

## Widening the window of persistence in seasonal pathogen–host systems

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### Abstract

Local instability of exploiter–victim systems is well-known in both theory and in nature. Victims can be too sparse to support exploiter reproduction (under-exploitation) or they can be too readily driven to extinction (over-exploitation). Exploiters of seasonal resources face the additional challenge of surviving periods when victims are rare or unavailable. We formulate a fully stochastic model of highly seasonal pathogen–host dynamics and explore the interactions between an entomopathogenic nematode and its lepidopteran host. Our model suggests that if nematode populations experience the high rates of mortality predicted by short-term laboratory experiments, the paired threats of under- and over-exploitation should preclude the long-term persistence of this exploiter–victim system. We measured nematode mortality rates in the field and found that long-term mortality is lower than that predicted by short-term experiments. Incorporation of this new data into our model produces long-term persistence of local nematode populations across a range of initial nematode densities.

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### 1. Introduction

The fragility of exploiter–victim coexistence (Huffaker, 1958; Keeling et al., 2000; Murdoch and Oaten, 1975; Nicholson and Bailey, 1935) has been known since the seminal work of Gause (Gause, 1934). Long-term persistence of these systems is possible only if the paired risks of over- and under-exploitation are avoided. Natural selection on exploiters leads to a general

tendency for consumers to over-exploit resource populations. For pathogens with large numbers of infective propagules, the resulting depletion of hosts can lead to the extinction of the pathogen itself. Such over-exploitation of host populations is common in human diseases, where acquired immunity and/or deaths can exhaust the available hosts and lead to ‘fadeouts’ of disease epidemics (Keeling and Grenfell, 2002). Locally high host infection rates by parasites and parasitoids strongly suggest a common potential for over-exploitation (Gomez–Gutierrez et al., 2003; Lafferty and Kuris, 1996; Strong et al., 1996). A series of classic experiments (Huffaker, 1958) demonstrated the potential for predatory mites to drive victim populations to extinction, with subsequent collapse of the predator. Similar dynamics have been observed in a number of exploiter–victim systems, including *Didinium-Paramecia* (Luckinbill, 1973)

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and ciliates (Holyoak and Lawler, 1996). Consumer persistence is also threatened by under-exploitation; exploiter populations can go extinct via their inability to reproduce at low resource densities. Diseases, for example, die out if the mean reproduction number (expected number of secondary infections per primary infection) is less than one (Diekmann and Heesterbeek, 2000). Under-exploitation is also of considerable concern in applied ecology: both biological control efforts and accidental introductions of exploiter populations often fail when the introduced natural enemies cannot find sufficient prey or hosts (Stiling, 1993; Williamson, 1996).

Many exploiter populations live in seasonal environments, in which the conditions for their survival fluctuate dramatically and affect the probability of under and over-exploitation. Seasonally stressful abiotic conditions and periods of low victim availability are commonplace among viruses, nematodes, and fungal parasite–pathogens of univoltine insects (Briggs and Godfray, 1996; Dwyer et al., 2000; Elliot et al., 2002; Kohler and Wiley, 1997; Strong et al., 1996), mammals (Dimander et al., 2003), marine and freshwater invertebrates (Karvonen et al., 2003; Saarinen and Taskinen, 2003), and annual plants and agricultural crops (Aylor, 2003; Shaw, 1994). Dormant, resting, or resistant propagules notwithstanding, high mortality under seasonally stressful conditions is not unusual for the infectious propagules of pathogens (Decaestecker et al., 2003; Gomez–Gutierrez et al., 2003; Kohler and Hoiland, 2001; Lafferty and Kuris, 1996; Strong, 2002). Understanding the conditions that allow victim–exploiter persistence in the face of high exploiter mortality is germane to basic ecology as well as applied fields ranging from epidemiology to biological control. We construct a general seasonal model of over- and under-exploitation and apply it to the example of entomopathogenic nematodes.

Entomopathogenic nematodes are microparasites that are widespread enemies of soil insects (Hominick, 2002). They are commonly found in seasonal environments (Stuart and Gaugler, 1994). In such environments, entomopathogenic nematodes of the family Heterorhabditidae find and infect hosts during wet seasons and are inactive during dry seasons. Adults, feeding, and reproduction, of entomopathogenic nematodes occur only within the host cadaver; prey are pursued and infected by third-instar dauer larvae known as infective juveniles (IJs). The IJ enters a host through a spiracle or other orifice, and regurgitates a mutualistic bacterium that quickly kills, digests, and preserves the host with antibiotics. The bacterial population provides food for the growing nematode population inside. When the resources of the host cadaver are depleted, IJs emerge into the soil en masse and disperse in search of new hosts (Gaugler, 2002). A single large infected host produces

hundreds of thousands of free-living IJ nematodes (Preisser et al., in review). IJs move through the thin film of water surrounding soil particles, and they cannot move or kill prey in dry conditions (Grant and Villani, 2003). Thus, the IJs must survive the long dry season without hosts and suffer high mortality in dry, summer soil. Few survive from 1 year to the next, and mechanisms of persistence of their populations are poorly known (Strong, 2002).

Attack and infection rates of hosts can be extremely high (Strong et al., 1996), suggesting the potential for over-exploitation. Natural populations of these nematodes also die off even in the presence of live hosts (Strong, 2002), a that suggests under-exploitation. While this finding might be equally well-explained by the presence of the nematode's natural enemies, a series of laboratory and field experiments have found no evidence that EPN are controlled by predation at BMR (Jaffee and Strong, 2005; Jaffee et al., 1996). Models of non-seasonal control of hothouse pests also show the interaction of entomopathogenic nematodes and host flies to be unstable (Fenton et al., 2001).

The survival of Heterorhabditid nematodes in soil has been experimentally measured in several laboratory and agricultural field experiments (reviewed in Strong 2002). Most published mortality rates give cohort half-lives ( $\ln 2$ /daily mortality rate) for IJs in the soil of less than 10 days (Baur and Kaya, 2001; Strong, 2002). A half-life of 10 days reduces a cohort to 1/1000th of its starting size in 100 days, suggesting that dry seasons several months in length readily imperil cohorts of these microparasites. The lion's share of known entomopathogenic nematodes inhabit seasonal environments where hosts are unavailable for most of the year (Hominick, 2002). Given the susceptibility of active entomopathogenic nematodes to desiccation (Grant and Villani, 2003) and the lack of a desiccation-resistant resting stage in Heterorhabditids (Glazer, 2002), it is unclear how this microparasite–host system persists in a seasonal environment.

We explore the criteria for persistence of natural populations of the entomopathogenic nematode *Heterorhabditis marelatus* and their host, root-feeding host larvae of the ghost moth *Hepialus californicus*, in the Mediterranean climate of the California coast. We begin by presenting a seasonal model of the nematode–ghost moth interaction, then use a field experiment to generate estimates of long-term nematode survival independent of the short-term laboratory data traditionally used to parameterize dynamic models (Dugaw et al., 2004; Fenton et al., 2000, 2001). We compare the long-term persistence of the system predicted using the two mortality estimates, and highlight that measuring microparasite mortality under natural conditions can substantially increase the predicted probability of long-term persistence.

## 2. Mathematical model

To describe over- and under-exploitation, we analyze a fully nonlinear stochastic model of this exploiter–host system. We show that under-exploitation can be understood by the failure to have any infections. Because the exploiter’s fecundity is so high that a single infection prevents under-exploitation, under-exploitation can be analytically calculated as a linear stochastic process. Conversely, over-exploitation means large exploiter populations that exhaust their resources, allowing a tractable nonlinear deterministic model to approximate the stochastic model. We use our model to identify conditions favoring extinction in exploiter–victim associations, and the conditions that allow these associations to persist.

We derive our stochastic model by considering the dynamics within a year, similar to our earlier derivation of an analogous deterministic model (Dugaw et al., 2004). We divide the model into two seasons: the wet winter season when hosts are available and parasites are active, and the dry summer when parasites are quiescent. During the wet season, four events can occur: a parasite infects a host, a parasite dies, a host dies from causes other than parasite infection, and parasite offspring emerge from a host cadaver. The first three events are modeled as continuous time Markov processes (Taylor and Karlin, 1984). Infection occurs at a rate proportional to the product of the host and IJ populations. We ignore the possibility of multiple infections, because in nature the vast majority of hosts (>95%) are killed by a single hermaphroditic IJ (Strong and Preisser, unpublished data). Parasite and host deaths occur at rates proportional to their respective population sizes (Table 1). While a numerical response of nematode-trapping fungi to an increase in nematode populations has been suggested as a possible mechanism for density dependent death rates of these nematodes, experimental work has failed to find support for this hypothesis (Jaffee and Strong, 2005; Jaffee et al., 1996). Infections occur at a rate proportional to the product of the host and parasite population, and parasites emerge from hosts a fixed period of time,  $\tau$ , after an infection (Table 1). Parasites are unable to infect hosts during the dry season and experience only mortality (i.e. nematode deaths are the only events). Thus, the model reduces to a pure death process for the duration of the dry season (Taylor and Karlin, 1984). The parasites that survive the dry season become the initial population for the next wet season, and we assume that the new initial host population is Poisson-distributed with a mean independent of the local density of free-living parasites (Dugaw et al., 2004). This is a reasonable assumption because hosts disperse on a larger spatial scale than do localized microparasite populations (Wagner, 1985). Furthermore, the nematode is less

Table 1

The model is a continuous time stochastic process characterized by four possible events

Event	Transition	Rate
Nematode death	$N \rightarrow N-1$	$k_N N$
Host death	$H \rightarrow H-1$	$k_H H$
Infection	$N \rightarrow N-1$	$\beta H N$
	$H \rightarrow H-1$	

The first three are described in the table below.  $N$  and  $H$  represent the nematode and host population sizes,  $k_N$  and  $k_H$  are the nematode and host mortality rate constants and  $\beta$  is the infectivity. The fourth event, emergence, occurs  $\tau$  days after an infection, and the number of emerging infective juveniles is a saturating function of time, i.e.  $N \rightarrow N + \min\{M_0 e^{\tau t}, \Lambda_{\max}\}$ . (see Dugaw et al., 2004 for a discussion of this function).

frequent in space than the host ghost moth, and rhizospheres without the enemy produce most of the ghost moth recruits (Strong et al., 1996). Ghost moths are very strong flyers, and can lay eggs hundreds of meters away from their natal rhizosphere (Wagner, 1985). This pattern of long-distance dispersal supplies rhizospheres with host recruits independent of the local nematode densities.

## 3. Analysis

We begin our analysis of under-exploitation by realizing that

$$P[\text{extinction}] = P[\text{extinction \& noinfections}] + P[\text{extinction \& at least one infection}], \quad (1)$$

and that for the low infectivity or initial small parasite populations the second term is small. The term in Eq. (1) is given by the product:

$$P[\text{extinction}|\text{no infections}]P[\text{no infections}].$$

To approximate the probability of not having an infection we assume the parasite population is given by the solution to the corresponding deterministic model  $N(t) = N(0) \exp(-k_N t)$ . The probability of not having an infection then satis

$$\frac{dP[\text{no infections}](t)}{dt} = -\beta H N(t) P[\text{no infections}](t) \quad P[\text{no infections}](0) = 1. \quad (2)$$

We integrate Eq. (2) using the expression for  $N(t)$  given above to obtain the probability of having no infections.

$$P[\text{no infections}](t) = \exp\left[-\frac{\beta H N(0)}{\kappa_N} (1 - e^{-\kappa_N t})\right]. \quad (3)$$

If we assume there are no infections, then the only event that affects the nematode population is death, and the nematode dynamics reduce to a pure death process. Thus, the conditional probability of extinction for a single year, given no infections, is obtained from the solution to a pure death process (Taylor and Karlin, 1984)

$$P[\text{extinction}|\text{no infections}](t) = (1 - e^{-\kappa_N t})^{N(0)}. \quad (4)$$

When infection rates are low, or the initial parasite population is low, single wet season parasite extinction probabilities are well approximated by the product of Eqs. (3) and (4) evaluated at  $t = 365$ , an entire year (Fig. 2).

Over-exploitation is the main mode of extinction for nematode populations that are initially large or have high infectivity. Under these conditions there are typically several infections early in the season, and the nematode population remains large throughout the wet season. Thus, the wet season dynamics are well described by the corresponding deterministic model for the wet season:

$$\begin{aligned} \frac{dH(t)}{dt} &= -\beta H(t)N(t) = \kappa_H H(t), \\ \frac{dN(t)}{dt} &= -\beta H(t)N(t) - \kappa_N N(t) \\ &\quad + \beta H(t - \tau)N(t - \tau)\Lambda(t - \tau). \end{aligned} \quad (5)$$

Extinction may occur during the dry season, and we calculate this probability using the result of the deterministic model (Eq. (5)) as the initial condition for the stochastic dry season sub-model. Since, the dynamics are a pure death process in the dry season the extinction probability is given by an equation analogous to Eq. (4):

$$P[\text{dry season extinction}] = (1 - e^{-\kappa_N(365-T)})^{N(T)}, \quad (6)$$

where  $N(T)$  is the solution to the deterministic model for the wet season (Eq. (5)) evaluated at the end of the wet season, i.e.  $t = T$ . We obtained  $N(T)$  by numerically integrating Eq. (5).

As a complement to our analytic approximation approach, we also estimated extinction probabilities using Monte Carlo simulations of the full stochastic model. These simulations were coded in C using the randlib v1.3 library to simulate the random variates. We simulated exponential random variates to determine the timing between events (Taylor and Karlin, 1984), and then updated the state variables appropriately. We were able to calculate multiple year extinction probabilities by using the output of 1 year as the initial condition for the next. The extinction probability was estimated as the fraction of 10,000 simulations where the nematode population went to zero.

#### 4. Field experiment: methods

We conducted an experiment designed to determine the mortality rate of the entomopathogenic nematode *H. marelatus* in the field over long time scales. In coastal grasslands at the Bodega Marine Reserve (Bodega Bay CA, USA), we divided a  $4 \times 4$  m area into 16 contiguous  $1 \text{ m}^2$  blocks. We buried 40 sampling tubes (see below) in the root zone of each block (5–10 cm below ground). To minimize disturbance, we used shovels to pull up the upper grassland layer, placed the tubes underneath, and then replaced the upper grassland layer. Three different nematode density treatments were applied to the 40 sampling tubes in each block, with 10 tubes/treatment. The full analysis of the impact of each density treatment on nematode survival through time is developed elsewhere (Preisser et al., in review); accordingly, only results from the high-density (2500 IJ *H. marelatus*) treatment are discussed here. There was also a zero-nematode control treatment (Z) into which we pipetted distilled water rather than nematode solution. The experiment consisted of 320 sampling tubes (16 blocks  $\times$  20 tubes/block = 320 tubes) with 160 tubes assigned to each of the control and high-density treatments.

##### 4.1. Design of sampling tubes

We made sampling tubes by cutting the bottom off of 50 ml plastic centrifuge tubes (Falcon brand). We covered the bottom of each tube with fine ( $0.56 \text{ mm}^2$  mesh size) plastic mesh, and held it in place using plastic rings. The mesh excluded prey items from the tube (denying the nematodes a food source and preventing reproduction) while allowing air and moisture to move between the tube and surrounding soil. The design of the tubes also excluded both macro- and micro-invertebrate nematode predators, preventing predation from occurring and influencing the survival results. Each tube had 30 cc of damp (approximately  $0.2 \text{ ml H}_2\text{O/g}$  dry soil) soil added to it, into which we either pipetted 2500 nematodes from solution (the high-density treatment) or added an equal amount of distilled water (the zero-nematode control). Once the nematode solution/distilled water had been added, we capped each tube with screw-top lids; they remained sealed until retrieved from the field and sampled. In a subsequent experiment (Preisser et al., in review) with identically designed sampling tubes, we gathered data on the effect of the sampling tubes on soil moisture levels. We found no significant difference between mean soil moisture inside and outside of tubes buried in the same grassland used in this experiment.



## 4.2. Sampling protocol

All 16 blocks were buried in the coastal grassland in April 2001. We sampled eight times over 1 year, removing the last set of tubes in April 2002. On each sampling date, we selected two blocks using a random number generator, removed all the tubes in each block (20 tubes/block from each of the high density and control treatments = 40 tubes total), and immediately brought them inside. We added distilled water to each tube to increase the soil moisture to 15–20% H<sub>2</sub>O/g soil (3–5 ml H<sub>2</sub>O/tube). We added two ‘bait’ insects (‘waxworms’, larvae of the wax moth *Galleria mellonella*) to each tube, a standard method of censusing entomopathogenic nematodes (Kaya and Stock, 1997), then capped the tube and let it sit for a week. After a week, we removed the waxworms, scored them as nematode-infected or uninfected, and placed two new waxworms in the tube. We sampled the tubes for a total of 3 weeks (6 waxworms/tube). The highest number of nematode-infected waxworms occurred during the first week, and virtually none of the waxworms tested during the third week showed signs of nematode infection; we interpret these facts as suggesting that the 3-week sampling period censused nearly all of the surviving IJ nematodes.

Nematode-infected waxworms were briefly frozen to stop nematode development, placed in pepsin solution, and heated at 40 °C for 2 h. After pepsin digestion, we examined the digested waxworms and counted the number of *H. marelatius* nematodes.

## 5. Statistical analysis

We determined the nematode mortality rate by using linear regression on the log-transformed number of survivors versus time; the expected fraction of survivors after time  $t$  was  $\mu(t) = C \exp(-k_N t)$ . This method assumes that the error about the mean is log-normal and thus ignores process error. Entomopathogenic nematodes are so small that they must be sampled destructively; this fact prevented us from addressing process error in our analysis. We also fit a negative binomial model to the data, but the results were very close to the simple regression. Previous work on entomopathogenic nematodes has suggested that only a fraction of nematodes are viable; i.e. have the potential to infect hosts (Campbell et al., 1999). To address this possibility, we used two different methods of calculating the nematode mortality rate. In one case we assumed that all the nematodes that were initially placed in the tubes were viable, i.e. we fixed  $C = 1$ . In the other case we made no assumption about the fraction of initial number of viable nematodes,  $C$ , and back-calculated the intercept  $C$  using least squares. This provides two alternate fits to the model, one of which was derived

without any assumptions regarding the initial nematode density.

## 6. Results

### 6.1. Field experiment

Some nematodes survived for a year in the field. We recovered an average of  $135.35 \pm 12.65$  (se) *H. marelatius*/tube 1 month after beginning the experiment with 2500 nematodes/tube. After 1 year, this number had declined to  $0.95 \pm 0.58$  nematodes/tube. Of the 160 tubes in the control treatment, only one nematode was recovered. Using the known initial number of nematodes in the experiment we estimated the daily mortality rate was  $k_N = 0.032 \pm 0.0032$  ( $F$ -test:  $p < 0.0001$ ). When we made no assumptions about the initial number of nematodes, the daily mortality rate was  $k_N = 0.012 \pm 0.0025$  and the estimated fraction of nematodes that were viable was  $C = 0.0156 \pm 0.0001$  ( $F$ -test:  $p = 0.0003$ ). Both estimates of nematode mortality are significantly lower than the previous published measurements which gave half lives less than 11 days, or mortality rates  $k_N > 0.063$  (Strong, 2002). Residual plots show a clear trend in the residuals over time in the case when the initial numbers was fixed, but there was no trend when the initial value was estimated (Fig. 1).

### 6.2. Model results

Model results generated with published mortality rates (Strong, 2002) and previously estimated parameter values (Dugaw et al., 2004) predict that long-term persistence of this exploiter–victim system should be extremely rare. Fig. 2 shows our analytic approximations of single-season nematode extinction probabilities as a function of initial nematode population size and results of simulations of the fully stochastic version. Fig. 3 shows the dependence of extinction probability on initial nematode population size and infectivity. Extinction due to over-exploitation and extinction due to under-exploitation are nearly mutually exclusive and exhaustive events for the high mortality rates measured under laboratory conditions. For low infectivity rates or small initial parasite populations, the population usually goes extinct because the parasites are unable to find hosts (under-exploitation). At higher rates of infectivity or large initial parasite populations, however, population extinction via over-exploitation is also nearly certain. Extinction from over-exploitation occurs because the parasites quickly infect and kill all of the hosts early in the wet season, leaving them without the future reproductive potential necessary to counter high dry season mortality. There is only a narrow range of parameter values where the probability of extinction for

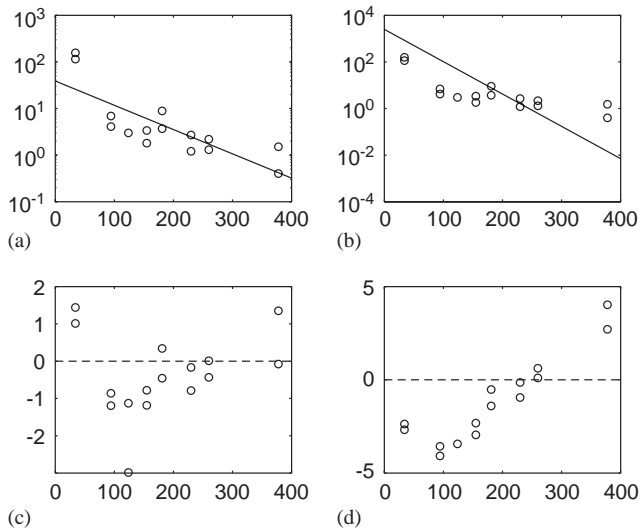


Fig. 1. Plots of the natural log of the number of surviving nematodes versus time for the field experiment. Panel (a) shows the results when we fit the intercept by back-calculating from the number of nematodes present in the tubes at each sampling date. The solid line represents the expected number of survivors predicted by the model. Panel (b) shows the results when the intercept was held fixed at the log of the number of nematodes that were put in the tubes,  $\ln(2500)$ . Panel (c) shows the residual for the fitted intercept model, and panel (d) shows the residuals when the initial number of nematodes was fixed.

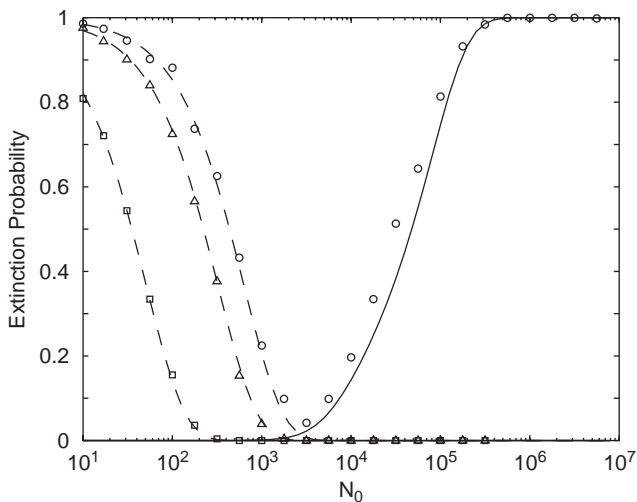


Fig. 2. Results from stochastic model analysis and simulation showing the dependence of single-year extinction probabilities on initial nematode population size. The dashed lines show the single-year extinction probability due to under-exploitation from Eqs. (2) and (3). The solid lines show the extinction probability due to over-exploitation from Eq. (4), and the points marked with circles, triangles, and squares are computed from 10,000 numerical simulations of the model. Parameters are the same for simulations and analytical results, mean initial host population size = 100, host mortality  $k_H = 0.0001 \text{ day}^{-1}$ , and nematode generation time  $\tau = 35$  days. The length of the wet season was  $T = 160$  days, and maximal host productivity was  $\Lambda_{\max} = 800,000$  nematodes per host,  $r = 0.09 \text{ day}^{-1}$ ,  $M_0 = 10,000$ ,  $\beta = 10^{-6}$  (see Table 1 for a summary of model & parameters). Results with nematode mortality  $k_N = 0.063 \text{ day}^{-1}$  are marked with circles,  $k_N = 0.032 \text{ day}^{-1}$  marked with triangles, and  $k_N = 0.012 \text{ day}^{-1}$  are marked with squares.

either reason is low and the exploiter–victim association can persist for a season. Even when the exploiter–victim system does initially persist, however, initial parasite densities the following year almost always fall outside the narrow window where persistence is likely. The probability of parasite populations persisting for 5 years is essentially zero for measured parameter values (Fig. 4).

Prior to extinction the year to year dynamics of the stochastic model are characterized by a noisy period two cycle, similar to the corresponding deterministic model (Dugaw et al., 2004). The model nematode populations can either go extinct after a high year (over-exploitation), or it can go extinct after a low year (under-exploitation).

Our model predicts that nematode populations are more likely to persist when we use the mortality rate we derived using the long-term experiment (all other parameter values were the same as above). The probability of extinction due to over-exploitation in a single year is reduced to almost zero (Fig. 3) and most persistence times are extended to five or more years (Fig. 4). The effect of decreased nematode mortality on persistence is stronger for small initial nematode populations due to the non-linear nature of over-exploitation. In contrast, increased nematode survivorship has a linear effect on under-exploitation (Figs. 2 and 3).

## 7. Discussion

Our method for calculating the extinction probabilities of an exploiter population produces simple formulae, applicable to a wide variety of exploiter–victim systems living in seasonal environments, which provide a fundamental understanding of the mechanisms leading to extinctions. Extinction due to over-exploitation of a seasonally limited resource occurs via exploiter mortality once the resource is depleted. Thus, a deterministic model yields the time to resource depletion and the resulting exploiter population size. Once the hosts have gone extinct, a linear stochastic model determines the extinction probability. This method of calculating extinction probabilities is very similar to a method derived for populations with non-overlapping generations (Iwasa and Mochizuki, 1988), but we allow for overlapping generations within a season. Our approach approximates under-exploitation in highly fecund microparasites by the failure to find hosts.

We initially modeled long-term nematode persistence in a natural system using parameters gathered from short-term laboratory experiments (Strong, 2002). This approach is similar to that of other microparasite–host models (Dugaw et al., 2004; Fenton et al., 2000, 2001). Based on these parameters, long-term persistence of

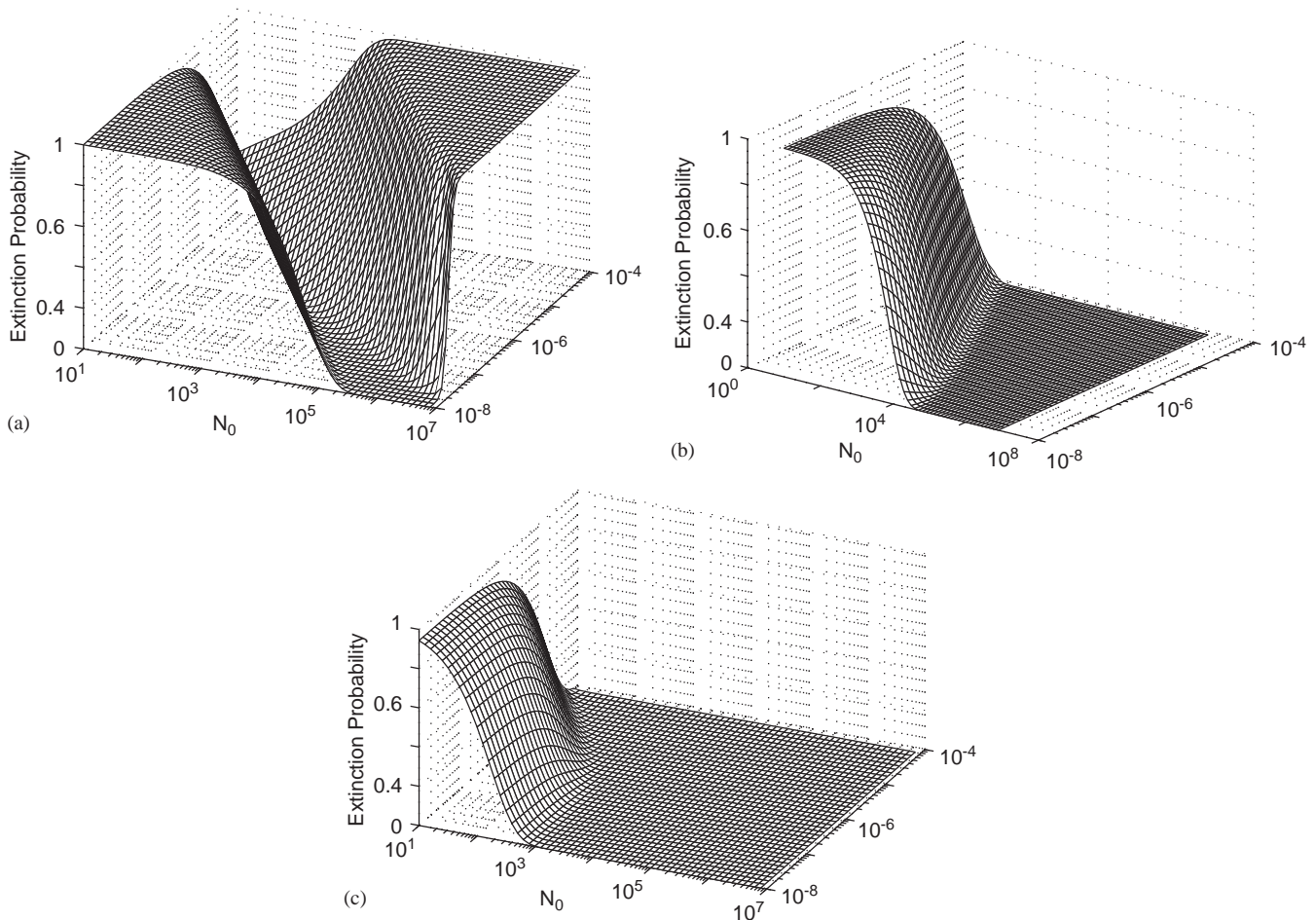


Fig. 3. Approximations to single year extinction probability as a function of initial nematode size and infectivity. Parameter values are the same as in Fig. 2. Nematode mortality  $k_N = 0.063 \text{ day}^{-1}$  in panel (a),  $k_N = 0.032 \text{ day}^{-1}$  in panel (b), and  $k_N = 0.012 \text{ day}^{-1}$  in panel (c).

local microparasite–host patches should be extremely rare (Fig. 2, open circles). Field observations, however, suggest that local persistence of such patches is more common than our model predicts. In a survey of 25 spatially separated areas on the Bodega Marine Reserve, three of the 25 areas maintained nematode populations over five sampling dates spread across 2 years (Preisser and Strong, unpublished data). Because each of the three areas was more than 3 m from the nearest other nematode population, repeated immigration into these areas is unlikely to account for the persistence of their nematode populations. Rhizosphere extinctions and colonization (Preisser and Strong, 2004; Strong, 1999) further indicate the dynamic nature of these local populations and the need for a modeling approach that incorporates field-estimated parameters. The lack of congruence between the model's predictions and our observations motivated our experimental measurement of long-term survivorship.

Long-term mortality of *H. marelatus* in its natural environment is lower than that predicted by laboratory and agricultural field experiments. When we incorporate

this lower mortality rate into our model, extinction of nematode populations due to over-exploitation occurs only at high initial population densities. Since the probability of under-exploitation is relatively insensitive to mortality, modifying exploiter mortality in our model predicts long-term persistence for a much wider range of initial nematode densities than was initially the case (Fig. 3). Our results imply that long-term 'single-patch' persistence of such exploiter–victim systems is extremely sensitive to exploiter mortality, and highlights the importance of measuring this parameter under the appropriate conditions.

The mechanistic basis for the long-term persistence of *H. marelatus* in our experiment is unclear. Heterogeneity in survival among individual nematodes is one possible explanation. Isolates of Heterorhabditid nematodes differ greatly in their short-term survival when exposed to low-moisture conditions (Glazer, 2002); it is reasonable to assume that such variation might affect long-term survival as well. Another factor might be abiotic heterogeneity. As soil dries during the summer, *H. marelatus* juveniles accumulate and survive within

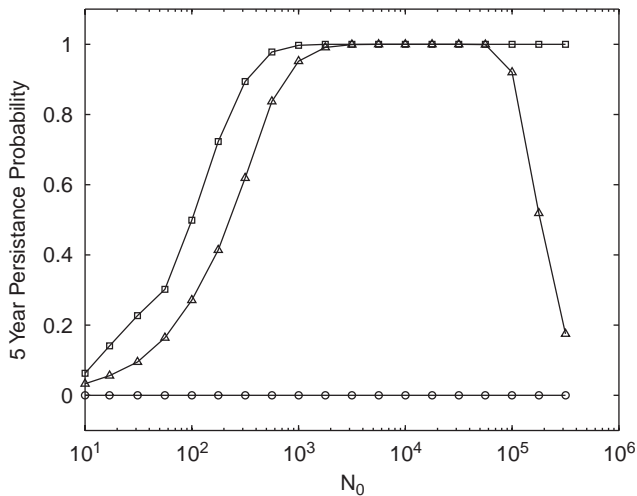


Fig. 4. Results from stochastic model simulation showing the dependence of probability of the nematode persisting for more than 5 years on the initial nematode population size and mortality rate. The probability of persistence is estimated by the fraction of 10,000 simulations that persist for at least 5 years. The parameter values used were mean initial host population size = 100, host mortality  $k_H = 0.0001 \text{ day}^{-1}$ , and nematode generation time  $\tau = 35$  days. The length of the wet season was  $T = 160$  days, and maximal host productivity was  $\Lambda_{\max} = 800,000$  nematodes per host,  $r = 0.09 \text{ day}^{-1}$ ,  $M_0 = 10,000$ ,  $\beta = 10^{-6}$  (see Table 1 for a summary of model & parameters). Results with nematode mortality  $k_N = 0.063 \text{ day}^{-1}$  are marked with circles,  $k_N = 0.032 \text{ day}^{-1}$  marked with triangles, and  $k_N = 0.012 \text{ day}^{-1}$  are marked with squares.

tiny soil aggregates (Strong, unpublished data) where the relative humidity is highest. Such soil aggregates are common in summer soils at BML; if they also formed within experimental tubes, nematode survival could be enhanced and/or heterogeneous among individuals. Heterogeneous survival rates can lead to a mortality rate (averaged over individuals) that decreases because the composition of the population changes over time (Vaupel and Carey, 1993). Specifically, individuals that have lower mortality rates are more likely to survive a longer period of time than individuals with high mortality rates, and the average population mortality rate decreases over time. Our estimates of mortality may be lower than previous estimates, because we averaged mortality over a longer period of time than most of the earlier laboratory experiments. We assumed a homogenous population in our statistical analysis so that we could compare our work with previous experiments and incorporate our results into a tractable stochastic model.

Seasonal microparasite–host systems squeezed into narrow windows of persistence by over- and under-exploitation should be common in nature. While the aggregated nature of infections is well known and consistent with over-exploitation (Anderson and May, 1986), the complementary threat to persistence is less transparent because parasite absence can be

due to causes other than under-exploitation. Conspicuous, localized episodes of high host mortality are clues that could indicate over-exploitation, but few studies examine both perils. Systems hemmed in by over- and under-exploitation may produce spatially isolated spikes of microparasite-induced host mortality in regions that appear to lack the disease or parasite. Candidates for such systems include ciliate diseases of krill (Gomez–Gutierrez et al., 2003), castrating parasites of crustacea (Lafferty and Kuris, 1996), and microsporidian diseases of caddis (Kohler and Hoiland, 2001). High survivorship of exploiter populations increases the chance of long-term persistence in such systems by decreasing the risks of both over- and under-exploitation.

Metapopulation dynamics (Hanski and Gilpin, 1997) may also play a role in maintaining locally unstable parasite–host interactions. While IJs of entomopathogenic nematodes can disperse short distances through wet soil, rates of colonization of locally extinct habitat patches by nematodes moving under their own steam are likely very low. However, a recent study found that a common invertebrate detritivore in California coastal prairies, the isopod *Porcellio scaber*, was capable of dispersing IJ *H. marelatus* under laboratory conditions (Eng et al., 2005). Phoretic movement of IJs upon the exterior of animals that they cannot kill is likely the mode of dispersal for these microparasites. These nematodes have low rates of mortality in moist soil (Preisser and Strong, 2004) and are believed to have refuges in marshy areas where their rates of mortality may be very low (Stock et al., 1999).

Migration of nematodes from a nearby source habitat may play a role in stabilizing this parasite–host system. *H. marelatus* was originally described as an inhabitant of seaside marshes (Liu and Berry, 1996), and a landscape-level survey found it primarily associated with marshes and wet soils (Stock et al., 1999). Small marshes are present near the Bodega Marine Reserve; such areas could serve as source populations for the occasional re-colonization of the coastal prairies. However, the lack of desiccation tolerance in Heterorhabditid nematodes suggests that most dispersing propagules are unlikely to survive (Grant and Villani, 2003), meaning that long-distance dispersal events are likely rare in this system. Short-distance dispersal between lupine bushes is more likely; in such cases, however, sub-populations all face the same dry-season conditions and the survival rate has to be high enough to weather the season without hosts. The relative roles of metapopulation dynamics within the prairie and a dispersal of nematodes from nearby marshes in stabilizing this parasite–host system is an open question that requires further study of dispersal rates and the potential source population.



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