

THE CONTRIBUTION OF LABORATORY EXPERIMENTS ON PROTISTS TO UNDERSTANDING POPULATION AND METAPOPOPULATION DYNAMICS

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Holyoak, M., and S. P. Lawler 2005. The contribution of laboratory experiments on protists to understanding population and metapopulation dynamics. *Advances in Ecological Research*, Vol. 37: Population Dynamics and Laboratory Ecology **37**:245-271.

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Running headline: Protozoan laboratory population experiments

Abstract

Several breakthroughs in ecological understanding of population dynamics have arisen through use of protists as model systems. The combination of rapid generation times, being large enough to count and small enough to manipulate make heterotrophic protozoa unparalleled in their utility for studies of population dynamics. Gains in understanding have come from three main areas: using laboratory experiments to test theory, developing new models to explain experimental results, and iterative rounds of model development and experimental testing. We review the contribution of protist experiments to population regulation, population responses to extrinsic perturbations, the role of space and habitat patchiness in creating predator and prey persistence, single species source-sink dynamics, and the stability of food chains with omnivores and intraguild predation, across productivity gradients. The results show that laboratory experiments with protists have played a key role in development and popular acceptance of a wide range of central theories in population ecology. We review these roles and also highlight new areas where protist model systems could provide similar advances.

Introduction

Laboratory experiments using heterotrophic protozoa have been central in the development of theory in population dynamics. There is a long tradition of ecologists using heterotrophic protists in microcosms to test ecological theory, beginning with classic research on competition models (e.g., Gause 1934, Vandermeer 1969; reviewed by Lawler 1998). Recently, an increasing number of researchers have been constructing simple food webs of protists and bacteria that are helping us understand the dynamic consequences of common food web modules, like linear food chains (e.g. Kaunzinger and Morin 1998), apparent competition (Lawler 1993), and intraguild predation (Morin 1999; Diehl and Feissel 2000). More complex protist assemblages have also been used in important tests of the relationship between biodiversity and ecosystem functioning (e.g., McGrady-Steed et al. 1997, Naeem and Li 1998). Here we concentrate on the utility of heterotrophic protists for studying population dynamics and do not extend beyond studies of three species food web modules. Our main aim is to illustrate the kinds of gains in our understanding of population dynamics that have been made as a result of laboratory experiments using protists, largely from the Kingdom Protozoa. We do not attempt to cover the large body of excellent work using autotrophic protists (algae). These studies often address different branches of ecological theory and because of space constraints, we elected to cover fewer topics in more detail.

A major problem that has arisen in ecology, starting in the 1920's and still carrying on today is the increasing gap between the development of ecological theory and empirical knowledge. The root of this problem was captured by So Fontanelle (1686; quoted in Kingsland 1995): "Grant a mathematician one little principle, he immediately draws a consequence from it, to which you must necessarily assent, and from this consequence another, till he leads you so far (whether you will or no) that you have much ado to believe him." As ecologists we might question whether the initial principle is correct and whether the elaboration of it is done in a biologically reasonable way. The outstripping of experimental tests by ecological theory is echoed by Kareiva (1989) who titled his paper "Renewing the dialogue between theory and experiments in population ecology" and proceeded to present an agenda for doing just this.

Laboratory experiments are done for many reasons and they represent just one part of a larger ecological literature (e.g., Resetarits and Bernardo 1998). In using laboratory experiments, ecologists may be endeavoring to understand particular field situations (e.g., Schindler 1998), to test and develop general ecological theory, or to test the effects of novel treatments. Novel

treatments often involve cases where there is no existing theory that is precise in its predictions, and the experimental results are intrinsically interesting because of interest in the treatment (e.g., effects of global warming on biodiversity and ecosystem functioning; Petchey et al. 1999). For tests of mechanisms to explain particular phenomena observed in the field, recent papers suggest that dimensional analyses and scaling rules can be used to improve the design of small scale experiments (e.g., Petersen and Hastings 2001, Englund and Cooper 2003). We do not address this topic further here, rather, we focus on the use of microcosm experiments to test general theory. The challenge posed for microcosm tests of theory is whether results “scale” between experiments at different spatial and temporal scales, or between the laboratory and field, thus providing good tests of general ecological principles (e.g., Gardner et al. 2001, Naeem 2001, Englund and Cooper 2003). Many ecologists recognize that there is a real need for model systems in ecology that are realistic for the organisms being studied, so that they will reflect ecological principles that also act in more natural systems and at larger scales.

In this review we begin by describing why protists make appropriate study organisms for laboratory population experiments. Next we describe some of the early work of Gause (1934), which provides a rich array of examples of testing and development of theories that are now regarded as the core of population ecology. We move onto the influence of density dependent feedback and extrinsic perturbations on populations, integrating early results with ongoing research. Next we expand to two species, predators and their prey, and review the effects of space and habitat patchiness on persistence and the insights gained from a search for persistence mechanisms. We briefly review laboratory experiments on source and sink dynamics, a topic that has proven difficult to explore in the field and offers much potential for future research. We end by expanding to studies of intraguild predation and review a variety of experimental work that develops close links with mathematical models and leads us in the direction of community ecology. We attempt to capture the state of knowledge in these areas and indicate directions that might prove fruitful for future study, especially in those areas where protist model systems indicate that field tests of theory might be productive. The theme that emerges is that researchers start with a theory, test it with the protist system, and these tests lead either to field studies, improved models, or both.

Protists as Model Systems

The diversity of protists means that there is a rich variety of species and traits to “mine” for suitable model systems. A recent estimate puts the number of protist species at 213,000, and rising as their taxonomy progresses (Corliss 2002). Taxonomically, protists are a heterogeneous group of single-celled (but sometimes colonial) eukaryotic organisms. According to Corliss (2002), these sophisticated cells are distributed among no less than five Kingdoms, two of which are dominated by non-colonial taxa. These are the Chromista (including zoosporic protists, opalinids, diatoms, some phytoflagellates), and the Kingdom Protozoa, which includes some of the best known, most diverse groups such as the ciliates, amoeboids, euglenoids, dinoflagellates, foramaniferans and radiolarians. Other single-celled or colonial eukaryotes lie within the Plantae (e.g., *Volvox*), Fungi (microsporidians), and Animalia (myxosporidians). The diversity of protists corresponds to a wealth of opportunity for study. Protists are also extremely important to the biosphere, because they are responsible for 40% of the earth's photosynthesis and almost all marine productivity (Reviewed by Corliss 2002). They have vital roles in terrestrial and freshwater ecosystems, especially in maintaining soil fertility and lake clarity through grazing bacteria.

The convenience of studying protists is difficult to overstate. Normal protist behaviors and even some intracellular processes can be easily observed under the microscope. Hundreds of generations of population dynamics may be observed within a few weeks. Thousands can be sacrificed in the name of science with nary an animal care protocol nor animal rights protestor in sight. Problems do occur, including contamination of cultures, cryptic species, difficulties in identifying field collected materials, and laboratory artifacts extraneous to the hypothesis being tested. With extra care, effort, and thought, most of these can be overcome. However, investigators would be wise to learn the biology of their species to guard against artifacts. Some aspects of biology differ from many other eukaryotes. For example, because they reproduce by fission, maternal effects are strong and can last more than one generation. Their sexual systems differ from many other organisms because they often involve several mating types, and sex is optional in more protists than in other eukaryotes (Bell 1988).

We believe that ecologists have only scratched the surface of ecological questions that can be asked using protists. Protists make convenient analogs of multicellular organisms that use similar ecological strategies, and have some adaptations that are worth studying in their own right. Protists have solved an enormous number of ecological and evolutionary challenges, all using single cells and occasionally cooperative behavior. Many perform DNA repair to such a level that a cell is potentially immortal (Bell 1988), while others senesce and die. Many form resting cysts, allowing study of “storage effects” (Chesson and Huntly 1997, e.g., McGrady-Steed and Morin 1997). Protists include producers, consumers, omnivores, internal and external parasites, and mutualists—and they possess a staggering number of adaptations to fill these trophic roles. Predators can select prey (Rapport et al. 1972, review: Laybourn-Parry 1988); prey can launch defenses that are specific to particular predation risks (Kusch 1993). There are sit-and-wait predators, active hunters, bottom feeders, filterers, engulfers and grazers. In short, convenient protistan models can be found for a host of important ecological traits, but this will only occur if ecologists learn more about them.

Of course not all ecological questions can be addressed with protists, and not all traits have protist analogs. Some questions can only really be answered within a particular system that one wants to understand. Nevertheless, there is a long tradition of successful protist models in ecology (Laybourn-Parry 1984; Kingsland 1995) which can be greatly expanded upon. The diversity of biologies possessed by protists sometimes causes them to have dynamics that are different from those predicted by simple models. However, these departures from theoretical expectation may reveal the importance of widespread aspects of biology that are absent from current models and which could usefully be added to them.

Early Experiments with Protozoa and the Birth of Population Ecology

Experiments with protozoa were central to the early development of population dynamic theory and for giving field ecologists more confidence in the validity of mathematically formulated theories, which they then tested in the field. The work of a Russian, G. F. Gause was central to this early progress. Gause’s work gives us several examples of experimental tests of theories that are central to modern day population ecology and also at least two examples where experiments led to what is now recognized as increased realism in mathematical models.

During the 1920’s the recently described logistic equation was controversial because the curve had not been tested even for short-term predictions and the main audience for it, demographers, were interested in long-term predictions. The curve was regarded as overly simplistic and detractors were suspicious because Pearl and Reed (1920) presented it as a generally applicable law with predictive ability. Gause set out to validate the Logistic equation

using bottle populations of a ciliate *Paramecium caudatum* and yeast, both of which he regarded as simplistic compared to field populations (Gause 1934). Through repeatedly censusing 63 replicate growing populations and plotting numbers against time he produced a very smooth S-shaped curve (Gause 1934). Hutchinson (1978) commented that an s-shaped curve was weak proof for the logistic theory and also likened populations of protists to an analogue computer: “What we have indeed done is to construct a rather inaccurate analogue computer for giving numerical solutions of our equation, using organisms for its moving parts. When we find that we have confirmed the logistic, what we have mainly confirmed is that the reduction in the rate of population growth is linearly dependent on the relative density of organisms. Actually, the beautiful S-shaped integral curve may be too insensitive a result to tell us how well we have established this conclusion.” Hutchinson (1978). It is not clear what Hutchinson would have regarded as an adequate test of the theory.

Gause came up with a creative and stronger test for the logistic theory. He did this by deriving equations with the same form as the logistic equation [$dN/dt=rN((K-N)/K)$], but which also included competition in a similar way to the recently-described Lotka-Volterra competition model (Volterra 1926; Lotka 1932):

$$\frac{dN_1}{dt} = rN_1 \frac{K_1 - (N_1 + \alpha_{1,2})}{K_1},$$

$$\frac{dN_2}{dt} = rN_2 \frac{K_2 - (N_2 + \alpha_{2,1})}{K_2},$$

where N_i are numbers of species i , r_i are intrinsic growth rates, and K_i are carrying capacities. The terms $\alpha_{1,2}$ and $\alpha_{2,1}$ are competition coefficients that modify the logistic equation to scale the effects on the growth rate of the target species of individuals of the other species. Gause then used two ciliates, *Paramecium aurelia* and *Stylonychia pustulata*, to experimentally test the principle of competitive exclusion for species utilizing a single resource. By testing whether extinction of one species resulted when two species were grown on a single resource, Gause succeeded in simultaneously demonstrating the utility of the logistic model and the competitive exclusion principle. Kingsland (1995) suggested that this demonstration was important because it encouraged Lack and Hutchinson (two of the most productive ecologists in the 1950's) to go out and test these ideas in the field.

Gause's work was also important for showing the practical utility of the niche concept and for linking the use of the term niche as an abstract space (Grinnell 1917) with the idea that it was based on feeding relationships within a community (Elton 1927). Gause experimentally demonstrated that *P. aurelia* and *P. bursaria* used different depths of bottles and suggested that this resulted in niche differentiation, which might explain their coexistence; there is no more precise work that we are aware of that tests the purported coexistence mechanism with these species. The idea that niches were measurable entities dramatically changed thinking about niches (Kingsland 1995) and this together with the competitive exclusion principle led to community ecology being dominated by niche and competition theory up until the early 1970's (e.g., Dobzhansky 1951, MacArthur 1958, Hutchinson 1961, Pianka 1966).

Gause's other major contribution was to demonstrate the utility of Lotka and Volterra's predator-prey model (Lotka 1925; Volterra 1926), thus contributing to the growth of predator and prey theory. Gause (1934) demonstrated short-term changes in density of a predatory ciliate, *Didinium nasutum*, and its prey *P. aurelia*, that were consistent with the oscillatory dynamics of the Lotka-Volterra predator and prey equations. Interestingly the test was rather weak by today's

standards: short-term observed rates of population change were observed to be consistent with long-term population trajectories and this was assumed to represent sufficient support for the model (Kareiva 1989). However, only after Gause (1934) showed the merits of the Lotka-Volterra equations did other ecologists explore their broader implications in field systems (Kareiva 1989). Perhaps not satisfied with the link between the Lotka-Volterra equations and his own experiments, Gause went on to perform further experiments where he varied predator and prey densities. In the Lotka-Volterra predator-prey equations, predator and prey densities have equal effects on the amplitude of oscillations, however Gause observed that the amplitudes of density oscillations depended more on the initial densities of predators than prey. This led Gause, Smaragdova and Witt (1936) to introduce a nonlinear functional response into the Lotka-Volterra predator-prey model, thereby making it accord with the experimental results. This was also the first time a nonlinear functional response was used, whereas today we assume (with much evidence) that most functional responses are nonlinear.

Population Control and Environmental Variation

Few problems in population ecology have been as controversial as the search for empirical evidence for the causes of population regulation. In the 1950's two camps emerged, with Andrewartha and Birch (1954) stressing the importance of density independent extrinsic factors, and Nicholson (1958), Lack (1954), Hutchinson, and MacArthur stressing intrinsic factors (competition) and density dependence (Kingsland 1995). This debate carried on through into the 1990's (Murdoch 1994), fueled by some miscommunication and misunderstandings (reviewed by Sinclair 1989), misleading statistical methods (e.g., Holyoak and Lawton 1992), and a lack of long-term data from field populations (e.g., Woiwod and Hanski 1992). While a consensus on the presence of density dependence in field populations was not reached until the 1990's (Sinclair 1989; Woiwod and Hanski 1992; Turchin 1995). Laboratory studies by Luckinbill and Fenton (1978) provided the first evidence from manipulative experiments for regulation in real populations (Harrison and Cappuccino 1995). Luckinbill and Fenton's (1978) experiments are also informative about the effects of extrinsic variation on populations.

Luckinbill and Fenton (1978) experimentally tested the effects of external perturbations on population fluctuations, which illustrated the effects of regulation and hence density dependent feedback (1970). Three species were used. Replicate populations of each were started either at their average density under experimental conditions, or either above or below this density. Each species returned to the average density at a speed inversely related to body size; this time period will be termed the characteristic return time. When replicate populations of two of the species were grown on resources that were sequentially perturbed downward and then upward with increasing frequency, the response varied between species. Densities were most constant for the largest-bodied species, *Paramecium primaurelia* and for this species they became less variable as perturbations became more frequent. The smaller-bodied ciliate *Colpidium campylum* showed larger amplitude oscillations than *P. primaurelia* and these increased in amplitude with an increasing frequency of perturbation until the species became extinct. Luckinbill and Fenton related their results to the reduced time it took to starve when food levels were low for smaller bodied *C. campylum* and the more rapid population growth when food was plentiful. The rapid changes in density of the small bodied species is consistent with the occurrence of over-compensating density dependence. This also concurs in the theoretical results by May (1974), where the degree of overcompensation in a discrete time logistic model is dependent on the intrinsic growth rate, r , which eventually produces deterministic chaos when r is sufficiently large. As a tool, density perturbations have been conducted in a variety of other

kinds of systems, but it is interesting that there was a long time period between Murdoch advocating them in 1970 (Murdoch 1970) and their wider use (Harrison and Cappuccino 1995). This indicates that Luckinbill and Fenton's (1978) study may have been instrumental in density perturbation experiments gaining popularity in other kinds of study systems.

Inspired by Luckinbill and Fenton's (1978) studies, Orland and Lawler (in press) conducted an experiment of similar design, but using a different species, *Colpidium cf. striatum*, and including a wider range of frequencies of perturbation. When Orland and Lawler increased the frequency with which resources were perturbed to intervals less than the characteristic return time they found that populations became less temporally variable. This result is analogous to Luckinbill and Fenton's findings for *P. primaurelia*; rather little effect was produced by resource perturbations that were too fast for the population density to match. Like Luckinbill and Fenton (1978), Orland and Lawler (in press) also found that resource perturbations at intervals greater than the characteristic return time increased the temporal variability of population densities. Under such circumstances the population would have had time to grow or decline in response to the altered conditions, which is a prerequisite for being able to overcompensate in response to changed conditions. This is consistent with *C. campylum* in Luckinbill and Fenton's experiment. The demonstration of increases and decreases in variability with different frequencies of perturbation in a single species shows that the results are not caused by interspecific differences.

So far we have only discussed resource perturbations. Extra insights are gained by considering the effects of other kinds of perturbations. The results of density perturbations can be seen in a study by Orland (2003), which was conducted under comparable conditions to Orland and Lawler (in press). Perturbing densities alternately upward and downward did not increase temporal variability in densities above that in unperturbed control treatments if perturbations were on the same frequency as the characteristic return time. However, perturbing densities more or less frequently produced greater temporal variability than controls. Density perturbations of a greater frequency than the return time are likely to have increased variability because the population could not respond sufficiently rapidly to fully counteract the direct perturbation. By contrast less frequent density perturbations could have produced density dependent feedback that caused populations to overcompensate, thereby increasing temporal variability above the control. This explanation is supported by a further treatment where resources were renewed at an interval that was approximately half of that of the return time; all density perturbations then increased temporal variability in population densities. Renewing nutrients would have short-circuited density dependent feedback that was mediated by resource availability. To date, these kinds of experiments investigating perturbations and long-term population dynamics are unique to protists in microcosms.

In the previous studies positive and negative perturbations occurred sequentially and were of similar magnitudes. In nature we are perhaps more likely to see random or structured sequences of perturbations that do not follow a strict balanced positive and negative sequence. A reddened spectrum is one where there is positive temporal (auto)correlation in environmental variation, such that events that have a negative effect on populations are likely to be followed by further negative events and vice-versa (positive events follow positive events). Reddening the spectra of environmental variability is therefore likely to increase the temporal variability of population densities and make extinction more likely. Reddened spectra appear to be frequent in ecology and are indicated by longer time series of abundances showing increased temporal population variability compared to shorter series (e.g., Pimm and Redfearn 1988, Inchausti and Halley 2001, Akcakaya et al. 2003). Interest amongst ecologists in the effects of the reddening of

spectra started with two laboratory experiments (Cohen et al. 1998; Petchey 2000). Cohen et al. (1998) programmed computer controlled incubators to generate either random (white spectra) or autocorrelated (red spectra) series of temperature fluctuations while holding the long-term average cumulative temperature constant (Figure 1a). Petchey (2000) then used this apparatus to look at the effects of different degrees of reddening on single species population dynamics using either *C. striatum* or *Paramecium tetraurelia*. They showed that both species tracked reddened temperature fluctuations more closely than random temperature fluctuations (Figure 1b). Petchey also showed that, like in population models, the change in temporal variability in densities to the reddening of temperature variation depended on an interaction between the intrinsic growth rate and the degree of reddening (Fig. 1c); again this result corresponds to the frequency effects seen in the work of Luckinbill and Fenton (1978) and Orland and Lawler (in press). The spectra of weather patterns are usually reddened and time series of population data also appear to be reddened regardless of the source of environmental variation (e.g., Petchey 2000, Akcakaya et al. 2003). It is therefore likely that the color of environmental variation is of broad importance in ecology, and much work remains to be done exploring the phenomenon for other kinds of populations and species interactions. The only experimental evidence for the importance of reddening of spectra for population dynamics comes from protists in laboratory microcosms. These phenomena clearly merit study in other kinds of systems.

Stabilizing Predator-prey Interactions in Populations and Metapopulations

Like for single species, it has been difficult to experimentally study the long-term population dynamics of predators and prey in the field, and the need for studies in simplified circumstances is augmented by the problem of studying species interactions and complex phenomena such as population cycles (e.g., Taylor 1990, 1991, Turchin 2003). Early laboratory experiments suggested that it was impossible to obtain persistence of predator and prey invertebrates for more than one or two density oscillations, or more than about ten generations (Gause 1934; Luckinbill 1973). This was likened to the neutral stability of the Lotka-Volterra model and the instability of the discrete-time Nicholson-Bailey model (Nicholson and Bailey 1935). In both experiments and models longer term persistence could, however, be obtained if something modified the basic predator-prey interaction. For example, Gause (1934) demonstrated that if a refuge was present for prey, or if a prey immigrant was added daily, then longer term persistence was possible for predatory *Didinium nasutum* and *Paramecium caudatum*. This was the first demonstration of a predator-prey coexistence mechanism and came from protist microcosms. Huffaker (1958) also showed that predator and prey mites could persist for longer in a spatially complex (subdivided) habitat. In this section we briefly review the contributions of laboratory experiments with protists exploring whether predator and prey persistence could be obtained in a homogeneous environment without repeated intervention, and then describe investigations of metapopulation dynamics in subdivided environments.

Luckinbill (1973) intuited that laboratory predator and prey populations were short lived because the small size of experimental arena prevented prey from becoming sufficiently scarce that predators could not find them, which would have forced predators to decline in abundance through starvation. Prey could then become more abundant again allowing both species to persist. Luckinbill used an inert thickening agent, methyl cellulose, to simulate a larger environment by slowing the movement of the protists, which reduced the frequency of contact between predators and prey. Different concentrations of methyl cellulose reduced encounters to different degrees. Luckinbill's main result was that the addition of methyl cellulose reduced the swimming rates of both predators and prey, prolonged persistence of both species and also

reduced the maximum density that predators achieved. Luckinbill's (1973) paper has had a broad influence on theory about predator and prey encounters, subsequent dynamics and alternative methods of stabilizing predator and prey interactions (see also Luckinbill 1974). Following Luckinbill and Fenton's lead, both Veilleux (1979) and Harrison (1995) investigated the form of functional responses caused by thickening the experimental medium with methyl cellulose and related changes in functional responses to gains in persistence in homogeneous environments using isoclines from simple models.

Early experiments in a variety of artificial systems showed the potential for habitat patchiness to prolong the persistence of specialist predators and their prey (e.g., Huffaker 1958, Maly 1978, Nachman 1981, 1987). However, these experiments did not achieve long-term persistence, nor tell us the mechanisms by which these species persisted. For example was it through a refuge for prey, or through metapopulation dynamics, or through other changes in the predator and prey interaction that were caused by the different environment? By contrast a rich variety of predator and prey metapopulation models were described, often inspired by Huffaker's work (reviewed by Kareiva 1990, Taylor 1990, 1991). Taylor (1990, 1991) failed to find any good examples of systems in the laboratory or field that could be said to persist via the mechanisms described in predator and prey metapopulation models; studies typically lacked evidence that movement was important or that local populations were prone to extinction. These deficiencies fueled us to try to test whether we could obtain long-term coexistence through predator and prey metapopulation dynamics.

Earlier experimental designs were improved on by using three replicated treatments: (1) Isolated bottles (patches) to test whether the basic predator-prey interaction was unstable. (2) Interconnected groups of nine or 25 bottles (subdivided multipatch environments) to look for spatial dynamics (Holyoak and Lawler 1996a, b). (3) The same total volume of habitat in undivided large bottles to test for effects of habitat size (e.g., Luckinbill 1974). By using bottles that were connected with tubes we could use clamps to isolate bottles, allowing us to obtain samples without unduly disrupting any spatial structure. We elected to use ciliate predator and prey species (*Didinium nasutum* and *Colpidium cf. striatum*) that do not especially feed along surfaces since we could not vary habitat patchiness without changing the surface area of our microcosms. The distance between patches in our subdivided microcosms was based on the little field data that was available, where Taylor and Berger (1980) found distances of about 15 cm between aggregations of protist species in a Canadian pond. We found that spatial subdivision did prolong persistence beyond that seen in either the single patches or large undivided volumes (Figure 2a); furthermore the predator and prey did not show signs of going extinct from subdivided microcosms when the experiment was ended after 130 days (or about 602 prey and 437 predator generations). Further analysis showed that within individual bottles (patches) of subdivided microcosms, prey extinctions and recolonizations were frequent (Figure 2b). For predators local extinctions and recolonizations were recorded infrequently. However, there was evidence that immigration raised local population densities and thereby rescued predator populations from extinction; densities of predators were increased in bottles of subdivided microcosms with more connecting tubes and which therefore would have permitted more immigration (Figure 2c). An independent experiment showed that migration rates of prey between adjacent bottles in subdivided microcosms were low, as expected for repeated local extinction and colonization, and that predator movement rates were somewhat greater, which was consistent with rescue as opposed to local extinction. Density fluctuations of each species in different patches of subdivided microcosms were also only partly synchronous, which was

consistent with metapopulation structure (Figure 2d). Altogether the results provided the first clear example of how spatial dynamics generated predator and prey persistence in multipatch subdivided habitats. This was via extinction-colonization dynamics of the prey and rescue effects in predators. A comparison with the predictions from mathematical models for predator and prey metapopulations (e.g., Crowley 1981, Reeve 1988) showed that the effects of dispersal on dynamics were entirely consistent with these models. This initial study prompted others to use similar experimental designs, it opened the way for Holyoak and others to conduct some of the first tests of untested theory, and led to tighter model-empirical linkages. For example, concurrent development of a model and experiments demonstrated the utility of an individual-based model for predicting temporal dynamics and persistence of a predator and prey populations, thereby increasing the testability of persistence mechanisms (Holyoak et al. 2000).

A further experiment (Holyoak 2000) evaluated the role of nutrient enrichment on predator and prey metapopulations. This experiment was based on a theoretical paper by Jansen (1995). Raising the carrying capacity within single patches (and patches that were connected by migration) was expected to produce predator and prey oscillations of larger amplitude, as predicted by Rosenzweig (1971), and which was termed the paradox of enrichment. Jansen (1995) predicted that metapopulations could persist despite enrichment if local dynamics remained asynchronous in different patches. The experiment (Holyoak 2000) provided support for Jansen's model with prolonged persistence in subdivided habitats and a large amount of asynchrony despite enrichment. One difference from Jansen's model was that in the experiment predator populations became more synchronous across patches with enrichment, whereas this did not happen in Jansen's simulations. The explanation was that predators were more likely to experience very low prey densities with enrichment. Independent experiments showed that predators had a delayed response where they increased their interpatch movement rate when they were starving, which might cause more dispersal with enrichment and thereby increase the degree of synchrony across patches. This represents the kind of behavior that is often missing from simple models and given that it is possessed by rather simple organisms we might question whether it should be added to models.

Altogether this series of experiments have helped to bring predator and prey metapopulation theory and empirical evidence somewhat closer together. There are a growing number of studies that have been exploring predator-prey (or other exploiter-victim) interactions in the field, e.g., Van Nouhuys and Hanski (1999, 2002), Weisser (2000), Berendonk and Bonsall (2002), Schops (2002). The experiments reviewed in this section provided greater congruence between experiments and theory, the first demonstrations of several widely accepted areas of population dynamic theory, and unexpected results that have suggested that theory might need to be modified.

Source and Sink dynamics

Source and sink dynamics represent another current area of ecological theory that has proven difficult to test fully in the field and where the existing tests look only at short term dynamics. In a literature review Diffendorfer (1998) could not find a single example of a study that adequately distinguished between source-sink dynamics (Pulliam 1988) and movement that resulted from optimal foraging ("balanced dispersal"; McPeck and Holt 1992). A survey of the literature by Donahue et al. (2003) found that only about 28% of empirical studies about source and sink dynamics contained any data on movement and in all of these cases the information was inadequate for distinguishing whether movement was from sources or sinks or was equal between different kinds of patches (balanced dispersal). A further complexity is that immigration

may produce density-dependent reductions in population growth rates, making otherwise viable populations appear as sinks (termed pseudosinks by Watkinson and Sutherland 1995). The difference between sinks and pseudosinks is that if interpatch movement were to cease, sink populations would decline to extinction whereas pseudosinks would remain viable. The complexities of source and sink dynamics are such that it is a topic where substantial progress has been made by coupling mathematical models with protists experiments.

Fueled by the absence of data, Donahue et al. (2003) investigated the patterns of movement and the influence of density changes mimicking movement on spatial dynamics. Experiments used *Colpidium cf. striatum*, a mixed flora of bacteria and millet seeds as resources (to alter habitat quality). Side experiments measuring dispersal rates predicted that throughout the main experiment there should be a net flux of protists from high to low resource patches. Simple source and sink models (Pulliam 1988) predict that high dispersal will produce the greatest population abundance in sink patches (assuming that the source is not depleted by emigration). By contrast, in experimental treatments that permitted different levels of dispersal (with no tubes, long or short tubes), intermediate dispersal rates produced the greatest abundances in low resource patches. Donahue et al. parameterized a two-patch model and used this to test whether density dependent feedback caused by immigration (pseudosink effects) could account for densities not being greatest in low resources patches at the highest dispersal rates. The results showed that pseudosink effects were feasible. There have been rather fewer attempts to look at pseudosink effects in field populations, although one field study did find some evidence for them (Boughton 1999). A second novel aspect of this study was that over hundreds of generations sources and sinks converged in their population densities. It is likely that differences in the body size of protists leaving sources (large) versus sinks (small) created a large flow of nutrients from sources to sinks, which altered sink conditions. This kind of feedback between movement and local conditions has been observed with concentrations of grazing herbivores in the Serengeti depositing nitrogenous wastes that fertilize already nutrient-rich areas (McNaughton et al. 1997). There are few examples of changes in source and sink status (although see Boughton 1999) and none that we are aware of that have examined long-term dynamics. Another set of investigations using protists in laboratory experiments and models showed that reddened environmental variability can inflate the abundances observed in sink populations, which could transform some sinks into sources (Gonzalez and Holt 2002; Holt et al. 2003). This phenomenon has no tests in other kinds of empirical systems. Clearly more field investigations of source and sink dynamics and their consequences are merited.

Omnivory and stability

Omnivory was once thought to be rare in food webs (e.g., Pimm 1980), however it is now recognized that many consumers feed at more than one trophic level (reviews: Polis 1994, Morin and Lawler 1995, Coll and Guershon 2002; see also Link 2002). Feeding at more than one trophic level is our operational definition of omnivory for this paper (Pimm and Lawton 1977). In early papers, the apparent rarity of omnivory was attributed to either dynamical constraints (Pimm and Lawton 1977), or to difficulties inherent in feeding on prey that differ in structure, size, and chemical makeup (e.g., Yodzis 1984, Stenseth 1985, Lawton 1989). Recognition of the prevalence of omnivory raised the challenge of figuring out why these potential constraints on omnivores did not prevent them from succeeding.

Protists have been a valuable model system for understanding the dynamical consequences of omnivory. First we outline a portion of the many theoretical treatments of omnivory, and then review empirical tests that used protist food chains. Early analysis of Lotka-

Volterra style food web models found that models that included omnivores tended to be unstable (prone to extinction of one or more species), or such models had a long return time to equilibrium behavior (Pimm and Lawton 1977). They suggested that the “intraguild predation” form of omnivory, where a top predator consumes both a prey and the prey's food, might be particularly unstable because it places the prey in a sort of double jeopardy (Pimm and Lawton 1977, Polis and Holt 1992). This form is called “intraguild predation” (hereafter IGP) because the top and intermediate consumers share prey. However, a review by Polis et al. (1989) found that IGP seems common and important to food web dynamics in many systems. They modeled this subweb configuration, and found that omnivores could either stabilize food chain dynamics if predation on the lowest trophic level was weak, or destabilize it if omnivores fed efficiently enough to out-compete intermediate prey for the resource. Additional work by McCann and Hastings (1997) and McCann et al. (1998) reinforced this theory using nonlinear models.

An initial study by Lawler and Morin (1993) tested Pimm and Lawton's model result that simple food chains containing omnivores would be less stable. Our empirical definition of stability was the combination of low population fluctuations and high population size (see Morin and Lawler 1996 and Holyoak and Sachdev 1998 for discussion of empirical stability). Lawler and Morin (1993) constructed three-link food chains of bacteria, bacterivorous *Colpidium cf. striatum*, and a predator. The top predator was either the omnivorous protist *Blepharisma americanum*, or either of the protist predators *Amoeba proteus* or *Actinosphaerium eichhornii*. The predators were not strict predators, in that they consume some bacteria. However, they were unable to divide if only given bacteria to consume, while *Blepharisma* could reproduce on a diet of either protists or bacteria. Results showed that bacterivores had no consistent population responses to the type of top predator, sometimes persisting at relatively steady abundance and sometimes varying widely or going extinct. However the omnivore always had more abundant, less variable populations than the predators, when it fed as an omnivore. This result was intriguing because it showed that the purported dynamical limitations to omnivory in food webs might not be common in real systems (Yodzis and Innis 1992). An extension of this study to include a second omnivore, *Tetrahymena vorax*, and four other predators, found similar results (Morin and Lawler 1996). Effects of omnivores and predators on intermediate prey were idiosyncratic, however omnivore populations were often more abundant and fluctuated less than populations of predators.

As mentioned above, the predators in the studies by Morin and Lawler were actually omnivorous to some unknown extent, in that they probably consumed bacteria as well as smaller protists. Could “degree of omnivory” explain some of the idiosyncratic results? Holyoak and Sachdev (1998) did a more sophisticated study using many of the same species, but with the addition of a “ranking” of consumers by their degree of omnivory. If a species was known to eat bacteria, or took longer to starve when more bacteria were available, it was assigned a higher omnivory ranking. Cannibals also received a higher ranking, because they fed at their own trophic level as well as at least one below. In empirical terms it was expected that if omnivory was stabilizing, populations of more omnivorous species would persist better and fluctuate less in abundance, and that omnivory in predators would not necessarily cause prey to fluctuate more or go extinct sooner. As predicted, species that were more omnivorous fluctuated less and persisted longer than less omnivorous species. Intriguingly, effects of predators on prey persistence or fluctuations had no detectable relationship to omnivory.

To our knowledge, few if any field studies have attempted to relate “degree of omnivory” to population dynamics, and we hope that highlighting this study will encourage other ecologists

to explore their systems for this effect. For example, it might be fruitful to focus on terrestrial food chains involving parasitoids and hyperparasitoids, because omnivory is known to affect the dynamics of these systems (e.g., Brodeur and Rosenheim 2000, Montoya et al. 2003).

Recent theory holds that although weak omnivory can be stabilizing, strong omnivorous links could still destabilize food webs (e.g., McCann and Hastings 1997, McCann et al. 1998, Mylius et al. 2001, Kuijper et al. 2003 and references therein). The original theory by Polis et al. (1989) also points out that the top omnivore cannot be a superior competitor for basal resources. Therefore the positive empirical relationship between degree of omnivory and “stability” needs further exploration—a more detailed quantification of interaction strengths within the protist system would help us understand whether the strength of omnivorous links falls into the range that is thought to be stabilizing. For example, the omnivores we used might not consume bacteria efficiently enough to have much effect on bacterivores. Here the main limiting factor is that it is empirically difficult to measure interaction strengths (Berlow et al. 1999). Work by Morin (1999) and Diehl and Feissel (2001) does support this suggestion for one omnivore.

Several protistan omnivores switch between morphs that feed either mostly on bacteria or mostly on bacterivores, allowing a change in feeding efficiency on the different trophic levels that responds to the availability of prey at each level. This aspect of the system inspired an intriguing extension of intraguild predation models to examine the dynamical consequences of including optimal foraging (Krivan 2000). Krivan (2000) found that optimal foraging by intraguild predators could help stabilize food webs (see also Matsuda et al. 1986). Not only can protists serve as models for adaptive changes in predators, but they are excellent models for studying the population-dynamic effects of inducible defenses in prey (e.g., Kusch 1998). Inducible defenses are being found in an increasing variety of organisms (review: Tollrian and Harvell 1999; see also Johansson and Wahlstrom. 2002; Trussell and Nicklen 2002; Relyea 2002), yet their effects on population dynamics are rarely studied because of the long generation times of many organisms.

The Interaction Between Productivity and Intraguild Predation

The ability of the IGP system to persist is predicted to vary with the productivity of the system and the relative impacts of top and intermediate predators on basal prey (Polis et al. 1989; Holt and Polis 1997; Diehl and Feissel 2000, 2001). For the system to persist under any condition, the intermediate species must be the better competitor for basal prey. Otherwise this population cannot withstand the dual impacts of a superior competitor that eats them. At low levels of productivity, the intermediate species can outcompete the top omnivore, because it reduces basal prey to a low level, yet it is not itself abundant enough to sustain a population of the omnivore. At moderate productivity, all three can persist because populations of the intermediate can support the top omnivore, yet basal prey are sparse enough so that the top omnivore must rely on intermediate prey. At higher productivities, basal prey can sustain the top omnivore, and the top omnivore increasingly begins to suppress intermediate prey. With further enrichment under these circumstances, basal prey and the top omnivore increase until predation by the omnivore outstrips the intermediate prey's reproductive rate, and the system collapses to a predator-prey system.

Morin (1999) and Diehl and Feissel (2000, 2001) provided elegant tests of this theory. Morin (1999) grew the omnivore-consumer-basal prey IGP system *Blepharisma americanum*-*Colpidium cf. striatum*-bacteria under low and high nutrient conditions. At low nutrient levels, the intermediate consumer *Colpidium* excluded the top omnivore, even though *Blepharisma* could eat *Colpidium*. Exclusion was proven by the fact that *Blepharisma* could persist in low

nutrient microcosms without *Colpidium*. A side experiment showed that *Colpidium* drove bacteria to lower levels than the top omnivore. The idea that a prey could exclude its predator was counter-intuitive at the time! At the higher nutrient level, both coexisted. This study established that enrichment caused most of the predicted changes in population levels, persistence and dynamics. However, nutrient levels were not high enough in the Morin study to test the prediction that further enrichment would cause extinction of the intermediate consumer.

Diehl and Feissel (2000) used a very similar system (*Blepharisma americanum*-*Tetrahymena pyriformis*-bacteria) and a wider range of nutrient levels to see if all three conditions could be attained: competitive exclusion of the top omnivore, coexistence, and predatory exclusion of the intermediate consumer. The three conditions were indeed attained at the appropriate nutrient levels. A follow-up paper (Diehl and Feissel 2001) demonstrated the mechanisms underlying these phenomena, that is, that competition was responsible for exclusion of the omnivore at low nutrients, predation caused lower abundances of *Tetrahymena* as the system was enriched, and the intermediate consumer benefited the top omnivore at intermediate levels of enrichment (see also Lawler and Morin 1993). Two field studies now also show similar patterns of coexistence and exclusion across productivity gradients in parasitoid-host-plant systems (Amarasekare 2000, Borer et al. 2003), confirming that the theory and the protist model system have real-world relevance.

These results show that it may be possible to predict the outcome of IGP in advance, by measuring the relative competitive abilities of the top omnivore and intermediate consumer on shared prey. This could have implications for predicting the consequences of species invasions, when invasives are likely to cause IGP food web configurations. Nutrient enrichment of the environment is one of the prevailing conservation challenges on the planet, and these experiments also show that excess nutrients could put some species of intermediate consumers at risk (Diehl and Feissel 2001).

Conclusion

The combination of rapid generation times, being large enough to count, and small enough to grow and manipulate in large numbers make protozoa unparalleled in their utility for performing population experiments. The most potent use of these experiments is to use them to test general ecological theories that either cannot be tested or cannot be tested as thoroughly in other kinds of systems. Similarity of results between general models and laboratory studies adds generality to the laboratory findings and often allows additional tests of mechanisms that help to validate the models, thereby also strengthening inference. Parallel or iterative development of models and experiments, such as in the work on intraguild predation and the cases of Holyoak et al. (2000) and Donahue et al. (2003), illustrated cases where models were necessary to interpret the original experiment and further experiments were necessary to parameterize the models. Some cases show that protist experiments gave the broader community of ecologists confidence that theories were worth exploring in field systems. Experiments with protists in the laboratory clearly play a valuable role in a modern integrative population ecology that brings together theory, observations and experiments in a wide variety of types of study system.

Acknowledgments

We thank Robert Desharnais for inviting us to write this piece. MH was supported by NSF DEB-0213026 to M.H. and Alan Hastings.

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Figure 1. A. The influence of reddened (autocorrelated) stochastic variation and white (uncorrelated) stochastic variation in temperature in computer controlled incubators. B. The correlation between population density and temperature in *Colpidium cf. striatum* and *Paramecium aurelia*. C. The coefficient of variation of population density for populations grown under white and red noise. Bars represent standard errors in B and C. Further details in Petchey (2000). Redrawn from Petchey (2000).

Figure 2. A. Persistence times of predatory *Didinium nasutum* and its prey *Colpidium cf. striatum* in isolated 30 mL patches, large undivided 270 mL patches, large undivided 750 mL patches, and subdivided nine- or 25-patch microcosms (“arrays”, e.g., see panel D). Both nine and 25-patch subdivided microcosms are shown as a single bar because both species persisted for the duration of the experiment in all microcosms of these types. B. The estimated number of prey extinctions occurring in individual 30 mL bottles within subdivided microcosms of 25 patches during a 40 day period. C. Mean predator densities in bottles of nine-patch microcosms in relation to numbers of tubes connecting bottles; elevated densities with greater numbers of tubes indicate rescue effects as did a reduced number of local extinctions (data not shown). D. The average correlation between prey densities in bottles of 25-patch subdivided microcosms that were separated by different numbers of tubes (1, 2=2 tubes and one bottle, 3=3 tubes and 2 bottles, etc.). Correlations for predators were broadly similar indicating substantial independence of dynamics in different patches. Error bars in A and D indicate standard errors. Redrawn from Holyoak and Lawler (1996a).





