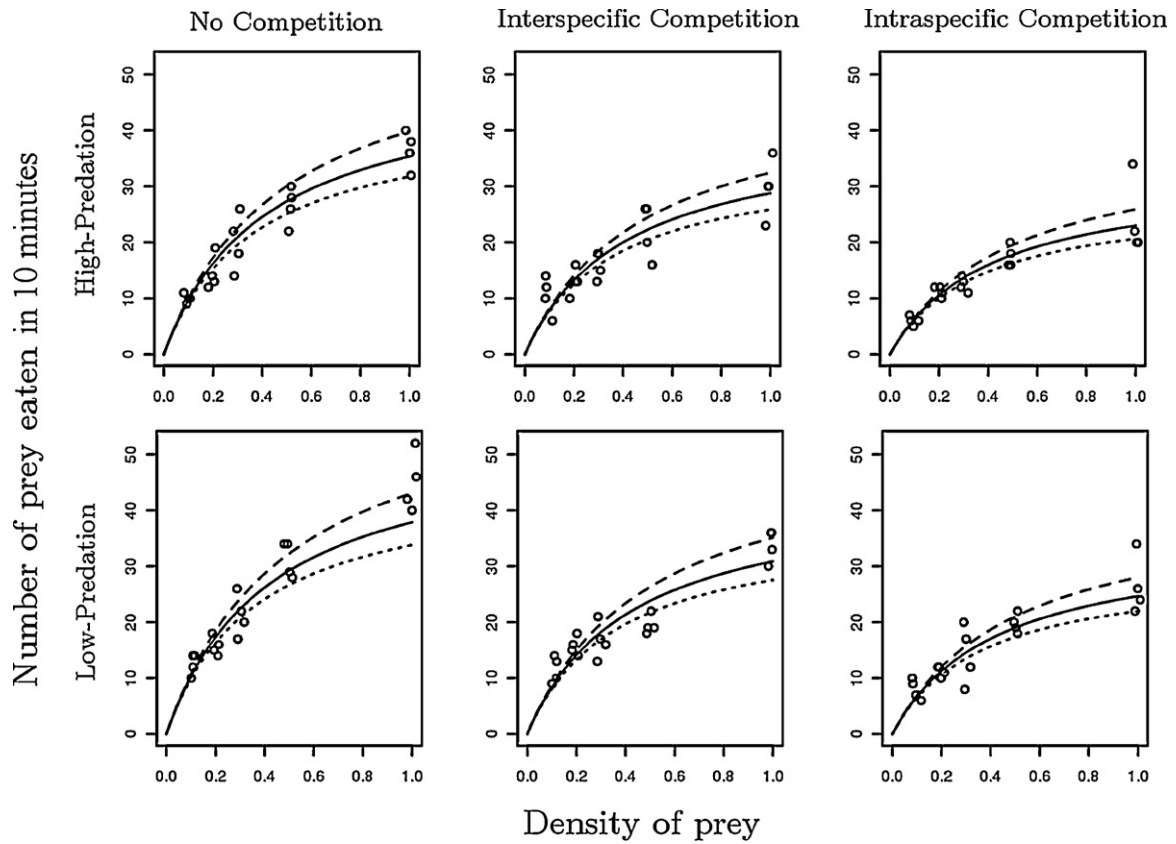


Fig. 1. Functional responses of guppies for the six treatment combinations. Number of resources items eaten during the 10 min of observations. Fitted lines represent the predictions of the best model for a fish of 18 mm (dotted), 20 mm (solid) and 22 mm (dashed) of standard length.

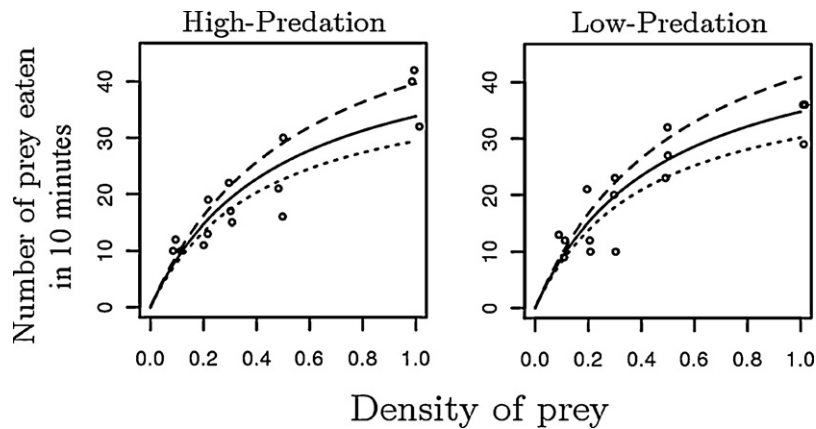


Fig. 2. Functional responses of high and low predation *Rivulus* killifish with no competition. Number of resources items eaten during the 10 min of observations. Fitted lines represent the predictions of the best model for a fish of 24 mm (dotted), 27 mm (solid) and 30 mm (dashed) of standard length.

Table 3
Parameter estimates of the final CM-type competition model.

Parameter	Estimate	SD
a_0	11.380	2.55
a_{pop}	0.703	1.01
a_{size}	0.034	0.12
a'_0	5.180	10.01
a'_{pop}	0.370	1.23
a'_{size}	0.190	0.37
h_0	0.350	0.11
h_{pop}	−0.014	0.02
h_{size}	−0.008	0.005
c	5.37	0.62
c'	2.27	0.47

handling time in the model, i.e. a Type II curve. Fits of the average models of the killifish functional response are shown in Fig. 2. In contrast with the guppy model, the complete model's AIC supported a simple Poisson as appropriate for describing the error structure ($\Delta\text{AIC}_c = 2$ over a double Poisson). Table 3 shows the parameter estimates derived for the CM-type competition models after model averaging. Note that parameters related to the search efficiency a of killifish are derived from the single killifish experiments also after model averaging.

Table 2 shows the estimates and standard deviations for the interference competition coefficients c and c' estimated from the averaged guppy model. From these, we can calculate the relative importance of both types of competition as their quotient $c/c' = 2.5 \pm 0.7$. The relevance of competition in our model is stressed by the high cumulative weight ($\gg 0.99$) of models incorporating two separate competition terms (Table 1). The ratio indicates a much greater importance of intraspecific versus interspecific competition. The estimated values of ah for a 20 mm fish are 4.25 ± 1.82 and 4.31 ± 1.90 for high and low predation fish, respectively.

6. Discussion

We have illustrated how to expand commonly used functional response equations to incorporate the effects of inter-specific competitors. More importantly, we have shown how the parameterization and analysis of such equations with response-surface experiments can be used to gain mechanistic understanding of the nature of competition. In our case study with guppies and killifish, for example, we have learnt three main lessons. First, foraging interference can occur during handling as well as the searching phase. In other words, foragers can prolong the handling time of captured prey due to interference. We can infer this because the guppy functional response follows a CM and not a BD model, which assumes that guppies are interfering with each other even when they're not searching for preys. Since the handling phase is very short and can be interfered upon, it is likely that it does not represent digestion but, rather, ingestion or other external manifestations of prey handling. Second, intra-specific competition is likely to be more important than competition between species for drift invertebrate feeding, the main food source for *Rivulus* in nature (Fraser et al., 1999; Owens, 2010).

The importance of intra-specific competition is significant for the evolution of life-histories, which are known to evolve rapidly in the guppy in response to changes in predation pressure (Reznick et al., 1990, 1997). When predation pressure declines and inter-specific competition is weak, the consequent increase in population density can increase the importance of intra-specific competitive as the main selective force (Miller and Travis, 1996). To detect such indirect effects it is important to perform experiments addressing the mechanisms behind intra- and inter-specific competition, such as functional responses, rather than the demographic patterns.

There is a vast array of functional response equations that incorporate a variety of intra-specific behavioural and physiological mechanisms (Jeschke et al., 2002; Skalski and Gilliam, 2001). Combined with consumer–resource models, they provide an extremely valuable tool to gain mechanistic understanding on consumer–resource dynamics. Several studies point at the importance of predator behaviour on predator–resource dynamics (e.g. Abrams and Matsuda, 2004; Coolen et al., 2007; Krivan et al., 2008). More generally, derivation of ecological patterns from individual mechanisms has been advocated as having a higher predictive power, particularly in the face of environmental change (Sutherland, 2006; Sutherland and Norris, 2002). If we are to extend this approach to the understanding of more complex systems, functional responses need to incorporate behavioural interactions among multiple consumer species or resource types. Our development is a first step in this direction, by incorporating interference competition between two consumer species. The approach could be extended to incorporate other foraging interactions between species such as inter-specific attraction or commensalism, as well as interactions between multiple resources (e.g. between different prey species), such as mutualistic defence strategies or mimicry. This way, just as population biology has gained enormously from the incorporation of individual processes in population models (Sutherland, 1996), we can increase our mechanistic understanding of community ecology by incorporating inter-specific behaviours into community models via multi-species functional response equations.

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Appendix A. Derivation functional response equations with interspecific competition

A.1. Beddington–DeAngelis type

The feeding functional response of a given individual will depend on the density of resources N , the density of inter-specific competitors C and the density of conspecific consumers (excluding the focal individual), which we denote as F and is defined as the inverse of the average time T elapsed between the acquisition of two food items. For the one-species Beddington–DeAngelis derivation, this time is decomposed into the time spent searching (T_S), handling resources (T_H) and wasted in interference competition (T_W). The incorporation of inter-specific competition requires the decomposition of T_W into conspecific (T_{WC}) and inter-specific interference (T_{WI}). Hence:

$$T = T_S + T_H + T_{WC} + T_{WI} \quad (\text{A1})$$

We follow the standard assumption that consumers and resources are identical and homogeneously distributed throughout the volume. If a is the search efficiency (attack rate), defined as the volume monitored by a consumer per unit time, the number of resource items a given consumer encounters per unit time is aN ,

and thus the time spent searching for a given resource items is

$$T_S = \frac{1}{aN}. \quad (A2)$$

The time wasted in interference with the conspecific population F can be calculated as the number of encounters with conspecifics (n_c) multiplied by the time wasted per encounter (d). If b is the *per capita* consumer encounter rate and we assume that handling and interference time are small with respect to searching time, the probability of a searching consumer encountering another searching consumer is bF , which results in:

$$T_{WC} = d \cdot n_c = d \cdot T_S \cdot bF = T_S \cdot cF \quad (A3)$$

where c is the intra-specific competition coefficient $c = bd$.

Denoting the inter-specific competition coefficient as c' we can equally derive the total time wasted in interference with intra-specific competitors, which will now depend on the competitor's encounter rate as:

$$T_{WI} = T_S c' C \quad (A4)$$

Finally, if we rewrite the handling time T_H as h , the frequency of ingestion is

$$f(N, F, C) = \frac{1}{T_S + h + T_{WC} + T_{WI}}$$

which, using Eqs. (A2)–(A4) can be re-written as:

$$f(N, F, C) = \frac{aN}{1 + ahN + cF + c' C}$$

A.2. Crowley–Martin type

If we assume that either consumer species can waste interference time both at the searching and handling stages, we need to decompose wasted time T_W into a searching and handling component. The time wasted interfering in the searching stage is equivalent to Eqs. (A3) and (A4). The times wasted in interfering with conspecifics while handling equals:

$$T_{WHC} = h \cdot cF \quad (A5)$$

where $h \cdot cF$ is the probability of encountering a competitor while handling. Similarly, we can calculate the time wasted in inter-specific competition while handling as:

$$T_{WHI} = h \cdot c' C \quad (A6)$$

Eqs. (A5) and (A6) lead to

$$f(N, F, C) = \frac{1}{T_S + h + T_{WSC} + T_{WHC} + T_{WHI}}$$

Poisson which, using Eqs. (A2)–(A6) can be written as:

$$f(N, F, C) = \frac{aN}{(1 + ahN) \cdot (1 + cF + c' C)}$$

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