

Linked exploitation and interference competition drives the variable behavior of a classic predator–prey system

John P. DeLong and David A. Vasseur

J. P. DeLong (jpdelong@unl.edu) and David A. Vasseur, Dept of Ecology and Evolutionary Biology, Yale Univ., New Haven, CT 06520-8106, USA. Present address for JPD: School of Biological Sciences, Univ. of Nebraska, Lincoln, NE 68588, USA.

The potential connection between exploitation and interference competition was recognized long ago but has not been evaluated. We measured the levels of both forms of competition for the protist *Didinium* preying upon *Paramecium*. Across populations, exploitation intensity was tightly linked to interference intensity, and the form of this relationship follows from a simple model of interaction speeds. The variation in interference competition was as large across populations of *Didinium* as has been observed previously across species from a variety of taxa including birds, mammals, insects, crustaceans, flatworms and protists. The link between exploitation and interference competition alters our understanding of how interference competition influences population dynamics. Instead of simply stabilizing systems, variation in interference levels can shift population dynamics through qualitatively different regimes because of its association with exploitation competition. Strong interference competition pushes a system to a regime of deterministic extinction, but intermediate interference generates a system that is stable with a high competitive ability. This may help to explain why the distribution of interference values is unimodal and mostly intermediate in intensity.

Competitive interactions influence foraging rates and the subsequent ability of organisms to support maintenance, growth and reproduction with food energy (Gause 1934, Park 1954). The nature and type of competitive interactions are thus of fundamental significance to ecological processes such as population dynamics and community assembly. Despite such importance, there is little clarity in the literature about the relative contribution of the two major types of competition – exploitation and interference – in driving ecological processes. A link between the two forms of competition was suggested long ago by Park (1954), but this possibility has received little empirical or theoretical attention.

Exploitation and interference competition jointly influence foraging rates (Fig. 1) (Hassell and Varley 1969, Salt 1974). Exploitation competition occurs when competitors reduce the amount of resource available in the environment, and interference competition reduces the amount of available resource that can be acquired due to the presence of competitors, even when resource levels are held constant (Park 1954, Smallegange et al. 2006). Therefore, foraging rates may be dependent on the density of both predators and their prey (Arditi and Ginzburg 1989, Abrams and Ginzburg 2000).

Existing functional response models can incorporate both forms of competition. The Holling disc equation, $f(R) = \frac{aR}{1 + abR}$, depicts a saturating foraging rate for a

consumer foraging on a resource species, R , with handling time, b , and area of capture, a (Holling 1959, van der Meer and Smallegange 2009). We will use the parameter a as a proxy for exploitation competition, for two reasons. First, a determines how much space a consumer can clear of resources per unit time (DeLong and Vasseur 2012a) and so is literally a measure of the rate of exploitation. Second, a also determines how quickly foraging rate drops with a decline in resource abundance. Any two species with the same b will have the same maximum foraging rate, but when R declines, the species with the highest a will experience a more rapid drop in foraging rate when prey density becomes low. In this way, a also characterizes the indirect effect of exploitation by competitors.

A common modification of the disc equation introduces interference competition as an exponent, m for ‘mutual’ interference, on consumer density that is added to both the numerator and denominator (Hassell and Varley 1969, Arditi and Akçakaya 1990, Skalski and Gilliam 2001, DeLong and Vasseur 2011):

$$f(R, C) = \frac{aRC^m}{1 + abRC^m} \quad (1)$$

The exponent m describes how fast foraging rates decline with the density of competing consumers, independent of resource levels. More negative values of m depress foraging rates to a greater degree, and therefore m is a measure of

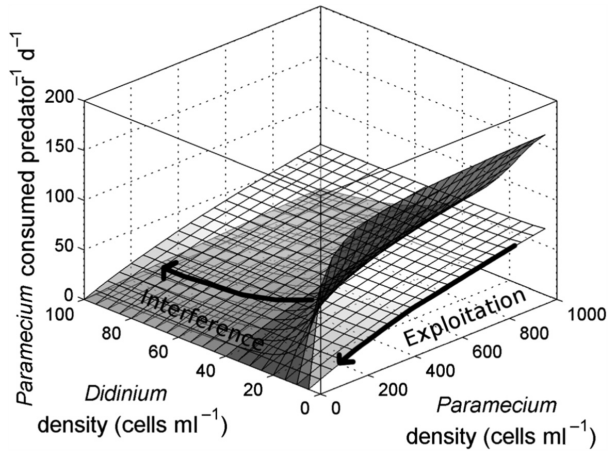


Figure 1. The effects of exploitation and interference competition on foraging rate. In this figure, foraging is portrayed as a function of both prey and predator density. Exploitation competition occurs along the x-axis, as reduced food availability reduces foraging rates according to the area of capture parameter, a . Interference competition occurs along the y-axis, as increased predator density reduces foraging rates according to the mutual interference parameter, m . Two different surfaces are shown, representing the extremes of the functional responses displayed by *Didinium* preying upon *Paramecium* in this study (Fig. 2, Table 1). The dark surface represents the experiment with the highest level of interference, whereas the light surface represents the experiment with the lowest level. Notice that the dark surface shows both a steep drop in foraging rate with predator density and a steep increase in foraging rate with prey density, while the reverse is true for the light surface.

interference competition intensity in the same way that a is a measure of exploitation competition. Equation 1 describes very well numerous data sets on foraging rates that vary with consumer and resource levels (DeLong and Vasseur 2011).

Mutual interference is often thought to vary among species or populations along a continuum from 0 to -1 (Abrams and Ginzburg 2000, Ginzburg and Jensen 2008, DeLong and Vasseur 2011). A compilation from the literature showed that mutual interference tends to be intermediate in this range, with a mode around -0.7 to -0.8 , but with some values as low as -2.5 (Fig. 2; after DeLong and Vasseur 2011, with additional data added, see figure legend). It is unknown why intermediate levels are most common, or why there is a unimodal rather than a bimodal or uniform distribution of values, but the pattern may suggest the existence of an underlying tradeoff.

It is unclear what generates mutual interference, although it is generally thought of as linked to physical encounters among competitors (Smallegange et al. 2006). Such encounters may be thought of as resulting from the same type of mass-action process that generates encounters between predator and prey. We therefore hypothesized that the level of interference competition could be linked to the magnitude of exploitation competition because both forms hinge upon the rate of encounters between individuals. Higher levels of exploitation ability require greater rates of encounter between predators and their prey (Aljetlawi et al. 2004), and increasing those encounters should increase the rate of

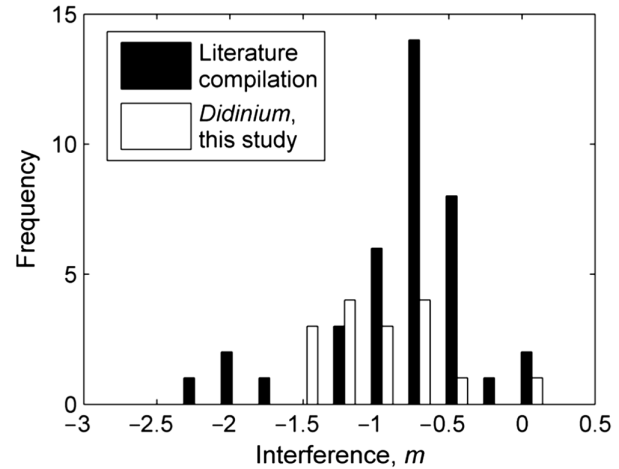


Figure 2. The distribution of interference values, m . Black bars are values from the literature, based on a compilation of values taken for arthropods, birds, mammals, fish, protists, and a flatworm, from DeLong and Vasseur (2011). Additional values were added to the original data set (Helgen 1987, Fussmann et al. 2005), following the methods in DeLong and Vasseur (2011). The mean of literature values was -0.8 ($SE = 0.09$, $n = 38$). White bars are values for *Didinium* from separate foraging experiments from this study. The mean of these values was -0.93 ($SE = 0.11$, $n = 16$).

competitor–competitor encounters as well. Thus, we predicted a link between the intensity of exploitation and interference competition, and therefore a negative relationship between a and m (interference is stronger when m is more negative).

We tested for within-species variation in exploitation (a) and interference (m) competition by conducting multiple experiments to quantify the functional response of the ciliate predator *Didinium nasutum* foraging on *Paramecium aurelia*. This classic predator–prey system displays a tendency to go rapidly extinct, but under some conditions – notably when the culture media is thickened such that the swimming speeds of the ciliates are reduced – the system displays oscillatory dynamics (Gause 1934, Luckinbill 1973, Salt 1974, Jost and Ellner 2000). We generated microcosms with a diverse range of environmental conditions, and then conducted independent foraging experiments on predators drawn from the different microcosms. Our data show that interference levels were indeed tightly linked to exploitation levels as predicted. Furthermore, we show mathematically that the precise relationship between a and m can be accounted for by random consumer interactions altering the consumer’s effective search velocity. Our interpretation is that high exploitation intensity imposes a considerable cost in the form of interference competition because the mass-action process that enables encounters between predators and prey also increases encounters among predators. Finally, we show that the link between a and m generates a range of dynamical patterns in which intermediate levels of interference and exploitation competition are likely to maximize competitive ability in an ecological context, explaining why most estimates of m are intermediate in magnitude.

Methods

Experimental methods

We acquired the ciliates *Didinium nasutum* and *Paramecium aurelia* (hereafter *Didinium* and *Paramecium*, respectively) from Carolina Biological Supply (Burlington, NC, USA). *Paramecium* was cultured in bottles at room temperature (23°C) with a mix of bacterial prey but initially inoculated with *Bacillus subtilis*. Multiple 50 mm-diameter plastic petri dishes were maintained with *Didinium* and *Paramecium* in an effort to generate a wide range of environmental conditions characterized by different culture age, prey and predator sizes, and nutrient levels. We took this approach because there is no prior information about what environmental factors are related to exploitation or interference levels within a species, so we could not a priori choose a method to generate variation in competition. Cultures of *Paramecium* were inoculated with *Didinium* and allowed to grow, and cultures were fed regularly with *Paramecium* pulled from different stock bottles to provide food of different quality and quantity. Cultures also were mixed to form new cultures with hybrid conditions.

We conducted foraging experiments by incubating 1, 2 or 4 *Didinium* cells under four levels of *Paramecium* density (a 3 by 4 factorial design) for about two hours (range, 1.5–2.5 h). In each of 16 experiments, *Didinium* were isolated from a single culture that had been allowed to grow undisturbed overnight (this is ~two generations). *Paramecium* stock cultures were first passed through a 70 µm cell strainer to remove bacterial flocs, and then *Paramecium* densities were varied by diluting the filtered stock culture with media from that culture passed through a 5 µm syringe filter. The target *Paramecium* densities were ~140, ~290, ~430, ~640 cells ml⁻¹, and our method ensured that bacteria levels, cloudiness and other environmental variables were kept constant across these different densities. Then, 0.05 ml of *Paramecium* culture was placed in the middle of a 50 mm petri dish, followed by 1, 2 or 4 *Didinium*, and covered with the lid of a 30 mm petri dish to make the cells in the drop easier to see and to minimize evaporation during the course

of the experiment. Drop volumes were maintained at the same level by adding the same amount of extra liquid regardless of how many *Didinium* were added (0.02 ml). The experiments were conducted over the course of a two-week period, with no more than three experiments conducted per day due to time constraints. Because of some consumer mortality, three of the 16 foraging experiments had less than the 12 target measurements (Table 1).

The number of *Paramecium* and *Didinium* were counted twice in each drop at the beginning and end of each foraging trial. The initial mean abundance of *Paramecium* was used as the quantity of resource, converted to densities given a volume of 0.07 ml. The mean between the beginning and end for *Didinium* was used as predator abundance, because of the occasional cell division, again converted to density given a volume of 0.07 ml. The number of *Paramecium* consumed was taken as the difference between the initial and final mean densities and was expressed as a per capita foraging rate given the duration of each trial and the mean number of *Didinium*. All data are included in Supplementary material Appendix A1.

Analytical methods

Because of prey depletion during the course of the experiment, we used a modified version of the random predator equation to analyze consumption rates (Rogers 1972, Bolker 2011):

$$R_c = R_0 - \frac{W(abR_0e^{-a(t-hR_0)})}{ab} \quad (2)$$

where R_c is the number of resource items eaten in time t , R_0 is the initial density of resource, and W represents the Lambert W function. We set $a = a_0C^m$, following the approach of Vucic-Pestic et al. (2011) and Lang et al. (2012). We treated each experiment as an independent trial, and the data from each trial was fitted separately to Eq. 2 to obtain independent estimates of the parameters a , m and h . We used the curve fitting toolbox in Matlab 2012b to fit Eq. 2 to each data set, using the least absolute residuals (LAR) robust option and constraining both a and h to be

Table 1. Results for each foraging experiment showing R^2 , sample size for run, and parameters (\pm 95% confidence interval) from Eq. 1. Some handling times were fixed at their limit in the fitting and thus have no cis.

Run	R^2	n	a (ml ind ⁻¹ d ⁻¹)	a 95% CIs	m	m 95% CIs	h	h 95% CIs
1	0.85	12	14.02	-96.26 to 124.3	-1.27	-3.1 to 0.57	0.010	-0.013 to 0.033
2	0.91	12	0.44	-0.55 to 1.43	-0.45	-0.94 to 0.05	0.004	-0.015 to 0.023
3	0.99	7	1.43	-1.45 to 4.32	-0.92	-1.42 to -0.42	0.008	0.0028 to 0.013
4	0.90	6	8.13	-5.88 to 22.15	-1.18	-1.77 to 0.60	1.62×10^{-13}	-
5	0.89	12	3.21	-3.19 to 9.61	-0.94	-1.42 to -0.47	0.002	-0.0082 to 0.012
6	0.80	12	0.79	-0.52 to 2.11	-0.62	-1.21 to -0.03	3.64×10^{-14}	-
7	0.86	11	1.81	-2.70 to 6.33	-0.68	-1.31 to -0.05	0.005	-0.001 to 0.011
8	0.96	12	1.23	0.42 to 2.04	-0.71	-0.93 to -0.48	2.23×10^{-14}	-
9	0.87	12	48.44	-151.3 to 248.2	-1.59	-2.60 to -0.57	0.019	0.01 to 0.028
10	1.00	12	13.40	9.35 to 17.45	-1.38	-1.49 to -1.27	3.68×10^{-14}	-
11	0.89	12	4.14	-13.3 to 21.57	-1.12	-2.22 to -0.03	0.003	-0.012 to 0.018
12	0.96	12	22.02	-27.93 to 71.97	-1.45	-2.1 to -0.79	0.006	0.0036 to 0.0081
13	0.97	12	4.87	-1.81 to 11.54	-1.16	-1.54 to -0.79	0.006	0.0024 to 0.0093
14	0.99	12	1.95	1.51 to 4.38	-0.85	-0.92 to -0.78	2.49×10^{-13}	-
15	0.93	12	1.08	-0.2204 to 2.37	-0.70	-1.11 to -0.29	2.34×10^{-14}	-
16	0.89	12	0.04	-0.0052 to 0.094	0.20	-0.12 to 0.51	2.67×10^{-14}	-

non-negative. We then used ordinary least squares regression to assess the relationship between $\ln(a)$ and m and Pearson's correlations to test for a relationship between b and both a and m . Given underlying uncertainty in the resulting parameter estimates, we conducted a full uncertainty analysis to evaluate the effect of error in the estimates of a and m on the slope of the relationship between these two variables (Supplementary material Appendix A2).

We extrapolated the effect of correlated exploitation and interference competition on the predator–prey dynamics of the system by solving a consumer–resource model for six different pairs of a and m that spanned the range of the a - m continuum (Results). The model was the MacArthur–Rosenzweig predator–prey model (Rosenzweig and MacArthur 1963, Hsu et al. 2008), commonly used to describe ciliate population dynamics (Vasseur and Fox 2009), modified by including Eq. 1 as the functional response:

$$\begin{aligned} \frac{dR}{dt} &= rR \left(1 - \frac{R}{K}\right) - C \frac{aRC^m}{1 + ahRC^m} \\ \frac{dC}{dt} &= eC \frac{aRC^m}{1 + ahRC^m} - \mu C \end{aligned} \quad (3)$$

where r is the maximum rate of population growth of the prey, K is the carrying capacity of the prey, e is the conversion efficiency of the predator, and μ is the natural mortality rate of the predator. The a and m pairs were determined by choosing a range of m values and using the fitted relationship between them to calculate the corresponding a . We also generated the predator and prey isoclines for each pair of parameters to overlay the temporal solution. Eq. 3 can be solved algebraically for the predator isocline: $C = \left(\frac{-\mu}{aR(\mu b - e)}\right)^{\frac{1}{m}}$.

In contrast, Eq. 3 cannot be solved algebraically for the prey isocline, so we numerically solved for this isocline over a range of prey values.

Values for the parameters used in the solutions and isoclines came from the observations on a and m as well as the estimates of b from these fits. The handling time was unrelated to either a or m (Results), and we therefore used in all simulations the mean value from the four fits where the confidence intervals of b did not include zero (Table 1; $\bar{b} = 0.008$ d). The values of K (841 cells ml⁻¹) and r (1.9 d⁻¹) were taken from previous work in our lab growing *Paramecium* under similar conditions (DeLong and Vasseur 2012b). The value of e (0.15) was taken as the mean from Veilleux (1979) as reported by Jost and Ellner (2000), which is close to other estimates for this species (Minter et al. 2011). The mortality parameter was estimated allometrically ($\mu = 0.1$ d⁻¹) using the data from Jackson and Berger (1984) re-analyzed in DeLong and Vasseur (2012a).

Results

We observed a wide range of interference competition levels across independent experiments (Table 1). The distribution of m values was broad and strongly resembled the unimodal distribution compiled from the literature for a wide range of

species (Fig. 2). Means of interference values did not differ significantly between the *Didinium* and literature samples ($t = 0.82$, DF = 52, $p = 0.42$). The extreme cases of no interference ($m = 0$) and values approaching -2 , as predicted by mass-action encounters, were observed both across species and within *Didinium*.

Levels of interference were positively related to levels of exploitation competition ($R^2 = 0.98$; Fig. 3; note again that m is negative). Increases in exploitation competition were accompanied by very rapid increases in interference intensity at first, but this relationship decelerated at higher levels of a and m , in a log-linear fashion. The value of a was not correlated with handling time ($r = 0.34$, $p = 0.20$), but m was slightly negatively correlated with handling time ($r = -0.51$, $p = 0.04$). The a - m relationship generated qualitatively different functional responses across experiments. Two pairs of a and m taken from either end of the continuum show the range of functional response shapes (Fig. 1).

The linking of a and m also generated qualitatively different types of population dynamics (Fig. 4). As the parameters moved along the a - m curve, the system transitioned from one with the slow stable attractor characteristic of the MacArthur–Rosenzweig model, toward a system with more rapid stabilization, and finally to one with rapid extinction. Along the a - m curve, the predator isocline shifts from a vertical line (characteristic of the MacArthur–Rosenzweig model) to one with an overall positive slope with interference that is concave up when $m < -1$ to straight when $m = -1$ and concave down when $m > -1$. The prey isocline shifts from one that is slightly negatively sloped close to the equilibrium point to one that is slightly positive. More importantly, because of the coupling of a and m , the height of the prey isocline drops as m increases, driving the intersection point of the isoclines to zero and generating deterministic extinction.

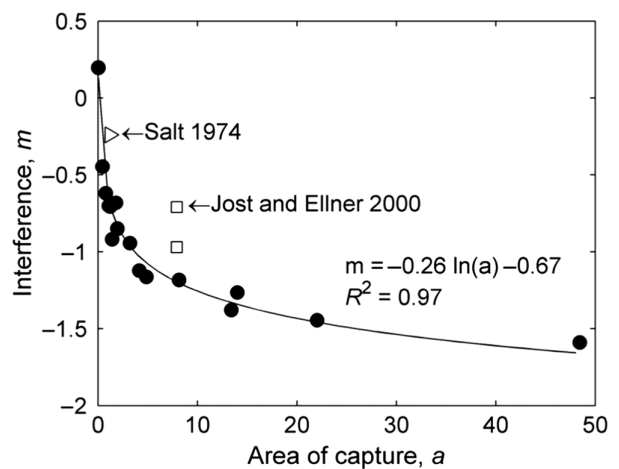


Figure 3. The relationship between level of exploitation competition, a , and interference competition, m , for *Didinium* preying upon *Paramecium*. Each point represents estimates of both a and m from an independent foraging experiment. The open triangle represents the study of *Didinium* and *Paramecium* by Salt (1974) re-analyzed in DeLong and Vasseur (2011), and the squares are data from Jost and Ellner (2000).

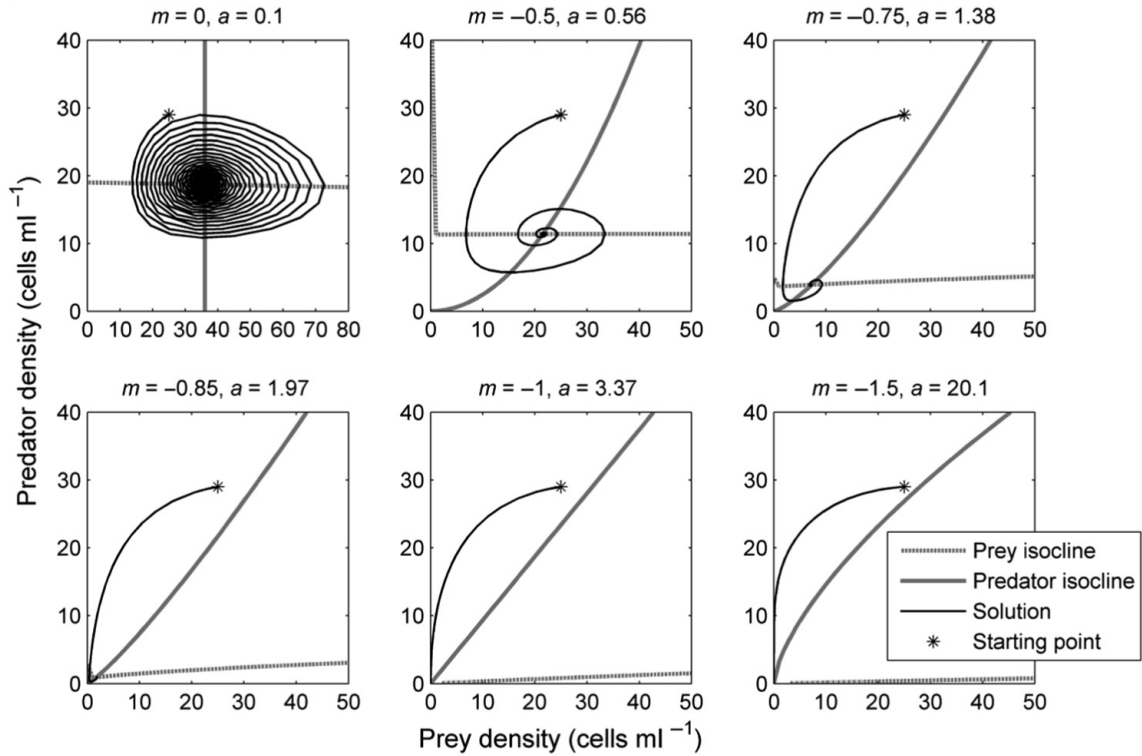


Figure 4. The changes in predator–prey population dynamics with correlated changes in the levels of exploitation and interference competition. From top left to bottom right, values of both exploitation (a) and interference (m) increase. The link between a and m is as empirically described in Fig. 3. The change from low competition to high competition generates a qualitative shift in dynamics, from one with the typical slow oscillatory dynamics of the MacArthur–Rosenzweig model to one with a more rapid stabilization to one that is characterized by deterministic extinction.

Discussion

Understanding the relative importance of exploitation and interference competition to ecological dynamics has been a challenge at least since Park (1954), who suggested that the two forms of competition might influence each other. How they influence each other, or even whether they are empirically linked, has remained unknown despite considerable research into both forms on their own. Here we showed that Park’s hunch was correct: the two forms of competition are tightly linked (Fig. 3). Using a series of independent foraging experiments with separate estimates of a and m across experiments, we demonstrated a tight positive link between exploitation (a) and interference (m) competition intensity in the *Didinium–Paramecium* predator–prey system. This pattern shows that as much variation in interference is possible within a species as among species (Fig. 2). This has significant implications for our understanding of the competitive structure of populations, and it indicates that point estimates of the magnitude of interference are insufficient to characterize a species.

We suggest that the correlation between a and m results from the fact that encounters both with resource items and other consumers depend on the same process of moving through space. Using the standard mass-action approach for deriving the area of capture parameter, we show that accounting for random interactions among consumers can generate a log-linear relationship between a and m following very

closely the pattern in Fig. 3. Area of capture (Aljetlawi et al. 2004, Pawar et al. 2012) is given by

$$a = A_d \sqrt{V_c^2 + V_r^2} \quad (4)$$

where V_c and V_r are the consumer and resource velocities, respectively, and A_d is the consumer’s area of detection, within which encounters lead to consumption events. Because search velocities are linear distances covered that actually enable encounters, they must decline with the presence of other consumers if interference is occurring. As with the random encounters between prey and predator, given by the product of R and C , random encounters among consumers can be characterized under mass-action by the product of C and C (C^2), which can be used to rescale V_c :

$$a = A_d \sqrt{\left(\frac{V_c}{C^2}\right)^2 + V_r^2} \quad (5)$$

This re-scaling makes a dependent upon C to a power whose value depends on the velocities. In the extremes, when V_r is 0, a depends on C^{-2} , and when V_c is 0, a depends on C^0 . Thus, Eq. 5 generates a dependence of a on C to an exponent x between 0 and -2 ($a \propto C^{-x}$), although x cannot be explicitly solved for unless one of the velocities is zero. Recognizing that the relationship between a and C generated from Eq. 5 is exactly that which modifies the disc equation in Eq. 1, the observed exponent x must be analogous to the

exponent m from Eq. 1. Note that when $C=1$, Eq. 5 collapses to Eq. 4, consistent with the notion that there must be at least two consumers for interference to occur. Importantly, Eq. 5 indicates that when V_c increases, both a and m (having identified m now as the emergent exponent) increase, which leads to a positive correlation between the two forms of competition.

We simulated this relationship in the following way to determine its shape. First, Eq. 5 produces estimates of both a and m , with a given explicitly and m found only by varying C and estimating its effect on a with regression. To do this, we set $A_d = 8.5$ and $V_r = 0.01$ (any set of non-zero parameters will work; here we selected values just to show it is possible to quantitatively find a match to the pattern in Fig. 3) and varied V_c from 0 to 8.4. For each level of V_c , we calculated a across a range of values of C (1–30) and regressed $\log(a)$ against $\log(C)$ to give an estimate of m as the slope of the regression line. Recall that the a in Eq. 1 is the maximum a , i.e. when $C=1$, so we therefore take the estimated m and the a when $C=1$ as our pair of points for that level of V_c . By varying V_c , we generated a data set of a and m values and examined the relationship between them. We compared that relationship to the observed relationship between a and m and found very strong correspondence between them (Fig. 5). Slight differences in the shape of the two curves may be due to additional variation in V_p , but our theory correctly predicts that a is positively correlated with m in an approximately log-linear fashion as observed. Although we do not have independent measures for any of these parameters in our system, the specific parameter values we used in the simulation do not alter this basic conclusion. This analysis also suggests that our experimental treatment induced variation in consumer speed across replicates. It is worth noting this new theory may be able to shed light on how and whether interference values should vary with temperature or body size (DeLong and Vasseur 2011).

Interference competition is typically viewed as having a strong stabilizing effect on population dynamics because it

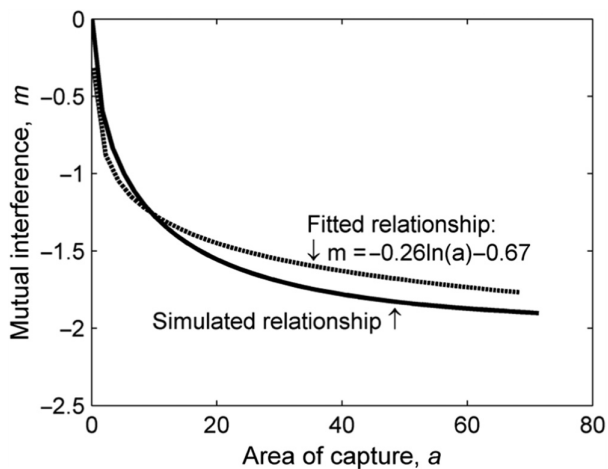


Figure 5. Simulated relationship between area of capture a and mutual interference m . Using Eq. 5, we varied the search velocity of the consumer and estimated the emergent m across a range of consumer densities. Given the underlying variation in velocity, a relationship emerged between a and m that closely mirrored our empirical results in Fig. 3.

tilts the predator isocline from a vertical line to one with a positive slope (Fig. 4) (Ginzburg and Jensen 2008, Hsu et al. 2008). It also may stabilize other kinds of interactions such as mutualisms (Wang et al. 2009). Theoretical studies, however, have varied the magnitude of interference competition independently of the parameters for exploitation competition, in particular area of capture. Our results indicate that interference and exploitation competition intensity are linked, which clearly alters the dynamical consequences of a change in interference. Instead of simply stabilizing the predator–prey system, increasing interference shifts the predator–prey dynamics from oscillatory, to one that is stabilized by interference, to one that shows deterministic extinction.

These dynamical shifts occur as a result of tandem movement of the predator and prey isoclines (Fig. 4). An increase in interference directly tilts the predator isocline to the right (Ginzburg and Jensen 2008), but it indirectly lowers the prey isocline through its connection to a . When interference is added independently of exploitation level, the system is stabilized by moving the equilibrium more to the right of the prey isocline’s hump (Rosenzweig 1971). But when interference is linked to exploitation, the equilibrium slowly moves to zero, removing the possibility of coexistence. This clarifies why the *Didinium–Paramecium* system shows different kinds of dynamics, from rapid extinction to stable oscillations (Luckinbill 1973, Veilleux 1979). With the addition of a thickening agent to the media, Luckinbill and Veilleux slowed the consumer search velocity. According to our new theory, this would have lowered both a and m , moving the system closer to the MacArthur–Rosenzweig idealism rather than a stabilized system with low a and high m . Similarly, our re-analysis of Salt’s data (DeLong and Vasseur 2011) produced estimates of a and m that place them in the area of stable oscillations along our curve (Fig. 3), which is what was observed in his study. Jost and Ellner’s (2000) re-analysis of Veilleux’s data indicated more intermediate levels of both interference (–0.6 to –1) and exploitation (S. P. Ellner pers. comm.) along with stable oscillations, but still in the range expected to produce them.

Our observations of a qualitative shift in dynamics also suggest why intermediate levels of interference competition are most common. Increasing a and m from low values stabilizes the system over a certain range, but raising them to a point above the most common values observed in the literature (–0.8 to –0.9) shifts the system to one that is deterministically driven to extinction. Furthermore, intermediate values of interference are those that lower the predator’s R^* – steady-state resource levels that are thought to reflect competitive ability at a population level – to the greatest degree (Fig. 4) (Tilman 1982). This effect can be seen in Fig. 4, bottom left panel, which shows a very low resource density at the stabilized steady-state at intermediate levels of m (in this panel $m = -0.85$), which is how R^* competitive ability is identified. Thus, intermediate interference maximally stabilizes a system without driving it to extinction, and simultaneously gives it a competitive edge against other populations. Given that extant populations must be competitive without going extinct, we suggest that intermediate levels of interference are those that most often allow species to pass through competitive ecological filters.

In showing the direct connection between exploitation and interference competition, we also reinforce the necessity of considering interference competition for trophic interactions in general. Interference is generally avoided when attempting to construct models of population dynamics, communities, and food-webs. For example, recent advances considering non-trophic interactions are proceeding considering the effect of exploitation competition but not the effect of interference competition (Kéfi et al. 2012). About 95% of all studies that have measured mutual interference competition have found significant (non-zero) levels, and our results show that even some of the observed low levels may be context-specific and not species-level values. Our results show that broad attempts to understand ecological dynamics that avoid considering the effects of interference competition are likely to miss important dynamic behaviors (Fig. 4).

It is also possible that covariation in exploitation and interference competition may extend to variation among individuals within a population. Mutual interference is by definition a group-level trait, but variation in body size or other traits may cause variation in exploitation intensity among individuals, potentially altering interference intensity at the individual level. At this time, there is no information about how age, size, or other traits within a population could induce variation in interference intensity among individuals, and we have therefore focused on the effects of variation in mean levels of exploitation and interference competition across populations. Future work investigating the drivers of variation in competitive intensity could allow us to explore how variation in exploitation and interference intensity among and within populations would influence population and community level dynamics.

In conclusion, we have shown that interference competition is not species-specific but may vary as much within a species as across species. Exploitation competition is tightly coupled to interference competition, and we propose that the coupling may be due to random encounters between consumers reducing the search velocity of the consumer. This coupling of competition alters the dynamic consequences of interference competition relative to current ecological thinking. Finally, this link also may supply the answer to the question of why interference competition is mostly intermediate in magnitude. Given the importance of interference and exploitation competition to issues of coexistence and community processes in general (DeLong and Vasseur 2012b), further work disentangling the interference and exploitation effects on ecological and evolutionary processes seems merited.

Acknowledgements – JPD was supported by a Yale Univ. Brown Fellowship. We thank Gabrielle Corradino and Anastasia Linger for laboratory assistance, Stephen Ellner and Christian Jost for providing unpublished information on the area of capture parameter from the study of Jost and Ellner (2000), Björn Rall for assistance with fitting functional response models, and Daisaburo Shizuka and Pavel Kratina for editorial assistance.

References

Abrams, P. A. and Ginzburg, L. R. 2000. The nature of predation: prey dependent, ratio dependent or neither? – *Trends Ecol. Evol.* 15: 337–341.

- Aljetlawi, A. A. et al. 2004. Prey–predator size-dependent functional response: derivation and rescaling to the real world. – *J. Anim. Ecol.* 73: 239–252.
- Arditi, R. and Ginzburg, L. 1989. Coupling in predator–prey dynamics: ratio-dependence. – *J. Theor. Biol.* 139: 311–326.
- Arditi, R. and Akçakaya, H. R. 1990. Underestimation of mutual interference of predators. – *Oecologia* 83: 358–361.
- Bolker, B. M. 2011. *Ecological models and data in R*. – Princeton Univ. Press.
- DeLong, J. P. and Vasseur, D. A. 2011. Mutual interference is common and mostly intermediate in magnitude. – *BMC Ecol.* 11: 1.
- DeLong, J. P. and Vasseur, D. A. 2012a. Size-density scaling in protists and the links between consumer–resource interaction parameters. – *J. Anim. Ecol.* 81: 1193–1201.
- DeLong, J. P. and Vasseur, D. A. 2012b. Coexistence via resource partitioning fails to generate an increase in community function. – *PLoS ONE* 7: e30081.
- Fussmann, G. F. et al. 2005. A direct, experimental test of resource vs. consumer dependence. – *Ecology* 86: 2924–2930.
- Gause, G. F. 1934. *The struggle for existence*. – Williams and Wilkins, Baltimore (Reprinted 1964 by Hafner).
- Ginzburg, L. R. and Jensen, C. X. J. 2008. From controversy to consensus: the indirect interference functional response. – *Verh. Internat. Verein. Limnol.* 30: 297–301.
- Hassell, M. P. and Varley, G. C. 1969. New inductive population model for insect parasites and its bearing on biological control. – *Nature* 223: 1133–1137.
- Helgen, J. C. 1987. Feeding rate inhibition in crowded *Daphnia pulex*. – *Hydrobiologia* 154: 113–119.
- Holling, C. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. – *Can. Entomol.* 91: 293–320.
- Hsu, S.-B. et al. 2008. Global dynamics of a predator–prey model with Hassell–Varley type functional response. – *Discrete Continuous Dynamical Systems B* 10: 857–871.
- Jackson, K. M. and Berger, J. 1984. Survival of ciliate protozoa under starvation conditions and at low bacterial levels. – *Microb. Ecol.* 10: 47–59.
- Jost, C. and Ellner, S. P. 2000. Testing for predator dependence in predator–prey dynamics: a non-parametric approach. – *Proc. R. Soc. B* 267: 1611–1620.
- Kéfi, S. et al. 2012. More than a meal... integrating non-feeding interactions into food webs. – *Ecol. Lett.* 15: 291–300.
- Lang, B. et al. 2012. Warming effects on consumption and intraspecific interference competition depend on predator metabolism. – *J. Anim. Ecol.* 81: 516–523.
- Luckinbill, L. S. 1973. Coexistence in laboratory populations of *Paramecium aurelia* and its predator *Didinium nasutum*. – *Ecology* 54: 1320–1327.
- Minter, E. J. A. et al. 2011. Prey-dependent mortality rate: a critical parameter in microbial models. – *Microb. Ecol.* 62: 155–161.
- Park, T. 1954. Experimental studies of interspecies competition. II. Temperature, humidity and competition in two species of *tribolium*. – *Phys. Zool.* 27: 177–238.
- Pawar, S. et al. 2012. Dimensionality of consumer search space drives trophic interaction strengths. – *Nature* 486: 485–489.
- Rogers, D. 1972. Random search and insect population models. – *J. Anim. Ecol.* 41: 369–383.
- Rosenzweig, M. 1971. Paradox of enrichment: destabilization of exploitation ecosystems in ecological time. – *Science* 171: 385–387.
- Rosenzweig, M. and MacArthur, R. 1963. Graphical representation and stability conditions of predator–prey interactions. – *Am. Nat.* 97: 209–223.
- Salt, G. W. 1974. Predator and prey densities as controls of the rate of capture by the predator *Didinium nasutum*. – *Ecology* 55: 434–439.

- Skalski, G. T. and Gilliam, J. F. 2001. Functional responses with predator interference: viable alternatives to the Holling type II model. – *Ecology* 82: 3083–3092.
- Smallegange, I. M. et al. 2006. Disentangling interference competition from exploitative competition in a crab–bivalve system using a novel experimental approach. – *Oikos* 113: 157–167.
- Tilman, D. 1982. Resource competition and community structure. – Princeton Univ. Press.
- Vasseur, D. A. and Fox, J. W. 2009. Phase-locking and environmental fluctuations generate synchrony in a predator–prey community. – *Nature* 460: 1007–1010.
- van der Meer, J. and Smallegange, I. M. 2009. A stochastic version of the Beddington–DeAngelis functional response: modelling interference for a finite number of predators. – *J. Anim. Ecol.* 78: 134–142.
- Veilleux, B. G. 1979. An analysis of the predatory interaction between *Paramecium* and *Didinium*. – *J. Anim. Ecol.* 48: 787–803.
- Vucic-Pestic, O. et al. 2011. Warming up the system: higher predator feeding rates but lower energetic efficiencies. – *Global Change Biol.* 17: 1301–1310.
- Wang, R.-W. et al. 2009. Interference competition and high temperatures reduce the virulence of fig wasps and stabilize a fig-wasp mutualism. – *PLoS ONE* 4: e7802.

Supplementary material (available online as Appendix oik-00418 at <www.oikosoffice.lu.se/appendix>). Appendix A1–2.