

Supporting Information:
Hidden layers of density dependence in consumer
feeding rates

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1 Empirical datasets

Table S1: A summary of single-resource consumer dependence datasets. “Dataset” refers to the specific experiment from the study, and ‘-’ implies there was only one dataset available. “Nobs” indicates the sample size. “Replaced” refers to whether the consumed resource was replaced during the study, which dictated our use of a binomial versus a Poisson likelihood. “Consumer” refers to the whether the consumer was a predator or a parasitoid. “Raw” refers to whether we were able to use the raw data at the level of each treatment replicate, or whether we instead used means and associated uncertainty intervals to produce bootstrapped datasets. “Type” refers to whether the data was provided to us by the author, or whether an online repository, or was extracted from the publication. “Source” refers to the figures and tables from which the data were extracted.

Study	Dataset	Nobs	Replaced	Consumer	Raw	Type	Source	Citation
Chan <i>et al.</i> (2017)	ch	10	Yes	Predator	Yes	Provided	-	Chan <i>et al.</i> (2017)
Chan <i>et al.</i> (2017)	cs	10	Yes	Predator	Yes	Provided	-	Chan <i>et al.</i> (2017)
Chan <i>et al.</i> (2017)	lh	10	Yes	Predator	Yes	Provided	-	Chan <i>et al.</i> (2017)
Chan <i>et al.</i> (2017)	ls	10	Yes	Predator	Yes	Provided	-	Chan <i>et al.</i> (2017)
Chan & Turnbull (1966)	-	15	No	Predator	Yes	Extracted	Table 2	Novak & Stouffer (2020)
Chong & Oetting (2006)	-	126	Yes	Parasitoid	Yes	Provided	-	Chong (2020)
Crowley & Martin (1989)	-	60	Yes	Predator	No	Extracted	Fig. 2	Novak & Stouffer (2020)
Edwards (1961)	nm	97	Yes	Parasitoid	Yes	Extracted	Tables 1, 2 & 3	Novak & Stouffer (2020)
Edwards (1961)	ts1	75	Yes	Parasitoid	Yes	Extracted	Tables 1, 2 & 3	Novak & Stouffer (2020)
Edwards (1961)	ts2	17	Yes	Parasitoid	Yes	Extracted	Tables 1, 2 & 3	Novak & Stouffer (2020)
Elliott (2005)	i2	400	Yes	Predator	Yes	Provided	-	Elliott (2020a)
Elliott (2005)	i3	400	Yes	Predator	Yes	Provided	-	Elliott (2020a)
Elliott (2005)	i4	400	Yes	Predator	Yes	Provided	-	Elliott (2020a)
Elliott (2005)	i5	400	Yes	Predator	Yes	Provided	-	Elliott (2020a)
Eveleigh & Chant (1982)	aa	111	No	Predator	No	Extracted	Tables 4, 5 & 8	Novak & Stouffer (2020)
Eveleigh & Chant (1982)	ad	226	No	Predator	No	Extracted	Tables 4, 5 & 8	Novak & Stouffer (2020)
Eveleigh & Chant (1982)	ap	267	No	Predator	No	Extracted	Tables 4, 5 & 8	Novak & Stouffer (2020)
Eveleigh & Chant (1982)	pa	111	No	Predator	No	Extracted	Tables 4, 5 & 8	Novak & Stouffer (2020)
Eveleigh & Chant (1982)	pd	278	No	Predator	No	Extracted	Tables 4, 5 & 8	Novak & Stouffer (2020)
Eveleigh & Chant (1982)	pp	298	No	Predator	No	Extracted	Tables 4, 5 & 8	Novak & Stouffer (2020)
Fussmann <i>et al.</i> (2005)	-	101	Yes	Predator	Yes	Provided	-	Fussmann (2020)
Griffen & Delaney (2007)	fla	108	No	Predator	No	Extracted	Fig 1 & Fig A1	Novak & Stouffer (2020)
Griffen & Delaney (2007)	flb	108	No	Predator	No	Extracted	Fig 1 & Fig A1	Novak & Stouffer (2020)
Griffen & Delaney (2007)	fA1a	32	No	Predator	No	Extracted	Fig 1 & Fig A1	Novak & Stouffer (2020)
Griffen & Delaney (2007)	fA1b	32	No	Predator	No	Extracted	Fig 1 & Fig A1	Novak & Stouffer (2020)
Hassan (1976)	Ag	100	Yes	Parasitoid	No	Extracted	Table 1	Novak & Stouffer (2020)
Hassan (1976)	Br	100	Yes	Parasitoid	No	Extracted	Table 1	Novak & Stouffer (2020)
Hassan (1976)	Pp	100	Yes	Parasitoid	No	Extracted	Table 1	Novak & Stouffer (2020)
Hossie & Murray (2016)	cl	42	No	Predator	Yes	Provided	-	Hossie & Murray (2020)
Hossie & Murray (2016)	ev	42	No	Predator	Yes	Provided	-	Hossie & Murray (2020)
Huffaker & Matsumoto (1982)	-	40	Yes	Parasitoid	No	Extracted	Table 1	Novak & Stouffer (2020)
Johnson (2006)	-	45	No	Predator	Yes	Extracted	Fig. 1	Novak & Stouffer (2020)
Jones & Hassell (1988); Jones (1986)	e4	125	No	Parasitoid	Yes	Extracted	Fig. 1a & 3	Novak & Stouffer (2020)
Jones & Hassell (1988); Jones (1986)	e5	140	No	Parasitoid	Yes	Extracted	Fig. 1a & 3	Novak & Stouffer (2020)
Katiz (1985)	-	112	No	Predator	No	Extracted	Table 1	Ardit & Akçakaya (1990)
Kfir (1985)	-	120	No	Parasitoid	No	Extracted	Table 1	Novak & Stouffer (2020)
Kratina <i>et al.</i> (2009)	-	67	No	Predator	Yes	Provided	-	Kratina (2020)

Table S1: (continued)

Study	Dataset	Nobs	Replaced	Consumer	Raw	Type	Source	Citation
Krylov (1992)	i	28	No	Predator	No	Extracted	Table 1 & Fig. 1L	Novak & Stouffer (2020)
Kumar & Tripathi (1985)	Cc	90	No	Parasitoid	No	Extracted	Tables 1 & 2 & Figs. 1 & 2	Novak & Stouffer (2020)
Kumar & Tripathi (1985)	DI	90	No	Parasitoid	No	Extracted	Tables 1 & 2 & Figs. 1 & 2	Novak & Stouffer (2020)
Kumar & Tripathi (1985)	Sm	90	No	Parasitoid	No	Extracted	Tables 1 & 2 & Figs. 1 & 2	Novak & Stouffer (2020)
Lang <i>et al.</i> (2012)	Po 10	185	No	Predator	Yes	Provided	-	Lang (2020)
Lang <i>et al.</i> (2012)	Po 20	181	No	Predator	Yes	Provided	-	Lang (2020)
Lang <i>et al.</i> (2012)	Pt 10	184	No	Predator	Yes	Provided	-	Lang (2020)
Lang <i>et al.</i> (2012)	Pt 20	186	No	Predator	Yes	Provided	-	Lang (2020)
Long <i>et al.</i> (2012b)	-	50	No	Predator	Yes	Provided	-	Long (2020a)
Mansour & Lipcius (1991)	-	36	No	Predator	No	Extracted	Fig. 1a	Novak & Stouffer (2020)
Médoc <i>et al.</i> (2013)	-	48	Yes	Predator	Yes	Provided	-	Médoc <i>et al.</i> (2020b)
Médoc <i>et al.</i> (2015)	be	76	Yes	Predator	Yes	Provided	-	Médoc <i>et al.</i> (2020a)
Médoc <i>et al.</i> (2015)	dv	76	Yes	Predator	Yes	Provided	-	Médoc <i>et al.</i> (2020a)
Médoc <i>et al.</i> (2015)	pu	76	Yes	Predator	Yes	Provided	-	Médoc <i>et al.</i> (2020a)
Mertz & Davies (1968)	-	120	No	Predator	Yes	Extracted	Table 1	Novak & Stouffer (2020)
Mills & Lacaan (2004)	-	179	Yes	Parasitoid	Yes	Extracted	Fig. 1a-c	Novak & Stouffer (2020)
Montoya <i>et al.</i> (2000)	-	528	Yes	Parasitoid	No	Extracted	Table 1	Novak & Stouffer (2020)
Omkar & Pervez (2004)	-	90	No	Predator	Yes	Provided	-	Omkar & Pervez (2004)
Prokopenko <i>et al.</i> (2017)	-	80	Yes	Predator	Yes	Provided	-	Prokopenko (2020)
Prokopenko <i>et al.</i> (2018)	-	60	Yes	Predator	Yes	Provided	-	Prokopenko (2020)
Reeve (1997)	-	26	No	Predator	Yes	Provided	-	Pusack (2020)
Salt (1974)	-	50	Yes	Predator	No	Extracted	Fig. 3 & Table 1	Reeve (2020)
Utley (1980)	i1	168	No	Predator	No	Extracted	Figs. 4.3.1, 4.3.2, 4.3.3, 8.3.1 & 8.3.2	Novak & Stouffer (2020)
Utley (1980)	i2	204	No	Predator	No	Extracted	Figs. 4.3.1, 4.3.2, 4.3.3, 8.3.1 & 8.3.2	Novak & Stouffer (2020)
Utley (1980)	i3	224	No	Predator	No	Extracted	Figs. 4.3.1, 4.3.2, 4.3.3, 8.3.1 & 8.3.2	Novak & Stouffer (2020)
Utley (1980)	n1	266	No	Predator	No	Extracted	Figs. 4.3.1, 4.3.2, 4.3.3, 8.3.1 & 8.3.2	Novak & Stouffer (2020)
Utley (1980)	n2	312	No	Predator	No	Extracted	Figs. 4.3.1, 4.3.2, 4.3.3, 8.3.1 & 8.3.2	Novak & Stouffer (2020)
Vahl <i>et al.</i> (2005)	k	10	No	Predator	Yes	Extracted	Fig. 4	Novak & Stouffer (2020)
Vahl <i>et al.</i> (2005)	t	10	No	Predator	Yes	Extracted	Fig. 4	Novak & Stouffer (2020)
Von Westernhagen & Rosenthal (1976)	2hr	80	No	Predator	No	Extracted	Fig. 3	Novak & Stouffer (2020)
Von Westernhagen & Rosenthal (1976)	4hr	120	No	Predator	No	Extracted	Fig. 3	Novak & Stouffer (2020)
Von Westernhagen & Rosenthal (1976)	8hr	100	No	Predator	No	Extracted	Fig. 3	Novak & Stouffer (2020)
Vucetich <i>et al.</i> (2002)	m14	118	Yes	Predator	Yes	Provided	-	Vucetich <i>et al.</i> (2002); Jost <i>et al.</i> (2005)
Vucetich <i>et al.</i> (2002)	m98	77	Yes	Predator	Yes	Provided	-	Vucetich <i>et al.</i> (2002); Jost <i>et al.</i> (2005)
Vucetich <i>et al.</i> (2002)	w14	44	Yes	Predator	Yes	Provided	-	Vucetich <i>et al.</i> (2002); Jost <i>et al.</i> (2005)
Vucetich <i>et al.</i> (2002)	w98	28	Yes	Predator	Yes	Provided	-	Vucetich <i>et al.</i> (2002); Jost <i>et al.</i> (2005)
Walde & Davies (1984)	-	60	Yes	Predator	No	Extracted	Fig 2 & 4	Novak & Stouffer (2020)
Wasserman <i>et al.</i> (2016b)	bg	38	No	Predator	Yes	Repository	-	Wasserman <i>et al.</i> (2016a)
Wasserman <i>et al.</i> (2016b)	mb	37	No	Predator	Yes	Repository	-	Wasserman <i>et al.</i> (2016a)
Wasserman <i>et al.</i> (2016b)	tü	39	No	Predator	Yes	Repository	-	Wasserman <i>et al.</i> (2016a)

Table S2: A summary of multi-resource dependence datasets. “Dataset” refers to the specific experiment from the study, and ‘.’ implies there was only one dataset available. “Nobs” indicates the sample size per resource consumed. “Replacement” refers to whether the consumed resources were replaced during the study, which dictated our use of a binomial versus a Poisson likelihood. “Consumer” refers to whether the consumer was a predator or a parasitoid. “Raw” refers to whether we were able to use the raw data at the level of each treatment replicate, or whether we instead used means and associated uncertainty intervals to produce bootstrapped datasets. “Type” refers to whether the data was provided to us by the author, was obtained from an online repository, or was extracted from the publication. “Source” refers to the figures and tables from which the data were extracted.

Study	Dataset	Nobs	Replaced	Consumer	Raw	Type	Source	Citation
Colton (1983; 1987)	1	108	No	Predator	Yes	Extracted	Table B3	Novak & Stouffer (2020)
Colton (1983; 1987)	2	108	No	Predator	Yes	Extracted	Table B3	Novak & Stouffer (2020)
Elliott (2006)	i2	290	Yes	Predator	No	Provided	-	Elliott (2020b)
Elliott (2006)	i3	290	Yes	Predator	No	Provided	-	Elliott (2020b)
Elliott (2006)	i4	290	Yes	Predator	No	Provided	-	Elliott (2020b)
Elliott (2006)	i4B	290	Yes	Predator	No	Provided	-	Elliott (2020b)
Elliott (2006)	i5	290	Yes	Predator	No	Provided	-	Elliott (2020b)
Elliott (2006)	i5B	290	Yes	Predator	No	Provided	-	Elliott (2020b)
Iyer & Rao (1996)	Bc	192	No	Predator	No	Extracted	Fig. 1 & 2	Novak & Stouffer (2020)
Iyer & Rao (1996)	Bp	192	No	Predator	No	Extracted	Fig. 1 & 2	Novak & Stouffer (2020)
Iyer & Rao (1996)	Br	192	No	Predator	No	Extracted	Fig. 1 & 2	Novak & Stouffer (2020)
Kalinkat <i>et al.</i> (2011)	A	48	Yes	Predator	Yes	Provided	-	Kalinkat <i>et al.</i> (2018)
Kalinkat <i>et al.</i> (2011)	C	48	Yes	Predator	Yes	Provided	-	Kalinkat <i>et al.</i> (2018)
Kalinkat <i>et al.</i> (2011)	H	48	Yes	Predator	Yes	Provided	-	Kalinkat <i>et al.</i> (2018)
Kalinkat <i>et al.</i> (2011)	P	70	Yes	Predator	Yes	Provided	-	Kalinkat <i>et al.</i> (2018)
Kalinkat <i>et al.</i> (2011)	T	137	Yes	Predator	Yes	Provided	-	Kalinkat <i>et al.</i> (2018)
Krylov (1992)	ii	56	No	Predator	No	Extracted	Fig. 1 & Fig. 2	Novak & Stouffer (2020)
Lester & Harmsen (2002)	Af d	60	Yes	Predator	Yes	Provided	-	Lester (2020)
Lester & Harmsen (2002)	Af e	60	Yes	Predator	Yes	Provided	-	Lester (2020)
Lester & Harmsen (2002)	Ty d	60	Yes	Predator	Yes	Provided	-	Lester (2020)
Lester & Harmsen (2002)	Ty e	60	Yes	Predator	Yes	Provided	-	Lester (2020)
Long <i>et al.</i> (2012a)	-	94	No	Predator	Yes	Provided	-	Long (2020b)
Mattila & Bonsdorff (1998)	-	37	No	Predator	No	Extracted	Fig. 3a & 4	Novak & Stouffer (2020)
Nachappa <i>et al.</i> (2006)	-	158	No	Predator	Yes	Provided	-	Nachappa <i>et al.</i> (2006)
Ranta & Nuutinen (1985)	10	123	Yes	Predator	No	Extracted	Fig. 2 & 3 & Tables 2 & 5	Novak & Stouffer (2020)
Ranta & Nuutinen (1985)	13	123	Yes	Predator	No	Extracted	Fig. 2 & 3 & Tables 2 & 5	Novak & Stouffer (2020)
Ranta & Nuutinen (1985)	18	123	Yes	Predator	No	Extracted	Fig. 2 & 3 & Tables 2 & 5	Novak & Stouffer (2020)
Ranta & Nuutinen (1985)	Ad	123	Yes	Predator	No	Extracted	Fig. 2 & 3 & Tables 2 & 5	Novak & Stouffer (2020)
Wong & Barbeau (2005)	rc	48	Yes	Predator	Yes	Provided	-	Wong & Barbeau (2020)
Wong & Barbeau (2005)	ss	48	Yes	Predator	Yes	Provided	-	Wong & Barbeau (2020)

2 Maximum-likelihood parameter estimation

For both single-resource and multiple-resource datasets in which consumed resources were continually replaced, we assumed that observed *counts* of resources consumed were drawn from a Poisson distribution parameterized by the feeding rate of the functional response. For datasets in which consumed resources were not replaced, we assumed that observed *proportions* of resources consumed were drawn from a binomial distribution parameterized by the feeding rate of the functional response and by the total number of available resources at the start of the experiment. For non-replacement datasets with a single resource, we generated analytical predictions for the proportion of resources consumed using the Lambert W function to account for continuous resource depletion (Okuyama & Ruyle, 2011; Lehtonen, 2016; Rosenbaum & Rall, 2018). For non-replacement datasets with multiple resources, we determined the proportion of both resources consumed via numerical integration of the coupled differential equations (Keitt, 2017). For multiple-resource datasets the likelihood was calculated as the sum of the likelihoods of each of the two resources. This is because the functional response parameters for each resource influence both feeding rates (except in the limiting cases) and hence require simultaneous estimation.

3 Parametric bootstrapping of empirical datasets

For each dataset comprised of treatment means and associated uncertainties, we generated parametrically-bootstrapped datasets as follows. For a treatment level consisting of n replicates with mean number of resources consumed μ and standard error s , we first drew n random values x from a Gaussian distribution with mean μ and standard deviation $\sigma = s\sqrt{n}$. To mirror our inference process and ensure data consistent with the underlying likelihood functions, we then used these random values to parameterize Poisson or binomial processes depending on whether the original dataset corresponded to a replacement or non-replacement study design, respectively. For Katz (1985) where we could not obtain estimates of uncertainty, we used the available means as raw data.

To maintain biologically sensible predictions, we replaced any random value $x < 0$ with 0 for both experiment types since this is the lower limit of observable feeding. In non-replacement

datasets, we replaced any value of $x > N$ with N since this is the upper limit of observable feeding. For the multi-resource datasets, we were able to obtain uncertainties of feeding on both resources but not the covariance between them. We therefore simulated these paired observations as independent random variables.

4 Limit of one implicit density-dependent process per predictor density

Consider a single consumer k foraging on individuals from a single resource species i , and experimental data which provide estimates of feeding rate F_{ki} as a function of varying density of resource N_i . In this case, our functional response can only be a linear or non-linear function of a single predictor density: N_i . Rather than a single “handling time” quantified with the parameter h_{ki} as occurs in a Holling Type II model, imagine that we also wish to separate handling into “capture time” γ_{ki} and “digestion time” δ_{ki} (Jeschke *et al.*, 2002). Similar to the main text, we can define the feeding rates F_{ki} as

$$F_{ki}(N_i) = a_{ki}N_i(1 - \gamma_{ki}F_{ki} - \delta_{ki}F_{ki}) . \quad (\text{S1})$$

If we rearrange this equation algebraically to solve for F_{ki} , we obtain

$$F_{ki}(N_i) = \frac{a_{ki}N_i}{1 + a_{ki}(\gamma_{ki} + \delta_{ki})N_i} , \quad (\text{S2})$$

which implies that resource-dependent variation in feeding rates alone is insufficient for us to distinguish between capture and digestion in the absence of additional, independent information with which to estimate one or both of the parameters γ_{ki} and δ_{ki} .

Now consider a dataset with varying densities N_k of the consumer k foraging on varied densities N_i of a single resource species i . In this case, our functional response can only be a linear or non-linear function of two predictor densities: N_i and P_k . Rather than a single interference process occurring between conspecific consumers, we wish to distinguish between direct antagonistic interactions between consumers, which has an associated “antagonism” time ξ_k (during which consumers cannot feed), and avoidance of interactions between consumers, which has an associated “avoidance” time κ_k (also during which consumers cannot feed). Similar to the main

text, we can define the feeding rate F_{ki} , the interference rate I_k , and the avoidance rate A_k as

$$I_k(N_i, P_k) = \alpha_k(P_k - 1)(1 - h_{ki}F_{ki} - \kappa_k A_k - \xi_k I_k) \quad (\text{S3})$$

$$A_k(N_i, P_k) = \eta_k(P_k - 1)(1 - h_{ki}F_{ki} - \kappa_k A_k - \xi_k I_k) \quad (\text{S4})$$

$$F_{ki}(N_i, P_k) = a_{ki}N_i(1 - h_{ki}F_{ki} - \kappa_k A_k - \xi_k I_k) . \quad (\text{S5})$$

If we rearrange this equation algebraically to solve for F_{ki} , we obtain

$$F_{ki}(N_i, P_k) = \frac{a_{ki}N_i}{1 + a_{ki}h_{ki}N_i + (\alpha_k\xi_k + \eta_k\kappa_k)(P_k - 1)} , \quad (\text{S6})$$

which implies that resource- and consumer-dependent variation in feeding rates is insufficient for us to distinguish between antagonism and avoidance in the absence of additional, independent information about one or both of I_k and A_k .

Another way to understand this limitation is to consider the statistical identifiability of the parameters in the functional responses given by Eq. (S2) & (S6). In order for a set of parameters to be identifiable, the derivatives of the generating function with respect to those parameters should all be unique (Beck & Arnold, 1977). This does not hold true for either of the examples above; for example, looking at Eq. (S2)

$$\frac{\partial F_{ki}}{\partial \gamma_{ki}} = \frac{\partial F_{ki}}{\partial \delta_{ki}} = \frac{-(a_{ki}N_i)^2}{(1 + a_{ki}(\gamma_{ki} + \delta_{ki})N_i)^2} . \quad (\text{S7})$$

A somewhat counter-intuitive consequence of this is that the limit of one implicit process per predictor density holds only so long as the order of that density remains the same, where order reflects the implicit or explicit exponent of the predictor density (e.g., N_i is order 1, $(N_i)^2$ is order 2, and so on). Therefore, one cannot separate capture time from digestion time in our example because both are order $(N_i)^1$ processes in that they occur *per resource consumed*. If one process was order 1 (i.e., depended on $(N_i)^1$) and the other was order 2 (i.e., depended on $(N_i)^2$), both *could* be inferred simultaneously. Indeed, this is the reason why we can infer additional parameters that are multiplicative *combinations* of predictor densities in the models introduced here and also the reason why it is possible to shift from a linear Holling Type I model to the non-linear Holling Type II model when we have a single order 1 predictor density N_i .

5 Multi-resource dependence and prey electivities

In a multi-resource context, it is common to think about variation in feeding rates across resources as being driven by “prey electivities” or “predator preferences” (Ivlev, 1961; Chesson, 1983; 1989; Murdoch, 1969; Oaten & Murdoch, 1975). Given a choice of multiple resources (prey), the optimal foraging strategy of a given consumer (predator) may vary depending on resource availability. For example, a high feeding rate on of one type of resource due to that resource being abundant may lead to the consumer feeding differentially on another resource to achieve nutritional balance. In a functional-response context, one way to determine preferences is based on the ratio of attack rates. From this perspective, our generalized multi-resource Type II functional response (Eq. 10) is consistent with consumers having fixed preferences because the attack rates are constant. Analytically, this constancy of attack rates can also be seen by virtue of the fact that there is no common factor with which any a_{ki} is multiplied in both the numerator *and* denominator of Eq. (10).

That said, the ratio of attack rates only fully captures realized preferences and realized differences in relative consumption when handling times are negligible. One can alternatively quantify preferences and/or switching behaviour based on the proportion of resources consumed relative to the proportion of resources available (i.e., F_{ki}/F_{kj} versus N_i/N_j (Murdoch, 1969; van Leeuwen *et al.*, 2013). For Eq. (10) from the main text, we thereby obtain

$$\frac{F_{ki}}{F_{kj}} = \frac{a_{ki} \left[1 + \left(1 - \phi_{F_{ki}F_{kj}} \right) a_{kj} h_{kj} N_j \right]}{a_{kj} \left[1 + \left(1 - \phi_{F_{kj}F_{ki}} \right) a_{ki} h_{ki} N_i \right]} \times \frac{N_i}{N_j}. \quad (\text{S8})$$

This perspective allows us to see how non-independent feeding (and the parameters $\phi_{F_{ki}F_{kj}}$ and $\phi_{F_{kj}F_{ki}}$) induce apparent switching behaviour because the proportionality constant in front of $\frac{N_i}{N_j}$ is only constant when $\phi_{F_{ki}F_{kj}} = \phi_{F_{kj}F_{ki}} = 1$. An equivalent inference is obtained when quantifying preferences by normalizing prey-specific foraging by the total foraging (i.e., $F_{ki}/(F_{ki} + F_{kj})$). With the caveat that the multiple-resource datasets in our collection are primarily laboratory-based, this scenario appears to be rare (see Fig. 3 and the estimates of $\phi_{F_{ki}F_{kj}}$ and $\phi_{F_{kj}F_{ki}}$).

Conspicuously absent from Eq. (S8) are N_i in the numerator and N_j in the denominator of the proportionality constant (c.f. van Leeuwen *et al.*, 2013). Such density dependence can be

obtained by modifying Eqs. (8) & (9) of the main text to make the attack rates explicit functions of the other resources' density. Although this phenomenological manipulation of the model stands in contrast to the way density-dependent handling times “emerge” as shown in the main text, it nonetheless provides a useful basis of comparison.

For example, we could include linearly-dependent attack rates as

$$\tilde{F}_{ki}(N_i, N_j) = \tilde{a}_{ki}N_i \left(1 - h_{ki}\tilde{F}_{ki} - \phi_{\tilde{F}_{ki}\tilde{F}_{kj}}h_{kj}\tilde{F}_{kj}\right) \quad (\text{S9})$$

$$\tilde{F}_{kj}(N_i, N_j) = \tilde{a}_{kj}N_j \left(1 - \phi_{\tilde{F}_{kj}\tilde{F}_{ki}}h_{ki}\tilde{F}_{ki} - h_{kj}\tilde{F}_{kj}\right) \quad (\text{S10})$$

$$\tilde{a}_{ki} = a_{ki} (1 + \alpha_{kij}N_j) \quad (\text{S11})$$

$$\tilde{a}_{kj} = a_{kj} (1 + \alpha_{kji}N_i), \quad (\text{S12})$$

introducing two new parameters, α_{kij} and α_{kji} , that control the effect of the abundance of one resource on the consumer's attack rate on the other resource. Since these changes directly modify the attack rates, they can be carried through upon solving for \tilde{F}_{ki} and \tilde{F}_{kj} , just as shown in the main text. The resulting expression for \tilde{F}_{ki} is

$$\tilde{F}_{ki}(N_i, N_j) = \frac{\tilde{a}_{ki}N_i \left[1 + \left(1 - \phi_{\tilde{F}_{ki}\tilde{F}_{kj}}\right)\tilde{a}_{kj}h_{kj}N_j\right]}{\left(1 + \tilde{a}_{ki}h_{ki}N_i\right)\left(1 + \tilde{a}_{kj}h_{kj}N_j\right) - \phi_{\tilde{F}_{ki}\tilde{F}_{kj}}\phi_{\tilde{F}_{kj}\tilde{F}_{ki}}\tilde{a}_{ki}h_{ki}\tilde{a}_{kj}h_{kj}N_iN_j}, \quad (\text{S13})$$

which is equivalent to Eq. (10) but with a_{ki} replaced by \tilde{a}_{ki} and a_{kj} replaced by \tilde{a}_{kj} . The corresponding expression for predator preferences (defined as above) is

$$\frac{\tilde{F}_{ki}}{\tilde{F}_{kj}} = \frac{a_{ki} (1 + \alpha_{kij}N_j) \left[1 + \left(1 - \phi_{\tilde{F}_{ki}\tilde{F}_{kj}}\right) a_{kj} (1 + \alpha_{kji}N_i) h_{kj}N_j\right]}{a_{kj} (1 + \alpha_{kji}N_i) \left[1 + \left(1 - \phi_{\tilde{F}_{kj}\tilde{F}_{ki}}\right) a_{ki} (1 + \alpha_{kij}N_j) h_{ki}N_i\right]} \times \frac{N_i}{N_j}. \quad (\text{S14})$$

Notably, the proportionality constant in this expression includes N_i in the numerator and N_j in the denominator. These densities are *always* multiplied by the density of the “other” resource. This implies that the only way to have these densities appear alone is to introduce them in our expressions for density-dependent attack rates (Eqs. S11 & S12). (Note that the functional form of density-dependent preferences achieved phenomenologically and those as captured by Eq. (S13) are *identical* when $\phi_{F_{ki}F_{kj}} = \phi_{F_{ki}F_{ki}} = 1$.)

As might be expected, including density-dependent attack rates *and* non-independent feeding (via $\phi_{F_{ki}F_{kj}}$ and $\phi_{F_{kj}F_{ki}}$) creates many additional higher-order terms in the resulting functional responses. That is, the numerator and denominator of Eq. (S13) could include terms in the

numerator and denominator of order 2 that depend on $(N_i)^2$, $(N_j)^2$, $(N_i)^2 (N_j)^1$, $(N_i)^1 (N_j)^2$, etc. The only exception is when feeding on each resource is 100% independent of feeding on the other (i.e., $\phi_{F_{ki}F_{kj}} = \phi_{F_{ki}F_{kj}} = 0$), in which case the order of Eq. (S13) is equivalent to that of Eq. (10). Again with the caveat that the multiple-resource datasets in our empirical collection are primarily laboratory-based, this scenario also appears to be rare (see Fig. 3 and the estimates of $\phi_{F_{ki}F_{kj}}$ and $\phi_{F_{ki}F_{kj}}$).

References

- Arditi, R. & Akçakaya, H.R. (1990). Underestimation of mutual interference of predators. *Oecologia*, 83, 358–361.
- Beck, J.V. & Arnold, K.J. (1977). *Parameter Estimation in Engineering and Science*. John Wiley & Sons, Inc., New York, NY, USA.
- Chan, K., Boutin, S., Hossie, T.J., Krebs, C., O’Donoghue, M. & Murray, D.L. (2017). Improving the assessment of predator functional responses by considering alternate prey and predator interactions. *Ecology*, 98, 1787–1796.
- Chant, D.A. & Turnbull, A.L. (1966). Effects of predator and prey densities on interactions between goldfish and *Daphnia pulex* (De Geer). *Canadian Journal of Zoology*, 44, 285–289.
- Chesson, J. (1983). The estimation and analysis of preference and its relationship to foraging models. *Ecology*, 64, 1297–1304.
- Chesson, J. (1989). The effect of alternative prey on the functional response of *Notonecta Hoffmani*. *Ecology*, 70, 1227–1235.
- Chong, J.H. (2020). Data from: Functional response and progeny production of the Madeira mealybug parasitoid, *Anagyrus sp. nov. nr. sinope*: the effects of host and parasitoid densities. *Figshare*: <https://doi.org/10.6084/m9.figshare.12781250.v1>.
- Chong, J.H. & Oetting, R.D. (2006). Functional response and progeny production of the Madeira mealybug parasitoid, *Anagyrus sp. nov. nr. sinope*: the effects of host and parasitoid densities. *Biological Control*, 39, 320–328.
- Colton, T.F. (1983). *Predation by damselfly naiad on two species of zooplankton: preference, switching, and the modelling of predation*. Ph.D. thesis, Duke University.
- Colton, T.F. (1987). Extending functional response models to include a second prey type: an experimental test. *Ecology*, 68, 900–912.

- Crowley, P.H. & Martin, E.K. (1989). Functional responses and interference within and between year classes of a dragonfly population. *Journal of the North American Benthological Society*, 8, 211–221.
- Edwards, R.L. (1961). The area of discovery of two insect parasites, *Nasonia vitripennis* (Walker) and *Trichogramma evanescens* (Westwood), in an artificial environment. *The Canadian Entomologist*, 93, 475–481.
- Elliott, J.M. (2005). Ontogenetic shifts in the functional response and interference interactions of *Rhyacophila dorsalis* larvae (Trichoptera). *Freshwater Biology*, 50, 2021–2033.
- Elliott, J.M. (2006). Prey switching in *Rhyacophila dorsalis* (Trichoptera) alters with larval instar. *Freshwater Biology*, 51, 913–924.
- Elliott, J.M. (2020a). Data from: Ontogenetic shifts in the functional response and interference interactions of *Rhyacophila dorsalis* larvae (Trichoptera). *Figshare*: <https://doi.org/10.6084/m9.figshare.13028114.v1>.
- Elliott, J.M. (2020b). Data from: Prey switching in *Rhyacophila dorsalis* (Trichoptera) alters with larval instar. *Figshare*: <https://doi.org/10.6084/m9.figshare.13028129.v1>.
- Eveleigh, E.S. & Chant, D. (1982). Experimental studies on acarine predator–prey interactions: the effects of predator density on prey consumption, predator searching efficiency, and the functional response to prey density (Acarina: Phytoseiidae). *Canadian Journal of Zoology*, 60, 611–629.
- Fussmann, G.F. (2020). Data from: A direct, experimental test of resource vs. consumer dependence. *FigShare*: <https://doi.org/10.6084/m9.figshare.12782297.v1>.
- Fussmann, G.F., Weithoff, G. & Yoshida, T. (2005). A direct, experimental test of resource vs. consumer dependence. *Ecology*, 86, 2924–2930.
- Griffen, B.D. & Delaney, D.G. (2007). Species invasion shifts the importance of predator dependence. *Ecology*, 88, 3012–3021.

- Hassan, S.T. (1976). The area of discovery of *Apanteles glomeratus* (Hymenoptera: Braconidae), *Pteromalus puparum* (Pteromalidae) and *Brachymeria regina* (Chalcididae). *Entomologia experimentalis et applicata*, 20, 199–205.
- Hossie, T.J. & Murray, D.L. (2016). Spatial arrangement of prey affects the shape of ratio-dependent functional response in strongly antagonistic predators. *Ecology*.
- Hossie, T.J. & Murray, D.L. (2020). Data from: Spatial arrangement of prey affects the shape of ratio-dependent functional response in strongly antagonistic predators. *Figshare*: <https://doi.org/10.6084/m9.figshare.12739181.v1>.
- Huffaker, C.B. & Matsumoto, B.M. (1982). Group versus individual functional responses of *Venturia [= Nemeritis] canescens* (Grav.). *Researches on Population Ecology*, 24, 250–269.
- Ivlev, V.S. (1961). *Experimental Ecology of the Feeding of Fishes*. Yale University Press, New Haven, CT, USA. Translated from the Russian by Douglas Scott.
- Iyer, N. & Rao, T. (1996). Responses of the predatory rotifer *Asplanchna intermedia* to prey species differing in vulnerability: laboratory and field studies. *Freshwater Biology*, 36, 521–533.
- Jeschke, J.M., Kopp, M. & Tollrian, R. (2002). Predator functional responses: Discriminating between handling and digesting prey. *Ecol. Monogr.*, 72, 95–112.
- Johnson, D.W. (2006). Predation, habitat complexity, and variation in density-dependent mortality of temperate reef fishes. *Ecology*, 87, 1179–1188.
- Jones, T.H. (1986). *Patterns of parasitism by Trybliographa rapae (Westw.), a cynipid parasitoid of the cabbage root fly*. Ph.D. thesis, University of London, Imperial College.
- Jones, T.H. & Hassell, M.P. (1988). Patterns of parasitism by *Trybliographa rapae*, a cynipid parasitoid of the cabbage root fly, under laboratory and field conditions. *Ecological entomology*, 13, 309–317.

- Jost, C., Devulder, G., Vucetich, J.A., Peterson, R.O. & Arditi, R. (2005). The wolves of isle royale display scale-invariant satiation and ratio-dependent predation on moose. *Journal of Animal Ecology*, pp. 809–816.
- Kalinkat, G., Rall, B.C., Vucic-Pestic, O. & Brose, U. (2011). The allometry of prey preferences. *PLoS ONE*, 6, e25937.
- Kalinkat, G., Rall, B.C., Vucic-Pestic, O. & Brose, U. (2018). Kalinkat et al. 2011 data. *Figshare*: <https://doi.org/10.6084/m9.figshare.6360506.v1>.
- Katz, C.H. (1985). A nonequilibrium marine predator-prey interaction. *Ecology*, 66, 1426–1438.
- Keitt, T.H. (2017). *odeintr: C++ ODE Solvers Compiled on-Demand*. R package version 1.7.1.
- Kfir, R. (1983). Functional response to host density by the egg parasite *Trichogramma pretiosum*. *Entomophaga*, 28, 345–353.
- Kratina, P. (2020). Data from: Functional responses modified by predator density. *Figshare*: <https://doi.org/10.6084/m9.figshare.12794816.v1>.
- Kratina, P., Vos, M., Bateman, A. & Anholt, B.R. (2009). Functional responses modified by predator density. *Oecologia*, 159, 425–433.
- Krylov, P.I. (1992). Density-dependent predation of *Chaoborus flavicans* on *Daphnia longispina* in a small lake: the effect of prey size. *Hydrobiologia*, 239, 131–140.
- Kumar, A. & Tripathi, C.P.M. (1985). Parasitoid–host relationship between *Trioxys (Binodoxys) indicus* Subba Rao & Sharma (Hymenoptera: Aphidiidae) and *Aphis craccivora* Koch (Hemiptera: Aphididae): effect of host plants on the area of discovery of the parasitoid. *Canadian Journal of Zoology*, 63, 192–195.
- Lang, B. (2020). Data from: Warming effects on consumption and intraspecific interference competition depend on predator metabolism. *Figshare*: <https://doi.org/10.6084/m9.figshare.12789986>.

- Lang, B., Rall, B.C. & Brose, U. (2012). Warming effects on consumption and intraspecific interference competition depend on predator metabolism. *Journal of Animal Ecology*, 81, 516–523.
- van Leeuwen, E., Brännström, A., Jansen, V.A.A., Dieckmann, U. & Rossberg, A.G. (2013). A generalized functional response for predators that switch between multiple prey species. *J. Theor. Biol.*, 328, 89–98.
- Lehtonen, J. (2016). The Lambert W function in ecological and evolutionary models. *Methods Ecol. Evol.*, 7, 1110–1118
- Lester, P.J. (2020). Data from: Functional and numerical responses do not always indicate the most effective predator for biological control: an analysis of two predators in a two-prey system. *Figshare*: <https://doi.org/10.6084/m9.figshare.12838352>.
- Lester, P.J. & Harmsen, R. (2002). Functional and numerical responses do not always indicate the most effective predator for biological control: an analysis of two predators in a two-prey system. *Journal of Applied Ecology*, 39, 455–468.
- Long, W.C. (2020a). Data from: Cannibalism in red king crab, *Paralithodes camtschaticus* (Tilesius, 1815): Effects of habitat type and predator density on predator functional response. *FigShare*: <https://doi.org/10.6084/m9.figshare.12780440>.
- Long, W.C. (2020b). Data from: Density-dependent indirect effects: apparent mutualism and apparent competition coexist in a two-prey system. *FigShare*: <https://doi.org/10.6084/m9.figshare.12780455.v1>.
- Long, W.C., Gamelin, E.F., Johnson, E.G. & Hines, A.H. (2012a). Density-dependent indirect effects: apparent mutualism and apparent competition coexist in a two-prey system. *Marine Ecology Progress Series*, 456, 139–148.
- Long, W.C., Popp, J., Swiney, K.M. & Van Sant, S.B. (2012b). Cannibalism in red king crab, *Paralithodes camtschaticus* (Tilesius, 1815): Effects of habitat type and predator density on predator functional response. *Journal of Experimental Marine Biology and Ecology*, 422, 101–106.

- Mansour, R.A. & Lipcius, R.N. (1991). Density-dependent foraging and mutual interference in blue crabs preying upon infaunal clams. *Marine Ecology Progress Series*, 72, 239.
- Mattila, J. & Bonsdorff, E. (1998). Predation by juvenile flounder (*Platichthys flesus* L.): a test of prey vulnerability, predator preference, switching behaviour and functional response. *Journal of Experimental Marine Biology and Ecology*, 227, 221–236.
- Médoc, V., Albert, H. & Spataro, T. (2015). Functional response comparisons among freshwater amphipods: ratio-dependence and higher predation for *Gammarus pulex* compared to the non-natives *Dikerogammarus villosus* and *Echinogammarus berilloni*. *Biological Invasions*, 17, 3625–3637.
- Médoc, V., Albert, H. & Spataro, T. (2020a). Data from: Functional response comparisons among freshwater amphipods: ratio-dependence and higher predation for *Gammarus pulex* compared to the non-natives *Dikerogammarus villosus* and *Echinogammarus berilloni*. *Figshare*: <https://doi.org/10.6084/m9.figshare.12937841.v1>.
- Médoc, V., Spataro, T. & Arditi, R. (2013). Prey: predator ratio dependence in the functional response of a freshwater amphipod. *Freshwater Biology*, 58, 858–865.
- Médoc, V., Spataro, T. & Arditi, R. (2020b). Data from "prey:predator ratio dependence in the functional response of a freshwater amphipod". *Figshare*: <https://doi.org/10.6084/m9.figshare.12937670.v1>.
- Mertz, D.B. & Davies, R.B. (1968). Cannibalism of the pupal stage by adult flour beetles: An experiment and a stochastic model. *Biometrics*, pp. 247–275.
- Mills, N.J. & Lacan, I. (2004). Ratio dependence in the functional response of insect parasitoids: evidence from *Trichogramma minutum* foraging for eggs in small host patches. *Ecological Entomology*, 29, 208–216.
- Montoya, P., Liedo, P., Benrey, B., Barrera, J.F., Cancino, J. & Aluja, M. (2000). Functional response and superparasitism by *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae), a parasitoid of fruit flies (Diptera: Tephritidae). *Annals of the Entomological Society of America*, 93, 47–54.

- Murdoch, W.W. (1969). Switching in general predators: Experiments on predator specificity and stability of prey populations. *Ecol. Monogr.*, 39, 335–354.
- Nachappa, P., Braman, S.K., Guillebeau, L.P. & All, J.N. (2006). Functional response of the tiger beetle *Megacephala carolina carolina* (Coleoptera: Carabidae) on twolined spittlebug (Hemiptera: Cercopidae) and fall armyworm (Lepidoptera: Noctuidae). *Journal of Economic Entomology*, 99, 1583–1589.
- Novak, M. & Stouffer, D.B. (2020). Data extracted for “Hidden layers of density dependence in consumer feeding rates”. *Figshare*: <https://doi.org/10.6084/m9.figshare.12830792.v1>.
- Oaten, A. & Murdoch, W.W. (1975). Switching, functional response, and stability in predator-prey systems. *Am. Nat.*, 109, 299–318.
- Okuyama, T. & Ruyle, R.L. (2011). Solutions for functional response experiments. *Acta Oecol.*, 37, 512–516.
- Omkar & Pervez, A. (2004). Functional and numerical responses of *Propylea dissecta* (Col., Coccinellidae). *Journal of Applied Entomology*, 128, 140–146.
- Prokopenko, C.M. (2020). Data from: Evaluation of alternative prey-, predator-, and ratio-dependent functional response models in a zooplankton microcosm. *Figshare*: <https://doi.org/10.6084/m9.figshare.12813209.v1>.
- Prokopenko, C.M., Turgeon, K. & Fryxell, J.M. (2017). Evaluation of alternative prey-, predator-, and ratio-dependent functional response models in a zooplankton microcosm. *Canadian Journal of Zoology*, 95, 177–182.
- Pusack, T.J. (2020). Size-dependent predation and intraspecific inhibition of an estuarine snail feeding on oysters. *Dryad Dataset*, <https://doi.org/10.5061/dryad.ffbg79crw>.
- Pusack, T.J., White, J.W., Tillotson, H.G., Kimbro, D.L. & Stallings, C.D. (2018). Size-dependent predation and intraspecific inhibition of an estuarine snail feeding on oysters. *Journal of Experimental Marine Biology and Ecology*, 501, 74–82.

- Ranta, E. & Nuutinen, V. (1985). Foraging by the smooth newt (*Triturus vulgaris*) on zooplankton: functional responses and diet choice. *The Journal of Animal Ecology*, pp. 275–293.
- Reeve, J.D. (1997). Predation and bark beetle dynamics. *Oecologia*, 112, 48–54.
- Reeve, J.D. (2020). Data from: Predation and bark beetle dynamics. *Figshare*: <https://doi.org/10.6084/m9.figshare.12784175.v1>.
- Rosenbaum, B. & Rall, B.C. (2018). Fitting functional responses: Direct parameter estimation by simulating differential equations. *Methods Ecol. Evol.*, 9, 2076–2090.
- Salt, G.W. (1974). Predator and prey densities as controls of the rate of capture by the predator *Didinium nasutum*. *Ecology*, 55, 434–439.
- Uttley, M.G. (1980). *A laboratory study of mutual interference between freshwater invertebrate predators*. Ph.D. thesis, University of York.
- Vahl, W.K., Van der Meer, J., Weissing, F.J., Van Dullemen, D. & Piersma, T. (2005). The mechanisms of interference competition: two experiments on foraging waders. *Behavioral Ecology*, 16, 845–855.
- Von Westernhagen, H. & Rosenthal, H. (1976). Predator-prey relationship between pacific herring, *Clupea harengus pallasi*, larvae and a predatory hyperiid amphipod, *Hyeroche medusarum*. *Fishery Bulletin*, 74.
- Vucetich, J.A., Peterson, R.O. & Schaefer, C.L. (2002). The effect of prey and predator densities on wolf predation. *Ecology*, 83, 3003–3013.
- Walde, S.J. & Davies, R.W. (1984). The effect of intraspecific interference on *Kogotus nonus* (Plecoptera) foraging behaviour. *Canadian Journal of Zoology*, 62, 2221–2226.
- Wasserman, R.J., Alexander, M.E., Dalu, T., Ellender, B.R., Kaiser, H. & Weyl, O.L. (2016a). Data from: Using functional responses to quantify interaction effects among predators. *Dryad Dataset* <https://doi.org/10.5061/dryad.4v2s0>.

- Wasserman, R.J., Alexander, M.E., Dalu, T., Ellender, B.R., Kaiser, H. & Weyl, O.L. (2016b). Using functional responses to quantify interaction effects among predators. *Functional Ecology*, 30, 1988–1998.
- Wong, M.C. & Barbeau, M.A. (2005). Prey selection and the functional response of sea stars (*Asterias vulgaris* Verrill) and rock crabs (*Cancer irroratus* Say) preying on juvenile sea scallops (*Placopecten magellanicus* (Gmelin)) and blue mussels (*Mytilus edulis* Linnaeus). *Journal of Experimental Marine Biology and Ecology*, 327, 1–21.
- Wong, M.C. & Barbeau, M.A. (2020). Data from: Prey selection and the functional response of sea stars (*Asterias vulgaris* Verrill) and rock crabs (*Cancer irroratus* Say) preying on juvenile sea scallops (*Placopecten magellanicus* (Gmelin)) and blue mussels (*Mytilus edulis* Linnaeus). *FigShare*: <https://doi.org/10.6084/m9.figshare.12780191.v1>.