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# PREDICTING EXTINCTION: PROGRESS WITH AN INDIVIDUAL-BASED MODEL OF PROTOZOAN PREDATORS AND PREY

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*Abstract.* Despite the importance of understanding persistence, there are few direct tests of the ability of models to predict predator and prey population persistence. We tested whether an individual-based model could forecast the dynamics and time to extinction in aquatic microcosms of a protist predator and prey: predatory *Didinium nasutum* and bacterivorous *Colpidium striatum*. By addressing both persistence and dynamics, the model increases the testability of mechanisms of extinction. Population-level equations modeled the functional response and prey growth. For individual predators, we simulated time since dividing and feeding, and number of prey consumed; these influenced the timing of division and death. We tested the model by comparing simulated dynamics to data from three experiments: (1) an experiment initiated with low predator–prey ratios in 30-mL bottles; (2) an experiment similar to Experiment 1, but in which immigrant predators, prey, or both were added during the first density cycle; (3) an experiment in 30-mL bottles, initiated with various predator–prey ratios.

Using only nine parameters measured in independent experiments, simulations gave satisfactory predictions of the period and amplitude of cycles of predator and prey densities, and predator and prey densities through time for Experiment 1. Adding stochasticity to the model also allowed it to reproduce observed prey and predator persistence and the proportion of replicates with prey extinctions. We used the improved model to forecast the results of Experiments 2 and 3. In Experiment 2, persistence changed with immigration. The model qualitatively reproduced these changes but underestimated their magnitude. Increasing the initial predator–prey ratio reduced persistence in Experiment 3. Simulations failed to qualitatively reproduce these results for 30-mL microcosms, unless we raised initial prey density.

This study demonstrates the use of an individual-based model to help identify and test mechanisms of extinction in predator–prey interactions. The combination of individual-based and population-level formalisms can maintain both model tractability and a close working relationship between models and accessible data.

*Key words: density perturbation; empirical tests of model predictions; functional response; immigration; individual-based model; microcosm; population persistence and extinction; population viability analysis; predation; predator–prey dynamics; predicted changes in individual state variables; starvation.*

## INTRODUCTION

Population extinction is a notoriously difficult process to study because of the long time scales involved and the problem of determining whether and when an extinction has occurred (Strong 1990). Yet, understanding the extinction process is essential to successfully conserving and managing species. This problem has attracted recent interest because of human-induced extinctions (reviewed by Lawton and May [1995]), such as habitat destruction (Groombridge 1992, Tilman et al. 1994) and fragmentation (Fahrig and Merriam 1994, Simberloff 1994, Burkey 1995, 1997, Fahrig 1997).

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Predator and prey dynamics are frequently cyclical, thus offering a special challenge for predicting population persistence (Renshaw 1991). Density cycles cause predator and prey populations to regularly reach low abundances where extinction through demographic stochasticity may be more likely. With cyclical dynamics, the timing and likelihood of extinction may be a function of the density cycles as well as more traditional factors, such as environmental stochasticity and catastrophes (Shaffer 1981, Goodman 1987). We begin by briefly reviewing the kinds of approaches that are potentially useful for understanding the persistence of such predator and prey interactions and then describe a promising approach that we have developed.

A number of statistical and observational approaches have been developed for studying extinction. Monitoring the occupancy of large numbers of habitat patches through time allows local extinctions to be recorded and statistical correlates of occupancy (such as patch isolation and size) to be sought (e.g., Hanski et al. 1994,

Smith and Quin 1996, Bolger et al. 1997; reviewed by Harrison and Taylor [1996]). For multiple species, the incidence or abundance of a predator or competitor across patches can also be correlated with observed extinctions of a focal species (Lei and Hanski 1997). Another approach is to correlate observations of extinctions with the temporal variability of populations (reviewed by Bengtsson and Milbrink [1995]). This approach assumes that spatial and temporal variability are separable; however, spatial and temporal variability may not be separable and are likely to be related to extinction in different ways (Gaston and McArdle 1994, Stewart-Oaten et al. 1995).

At least four modeling approaches have been used to predict persistence and evaluate management options (Goodman 1987, Lande and Barrowclough 1987, Burkey 1989, Caughley 1994):

1) If dynamics are at equilibrium, simple patch occupancy models can be used to estimate the rates of patch extinction and recolonization (e.g., Levins 1970). Such approaches would be complicated by nonequilibrium dynamics and are not amenable to the study of the population dynamic mechanisms of extinction within patches, because they do not consider within-patch dynamics. However, in some cases within-patch dynamics may not be important for persistence; for example, Nisbet and Gurney (1982: Chapter 10) show that persistence times of predator and prey mites in Huffaker's experiments (Huffaker 1958, Huffaker et al. 1963) can be adequately predicted using a stochastic birth–death model based on patch occupancy.

2) Population viability analyses use simple single species models to estimate probabilities of persistence from factors like population size, reproductive rate, and generation-to-generation variation in reproduction (reviewed by Foley [1996]).

3) Projection matrices can be used to calculate population trajectories, and/or elasticity analyses can be used to calculate mathematical stability (McDonald and Caswell 1993, Jensen 1995, 1996, Wisdom and Mills 1997, Menges and Dolan 1998).

4) Special-purpose numerical or analytical models can be used to generate population trajectories or reveal stability properties; the mathematical formalisms invoked for these purposes include differential equations (e.g., Lotka–Volterra equations), difference equations (e.g., Nicholson–Bailey equations), partial differential equations to analyze dynamics in spatially continuous environments (for reviews, see Kareiva [1990], Dunning et al. [1995]), stochastic birth–death models (e.g., Renshaw 1991, Foley 1996) and individual-based models (IBMs; Lomnicki 1991, Metz and de Roos 1991, Murdoch et al. 1992). For more than one species, such as interacting predators and prey, or competitors, models of types 2 and 3 become complex and have seldom been attempted (Caswell 1989, Foley 1996). Models of the fourth type are particularly useful for interacting species that undergo density cycles.

Which models within this fourth class are the most useful for studying and predicting extinction of cyclical predators and prey? Differential equation models are generally not appropriate for modeling persistence because of the following reasons: (1) Densities are numerically continuous, so that extinctions do not occur unless some minimum density is assumed to represent extinction (e.g., Harrison 1995). (2) Solutions to Lotka–Volterra and Nicholson–Bailey models are usually in terms of mathematical stability (see Case and Casten 1979) and not persistence. This difficulty is highlighted by strange attractors, which can generate extreme fluctuations that are hard to interpret in terms of population persistence (Armstrong and McGehee 1976). A lack of mathematical stability cannot, therefore, be equated with persistence, but the presence of mathematical stability can usually be equated with persistence. Thus, these models are useful as an indicator of a subset of parameter space where persistence is possible. (3) Dynamics may be qualitatively altered by demographic stochasticity caused by the discreteness of events when there are few individuals. Renshaw (1991) showed that neutrally stable cycles in a Lotka–Volterra model were replaced by extinction of prey in the first oscillation in an equivalent birth–death formulation, and in another case a stable point equilibrium was replaced by sustained oscillations. (4) Individual variation in parameters may be important to dynamics when populations are small, or when age, size, or social structure is present.

For simple predator–prey interactions, we can analyze dynamics using stochastic birth–death models that explicitly represent individuals (Leslie and Gower 1960, Poole 1974, Renshaw 1991). Individual-based models (IBMs) offer a more flexible formalism that allows both temporal dynamics and the frequency distribution of times to extinction to be evaluated in a single formalism. Simulation of IBMs can estimate the variation in dynamics generated by stochastic models that cannot be solved analytically, and can portray population dynamics that are far from equilibrium. Here, we develop and parameterize an IBM to simulate predator and prey population persistence and density trajectories, and we show that the model can predict actual dynamics. Our focus is on the distribution of times to extinction and how they are altered by various density perturbations. The aim is to illustrate the utility of IBMs for modeling persistence and their flexibility for representing dynamics in ways that can easily be measured. We therefore do not compare results from different model formalisms.

The major cost of using models that explicitly represent individuals is that they are almost always analytically intractable, necessitating the use of simulations. The inability to generate general solutions directly typically requires many different, well-chosen simulations to uncover the most important patterns, which is the sort of analysis presented here. It is fre-

quently assumed that, if appropriate processes for individuals are specified in a model, population- or community-level patterns will emerge naturally (DeAngelis et al. 1994). Often the complexity of IBMs make it difficult to identify community or population patterns, and the reality is that usually we need much more careful tests of IBMs (Grimm 1999).

Individual-based models also differ enormously in their aims (reviewed by Grimm [1999]). For those aiming to predict population-level phenomena, tests can be conducted at a number of different levels. Population dynamic models should be tested at the population level, both for conditions similar to those under which the model was parameterized, and for altered conditions that test the robustness of the model. Second, tests should attempt to validate the mechanisms of behavior, physiology (etc.) that lead to higher level phenomena. This task may not be as daunting as it sounds; often the model can be broken down into many submodels and functions that can be tested separately. Third, it is sensible to try to remove unnecessary complexity from an IBM and to understand how population- and community-level phenomena arise. This can be achieved by applying statistical or mathematical simplification techniques (e.g., Fahse et al. 1998), or a suite of models of differing complexity could be used to see what is gained in terms of model behavior as additional features are added (e.g., Murdoch et al. 1992). In a review of 50 selected IBMs, Grimm (1999) found that models were tested rather infrequently (e.g., only 14% of 50 models were tested under altered conditions). However, this criticism could also be applied to many other types of model. Whilst we have conducted preliminary investigations of the second and third type, we reserve them as a focus of a future paper, and here focus on tests of population-level dynamics.

We chose to investigate a predator–prey interaction between two ciliated protists, predatory *Didinium nasutum* Müller feeding on bacterivorous *Colpidium* cf. *striatum* Stokes in laboratory microcosms. The short generation times of the species involved allows predator and prey persistence to be directly measured in replicate populations. Here we present a case study of a simple manipulable system that we believe will advance the convergence between models for predicting persistence and empirical data.

*D. nasutum* and *C. striatum* are free-living, freshwater species that are commonly found together, and both reproduce by binary fission (Laybourn and Stewart 1974). *D. nasutum* is an active, voracious predator (Laybourn 1977) that starves quickly in the absence of prey. *D. nasutum* is capable of forming long-lived cysts when feeding on *Paramecium* (Beers 1935), but not when reared on *C. striatum.*

Our goal was to develop a numerical model of predator–prey dynamics that predicts both density fluctuations and times to extinction of predators and prey. We first describe an IBM that we used to simulate predator and prey dynamics in our experiments. Our model is motivated by knowledge of this experimental system from both published sources and our own experience (Holyoak and Lawler 1996*a, b*). Experimental evidence for the forms of equations used and independent experiments that were used to measure model parameters are described in the Appendix. Next we describe three additional independent experiments that were used to evaluate the model and to learn from discrepancies between simulations and empirical observations. We first tested the model under a set of "baseline experimental conditions," which were as similar as possible to the conditions under which the model was parameterized. Under these conditions, we used 45 predator and prey populations to establish the pattern of persistence and temporal dynamics that we attempted to simulate. A second experiment, the "immigration experiment," tested the effects on experimental dynamics of adding a single pulse of immigrant predators, prey, or both during the first density cycle. This represents a density perturbation that is commonly used to investigate the dynamical behavior of population models when perturbed away from densities that are usually achieved. A third experiment was motivated partly by ideas of alternative stable states, where different starting conditions might lead to different equilibria, and partly by experimental reports that initial predator–prey ratios influence predator and prey dynamics (e.g., Tanigoshi and McMurtry 1977). The "initial predator–prey ratio experiment" therefore varied initial predator densities to investigate the robustness of the model to deviations in experimental conditions. For each experiment, we conducted quantitative comparisons of simulated and observed dynamics.

## Model Structure and Analysis

### *Overview*

Our model blends population-level and individual-based formalisms. Population-level features were predation, controlled by a type II functional response (Holling 1959), and logistic prey population growth. Both prey and predators experienced density-independent mortality, which simulated the removal of 6% of the volume of microcosms every 48 h (see *Experimental methods: Baseline experimental conditions*). In experiments, these samples were replaced by fresh nutrient medium, which represents a small periodic perturbation. However, we were unable to find any associated changes in time series of predator and prey densities using spectral analysis.

Predator individuals varied in a number of individual state variables. Predators divide by binary fission at time intervals controlled both by feeding and the cell-cycle; this was represented by tracking the time since division and number of prey consumed for individual predators. Additionally, all predators were assumed to have identical predatory ability, so that each of the prey

consumed (calculated from a population-level functional response) were assigned to randomly selected individuals that had not yet consumed sufficient prey to divide. Predators that had consumed enough prey to divide, but could not do so until the cell cycle permitted, were referred to as "satiated" and remained unable to feed until the required time after the previous division. A separate experiment (see the Appendix) showed that predators died mainly from starvation, which was realistically represented by tracking the time since feeding for individual predators. Another experiment (also see the Appendix) showed that during starvation some predators became unable to feed, although they were still actively swimming; these predators were termed "moribund" and, for simplicity, were removed from simulations.

To simulate times to extinctions of predators and prey, and the proportion of replicates in which prey went extinct, it was necessary to add stochasticity to predator density. This was done by multiplying predator density by a normally distributed independent random deviate, $\Xi(t)$, with a mean of zero and a variance of $\xi$. The stochastic variation thus introduced was proportional to the square root of predator density (Leslie and Gower 1960, Poole 1974); like demographic stochasticity, this influenced dynamics more at low densities than high densities. Also, because stochasticity added to simulations of persistence was not parameterized independently of experiments in 30-mL bottles (see *Results: Persistence with baseline experimental conditions*), we prefer to present simulations without added stochasticity for factors unaffected by it. No stochasticity was added when we simulated population densities through time, mean, minimum or peak density, variation in density, or the period and amplitude of cycles. A second form of stochasticity arose in probabilistic events that needed to be resolved to events actually happening (or not) by comparing the probability of the event occurring with an evenly distributed random deviate in the range zero to one.

### *Model details*

All equations used in the model are given in Table 1. Constants are defined and their estimated values (see *Measuring parameters*) are given in Table 2. Table 1 should be self-explanatory; however, certain processes for predators are not easily represented by equations. When a predator divided, it was replaced by two daughter cells that were assumed to have just eaten (controlling starvation and becoming moribund) but to have consumed zero prey (influencing division and satiation; see *Model structure and analysis: Overview*). For simplicity, newly divided predators could not feed until the time step after division.

Prey consumption was a function of the predator's functional response ($f(x(t))$, where $x(t)$ is prey density at time $t$) and the number of predators ($Y(t)$) less the number of satiated predators ($Y_S(t)$). Hence, $f(x(t))\cdot(Y(t)-Y_S(t))\cdot\delta$ prey were consumed in a time step of length $\delta$ (Table 1: Eq. 9). Each prey eaten was assigned to a randomly selected nonsatiated predator. Predators that died or became moribund were removed from simulations. For density-independent mortality, randomly selected predators (and prey) were removed. To represent experimental observations, satiated predators were assumed unable to starve to death. Likewise for stochasticity added to predator densities through $\Xi(t)$ (Table 1: Eq. 10), randomly selected predators were removed (for $\Xi(t) < 0$). For stochastic increases in predator density ($\Xi(t) > 0$), we added predators with a random distribution of times since division (in the range $0$–$\tau$; Table 2) that had just fed and had consumed $0$–$\sigma$ prey (Table 2); Exploratory analyses showed that these decisions had very little impact on persistence.

All simulations began with random predator ages (drawn from a uniform distribution within $0$–$\tau$), and numbers of prey eaten (uniformly distributed within $0$–$\sigma$). Predators had fed in the present time step. Starting densities of both species were as in the experiments described in *Experimental methods.*

During each time step, events were calculated based on conditions in the previous time step, and conditions were not updated until all events had been calculated. This is the simplest way of minimizing the effect that the sequence of events within time steps has on dynamics. If certain events occur sequentially within a time step, artifacts may be generated in the population dynamics (McCauley et al. 1993). Each population-level calculation in the model causes a change in abundance that generally is not an integer. The whole number part of the change in abundance was added to or subtracted from the abundance (depending on the event). The fractional part of population change was interpreted as the probability of a single individual being added to or subtracted from the population, which creates demographic stochasticity. The amount of demographic stochasticity depends on the length of time steps, such that shorter time steps will generate more fractional individuals per unit time, resolved as probabilities of unit change in abundance. Exploratory analyses showed that the length of time steps did not alter persistence from the model, if time steps were kept $<0.2$ h. This time period is reasonable, given that predation is the most frequent event in the model and that it occurred at a maximum rate not much greater than one predation event per 0.2-h time step.

### *Measuring parameters*

Separate experiments measured all parameters used in the model, except for variance of stochasticity added to predator densities ($\xi$; Table 2). Because our main aim is to assess the utility of the individual-based model for predicting dynamics and extinction, we have placed the detailed experimental and statistical protocols for measuring parameters in the Appendix.

TABLE 1. The model structure. Constants are defined in Table 2.

| Variable | Definition |
|---|---|
| **Population state variables** | |
| $X(t)$ | No. prey at time $t$ |
| $x(t)$ | Density of prey at time $t$ ($x(t) = X(t)/v$) |
| $Y(t)$ | No. predators at time $t$ |
| $Y_S(t)$ | No. satiated predators at time $t$ |
| **Predator individual state variables** | |
| $\varepsilon_i(t)$ | Cumulative no. prey eaten by predator $i$ since division at time $t$ |
| $a_i(t)$ | Age: No. time steps since division for predator $i$ at time $t$ |
| $t_{f(i)}(t)$ | No. time steps since feeding for predator $i$ at time $t$ |
| **Other variables** | |
| $z_{.(i)}$ | An independent uniformly distributed random deviate in the range 0–1 that was redrawn for every individual ($i$) and every event (the dot notation is used to replace subscripts $R$, $D$, or $M$) |
| $\Xi(t)$ | An independent normally distributed random deviate with a mean of zero and variance of $\xi$ used to add stochasticity to predator abundances |
| **Functions for predator individuals** | |
| $P_{R(i)}(t)$ | Probability of predator $i$ reproducing in a time step: $$P_{R(i)}(t) = \begin{cases} 1 & \text{for } \varepsilon_i = \sigma \text{ and } a_i \geq \tau \\ 0 & \text{for } \varepsilon_i < \sigma \text{ or } a_i < \tau \end{cases} \quad (1)$$ |
| $P_{S(i)}(t)$ | Probability of predator $i$ becoming satiated during a time step: $$P_{S(i)}(t) = \begin{cases} 1 & \text{for } \varepsilon_i = \sigma \\ 0 & \text{for } \varepsilon_i < \sigma \end{cases} \quad (2)$$ |
| $P_{D(i)}(t)$ | Probability of predator $i$ surviving for $t_{f(i)}$ hours without feeding but starving to death during a time step: $$P_{D(i)}(t) = \begin{cases} \delta_t/[t_0 - (t_{f(i)}\delta)] & \text{for } t_{f(i)} < t_0 - \delta \\ 1 & \text{for } t_{f(i)} \geq t_0 - \delta \end{cases} \quad (3)$$ |
| $P_{M(i)}(t)$ | Probability of predator $i$ becoming moribund within a time step at time $t_{f(i)}$ since feeding: $$P_{M(i)}(t) = \frac{\exp(u - wt_{f(i)}\delta)}{1 + \exp(u - wt_{f(i)}\delta)} - \frac{\exp[u - w(t_{f(i)} + 1)\delta]}{1 + \exp[u - w(t_{f(i)} + 1)\delta]} \quad (4)$$ |
| **Within-time step changes in predator populations** | |
| $\Delta R(t)$ | No. predators that divided: $$\Delta R(t) = \sum_{i=1}^{Y} (z_{.(i)} < P_{R(i)}) \quad (5)$$ |
| $\Delta S(t)$ | No. predators becoming satiated: $$\Delta S(t) = \sum_{i=1}^{Y} P_{S(i)} \quad (6)$$ |
| $\Delta D(t)$ | No. predators dying from starvation; satiated predators could not die from starvation: $$\Delta D(t) = \sum_{i=1}^{Y-Y_S} (z_{.(i)} < P_{D(i)}) \quad (7)$$ |
| $\Delta M(t)$ | No. predators becoming moribund; satiated predators could not become moribund: $$\Delta M(t) = \sum_{i=1}^{Y-Y_S} (z_{.(i)} < P_{M(i)}) \quad (8)$$ |
| **Balance equations** | |
| $\Delta X(t)$ | Change in prey density within a time step: $$\Delta X(t) = rX(t)\delta[1 - x(t)/K] - f(x(t))(Y - Y_S)\delta - P_I X(t) \quad (9)$$ |
| $\Delta Y(t)$ | Change in predator density within a time step: $$\Delta Y(t) = \Delta R(t) - \Delta S(t) - \Delta D(t) - \Delta M(t) - Y(t)P_I + \Xi(t)\sqrt{Y(t)} \quad (10)$$ |
| $X(t + \delta)$ | Prey densities were updated at the end of each time step: $$X(t + \delta) = X(t) + \Delta X(t) \quad (11)$$ |
| $Y(t + \delta)$ | Predator densities were updated at the end of each time step: $$Y(t + \delta) = Y(t) + \Delta Y(t) \quad (12)$$ |
| **Additional relationships** | |
| $f(x(t))$ | The killing rate per predator, following a type II functional response: $$f(x(t)) = ax(t)/[1 + aT_h x(t)] \quad (13)$$ |
| $Y_S(t)$ | No. satiated predators at time $t$: $$Y_S(t) = \sum_{i=1}^{Y} [a_i(t) > (\sigma - 1)] \quad (14)$$ |

## EXPERIMENTAL METHODS

In this section, we describe a set of "baseline experimental conditions" used to define the predator–prey dynamics that we attempted to simulate. The baseline experiment represents a standardized set of conditions, which were as close as possible to those under which the model was parameterized. We then describe two experiments that evaluate the generality of the model by conducting them under slightly different conditions to the baseline experiment. The "immigration experiment" tested the effect on persistence of a density perturbation caused by addition of a single pulse of immigrant predators, prey, or both. The "initial predator–prey ratio experiment" was conducted at greater initial predator–prey ratios than the previous experiments, which makes persistence times dependent on the initial predator–prey ratio. We varied the initial ratio of predators to prey in bottles and examined persistence of both species.

For all the parameters that we report, confidence limits are standard deviations (1 SD) unless indicated to be standard errors (1 SE), or 95% confidence intervals (95% CI).

TABLE 2. Parameter estimates for constants used in the model.

| Symbol | Value† | Definition |
|---|---|---|
| $\delta$ | 0.1 h | Length of a time step |
| $v$ | 30 mL | Microcosm volume |
| $r$ | 0.089 (0.006) $h^{-1}$ | Prey intrinsic growth rate |
| $K$ | 770 (154) $mL^{-1}$ | Prey carrying capacity (per unit volume) |
| $\tau$ | 7.00 (0.27) h | Minimum age at which predators can divide |
| $\sigma$ | 18.05 (1.84) | No. prey required to be eaten for predator division |
| $a$ | 0.0178 (0.007) mL/h | Predator attack rate |
| $T_h$ | 0.0769 (0.031) h | Time for a predator to subdue and ingest a prey individual |
| $P_I$ | 0.06 $h^{-1}$ | Density independent mortality rate for predators or prey |
| $t_0$ | 67.2 h | Time after feeding when predator survival reaches zero |
| $u$ | 6.549 | Logistic regression intercept for the proportion of predators capable of feeding (not moribund) during starvation |
| $w$ | 0.2237 $h^{-1}$ | Logistic regression slope for the proportion of predators capable of feeding (not moribund) during starvation |
| $\xi$ | $3 \times 10^{-5}$§ | Variance of random deviates used to introduced stochastic variation into predator abundance via $\Xi(t)$ |

*Note:* Parameters $r$ and $K$ were estimated from the "immigration experiment"; and $a$, $T_h$, $\sigma$, $\tau$, $t_0$, $u$, and $w$ were measured in separate experiments.

† Mean values reported, with 1 SD included parenthetically as indicated. No units indicated for dimensionless variables.

§ The value of $\xi$ comes from Fig. 1.

### *Baseline experimental conditions*

The predator *Didinium* and its bacterivorous prey *Colpidium* were supported on a mixed bacterial suspension in semicontinuous batch culture, using aqueous nutrient medium made from Protozoan Pellets (Carolina Biological Supply, Burlington, North Carolina, USA). Cultures were kept in 45 polypropylene bottles, each containing 30 mL of medium plus a millet seed to provide a slow release of additional nutrients. One drop (0.028 mL) of a mixed inoculum of bacteria was added to each (otherwise sterile) bottle. Bacteria were obtained by filtering *Colpidium* cultures through a 5-$\mu$m nylon filter, which retains protests, but not bacteria. The baseline experimental conditions were defined by two experiments: the first consisted of 15 30-mL control bottles of the immigration experiment, and the second consisted of 30 bottles. After 24 h, ~12 *Colpidium* were added to each bottle, and after an additional 48 h, four *Didinium* were added to each bottle. Two additional 30-mL bottles contained prey, but no predators, and were used solely to calculate the prey-carrying capacity. In the second experiment, initial prey density was 141 prey/mL (1 SD = 22), and four predators were added. Mean room temperature did not differ between experiments (23 ± 2.5°C vs. 22 ± 2°C).

Experiments were sampled every two days by mixing bottle contents with a Pasteur pipette and removing 1.8 mL. Samples were replaced with fresh sterile nutrient medium. *Colpidium* and *Didinium* were counted under a binocular microscope in a three-drop subsample from the 1.8 mL. If fewer than three individuals were present, the rest of the sample was censused. In preliminary experiments, this sampling procedure yielded a coefficient of variation between samples of 0.16 for predators and 0.09 for prey ($n$ = 90). Sampling ceased when predators were recorded as absent in at least three consecutive samples at two-day intervals and in presence/absence checks between these samples; if predators were recorded on any of these five days, sampling continued until extinctions were confirmed for five consecutive days. Prey never went extinct in the absence of predators during these experiments.

We calculated persistence, mean densities, mean minimum and maximum densities for predators and prey, and the period of predator–prey cycles in each bottle. The two experiments did not differ in these parameters using Student's $t$ tests and a Tukey's test. Similarly, there was no difference between experiments in the proportion of replicates where prey went extinct (using a $G$ test). The period of cycles was measured as the time between successive maxima or minima in densities (termed "turning-point methods" by Kendall and Stuart 1969). We also calculated the lag between predator and prey maxima or minima. We did not apply tests of whether the distribution of periods was random, because these are of low statistical power. Instead, we averaged the periods within density sequences from each individual bottle and used Student's $t$ tests to determine whether the periods of cycles differed.

Observed values of these statistics were compared with 10 000 simulations using the parameter values in Table 2, and starting conditions as in the 15 bottles that were controls in the immigration experiment. No stochasticity was added to these simulations, except when calculating persistence and the proportion of replicates with prey extinct. The 10 000 replicates were used to calculate nonparametric 95% confidence intervals. All confidence limits given for simulations are nonparametric.

### *Methods for the immigration experiment*

This experiment used 15 of the 30-mL bottles as controls, plus 15 additional bottles. Four days after *Didinium* were added, extra predators, prey, or both were added to each of five bottles. The remaining 15 control bottles received no extra predators or prey. The

numbers added were (arbitrarily) 10% of density maxima observed during the first four days after predator addition: 3314 *Colpidium* (1 SD = 124) and/or 49 *Didinium* in 2.86 mL. The same volume (2.86 mL) of medium was added to the 15 controls.

Bottles were followed until extinction of prey or both species, and we compared the proportion in which prey went extinct in different treatments using $G$ tests. Additionally, for each species, we compared natural-log-transformed persistence between treatments using one-way ANOVAs. Only replicates where the species being tested went extinct were included in these ANOVAs. Prior to conducting ANOVAs, we confirmed that log-transformed persistence was normally distributed using $\chi^2$ tests, and variances were indistinguishable across treatments (Bartlett's test for homogeneity of variances).

Immigrant predators came from an actively dividing predator culture containing abundant predators and prey. In simulations, we assumed that immigrant predators had ages that were uniformly distributed within $1-\tau$, had eaten $1-\sigma$ prey, and had just fed.

### *Methods for the initial predator–prey ratio experiment*

We conducted an experiment to measure the effect of initial predator–prey ratio on persistence of predators and prey in 30-mL bottles. We selected initial predator densities that gave a starting predator–prey ratio of 0.05 (two bottles), 0.2 (four bottles), 0.6 (four bottles) and 1.0 (five bottles). Initial prey densities were kept constant. Replication was uneven because of difficulty obtaining the large number of predators needed to begin the experiment. Ratios were high enough to cause predator and prey abundances to decline rapidly once predators were added. The absence of prolonged density cycles made it difficult to accurately measure dynamics. We therefore analyze only the times for predators and prey to reach a minimum density in the initial density cycle.

## RESULTS

### *Persistence with baseline experimental conditions*

Of 45 replicate 30-mL bottles, prey and predators both became extinct in eight bottles (18%), and, in the remainder of replicates, predators went extinct but prey survived. Prey persisted for a mean period of 12.3 ± 7.1 d ($n$ = 8) in the replicates where they ultimately became extinct. Predators persisted for a mean of 15.1 ± 10.9 d ($n$ = 37) in the replicates where prey survived. Predators persisted for a mean of 15.0 ± 10.2 d ($n$ = 45) from all replicates (including those where prey went extinct before predators).

In the absence of added stochasticity (i.e., $\xi = 0$), the model gave oscillations that frequently reached low densities, but predators were *never* observed to go extinct unless prey went extinct, and prey went extinct in 37% of 100 replicate runs of 83 d in length. We attempted to introduce stochasticity into the simulations in three ways: (1) by adding a normally distributed random deviate with a mean of zero (and a variety of variances) to any one of the parameters in Table 2 (other than $\delta$, $\nu$, or $\xi$) each time step. (2) Adding stochasticity to prey abundance in an analogous way to predator abundance in Eq. 10 (see Table 1). (3) Adding density-independent stochasticity to predator abundance as described in Eq. 10. The first two of these methods were rejected because low levels of stochasticity gave longer persistence than observed for real populations, and levels of stochasticity that were high enough to give realistic predator persistence gave very short prey persistence and caused prey extinction in more than the observed 18% of cases.

Addition of density-independent stochasticity to predator abundance in each time step (Eq. 10; Table 1) gave satisfactory results. Fig. 1 shows that an intermediate level of stochasticity ($\xi = 3.0 \times 10^{-5}$) gave mean persistence of 11.5 d (95% CI = 4.6–25.4, $n$ = 1821) for prey and 17.2 d (95% CI = 8.9–36.4, $n$ = 8179) for predators; neither of these values differs significantly from the observed values ($P$ = 0.29, and $P$ = 0.54, respectively, from 10 000 replicate simulations). Simulated prey went extinct in 18.2% of cases, compared to the almost identical 17.7% of observed cases. Predators persisted for a mean of 15.2 d (95% CI =7.0–36.0, $n$ = 10 000) in all replicates, regardless of whether prey went extinct first; the confidence limits from the simulated values encompass the experimental value of 15.0 d. Henceforth, all simulations of persistence used $\xi = 3.0 \times 10^{-5}$.

Stochasticity added through $\xi$ caused very little variation in trajectories other than at low predator and prey densities; consequently the period and lag of cycles, the shape of trajectories (Figs. 2 and 3), and none of the density characteristics reported in Table 3 differed for $\xi \leq 3.0 \times 10^{-5}$.

### *Density trajectories with baseline experimental conditions*

A phase plane diagram for 30 randomly selected 30-mL bottles is shown in Fig. 2A (only an arbitrary subset of all replicates is shown to improve clarity). Dynamics were cyclical with a mean period of 10.2 ± 0.3 d (1 SE) ($n$ = 45). The predator peak lagged behind the prey peak by 2.7 ± 0.3 d (1 SE) ($n$ = 45) and the predator minimum density lagged behind the prey minimum density by 3.3 ± 0.5 d (1 SE) ($n$ = 45). The model also gave cyclical dynamics (Fig. 2B) with a mean period of 9.8 d (95% CI = 8.1–12.2), which does not differ from the observed period. Equivalent lags in simulations were 2.1 d (95% CI = 1.5–2.4) for peak densities, and 3.7 d (95% CI = 2.0–4.2) at minimum densities. These lags encompass the experimental values. A comparison of Fig. 2A and B shows that the model gave predator and prey densities within the observed range.

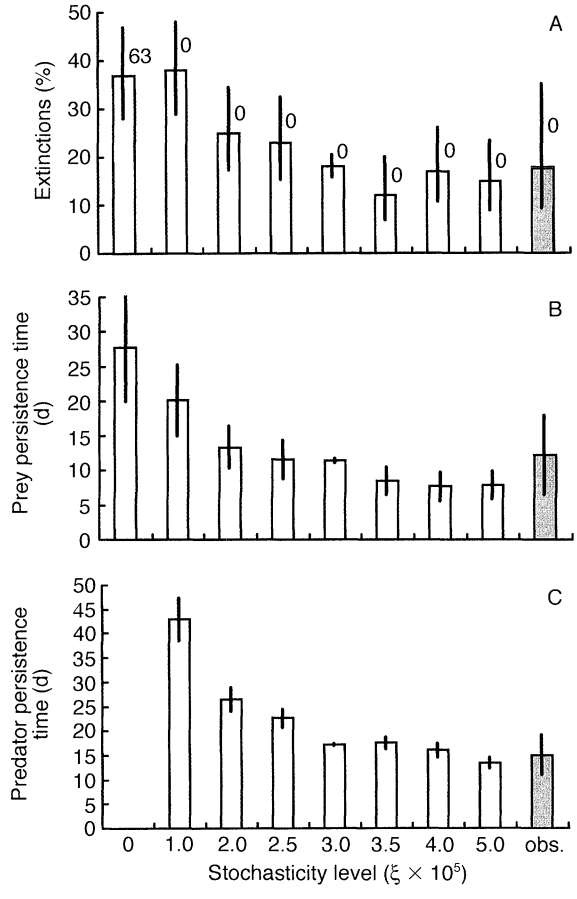


FIG. 1. The effect of adding stochasticity to a model of predator–prey dynamics (increasing $\xi$) on the proportion of cases with prey extinction, and on prey and predator persistence. Each graph shows results from simulations with various levels of stochasticity (unfilled bars) in addition to the observed value from unmanipulated 30-mL bottles (filled bar). Error bars give parametric 95% confidence limits. (A) Percentage of replicates in which prey went extinct. The number above each bar is the number of replicates in which no extinctions occurred within the 83.3 d simulated ($n = 100$ for simulations, except for $\xi = 3 \times 10^{-5}$ where $n = 10\,000$, and $n = 45$ for the experiments). Confidence limits were calculated using a binomial distribution. (B) Mean persistence for prey. (C) Mean persistence for predators. Model parameters are given in Table 2, and simulations began with the same initial abundances as the immigration experiment.

However, there is a much smaller amount of scatter in the simulated density trajectories (Fig. 2B, with $\xi = 3 \times 10^{-5}$) than the observed trajectories (Fig. 2A). At high values of $\xi$, observed and simulated density trajectories showed a similar amount of scatter, but persistence was unrealistically short (Fig. 1).

Dynamics in different 30-mL bottles diverged strongly after ~10 d, making it easier to compare changes in abundances through time during the first 10 d, and to use longer term dynamics to compare measures such as mean density that are less reliant on the phase of observed and simulated dynamics. Fig. 3 compares densities in nine randomly chosen control bottles from the immigration experiment with simulated values. An examination of correlation values showed that densities through time are as well-correlated to dynamics in experimental bottles as the bottles are to each other; for prey, correlations between observed and simulated prey densities were within the range 0.64–0.89 (mean $r = 0.82$, $P \leq 0.05$ in 87% of 15 cases), compared to 0.65–0.99 (mean $r = 0.93$, $P \leq 0.05$ in 80% of 14 cases) between pairs of replicate control bottles of the immigration experiment. Thus, the model did almost as well at predicting prey densities as the experiment. The model did only slightly less well at predicting predator densities; correlations between simulated and experimental data were 0.47–0.97 (mean $r = 0.82$, $P \leq 0.05$ in 60% of 15 cases), compared to 0.63–0.98 (mean $r = 0.87$, $P \leq 0.05$ in 81% of 14 cases) between replicates of the immigration experiment controls. Simulated predator densities declined more rapidly than observed predator densities (Fig. 3B), because predators that could no longer feed were removed from simulations, whereas these would have been counted in experiments. The dashed line in Fig. 3B shows a simulation in which starving predators that were unable to feed were not removed from simulations, which shows that simulated predator densities then declined at a similar rate to empirical values. These simulations required the use of an additional state variable to track whether individuals were capable of feeding, as well as the subtraction of the number of predators incapable of feeding from the total number of predators, $Y(t)$, in predation calculations (Table 1: Eq. 9).

Table 3 shows that the mean prey and predator densities in experimental 30-mL bottles were similar to those in simulations. The model correctly predicted the size of peak predator and prey densities, minimum densities at the trough of cycles, and temporal variability of predators or prey (Table 3).

### *Changes in state variables within simulated density cycles*

Fig. 4 shows the values of individual state variables through a typical simulated density cycle (shown in Fig. 4A). Mean no. prey consumed per predator (Fig. 4B), mean time since feeding (Fig. 4C), and mean predator age (Fig. 4D) all showed regular oscillations; these were least obvious for no. prey consumed per predator, but turning point tests indicated a cycle with a period similar to that of predator density cycles. During increases in predator density, prey were abundant and predators often consumed a high mean number of prey (e.g., days 0–2 or 8–12 in Fig. 4A, B), but no. prey consumed per predator fluctuated widely as cohorts of predators divided and returned to a simulated state of having consumed no prey. At this time, most predators fed at intervals of <1 h (Fig. 4C), and the average predator was at the maximum recorded value of 7 h ($\tau$) that is minimally required for division (Fig. 4D).

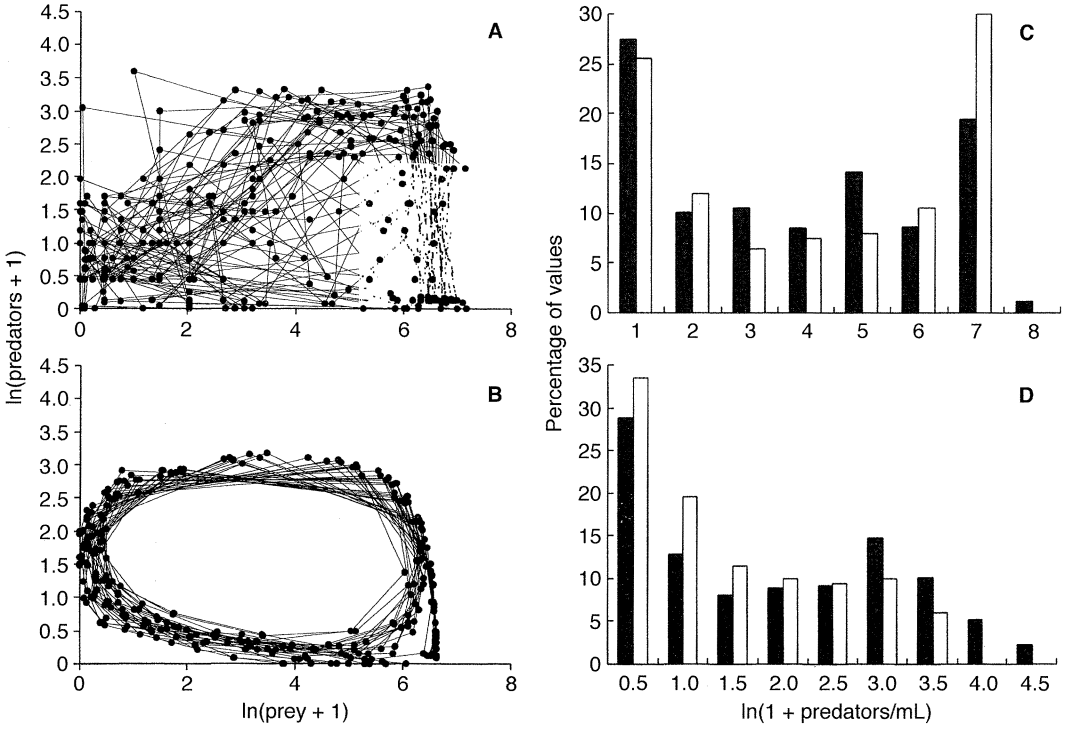


FIG. 2. Phase plane diagrams for experimental 30-mL bottles and simulations, and the distribution of predator and prey density values from a model of predator–prey dynamics: (A) ln(density + 1)-transformed values from 30 of the 45 bottles in which dynamics were not perturbed by adding immigrants; (B) a similar diagram for 30 replicates of simulations, using the same starting values as the immigration experiment; (C, D) distribution of transformed density values is plotted for experimental bottles (filled bars) and simulations (unfilled bars), using the same data as in (A) and (B), respectively. Parameter values are given in Table 2.

The increase in mean predator age during the first day of the density cycle is consistent with increased competition for prey limiting predator division, rather than a developmental delay. Later, as prey densities declined (e.g., days 4–8 in Fig. 4A), the mean time since predator feeding increased (Fig. 4C) causing starvation. At low predator densities, erratic fluctuations in individual state variables caused by the added stochasticity are apparent (Fig. 4 B–D); these reflect that individuals with random values of individual state variables were frequently added. The mean predator age and the average no. prey consumed per predator declined, suggesting that both limit predator division. Declines in prey consumption and mean predator age resulted in a net decrease in predator reproduction that adds to the decline in predator densities.

### *Effects of adding a single pulse of immigrants on observed and simulated dynamics*

In experimental bottles that did not receive immigrant predators or prey during the first density cycle (15 of the "control" bottles), prey went extinct in four of 15 bottles (26.7%). In the remaining 11 bottles (73.3%), prey survived until the termination of the experiment (five days after predators were last recorded in each bottle). Estimated lower and upper 95% confidence limits for the proportion of cases in which prey went extinct (from a binomial distribution) are 9.7% and 53.4% of replicates, respectively. Prey persisted for a mean of 14.0 d (95% CI = 12.0–15.8 d, $n = 4$) and predators persisted for 22.6 d (95% CI = 21.2–24.0 d, $n = 11$) (Fig. 5). There were no significant differences (at $P < 0.05$) in the period of cycles between treatments in $t$ tests.

Prey went extinct significantly more often in experimental bottles that were perturbed by predator addition, compared to controls (27% vs. 80%, $G_1 = 16.0$, $P < 0.001$). In simulations, prey also went extinct more often when predators were added. Extinctions occurred in 17.7% of controls vs. 38% predator addition treatments (300 replicates of each). This difference was significant in a $G$ test ($G_1 = 178.9$, $P < 0.0001$). The frequency of prey extinctions when immigrant predators (38% of replicates) were added in simulations was within the 95% confidence limits of the value of 80% from the experiment (95% CI from a binomial distribution = 34–99%). However, the wide confidence limits show that we do not have a good estimate of the rate of prey extinction from experiments when immigrant predators were added, because experimental sample sizes were small.

Adding prey, or both predators and prey, to exper-

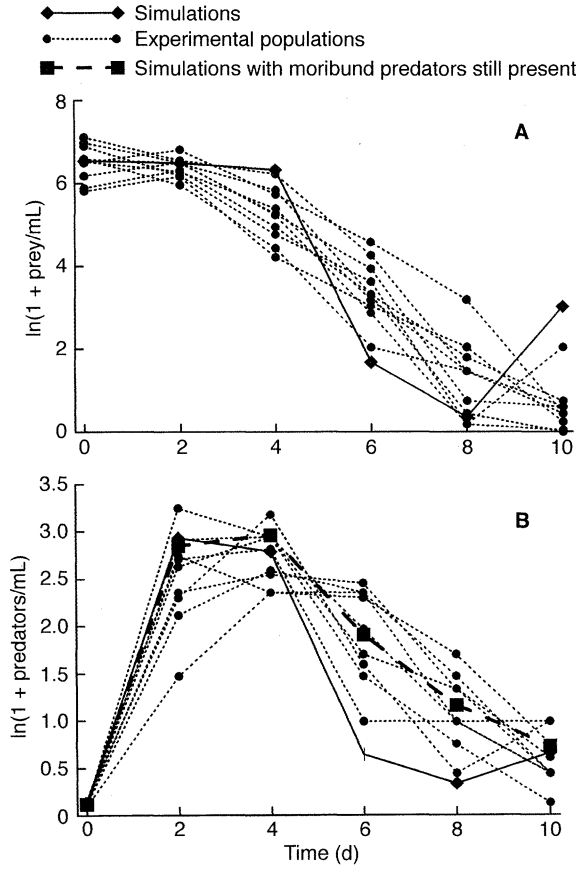


FIG. 3. The fit of model time series to observed densities of (A) prey and (B) predators. The solid line represents the simulated dynamics. Dotted lines are nine replicates from controls in the immigration experiment that was started under identical conditions. The dashed line in (B) represents predator densities where moribund predators were left in simulations. Starting values were $X(1) = 774$ prey/mL, $Y(1) = 4/30$ predators/mL, and $\xi = 0$; other parameters are listed in Table 2.

imental bottles did not alter the frequency of extinction of either species ($G$ tests, $P \gg 0.05$); prey went extinct in 40% (95% CI = 21–62%) and 20% (95% CI = 8–43%) of replicates, respectively. However, persistence of both predators and prey was greater in the prey addition treatments than in controls (which will be presented for comparison with simulations). Prey persisted for a mean of 14 d (95% CI = 12.0–15.8 d, $n = 4$) in control treatments and 23.5 d (95% CI = 20.3–27.2 d, $n = 2$) in prey addition treatments (considering only replicates where prey went extinct). Equivalent figures for predators were 22.6 d (95% CI = 21.2–24.0 d, $n = 11$) and 34.7 d (95% CI = 31.4–38.3 d, $n = 4$), respectively. Both of these differences were significant ($P < 0.05$) in one-way ANOVAs comparing ln(persistence).

In simulations, addition of immigrant prey caused the frequency of prey extinction to drop from 17.7% in controls to 9.3% of 300 replicates ($G_1 = 64.4$, $P < 0.001$). A power analysis on the experimental data shows that 163 replicates are required to attain an 80% chance of detecting a difference of this size; hence it is not surprising that this difference was not significant with only 20 replicates. Adding immigrant predators, or both predators and prey, to experimental bottles did not significantly change persistence. Fig. 5 shows that simulated prey and predators persisted for longer in prey addition treatments than in controls. These persistence times are significantly longer than the equivalent simulated persistence without immigration ($t_{598} = 3.03$, $P < 0.005$; and $t_{598} = 6.73$, $P < 0.001$; respectively). However, simulated persistence with prey immigration was also shorter than the equivalent experimental values (Fig. 5; $t_{34} = 6.27$, $P < 0.001$; and $t_{307} = 7.63$, $P < 0.001$; respectively, from log-transformed persistence). We conclude that the model qualitatively reproduced the effects of adding immigrant prey, but underestimated the amount by which persistence was increased.

TABLE 3. A comparison of observed and simulated dynamics in 30-mL bottles, reporting means and coefficients of variation (CV) of density, and the peak and minimum density in each cycle.

| Factor | Observed | | Simulated | | Comparison |
|---|---|---|---|---|---|
| | Mean | 95% CI | Mean | 95% CI | $P$ value |
| Mean prey density (no./mL) | 25.9 | 20.8–32.1 | 35.2 | 19.8–144 | 0.24 |
| Mean predator density (no./mL) | 5.42 | 4.62–6.34 | 4.38 | 2.65–5.29 | 0.41 |
| Minimum prey density (no./mL) | 0.28 | 0.18–0.39 | 0.38 | 0.17–0.55 | 0.53 |
| Peak prey density (no./mL) | 458 | 389–541 | 512 | 429–601 | 0.42 |
| Minimum predator density (no./mL) | 0.45 | 0.30–0.61 | 0.39 | 0.21–0.72 | 0.37 |
| Peak predator density (no./mL) | 30.2 | 25.4–35.9 | 24.3 | 21.5–38.7 | 0.62 |
| CV of prey density | 1.46 | 1.38–1.54 | 1.29 | 0.86–1.53 | 0.87 |
| CV of predator density | 1.20 | 1.10–1.30 | 1.40 | 1.09–1.81 | 0.12 |

*Notes:* For experimental values, densities were ln(density + 1)-transformed, and per-bottle averages were used to calculate back-transformed means and parametric 95% confidence limits, and peak and minimum densities (after testing per bottle means for normality with a $\chi^2$ test). Density was not transformed prior to taking the CV for each bottle. There were 45 bottles of 30 mL each (see *Experimental methods: Baseline experimental conditions).* For simulations, nonparametric 95% confidence limits and $P$ values from a comparison of the observed mean with the simulated distribution of values come from 10 000 replicates using parameters in Table 2 and initial conditions from the immigration experiment. All densities prior to extinction of either species were used in calculations.

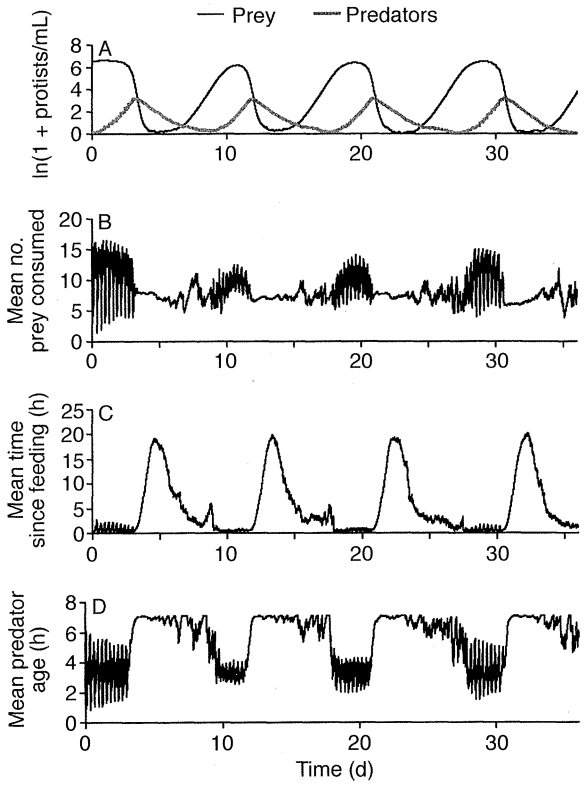


FIG. 4. Mean values of the individual state variables and predator and prey densities during a typical density cycle. (A) Mean prey and predator densities, which are ln(density + 1)-transformed. The thinner black line indicates prey, and the thicker line indicates predators. (B) Mean total number of prey consumed per predator. (C) Mean time since predator feeding. (D) Mean age of predator individuals. Parameter values were as in Fig. 3, except $\xi = 0.00003$.

### *Effects of initial predator–prey ratio on persistence and dynamics*

In the experiment in 30-mL bottles, higher initial predator–prey ratios caused more rapid declines in prey abundance, but did not affect the dynamics of the predator. Mean times for *Colpidium* to reach a minimum abundance in the first density cycle were 2.0 d with a predator–prey ratio of 1.0, 4.0 d with a ratio of 0.2 or 0.6, and 5 d with a ratio of 0.05 ($P < 0.001$, $\chi^2_3 = 23.3$, from a linear model). *Didinium* took 6.5 ± 1.9 d to reach minimum densities or go extinct, regardless of the initial predator–prey ratio. With the exception of one outlier (at the lowest ratio), all predator populations went extinct in ≤8 d. Comparison of these values to persistence of the controls of the immigration experiment (Fig. 5), where mean initial predator–prey ratio was 0.0002, shows that greater predator–prey ratios caused more rapid extinctions of both species. There was no indication that the experimental results depended on absolute density over the small range of densities that we used.

Simulations of 30-mL bottles produced opposite results to those in the experiment; increasing the predator–prey ratio led to increased persistence of both species and to prey extinctions in fewer replicates (Fig. 6). In simulations, predator and prey densities cycled with amplitudes that increased through time until extinction. Starting simulations with greater predator–prey ratios yielded a smaller amplitude initial density oscillation, consequently taking longer for cycles to reach sufficient amplitude for extinctions to occur. In contrast, for all but one replicate of the experiment, prey density declined after predator addition until prey went extinct, and greater initial predator–prey ratios caused more rapid prey declines. Exploratory simula-

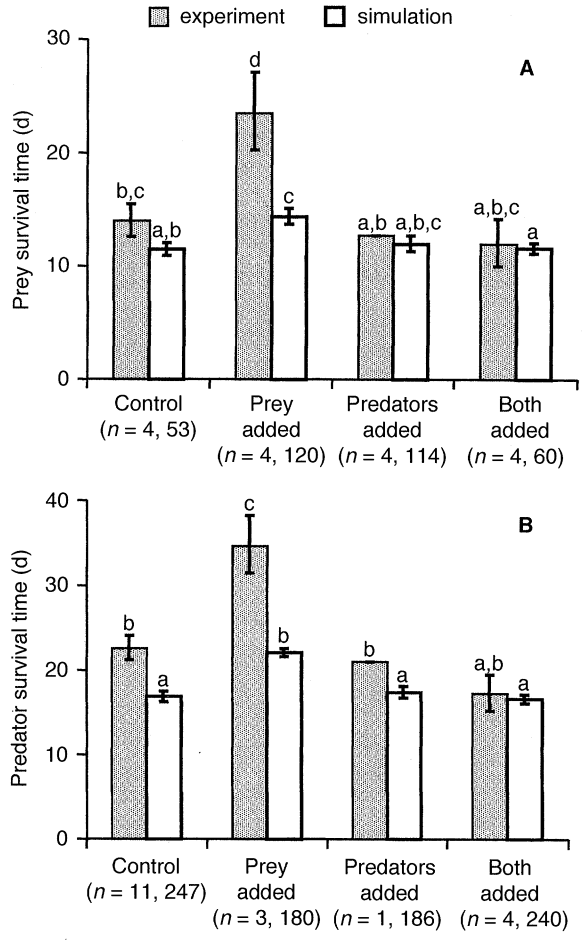


FIG. 5. Persistence of (A) prey and (B) predators in an experiment (shaded bars) or in simulations (unshaded bars) where part way through the initial predator–prey cycle either predators, prey, or both were added to 30-mL bottles. Control treatments received no immigrants. Immigrants were added four days after predators were introduced to prey cultures and at a rate of 10% of the maximum observed density during the first four days; $n$ is the sample size for the experiment and simulations, respectively. In calculating persistence of predators, only replicates where prey persisted were used. Within a species, bars with the same letter above them did not differ at $P < 0.05$ in Student's $t$ tests. Error bars indicate ± 1 SE. Parameter values in simulations were as in Fig. 4.

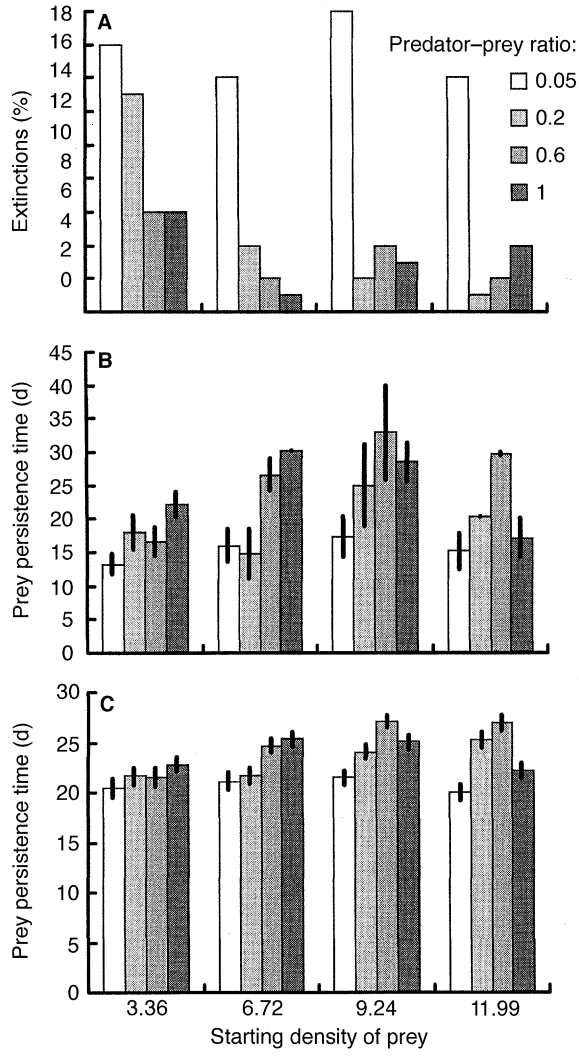


FIG. 6. The effects of initial predator–prey ratios on persistence in simulated 30-mL bottles started at low prey densities. Darker shading of bars represents greater initial predator–prey ratios (of 0.05, 0.2, 0.6, and 1.0). (A) Percentage of 100 replicates with prey extinctions. (B) Mean persistence for prey. (C) Mean persistence for predators. Error bars indicate ± 1 SE. In (A), a logistic model fitted using a maximum likelihood procedure (with binomial errors and weighting for sample size) and comparison of means using $t$ tests showed a greater frequency of prey extinction in the lowest ratio treatment ($\chi^2_3 = 25.9$, $P < 0.001$). In (B) and (C), one-way ANOVAs on ln-transformed persistence and $t$ tests showed increased prey and predator persistence at greater ratios ($F_{3,12} = 3.97$, $P < 0.05$, and $F_{3,12} = 4.30$, $P < 0.05$, respectively).

tions showed that the model correctly predicted the reduced persistence seen in 30-mL bottles when the initial prey density and predator–prey ratio were high. These results suggest that simulations at low prey densities failed to match the experiments, because predation rates at low prey densities were lower than in experiments. Additionally, data on the shape of the functional response were not obtained at such low prey densities (see the Appendix: Fig. A1). Both experimental results from 180-mL bottles and the match between simulations and experiments were qualitatively similar to those from 30-mL bottles. These results are not presented, because experimental sample sizes were small and results are therefore of limited meaning.

## DISCUSSION

This study used direct experimental tests to demonstrate the utility of an individual-based model (IBM) for predicting population persistence of predators and prey. In unmanipulated populations, the model successfully predicted observed values of three interrelated variables related to extinction: prey persistence, predator persistence, and the proportion of replicates with prey extinction. Few studies have tested predictions of persistence using data from real populations (Brook et al. 1997), and we found only one direct test of predicted predator and prey persistence times (Nisbet and Gurney 1982: Chapter 10). Predictions of population persistence most frequently come from population viability analyses (PVAs) using stochastic birth–death models. A weakness of PVAs is that it is often difficult to conduct direct tests of the proposed mechanisms of extinction (Hamilton and Moller 1995, Skelly and Meir 1997). A convenient feature of the IBM formalism is that it simulates both changes in densities and state variables through time, which provide tests of goodness-of-fit that are more straightforward to test than predictions about persistence. Finding concordance between simulated and observed temporal dynamics is a useful step along the way toward validating a mechanistic model of persistence; if such a model cannot predict temporal dynamics we would have little confidence in its ability to predict persistence.

Overall, the model gave good predictions of dynamics in unmanipulated predator and prey populations. In the model, all but one of the nine parameters were directly measured. The free parameter (stochasticity in predator abundance, $\xi$) was adjusted to generate quantitatively reasonable extinction behavior, but it had little effect on the period, amplitude, and trajectory of density oscillations. The simulations without added stochasticity successfully reproduced all of these factors in unmanipulated 30-mL bottles. Simulated phase plane diagrams also resembled those obtained from real populations (Fig. 2).

IBMs have been criticized because they lack generality (Judson 1994). One way to tackle this lack of generality is to represent factors that are widespread in nature (Uchmanski and Grimm 1996) or to address general ecological questions (Grimm 1999). The combination of individual-level and population-level processes in a single formalism makes models of this kind enormously flexible. Such models could be used to represent almost any predator–prey system, and could do so in ways that take advantage of parameters that are easily measured. For example, predator starvation (see the Appendix: Fig. A2) can easily be represented in a

model that tracks the time since feeding of individuals, but is more complex in purely population-level models. Predator reproduction via binary fission deviates from conventional reproductive modes, but is frequent in microbes. Models of this sort, that blend population and individual formalisms, will be useful for modeling field populations where parameters are more difficult to measure.

Although the basic model satisfactorily predicted many properties of population dynamics, the model produced unrealistically long prey persistence in the absence of added stochasticity, and predators never went extinct except when prey did. We solved this problem by adding stochasticity in the form of a small proportional change in predator abundance per time step. Its effects on predator (and prey) densities were not apparent until predator densities became low, when it increased the frequency with which the last few predators went extinct. The need for this adjustment to predator dynamics might result from a number of factors, including the following: (1) omission of an important state variable; for example, we do not explicitly consider bacterial population dynamics (Dive 1975); (2) predator dynamics may be stochastic if predators are sensitive to physical or chemical changes in their environment (e.g. temperature affects reproduction; Laybourn and Stewart 1974); (3) predators may show high demographic stochasticity if predator individuals vary systematically from one another (either genetically or phenotypically); (4) a process such as predation or prey reproduction that is treated as deterministic may actually be stochastic; and (5) a parameter value, or the form of an equation, may have been inadequately represented.

A number of parameters were not measured at the extremes of densities that occur in density cycles, and the representation of functions at low density values is difficult. We regard our measurements of the functional response and the conversion efficiency ($\sigma$) as the least accurate. The functional response showed a great deal of scatter because of prey reproduction (Fig. A1), so that alternative functional responses could not be statistically separated. The magnitude of $\sigma$ was estimated from only nine predators, and the value was not confirmed in a separate experiment. It would be sensible to confirm experimentally the measured parameters and forms of equations as a first step in deciding how the model could be improved. To date, we have broadly explored the effects of the functional response parameters on persistence, attempted to force the use of a type III functional response, and altered the form of the predator starvation curve (Fig. A2A) to reflect recent experimental evidence (Holyoak and Sachdev 1998) that predator mortality may increase sharply with time since feeding. None of these factors lead to an overall improvement in predicted persistence times. We feel that we need further experimental data on functional forms in order to proceed sensibly with a more thorough analysis of error propagation.

The model was able to predict qualitative changes in experimental dynamics when initial predator–prey ratios were manipulated or a single pulse of immigrants was added during the first density cycle. In both simulations and the experiment, prey addition lengthened persistence of both species, and predator addition caused prey extinction in more replicates. However, these perturbations had weaker effects in simulations than in the experiments, suggesting that the model is successful at making qualitative predictions, but that it would benefit from refinements that might improve quantitative predictions. At present, we do not have a good understanding of exactly why the density perturbations in the immigration experiment altered persistence times. Without a clearer understanding of this phenomenon, it is difficult to say more precisely why the simulations failed to reproduce the quantitative findings. Simulations might fail to accurately reproduce these changes either because dynamics are forced to densities where functions have not been parameterized, or because of any of the reasons we have proposed for the addition of stochasticity to the model.

The individual state variables (no. prey consumed per predator, time since feeding, and mean predator age) all show striking oscillations that contribute to the predator–prey density cycle. Changes in individual predator or prey state have also been found in a number of other cyclical predator–prey systems including small mammals and raptors (e.g., Krebs 1985), moose and wolves (Peterson et al. 1998), and grouse and foxes (Dobson and Hudson 1995). In future work, it would be interesting to track individual state variables empirically and to compare them with simulations in an effort to attempt to verify the mechanism as well as the phenomenology. Tracking the state variables directly would be difficult because measurement requires continuous observation of individual predators. One possibility is to track a surrogate variable, such as predator size, which is likely to be influenced by all three of the state variables. We would expect predator size to be greatest during predator increase, because then prey consumed per predator is high, mean age is high, and starvation is minimal. Mean predator size shows marked cyclical changes in *D. nasutum* when fed on *C. striatum* (M. Holyoak, *personal observation*), or *P. aurelia* (Salt 1975, Hewett 1988). An unreplicated experiment (M. Holyoak, *personal observation*) suggested that mean predator volume peaked at approximately two days after predator introduction, which accords with the changes in individual state variables in Fig. 4. However, mean prey size also shows cyclical oscillations, and further experimentation is needed to decipher the role of the state variable in determining predator cell size.

A future goal is to use this model to develop a predictive model of predator–prey metapopulation dynam-

ics. Although models of particular predator–prey metapopulations have been constructed (Nachman 1987*a, b*), only very general models have been compared with real dynamics (Holyoak and Lawler 1996*b*). For the present predator–prey pair, Holyoak and Lawler (1996*a, b*) demonstrated persistence via spatial dynamics in groups of 9 or 25 interconnected 30-mL bottles. The ability to predict extinction of local populations is important to understanding metapopulation dynamics, and makes the present model appropriate for simulating within-patch dynamics in a metapopulation. We also have good information on dispersal rates (Holyoak and Lawler 1996*a*; M. Holyoak, *personal observation*). The model presented here is readily adapted to multipatch dynamics. In contrast, delay differential equations represent dynamics using explicit time delays, and vital rates depend on past conditions in the natal patch. This makes consideration of movement between patches complex unless we know where individuals have come from. The use of individual state variables (age, prey consumed, etc.) in IBMs avoids these problems.

Previous comparisons between IBMs and empirical data from predator–prey systems are limited to within-generation studies (e.g., Rice et al. 1993). Ours is the first study that we know of in which temporal dynamics across many generations and persistence of predator–prey populations were predicted and tested using a single model. Physiologically driven IBMs of population dynamics have been constructed for a variety of natural populations, including *Daphnia spp.* and algae (Nisbet et al. 1989, McCauley et al. 1996) and a ciliate (*Tetrahymena pyriformis*) and bacterium (Jaworska et al. 1996). These models are parameter rich (containing 30 and 21 parameters, respectively, which were extracted from the literature); experimental measurements of parameters were therefore conducted under a variety of conditions. In our study, the use of carefully selected parameters allowed construction of a model in which all of the parameters, except a single stochasticity parameter $\xi$, could be measured. This increase in tractability from combining population-level and individual-level parameters could be exploited in other systems. Once individual state variables have been measured, it may also be possible to collapse individual equations down to a population-level formalism (Fahse et al. 1998). This could reduce the computer time required to simulate complex IBMs, while permitting the use of individual parameters that can often be easily measured.

In conclusion, we showed that a single model formalism is capable of predicting both changes in density through time and persistence of a predator–prey interaction. This study also demonstrates that the combination of individual-level and population-level formalisms into a single model creates an extremely flexible modeling framework that can be used to directly represent factors in ways that can be easily measured. We hope that by demonstrating how an IBM can be used to tie together data about persistence and temporal dynamics this study may serve as a springboard for studies of the persistence of more natural populations. The shortcomings of this study should also not be taken lightly. The need to add a relatively ad hoc stochasticity parameter to accurately predict persistence in a well-studied system and the difficulty in identifying why IBMs work or do not are widespread problems that challenge both theoreticians and empiricists. Mathematical tools that aid simplification and testing of IBMs (e.g., Fahse et al. 1998) are especially valuable.

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## APPENDIX

### Measuring Parameters

*Prey intrinsic growth rate and carrying capacity*

Two replicated experiments measured prey intrinsic growth rate, $r$. In the first experiment ln(density + 1) increased linearly with time for the first ~60 h after placing a single *C. striatum* in a vial containing 2 mL of bacterized medium. A constant prey density was reached after ~72 h. Using data from this experiment and the "immigration experiment," we calculated $r$ during the 48 h period prior to addition of predators, using $r$ = ln(final density/initial density)/48. Both experiments gave an intrinsic growth rate of 0.089 ± 0.006 $h^{-1}$ (mean ± 1 SD; parameter values are summarized in Table 2).

Prey carrying capacity, $K$, was calculated as the mean abundance of prey in two 30-mL bottles (see *Experimental methods: Immigration experiment*). We excluded the first 96 h to ensure that prey had reached $K$. This gave two carrying capacity estimates of 847 and 693 prey/mL, with a mean of 770 prey/mL. Values from later experiments showed that this was a representative value.

*Predator functional response*

Fitting a functional response to experimental data was complicated by a *reproductive* bias caused by prey reproduction during the time that it takes for measurable numbers of prey to be consumed. If prey in populations with predators reproduced at the same rate as those in predator-free control populations, consumption of prey prior to reproduction would make the estimated consumption rate exceed the actual consumption rate. We could reduce the duration of experiments by raising predator density, but this would also make predator densities unrealistically high. We therefore estimated the functional response parameters by fitting a model to the data that included both prey reproduction and predation. This could be accomplished either by simulation and then fitting to the experimental data, or by integrating the equations and fitting a more complicated equation to the data. We used simulations and a highly conservative fitting method, because the equation resulting from integration is complex and difficult to fit (see Houck and Strauss [1985] for a similar case).

Data from two experiments were combined to calculate the functional response of predators to prey density. In the first experiment, a stock culture of *Colpidium* at a density of 1030 prey/mL (1 SD = 195) was used to make dilutions of 10, 20, . . . , 100% (10 densities), and 1 mL of each dilution was placed into each of 13 vials (capacity, 4 mL). In the second experiment, 1 mL of prey at densities of 1554 (1 SD = 187) prey/mL, 1153 (144), 1109 (73), 904 (147), 523 (66), 336

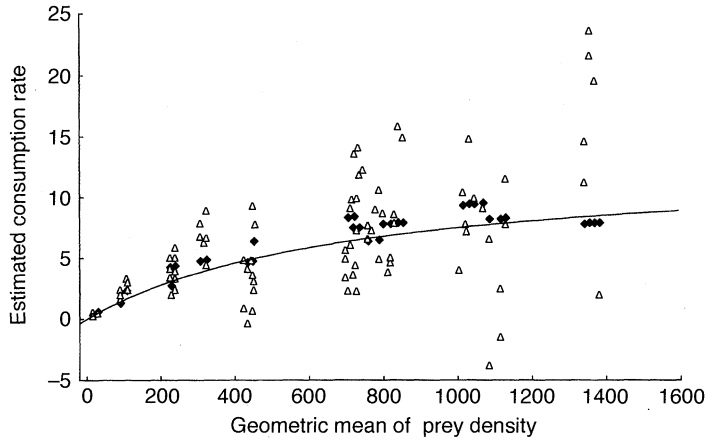


FIG. A1. Results of a predator functional response experiment. The open triangles show observed consumption rates of prey per predator per hour (Eq. A.1) plotted against the geometric mean of initial and final prey density for six or eight replicates at each of 17 prey densities. The filled diamonds show the predicted consumption rate from simulations using Eq. A.2 with the functional response from Eq. 13 ($T_h$ = 0.0769 predator-hours/prey and $a$ = 0.0178 mL·h$^{-1}$·[predator]$^{-1}$). Both predicted and observed consumption rates are biased by prey reproduction. See *Predator functional response* in this Appendix for a fitting procedure that dealt with this bias. The solid line shows prey consumption rates from the best-fitting functional response (Eq. 13 with parameters from Table 2), excluding measurement error due to prey reproduction.

(35), 125 (19), 36.3 (5.0), and 21.0 (2.1) prey/mL was placed into each of 12 vials. We added exactly 10 *Didinium* to 8 of the 13 vials at each concentration in the first experiment and 6 of 12 vials in the second experiment; the remaining vials of each concentration were controls that received no predators. Controls were used to calculate the intrinsic growth rate of prey, to adjust predator consumption rates for prey reproduction. After three hours, we censused *Didinium* in the entire 1 mL of predation treatments. We counted *Colpidium* in a 0.28–0.56 mL subsample (after thorough mixing) from each vial. In the second experiment, three control tubes were sampled immediately to estimate initial prey density, and the other three vials were sampled after three hours to estimate prey intrinsic growth rate. For both experiments, we plotted the final prey density of control flasks against initial density (estimated from the concentration in the first experiment). This relationship was linear, indicating that prey did not approach carrying capacity.

To calculate the number of prey consumed we conducted the following procedure:

1) We evaluated the mean of the final prey concentration from controls at each concentration ($C_d$, where $d$ is the concentration) and obtained a consumption rate for each bottle $\varepsilon_{b\subset d}$ (in units of prey per predator per hour) that included the reproductive bias. Let $b$ be the bottle number for each concentration $d$ (the $b \subset d$ notation symbolizes that bottle number is nested within concentration):

$$\varepsilon_{b\subset d} = \frac{C_d - P_{b\subset d}}{3\hat{Y}_{b\subset d}} \qquad (A.1)$$

where $P_{b\subset d}$ is the final prey density at concentration in bottle $b$ with concentration $d$; $\hat{Y}_{b\subset d}$ is the geometric mean of the initial and final number of predators in bottle $b$ with concentration $d$, and three hours is the duration of experiments. The reproductive bias causes $\varepsilon_{b\subset d}$ to exceed the actual consumption rate of prey.

2) We calculated the geometric mean of initial and final prey densities for each replicate with predators.

3) For control treatments at each concentration, we calculated the intrinsic growth rate of prey for each density ($r_d$ = ln[final density/initial density]/3). An arithmetic mean of $r_d$ (termed $\bar{r}_d$) was then calculated from the replicates for each concentration.

4) For each of the 1300 equally spaced values of $a$ within 0.001–1.3 mL·h$^{-1}$·predator$^{-1}$, and 3000 equally spaced values of $T_h$ within 0.001–3.0 predator-hours/prey we calculated a predicted value of the prey density after three hours, $\hat{P}_{b\subset d}$. These values were then used to calculate a predicted consumption rate with reproductive bias:

$$\hat{\varepsilon}_{b\subset d} = \frac{C_d - \hat{P}_{b\subset d}}{3\hat{Y}_{b\subset d}} \qquad (A.2)$$

where $\hat{P}_{b\subset d} = x(3)$, which is the predicted number of prey after three hours. To estimate the number of prey after three hours (the duration of the experiment) for each bottle, we iterated $x(t + \delta) = x(t) + \Delta x(t)$, where $x(t)$ is prey density at time $t$, $\delta$ is the length of a time step, and

$$\Delta x(t) = [x(t)\bar{r}_d - f(x(t))y(t)]\delta. \qquad (A.3)$$

The functional response $f(x(t))$ comes from Eq. 13 (Table 1). We assumed that predator density $y(t)$ started at 10 prey/mL and increased linearly with time to the final density observed in each replicate. Initial prey density is known from dilutions or measurement. We used time steps $\delta$ of 0.1 h, but also determined that our results were not sensitive to this arbitrary choice by using shorter time steps.

5) We found the values of $a$ and $T_h$ that minimized $\Sigma(\varepsilon_{b\subset d} - \Sigma(\hat{\varepsilon}_{b\subset d})^2$. Because this fitting procedure allows for the reproductive bias, the resulting values of $a$ and $T_h$ are not biased by reproduction.

For a type II functional response (Table 1: Eq. 13), $\hat{\varepsilon}_{b\subset d}$ accounted for a maximum of 32.3% of the variance in observed consumption rates ($\varepsilon_{b\subset d}$). A type III functional response (Holling 1959) accounted for only 0.4% more of the observed variance in consumption rates than Eq. 13 (Table 1), and was rejected because it included an additional parameter. Other studies of predation by *Didinium* on *Paramecium* have also found a type II functional response (Salt 1974, Veilleux 1979, Hewett 1980). Table 2 gives the best-fitting parameter values for Eq. 13, and Fig. A1 shows both the observed (unfilled triangular symbols) and estimated (solid diamond symbols) consumption rates, with reproductive bias plotted against prey density. The best-fitting functional response curve from Eq. 13 (which lacks the bias due to reproduction) is also plotted in Fig. A1. In the model, we treated predation as deterministic. We attempted to add stochasticity to either of the functional response parameters ($a$ or $T_h$), but this did not improve model behavior (see *Results: Persistence with baseline experimental conditions*).

Salt (1974) and Veilleux (1979) reported mutual interference between *Didinium* feeding on *Paramecium aurelia* at high predator densities (>40 predators/mL, compared to <28 predators/mL in our experiments). Yet, during nearly five hours of observations of predator–prey encounters at high predator densities (approximately 33 predators/mL), we did not see any event that could be construed as interference between predators. However, we have not investigated "pseudo-interference" caused by predators aggregating on clumps

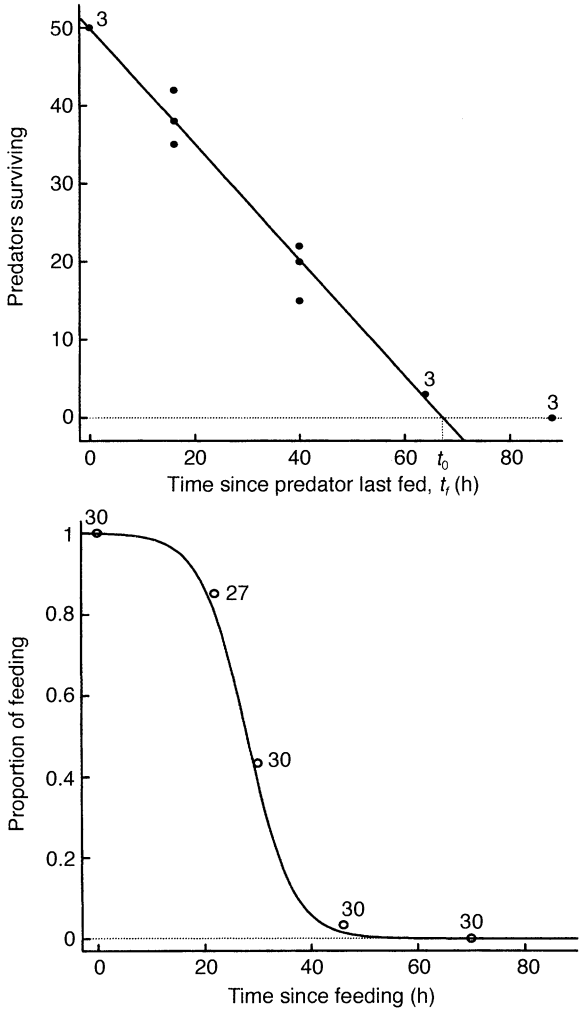


FIG. A2. (A) Survival time of predators in the absence of prey, and (B) proportion of predators capable of feeding after different periods of starvation. In (A), the final three points, at 88 h when no predators remained, were excluded from the linear regression because we do not know when the predators starved between 64 and 88 h. Numbers next to points on the graph list the numbers of overlapping points. Because the experiment was started with 50 predators, a linear regression was forced to have an intercept of 50; $F_{1,10} = 687$, $P < 0.0001$, slope $= -0.7418$ (1 SE = 0.0284). The line in (B) comes from a logistic regression (see *Predator starvation and ability to feed during starvation* in this Appendix and parameters $u$ and $w$ in Table 2 for other statistics). Numbers next to points on the graph show the numbers of individuals that were used to calculate the proportion. The value of the point at 72 h was assumed from (A).

of prey, which can reduce the per capita predation rate in a way that resembles mutual interference (e.g., May 1978). We do not consider interference further here, but the potential for pseudo-interference should be evaluated in future work.

*Generation time and conversion efficiency of predators*

We performed an experiment to calculate the minimum time between divisions of predators. We isolated nine pre-division *Didinium,* identified by their figure eight shapes, from cultures and let them complete division. We randomly took one of each pair of daughter cells and placed three individuals into each of three large drops of sterile water containing 150 prey (~ 0.3 mL/drop). This prey density (500 prey/mL) is slightly greater that the peak prey density (458 prey/mL) in experimental, predator–prey populations used to quantify dynamics and persistence (Table 3). We also prepared three similar drops to serve as controls to estimate the rate of prey starvation. Sterile water was used instead of nutrient medium to minimize prey division. We observed predators until they divided. After four hours, the predators had not yet divided, and mean prey abundance was 110 in controls and 79 in predator treatments. Predators were transferred to fresh drops containing 150 prey, and three fresh control drops were prepared. Predators divided after a mean of 7.00 h (SE = 0.15 h; $n = 3$, from three large drops each containing three predators). Final prey abundances were ~111 in controls and 89 in predator treatments. Predators ceased hunting at least an hour prior to division; this either represents satiation, or it represents activities that are incompatible with hunting and feeding. We factored out prey death in controls and calculated that each predator consumed a mean value of 18.05 prey between divisions (SD = 1.84, $n = 3$, from three large drops each containing three predators) .

We also calculated a predator generation time during the first 48 h after predator addition in the "immigration experiment" as ln(2) × 48/(ln[final density] − ln[initial density]). The immigration experiment gave a generation time of 7.14 h (SE =0.018, $n = 30$), which does not differ from the rate calculated above (Student's $t_{31} = 0.90$, $P \gg 0.05$). In the model, both the generation time and conversion efficiency were treated deterministically, because they had low variability in experiments.

*Predator starvation and ability to feed during starvation*

To estimate the predator starvation rate in the absence of prey, we placed 50 *Didinium* into 21 vials containing 3 mL of sterile medium, but no prey. We destructively sampled the entire 3 mL in three vials daily until no predators remained. Fig. A2 (panel A) shows that a constant number of predators died each day; a linear regression of numbers against time accounted for 98.6% of variance. From the regression equation, we can calculate the time when predator survival is zero (67.2 h) for use in Eq. 3 (Table 1). We assumed that predators, which came from cultures with abundant prey, had just fed prior to the start of the starvation experiment.

A second experiment calculated the proportion of predators capable of feeding after different periods of starvation. The experiment was set up in the same way as the previous experiment, except that it was started with predators that had just divided. After 0, 22, 30, and 46 h, a single surviving (swimming) predator was placed into each of 30 vials (capacity 3 mL) containing 2 mL of a solution with ~758 (SD = 215) prey/mL. Each vial was checked to ensure successful transfer of the predator. After 48 h the number of predators in each vial were counted, and those that had divided were recorded and discarded. If a vial contained no predators, that predator was judged to have been incapable of feeding. If there was only one predator present (two cases only) the predator was given a further 48 h to divide. In both cases, the predators died. Fig. A2 (panel B) shows the proportion of predators capable of feeding after the three starvation periods. A logistic regression of the proportion surviving against time since feeding was highly significant (see Table 2 for the intercept, $u$, and slope, $w$; $\chi^2 = 258$, df = 1, $P < 0.0001$) and accounted for 64% of the deviance in the proportion capable of feeding. For predator $i$, the proportions capable of feeding at time $t_{f(i)}$ after feeding and time $t_{f(i)} + \delta$ after feeding were calculated from the logistic regression equation and used to calculate the probability of becoming unable to feed during a time step of length $\delta$ at time $t_{f(i)}$ after feeding (Table 1: Eq. 4).