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Variable outcomes of protist–rotifer competition in laboratory microcosms

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A laboratory experiment examined competition for bacterial food between a protist and a rotifer. The experiment utilized a randomized 2 × 2 factorial design (+/0 rotifer sp., +/0 protist sp.). When grown monospecifically, the rotifer *Philodina* sp. and the protist *Paramecium multimicronucleatum* were similar in terms of mean efficiency of bacterial grazing in batch culture. When cultured together, the identity of the dominant species varied: *Philodina* dominated 3 of 5 replicates, while *Paramecium* dominated the remaining 2 replicates. The variable competitive outcome is predicted by variation in mean grazing efficiency when each species is raised alone.

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Protists are the major consumers of bacteria in most aquatic systems (Fenchel 1987, Laybourn-Parry 1992), and assemblages of bacterivorous protists are often dense and diverse (e.g. Taylor 1979, Fenchel 1987). Small rotifers, *Daphnia*, and other zooplankton may also be important consumers of bacteria in some systems (Ross and Munawar 1981, Starkweather 1987, Pace and Funke 1991). This diversity of potential consumers creates the possibility of competition among bacterivores, and raises the question of what form such competition will take.

In the classical Lotka-Volterra competition model, the outcome of competition between two species depends on the relative magnitude of each species' intraspecific and interspecific effects (assuming their carrying capacities are equal). The possible outcomes are unilateral dominance by the stronger interspecific competitor, stable coexistence, or dominance with the identity of the dominant species depending on initial conditions. The Lotka-Volterra model is phenomenological in that it says nothing about the mechanisms (e.g. exploitation, interference) of competition. In contrast, mechanistic models (e.g. Monod 1950, Schoener 1976, Tilman 1982) predict the outcome of exploitative competition depends on how efficiently each competing species utilizes the resource. Monod (1950) and Tilman (1982) identify more efficient species as those able to persist at lower resource levels. These models predict that competition can result either in predictable dominance by the most efficient competitor or stable coexistence of equally efficient competitors. Variable outcomes (priority effects) of exploitative competition are only predicted if sufficiently strong interspecific interference occurs simultaneously (Schoener 1976).

The Tilman (1982) model successfully predicts the outcome of competition between freshwater algae for silicate and phosphate (e.g. Tilman 1978, 1982, Grover 1989) and between rotifers (*Brachionus* spp.) for algae (Rothhaupt 1988). Hansen and Hubbell (1980) found that the analogous Monod (1950) model correctly predicts the outcome of competition for tryptophan between microbial strains in chemostats, and that equally efficient competitors can coexist indefinitely on a single resource. Mechanistic models may also be useful for

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understanding the dynamics of species competing for bacteria. Contrary to Lotka-Volterra predictions, these models suggest that, if bacteria constitute a single resource, exploitative competition for bacteria will result either in predictable dominance by a single species or stable coexistence. Results of laboratory experiments with protists are somewhat inconclusive. Luckinbill (1979) was able to order 5 ciliate species by competitive ability unambiguously, and Hairston et al. (1968) did the same for 3 *Paramecium* strains. However, neither study included quantification of grazing efficiency. Balciunas and Lawler (1995) found coexistence of *Chilomonas* sp. and *Colpidium* sp. despite significant interspecific variation in grazing efficiency, but suggested that interference of the less efficient grazer (*Chilomonas*) with the more efficient grazer (*Colpidium*) might be responsible. Interference may also explain the coexistence of *Chilomonas* with *Tetrahymena* (Lawler 1993a). None of these studies examined the possibility that intraspecific variation in exploitative efficiency might affect competitive outcomes. The theoretical prediction that identically efficient competitors will coexist indefinitely depends on characterizing each competitor's exploitative ability with a single number (such as Tilman's (1982) R^*) with zero variance. Hansen and Hubbell (1980) confirmed this prediction under tightly controlled conditions which all but eliminated intraspecific variability. Zero variability is unrealistic, but should be an adequate approximation when competing species differ greatly in exploitative ability. However, in nature, poor competitors should be quickly weeded out, leaving only those species which are relatively evenly matched. This suggests that intraspecific variation may often affect competitive outcomes.

This paper reports the results of a laboratory experiment which tested whether the outcome of competition for food between freshwater bacterivores is predictable from efficiency of resource use. The experiment focused on competition between the ciliate *Paramecium multimicronucleatum* and the rotifer *Philodina* sp., which coexist in nature. The species competed for the bacterium *Enterobacter aerogenes*. We used a single species of bacterium to standardize experimental conditions and to guard against the possibility that different bacterial species might constitute different resources for the consumers. Bacteria conform to Tilman's (1982) assumptions concerning resource properties. They exhibit some renewal even at low resource levels, have self-damped renewal, and reach an equilibrial abundance in the absence of consumption. Both *Paramecium* and *Philodina* fit many common assumptions concerning resource consumers. Population growth of protozoa and rotifers in laboratory microcosms conforms reasonably well to simple differential equations (Gause 1934, King 1967, Vandermeer 1969) and both our species exhibit relatively simple behavior. The experimental conditions maximize the probability that the two species will compete exploitatively, but are not so tightly controlled as to eliminate intraspecific variation in exploitative ability.

Methods

The experiment consisted of a factorial, completely randomized design with four treatments: bacteria alone, bacteria + *Paramecium*, bacteria + *Philodina*, and bacteria + *Paramecium* + *Philodina*. All cultures contained *Enterobacter aerogenes*, a bacterium eaten by both consumers. Treatments were replicated 5 times, for a total of 20 cultures. All organisms were obtained from Carolina Biological Supply.

We conducted the experiment in 50-ml glass beakers containing 35 ml of liquid culture medium prepared according to the procedure of Lawler (1993b). A single Protozoan Pellet (Carolina Biological Supply) was crushed into 1 l of commercial spring water; this liquid was autoclaved and stored at 4°C. To prepare cultures, the liquid was warmed to room temperature, agitated (to suspend undissolved Pellet debris), and poured into sterile 50-ml beakers. One sterile wheat seed (Carolina Biological Supply) was added to each culture as a nutrient supplement. Cultures were inoculated with a single loop of *Enterobacter aerogenes*, capped with foil, and incubated at 37°C for 24 h to allow the bacteria to reach a sufficient density to support consumers.

After the incubation period, cultures were assigned randomly to consumer treatments. Consumers (10 each of *Paramecium* and/or *Philodina*, as appropriate) were added individually via micropipette. Consumers were drawn from monoxenic stock cultures grown on *E. aerogenes*. Monoxenic stock cultures were established by putting individual *Paramecium* and *Philodina* through three washings in sterile medium before adding them to cultures of *E. aerogenes*. After addition of consumers, each culture was re-capped with foil and randomly positioned in a 5×4 array on a lab bench at ambient light and temperature. The experiment ran for 30 d.

Bacteria were sampled twice, once immediately before inoculation of consumers and once at the end of the experiment to estimate how much consumers reduced resource levels. Bacteria were sampled by agitating a culture, extracting 5 µl of liquid with an automatic pipette, diluting as necessary, and plating 100 µl onto LB agar (Ausubel et al. 1987). LB agar is a general medium suitable for a wide variety of bacteria and should facilitate detection of bacterial contamination of the cultures by allowing growth of a variety of contaminating bacteria (Ausubel et al. 1987). Plates were incubated at 37°C for 24 h and the number of colonies counted.

Platings at the end of the experiment indicated that two of five two-species cultures became contaminated with low densities (<20% of colonies) of an unknown bacteria. The contaminating species was likely *E. coli*; it produced smooth-edged white colonies when plated on LB agar, a colony form consistent with *E. coli* (and similar to *Enterobacter aerogenes*). Contaminants were included in all counts.

Paramecium and *Philodina* were sampled at the end of the experiment by counting the individuals in 2 ml of culture. This was done after vigorously agitating each culture (including scraping the sides and bottom with a spatula to dislodge attached *Philodina*), extracting 200 µl with an automatic pipette, and placing the extracted volume in a microtiter plate well. This procedure was repeated to fill a total of 10 wells. *Paramecium* and *Philodina* were then counted live with an inverted darkfield microscope. When a species was absent from a culture to which it had initially been added, approximately 10 ml of that culture was poured onto a Petri plate and the plate scanned under low power to confirm the extinction of the species. Results were analyzed using ANOVA of natural $\log_{10}$-transformed response variables.

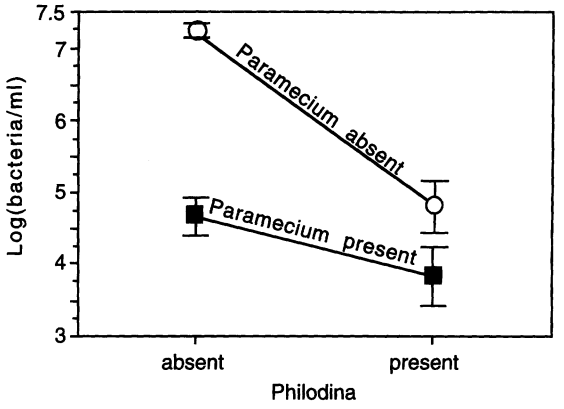

Fig. 1. Effect of *Paramecium mulitmicronucleatum* and *Philodina* sp., both alone and in combination, on densities of bacteria in batch culture. Initial presence/absence of *Philodina* is given on the *X* axis. Initial presence/absence of *Paramecium* is given by point type (open circles = absence, dark squares = presence). The *Y* axis shows mean $\log_{10}$-transformed abundance/ml of food bacteria. Error bars are ± SE.

Results

We analyzed bacterial densities as (log(abundance/ml) and consumer densities as (log((abundance/culture)+1)). Before addition of consumers, mean log-transformed bacterial density in the consumer-free cultures was 8.042 ± 0.211 (mean ± 1 SE). At the end of the experiment, bacterial densities in consumer-free cultures averaged 7.242 ± 0.102, a significant, though small, decline from initial densities (paired *t*-test, df = 4, P = 0.0302). When cultured alone, both *Paramecium* and *Philodina* significantly reduced bacterial densities below final densities in consumer-free cultures (Fig. 1, Table 1). When cultured together (hereafter, "mixed-species cultures"), the two consumers interacted to reduce bacteria to significantly lower densities than would have been predicted from their effects when grown alone (Fig. 1, Table 1). Final bacterial densities did not differ significantly between cultures containing either *Paramecium* or *Philodina* alone, although on average *Paramecium* reduced bacteria to a lower level (one-factor ANOVA, $F_{1,8} = 0.089$, $P = 0.7728$) (Fig. 1).

Since *Paramecium* and *Philodina* exhibited similar values of grazing efficiency when cultured alone (Fig. 1), we calculated the conditional probability of each species dominating a mixed-species culture, given the actual values of grazed bacterial densities seen in the 5 replicates of each grazer population. Mechanistic competition theory predicts that the dominant species will reduce bacteria to the lower level (Monod 1950, Tilman 1982). Let P_i = final bacterial density in *Paramecium* culture i and R_j = final bacterial density in *Philodina* culture j where $i, j = 1-5$. The probability of domination by *Paramecium* may be computed as the probability, for a randomly chosen P_i, that a randomly chosen R_j has a greater value, summed over all i. More formally,

Table 1. Effect of resource competition on densities of bacteria and bacterivores (*Paramecium multimicronucleatum* and *Philodina* sp.). Crossed, 2-factor design: *Paramecium* (initially present or absent) and *Philodina* (initially present or absent). "*Para.* × *Phil.*" denotes the interaction term. Bacteria were analyzed as $\log_{10}$-transformed abundance/ml. Consumers were analyzed as $\log_{10}$-transformed abundance/culture. For analysis of *Paramecium* and *Philodina* densities, only those cultures initially containing the consumer were included.

Dependent	Independent	df	SS	*F*	Pr > *F*
Bacterial density	*Paramecium*	1	15.797	35.592	≤0.0001
	Philodina	1	13.427	27.704	≤0.0001
	Para. × *Phil.*	1	3.209	6.622	0.0204
	Error	16	7.755		
Paramecium density	*Philodina*	1	2.643	12.774	0.0100
	Error	8	1.655		
Philodina density	*Paramecium*	1	0.523	0.989	0.3490
	Error	8	4.230		

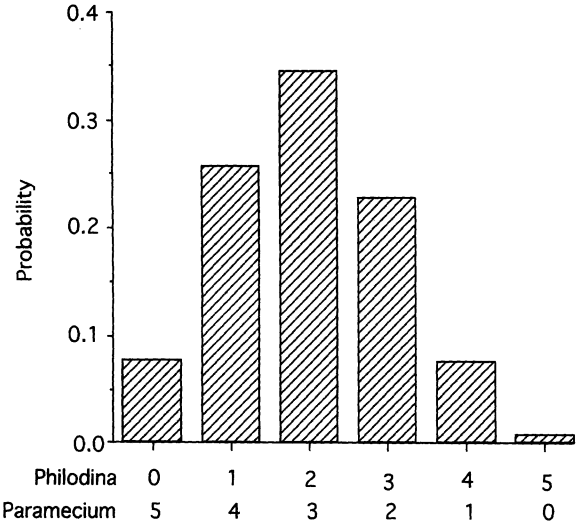

Fig. 2. Binomial probability distribution for the number of mixed-species cultures dominated by *Philodina* and *Paramecium*. The *X* axis gives the number of cultures dominated by each species. The *Y* axis gives the probability of each combination of outcomes, assuming binomial probabilities of 0.6 (domination by *Paramecium*) and 0.4 (domination by *Philodina*).

$$\sum_{\text{all } i} P(R_j > P_i \mid P_i) \quad (1)$$

The resulting probability of domination by *Paramecium* is 0.6 and the probability of domination by *Philodina* is 0.4.

We used binomial expansion of the probabilities generated by Eq. (1) to estimate the probability of *Philodina* dominating a given number of the 5 mixed-species replicates:

$$P(x) = n!/[x!(n-x)!]p^x(1-p)^{n-x} \quad (2)$$

where p denotes the probability of *Philodina* dominating ($=0.4$), x denotes the number of replicates dominated by *Philodina* and n denotes the total number of replicates ($=5$). The resulting probability distribution is given in Fig. 2. The distribution indicates that the most likely outcome of competition is *Paramecium* dominating 3 of 5 mixed-species cultures and *Philodina* dominating the other 2 ($P = 0.346$).

Philodina and *Paramecium* attained similar abundances when cultured alone (one-factor ANOVA, $F_{1,8} = 0.647$; $P = 0.4444$) (Fig. 3). When cultured together, *Philodina* attained higher abundances than *Paramecium* in 3 of the 5 cultures, while *Paramecium* attained higher abundances than *Philodina* in the remaining 2 cultures (Fig. 3). Eq. (2) gives the probability of this outcome as 0.230. The identity of the dominant species did not depend on bacterial contamination: *Paramecium* dominated one contaminated culture, *Philodina* the other. *Philodina* reduced *Paramecium* abundances in all 5 replicates below the lowest abundance attained by *Paramecium* alone, a significant difference (Fig. 3, Table 1). *Paramecium* had no significant effect on *Philodina* abundance; it reduced *Philodina* abundance below the lowest value attained by *Philodina* alone in only 2 of 5 replicates (Fig. 3, Table 1). The identity of the dominant consumer had no significant effect on final bacterial density (one-factor ANOVA, $F_{1,3} = 3.866$; $P = 0.1440$).

In both of the mixed-species cultures where one consumer species was absent from the 2-ml sample used to quantify consumer abundances, the absent consumer was present when an additional $\approx$10-ml of culture was scanned under low power. *Paramecium* was absent from one 2-ml sample; 2 individuals were seen in the subsequent 10-ml sample. *Philodina* was absent from one 2-ml sample; 4 individuals were seen in the subsequent 10-ml sample. Note that 10-ml samples were used only to confirm apparent extinctions. Because the volume examined in these samples was only approximate, the samples cannot be used to compute accurate whole-culture abundances.

Discussion

Mechanistic resource competition theory predicts that equally efficient species should coexist indefinitely (Monod 1950, Hansen and Hubbell 1980, Tilman 1982). Instead a variable outcome occurred: competition between *Philodina* sp. and *Paramecium multimicronucleatum* resulted neither in unilateral dominance nor coexistence. This variable outcome probably occurred because both consumers exhibited overlapping intraspecific variation in grazing efficiency. Mechanistic theories assume that a population's efficiency can be represented by a single value such as R^* (Tilman 1982). In our system, the competing species' similar mean efficiencies

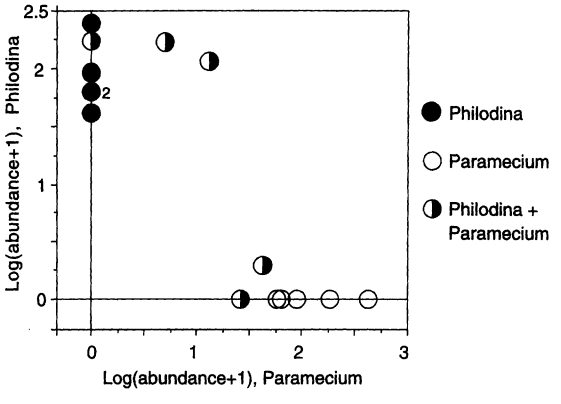

Fig. 3. Initial and final abundances of *Paramecium multimicronucleatum* and *Philodina* sp. The *X* and *Y* axes give $\log_{10}$-transformed abundance/culture of *Paramecium* and *Philodina*, respectively. Each point represents a single batch culture. One of the points, denoted by "2", represents a pair of identical values.

did not guarantee coexistence, since each species' efficiency varied slightly between cultures, probably due to slight variation in initial conditions and environmental factors. In nature, initial conditions and environmental factors vary greatly, making coexistence of similarly efficient species quite improbable in the absence of countervailing factors promoting coexistence.

Several alternative hypotheses do not fit our results. Possibly, since both consumers were still present in all mixed-species cultures at the end of the experiment, one of the two species might eventually have come to dominate all 5 replicates. However, *Paramecium multimicronucleatum* and *Philodina* sp. have short generation times (<48 h). In single-species cultures, both protists and rotifers multiply quickly to an equilibrium density and remain at that density for extended periods of time (e.g. Lawler and Morin 1993, Morin and Lawler 1995). In mixed-species cultures of exploitatively competing bacterivores, weaker species decline steadily to extinction (e.g. Gause 1934, Hairston et al. 1968, Vandermeer 1969). This makes it unlikely that either species' density was fluctuating dramatically. This also means that measured final bacterial densities likely represent equilibrium values. It is also unlikely that the rare species in the mixed-species cultures would have eventually increased to dominance. Prior work on competition among protozoa and rotifers in laboratory microcosms, and algae in chemostats, indicates that, after 30 d, the mixed-species cultures were likely asymptotically approaching equilibrium – most probably a single-species equilibrium (Gause 1934, Hairston et al. 1968, Vandermeer 1969, Gill 1972, Sommer 1983, 1985, Rothhaupt 1988). The rare species in each culture was probably on its way to exclusion, not domination. Even had it persisted at low levels for some time, the variability in the identity of the dominant species would remain. This variability in outcome is difficult to explain with mechanistic models which do not include intraspecific variation.

The presence of bacterial contamination in two of the mixed-species cultures cannot explain the variable outcome of competition. *Paramecium* and *Philodina* each dominated one of the two contaminated cultures. Tilman (1982) did propose that the outcome of exploitation competition between a pair of species will be variable when two potentially limiting resources are present and each consumer utilizes proportionately more of the resource that limits its competitor. The contaminating bacterium may have served as a second resource. Bacteria are known to differ in edibility to protozoa (Taylor and Berger 1976, Chrzanowski and Simek 1990), and different bacterial morphologies may vary in grazer resistance. However, both *E. coli* and *Enterobacter aerogenes* are non-toxic, gram-negative rods, and it is unclear why the two consumers used here would be differentially limited by similar bacteria species.

Alternatively, interactions may have involved more than resource competition. Schoener (1976) predicts the unstable outcome seen here when strong interspecific interference is present. We observed no predation or physical interference (e.g. interspecific avoidance) during extensive examinations of stock cultures containing both species. Certain protozoa, including species of *Paramecium*, are thought to inhibit one another through chemical secretions such as waste products (Gause 1934, Habte and Alexander 1978, Balciunas and Lawler 1995) or through bacterial endosymbionts (Gill 1972). If both *Philodina* and *Paramecium* inhibit each other chemically more than they inhibit themselves, then the first species to gain a slight numerical advantage in a mixed-species culture would come to dominate the culture, assuming the degree of inhibition to be proportional to the population density of the inhibiting species (Rothstein 1979). Although we cannot exclude the possibility of chemical interference, we have no positive evidence of it, and observed variation in grazing efficiency is sufficient to produce the observed competitive outcomes.

Because we kept the cultures covered during the experiment in order to prevent bacterial contamination, we could not renew nutrients through periodic addition of wheat seeds, as was done in similar studies (e.g. Lawler 1993b). As a result, bacteria declined during the experiment. However, the consumers were still able to grow, reproduce, and reduce bacteria well below the final densities exhibited in consumer-free cultures. The slight bacterial decline probably affected all cultures in a similar manner and cannot explain the variable competitive outcome.

Based on variation in grazing efficiency in the single-species cultures, we predicted that *Philodina* would dominate 2 of the 5 replicates. Although the observed outcome was not the most likely one ($P(3) = 0.230$), it is not substantially less probable than the most likely ($P(2) = 0.346$) (Fig. 3). The important point is that the outcome was variable, which suggests that local coexistence of equal competitors, just because they are equal, is not a biologically realistic possibility.

The result raises interesting issues concerning the structure of natural assemblages of exploitative competitors. It contrasts to the result of Hansen and Hubbell (1980), who obtained coexistence between two auxotrophic bacterial strains competing for tryptophan in continuous culture. Hansen and Hubbell (1980) precisely controlled the competitive efficiencies of their strains with additions of nalidixic acid. Under the less controlled conditions used here, species similar in mean efficiency failed to coexist. Local coexistence of similar species should be even less likely under uncontrolled natural conditions, because variation in efficiency should be greater. The theoretical possibility of identically efficient species coexisting locally in a fine-grained, homogeneous environment is unlikely to be important in practice. However, environmental heterogeneity in space and/or time might permit regional coexistence by

allowing different species to dominate different patches or altering the competitive hierarchy before exclusion occurs (Hutchinson 1961, Chesson 1986). Eddison and Ollason (1978) found that microcosms subjected to fluctuating temperatures (2–12°C/2 d) exhibited higher ciliate diversity than constant temperature controls (7°C), possibly because the relative competitive abilities of the ciliates varied with temperature (Gill 1972, Caron et al. 1986, Laybourn-Parry 1992).

Variation in the composition of communities which share a common source pool is often attributed to priority effects (e.g. Drake 1991). We have shown that such variability can also result when exploitative competitors exhibit overlapping intraspecific variation in efficiency of resource use. While the outcome of such competition will not be predictable in any given community, predicting the proportion of communities in which one competitor will dominate or exclude its rival may be possible.

Intraspecific variation in competitive ability is not unique to bacterivores. The exploitative (and interference) abilities of other taxa are known to vary with environmental conditions (e.g. Park 1954, DeBach and Sundby 1963). Whatever the mechanism, competitive ability is a property of the combination of a species and its environment, and is likely to vary in space and time.

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