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Evolutionary Dynamics of Prey Exploitation in a Metapopulation of Predators

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ABSTRACT: In well-mixed populations of predators and prey, natural selection favors predators with high rates of prey consumption and population growth. When spatial structure prevents the populations from being well mixed, such predators may have a selective disadvantage because they do not make full use of the prey's growth capacity and hence produce fewer propagules. The best strategy then depends on the degree to which predators can monopolize the exploitation of local prey populations, which in turn depends on the spatial structure, the number of migrants, and, in particular, the stochastic nature of the colonization process. To analyze the evolutionary dynamics of predators in a spatially structured predator-prey system, we performed simulations with a metapopulation model that has explicit local dynamics of nonpersistent populations, keeps track of the number of emigrants entering the migration pool, assumes individuals within local populations as well as within the migration pool to be well mixed, and takes stochastic colonization into account. We investigated which of the predator's exploitation strategies are evolutionarily stable and whether these strategies minimize the overall density of prey, as is the case in Lotka-Volterra-type models of competitive exclusion. This was analyzed by pairwise invasibility plots based on short-term simulations and tested by long-term simulation experiments of competition between resident and mutant predator-types that differed in one of the following parameters: the prey-to-predator conversion efficiency, the per capita prey consumption rate, or the per capita emigration rate from local populations. In addition, we asked which of these three strategies are most likely to evolve. Our simulations showed that under selection for conversion efficiency the predator-prey system always goes globally extinct yet persists under selection for consumption or emigration rates and that the evolutionarily stable (ES) exploitation strategies do not maximize local population growth rates. The most successful exploitation strategy minimizes the overall density of prey but does not make it settle exactly at the minimum. The system did not settle at the point where the mean time to co-invasion (i.e., immigration of a second predator

in a local prey population) equals the mean local interaction time (an idea borne out from studies on host exploitation strategies in host-pathogen systems) but rather where the mean time to co-invasion was larger. The ES exploitation strategies represent more prudent strategies than the ones that minimize prey density. Finally, we show that—compared to consumption—emigration is a more likely target for selection to achieve prudent exploitation and that prudent exploitation strategies can evolve only provided the prey-to-predator conversion efficiency is subject to constraints.

Keywords: exploitation, predator-prey interaction, evolutionarily stable strategy, natural selection, metapopulation model, virulence.

There is a long-standing debate on the evolution of prudent prey (host) exploitation, that is, predators (parasites) that do not overexploit their prey (host; Slobodkin 1968). In a homogeneous environment with well-mixed populations, individual predators should maximize their immediate harvest at the expense of long-term yields (Rosenzweig and MacArthur 1963; Maynard Smith 1982). Thus, natural selection favors predators with the highest consumption and population growth rate, and this will typically cause predator-prey dynamics to become unstable (May 1972).

In a structured environment, however, there is room for the evolution of prudent predators. This conclusion emerged from a multitude of models differing in whether spatial population structure is imposed by the environment or is caused by movement rules in a homogeneous environment. Grid models with one individual per cell and dispersal to neighboring cells (Boerlijst et al. 1993; Claessen and de Roos 1995; Rand et al. 1995; Savill and Hogeweg 1998, 1999) predict that prudent strategies evolve if local movement rules make the population sufficiently viscous because individuals then interact primarily with their own descendants. Metapopulation models, which assume global migration and only keep track of patch states (no local dynamics), in contrast, predict that complete avirulence evolves, unless a trade-off is assumed, for example, between transmission and disease-induced mortality (Levin and Pimentel 1981; May and Anderson 1983; Nowak and May 1994). The trade-off is generally modeled

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as an arbitrary function that should phenomenologically represent a local interaction among individuals within a patch. In this article, we investigate whether the trade-off indeed emerges if within-patch population dynamics are explicitly accounted for in metapopulation models with global migration between all available habitat patches.

Selection in a metapopulation occurs at two levels, within local populations (individual selection) and among local populations (group selection). The balance between these levels of selection is set by the frequency of invasions per local population (Eshel 1977; Wade and McCauley 1988; Harrison and Hastings 1996). A low frequency of invasions should allow more prudent strategies to evolve because individuals interact again primarily with their own type, just as in the grid-based models representing single individuals. To trace the consequences of local, within-patch competition between predator types that differ in exploitation strategy, it is therefore essential to explicitly model the local predator-prey dynamics. The outcome of competition depends on the rate at which the predator types enter the local population, while these immigration rates in turn depend on the number of predators that emigrated from local populations. For sufficiently low immigration rates, the invasion process becomes stochastic so that the invasion events determine who is competing with whom and when. The invasion history of a local population is crucial for understanding increased virulence, as is shown clearly by patch-state models that allow no more than two invasions (Nowak and May 1994; van Baalen and Sabelis 1995a; Mosquera and Adler 1998).

There have been few attempts to study evolution of exploitation strategies in a metapopulation model with global migration and explicit local dynamics (Gilpin 1975; van Baalen and Sabelis 1995b). Much like the assumptions underlying so-called haystack models for the evolution of altruistic traits (Maynard Smith 1964; Bulmer and Taylor 1980; Wilson and Colwell 1981), the model of van Baalen and Sabelis (1995b) was greatly simplified by ignoring feedback of the predators on prey density, by assuming synchronized and uniform start-up of local predator-prey dynamics, and by allowing predator immigration to take place only at the start. Here, we intend to explore the validity of the conclusions of van Baalen and Sabelis (1995b) in a simulation model in which these assumptions have been relaxed (at the expense of analytic tractability). We thus ask whether and how in a metapopulation with global and homogeneous migration between local patches prudent exploitation strategies may evolve as a result of the within-patch dynamics of prey and predators. We study the problem in a setting in which all predator-prey feedback loops are included.

Lotka-Volterra competition models of well-mixed populations predict the winning consumer type to be the one

that can sustain its population at the lowest level of the resource (MacArthur and Levins 1967). For much the same reasons, patch-state models with global migration predict the winning predator type to keep the number of prey patches at its minimum (Anderson and May 1982). Whether prey density minimization also holds in predator-prey metapopulation models with explicit local dynamics and stochastic immigration, and how this relates to the mean frequency of invasions, are questions to be answered by the simulations presented in this article.

Most models on prey exploitation consider only strategies that differ in the predation rate (Slobodkin 1974; Gilpin 1975). Alternatives to these strategies concern not only the prey-to-predator conversion efficiency but also the rate of emigration from a local population, as argued by van Baalen and Sabelis (1995b). All these strategies have in common that they affect the effective population growth rate of the predator and thereby the predation pressure on the prey population. Low consumption or conversion rates and nonzero emigration rates during the interaction ("milker" strategy) will allow the local prey population to represent a larger resource in the future, which in turn may benefit the final size of the local predator population. In contrast, high consumption or conversion rates and non-emigration during the interaction ("killer" strategy) will cause the predators to have a higher impact on the local prey population, thereby giving up opportunities to exploit the full growth capacity of the prey population. However, one may wonder which of these possible strategies are more likely to evolve.

In this article, we will discuss the simulation results from a model that keeps track of all invasion events, assumes deterministic local predator-prey dynamics, assumes deterministic emigration but stochastic invasion, and accounts for differences in exploitation strategies due to predation, conversion, and dispersal.

The Predator-Prey Model

Model Formulation

Predators and prey interact within a large number of patches (500 in our simulations) connected by global migration. Population sizes and time scales are discrete. Each time step, set to 1 d, involves three successive calculations: growth and predation within each patch, emigration, and immigration. The model of the within-patch population dynamics is inspired by observations on the interactions between prey and predatory mites. The experimental observations indicate that there is limited variance in population abundances over time after invasion by prey or predators has taken place (Sabelis and van der Meer 1986; Pels and Sabelis 1999). In other words, local population

growth after invasion is a rather deterministic process. In line with these observations, the model for local population dynamics is fully individual based, but with growth, predation, and emigration described as (approximately) deterministic processes (i.e., with little demographic stochasticity), whereas immigration is stochastic. In addition, the model parameters are set to default values representing the within-patch interaction between prey and predatory mites (table 1), thereby facilitating empirical tests of the model predictions.

Interaction. Predators and prey interact according to a model with exponential growth of predators (with per capita rate γ) and a constant per capita consumption rate (β ; Metz and Diekmann 1986; Diekmann et al. 1988; van Baalen and Sabelis 1995b). The consumption rate—and hence also the population growth rate—is constant because we assume that predators always forage at the plateau phase of their functional response, an assumption that is valid for a wide range of arthropod predator-prey systems (Janssen and Sabelis 1992; Sabelis et al. 1999). In addition, we assumed an upper size for the prey population (K ; i.e., a ceiling that prevents overshoot), a density-dependent growth rate of the prey, $a(N)$, with maximum α , and an upper value for the prey-to-predator conversion efficiency (ε). Thus, the maximum population growth rate of the predators equals $\gamma = \varepsilon\beta$. In its discrete form, the model is given by the following equations, where N_t^i and P_t^i are the numbers of prey and predators, respectively, in patch i at day t , and $N_t^{i(1)}$ and $P_t^{i(1)}$ are the numbers of prey and predators after growth and predation:

$$N_t^{i(1)} = N_t^i + a(N_t^i)N_t^i - b(N_t^i, P_t^i)P_t^i,$$

$$P_t^{i(1)} = P_t^i + \varepsilon b(N_t^i, P_t^i)P_t^i,$$

with

$$a(N_t^i) = \min\left(\alpha, \frac{K - N_t^i}{N_t^i}\right),$$

$$b(N_t^i, P_t^i) = \min\left(\beta, \frac{N_t^i + a(N_t^i)N_t^i}{P_t^i}\right).$$

The function $a(N)$ sets a limit K to the exponentially growing prey population, such that N_t^i never becomes larger than K and $a(N)$ remains positive. The function $b(N, P)$ represents the daily per capita predation rate. Note that this function expresses that each predator always consumes at a constant rate β , unless the number of predators P_t^i present is so large that the total predation pressure βP_t^i would cause the prey population to become negative.

In this latter case, the predators share all remaining prey on an equal per capita basis and the prey density becomes equal to 0.

Emigration. Prey leave a patch at a constant per capita migration rate (ν), whereas predators leave a patch at a per capita rate $m(N, P)$ that depends on the presence of prey and predators in the patch. In its discrete form, this yields the following equations, where $N_t^{i(2)}$ and $P_t^{i(2)}$ are the numbers of prey and predators in patch i at day t after emigration:

$$N_t^{i(2)} = N_t^{i(1)} - \nu N_t^{i(1)},$$

$$P_t^{i(2)} = P_t^{i(1)} - m(N_t^{i(1)}, P_t^{i(1)})P_t^{i(1)},$$

with

$$m(N_t^{i(1)}, P_t^{i(1)}) = \begin{cases} 0 & \text{if } N_t^{i(1)} > 0 \text{ and } P_t^{i(1)} = 1 \\ \mu & \text{if } N_t^{i(1)} > 0 \text{ and } P_t^{i(1)} > 1 \\ 1 & \text{if } N_t^{i(1)} = 0 \end{cases}.$$

The first expression of the function $m(N, P)$ guarantees that the first predator in a patch with prey never migrates without leaving offspring. The second and third expressions imply that predators leave at a constant rate μ as long as there are prey but leave instantaneously when all prey have been exterminated.

Immigration. Individuals that leave a patch enter a pool of migrants, one for the prey (\hat{n}) and one for the predators (\hat{p}):

$$\hat{n} = \sum_{i=1}^s \nu N_t^{i(1)},$$

$$\hat{p} = \sum_{i=1}^s m(N_t^{i(1)}, P_t^{i(1)})P_t^{i(1)}.$$

In the dispersal pool, prey and predators do not interact and do not reproduce. The number of immigrant prey and predators into each individual patch is determined by a Poisson distribution with mean $\sigma_N \hat{n}/s$ and $\sigma_P \hat{p}/s$, respectively. Hence, the number of prey and predators, $N_t^{i(3)}$ and $P_t^{i(3)}$, respectively, in patch i at day t after immigration are given by

$$N_t^{i(3)} = N_t^{i(2)} + \text{Poisson}\left(\frac{\sigma_N \hat{n}}{s}\right),$$

$$P_t^{i(3)} = P_t^{i(2)} + \text{Poisson}\left(\frac{\sigma_P \hat{p}}{s}\right).$$

Table 1: Definitions and dimensions of variables and parameters, together with their default values and ranges explored by simulation

Symbol	Meaning	Dimension	Default	Range
N_t^i	Number of prey in patch i at day t			
P_t^i	Number of predators in patch i at day t			
α	Per capita prey growth	day^{-1}	.5	
K	Prey carrying capacity	N	1,500	
β	Per capita attack rate	$NP^{-1} \text{ day}^{-1}$	2	.4–3
ε	Prey-to-predator conversion efficiency	PN^{-1}	.25	.2–.5
γ	Per capita migration rate of prey	day^{-1}	.01	
μ	Per capita migration rate of predators in presence of prey	day^{-1}	0	0–.3
σ_N	Per capita probability for prey to survive migration		.003	
σ_P	Per capita probability for predators to survive migration		.003	.002–.004
s	Number of patches		500	
δ_ε	Offset of ε mutants relative to the resident	PN^{-1}	.02	
δ_β	Offset of β mutants relative to the resident	$NP^{-1} \text{ day}^{-1}$.05	
δ_μ	Offset of μ mutants relative to the resident	day^{-1}	.01	

In these equations, s denotes the total number of patches in the metapopulation. The parameters σ_N and σ_P represent the probability that a dispersing prey or predator succeeds in finding a new patch at all. Hence, σ_N and σ_P take into account loss processes such as death during dispersal or failure to localize suitable habitat. These parameters have sufficiently low values to ensure that the total of all immigrants into the patches (which is the sum of the random Poisson deviates for all s patches) is smaller than the total number of dispersing prey and predators, \hat{n} and \hat{p} , respectively.

The three sequential events—interaction, emigration, and immigration—complete the update of one simulation day, so that

$$N_{t+1}^i = N_t^{i(3)},$$

$$P_{t+1}^i = P_t^{i(3)}.$$

Discrete Population Sizes. In the model, all population sizes (N 's and P 's) are treated as integers (i.e., natural numbers). However, the rules for both local interaction and emigration may specify changes in prey and predator density that have fractional parts. Whenever values with a fractional part occur, the changes in prey and predator densities are rounded up or down, in accordance with the sign of the difference between the fractional part and the result of a drawing from a uniform distribution between 0 and 1. More specifically, if the computed change equals $n + z$, where n is the integer and z is the fractional part of the value, it is rounded to n if a drawing from the uniform distribution is larger than z , while it is rounded to $n + 1$ otherwise. For a particular local population size, this

procedure allows for only two possible outcomes of the dynamic change, that is, n and $n + 1$. Generically, in individual-based models, binomial or gamma distributions determine the magnitude of the dynamic change. The latter distributions lead to a much larger variability in outcomes. Our procedure thus represents an individual-based process with as little demographic stochasticity in local dynamics as possible.

Our choice for the rounding procedure described above is strongly based on experimental observations (Sabelis and van der Meer 1986; Pels and Sabelis 1999), which indicate that local population growth is by and large deterministic. In addition, we consider the physiological processes underlying reproduction to be of a deterministic nature. In our experience, the organisms we study really do not gamble whether they reproduce or not but produce offspring following rather constant reproduction schedules. Combining deterministic local dynamics with multiple stochastic immigration events into a hybrid (deterministic/stochastic) model has been shown to be problematic (O. Diekmann, J. A. J. Metz, and V. A. A. Jansen, personal communication; see also Metz and Diekmann 1986). Gyllenberg and Hanski (1992) offer a solution leading to a single-species model in terms of partial differential equations. This model, however, incorporates the unrealistic assumption that immigration events are infrequent in patches without any prey or predators but sufficiently frequent in already occupied patches to have an impact on local population growth. Lacking an elegant and consistent solution to the problem of combining deterministic local dynamics and multiple stochastic immigration events, we decided to apply a rounding-off pro-

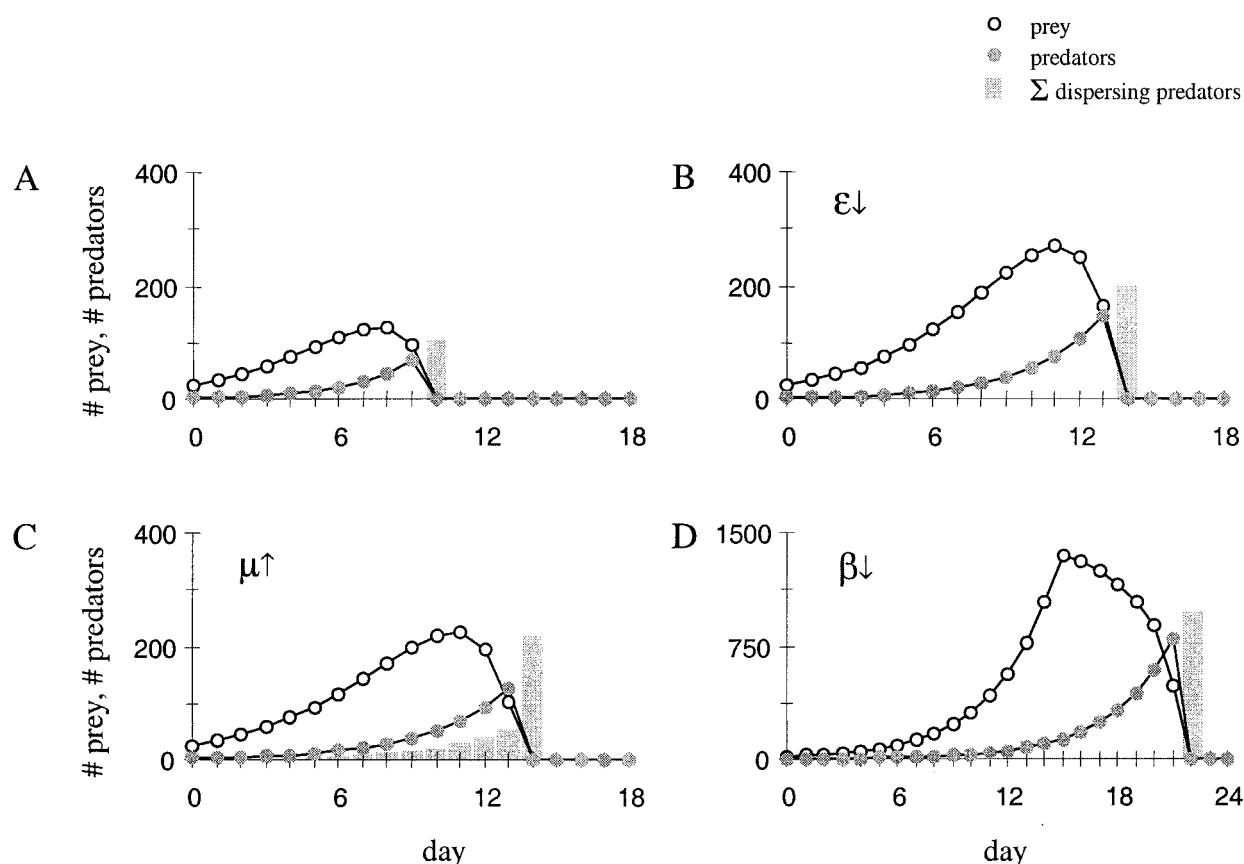


Figure 1: Local predator-prey dynamics initiated by 15 prey and two predators, for four predator types that differ in prey exploitation strategy: A, default values ($\epsilon = 0.25$, $\beta = 2$, and $\mu = 0$. For the other parameters, see table 1); B, as in A but with a reduced predator-to-prey conversion efficiency ($\epsilon = 0.2$); C, as in A but with an increased predator migration rate during the interaction ($\mu = 0.1$); D, as in A but with a reduced prey consumption rate ($\beta = 1.4$). In all cases, the local prey population is ultimately overexploited by the predators. Predators that have a lower exploitation efficiency (cf. B, C, and D to A) grow at a lower rate but produce a higher cumulative number of migrants. In C, the prey population first reaches carrying capacity before it declines.

cedure in order to convert the deterministic growth process into a growth in integer numbers.

Population Dynamics

The within-patch predator-prey interaction is always unstable. In the absence of predators, prey grow to carrying capacity, but once predators arrive in the patch, the local predator population grows exponentially, which results in extermination of the local prey population within a finite period after which all predators migrate. Each patch thus changes from the empty state (empty patch) via the state of being occupied by prey (prey patch), to the state of being occupied by prey and predators (predator-prey patch), and then to the empty state again. The duration of the interaction between predators and prey in a predator-prey patch and the number of predators that emerge

after overexploitation depend on, among other things, the initial predator-to-prey ratio and the predator's exploitation strategy (ϵ , β , μ). Predators that reduce their effective population growth rate, by reducing their consumption rate (β) or conversion efficiency (ϵ) and/or by increasing their migration rate (μ), need more time to eliminate the prey, allow the prey to reach larger numbers, and end the interaction with a higher cumulative number of dispersing predators (fig. 1). Note that our model of local predator-prey dynamics predicts a higher overall production of migrants for lower β and higher μ (even when expressed per unit of interaction time), but for ϵ this higher production of migrants occurs only if the prey gets eliminated before reaching its local carrying capacity.

The metapopulation persists only when, after overexploitation of a local prey population, at least one predator migrant is able to invade a new prey patch. The occurrence

of such an invasion depends on the total number of migrants emerging from a predator-prey patch, the probability of predators to survive migration and the number of prey patches. The number of migrants that emerge from a patch typically depends on the predator's exploitation strategy. This means that for the predator-prey interaction to persist, a minimum survival probability is required that depends on the predator's exploitation strategy. The theoretical limit of survival below which the metapopulation always vanishes is $1/Q$, with Q the number of predators that arise from a patch that was at the prey's carrying capacity at the moment of predator invasion. However, because of demographic stochasticity, the actual minimum required for persistence will always be slightly higher in the simulations.

Simulations of the model system over a range of values for survival showed that there also exists a maximum above which the metapopulation is not viable. With higher sur-

vival during migration, the predator-prey oscillations are stronger (fig. 2). The boundary where the oscillations blow up the predator-prey interaction depends on the predator's exploitation strategy. Numerical exploration revealed regions of persistence in the parameter space given by predator survival during migration (σ_p) and the consumption rate (β), conversion efficiency (ϵ), or the migration rate (μ) (fig. 3). Outside these regions, the metapopulation does not persist.

Evolution of Exploitation Strategies

We simulated exploitative competition among predators with different strategies (ϵ, β, μ) within a metapopulation. This involves the bookkeeping of their numbers for each exploitation strategy separately and their impact, that is, how fast they consume and grow within a patch. At the day on which prey are eliminated, the leftover prey are

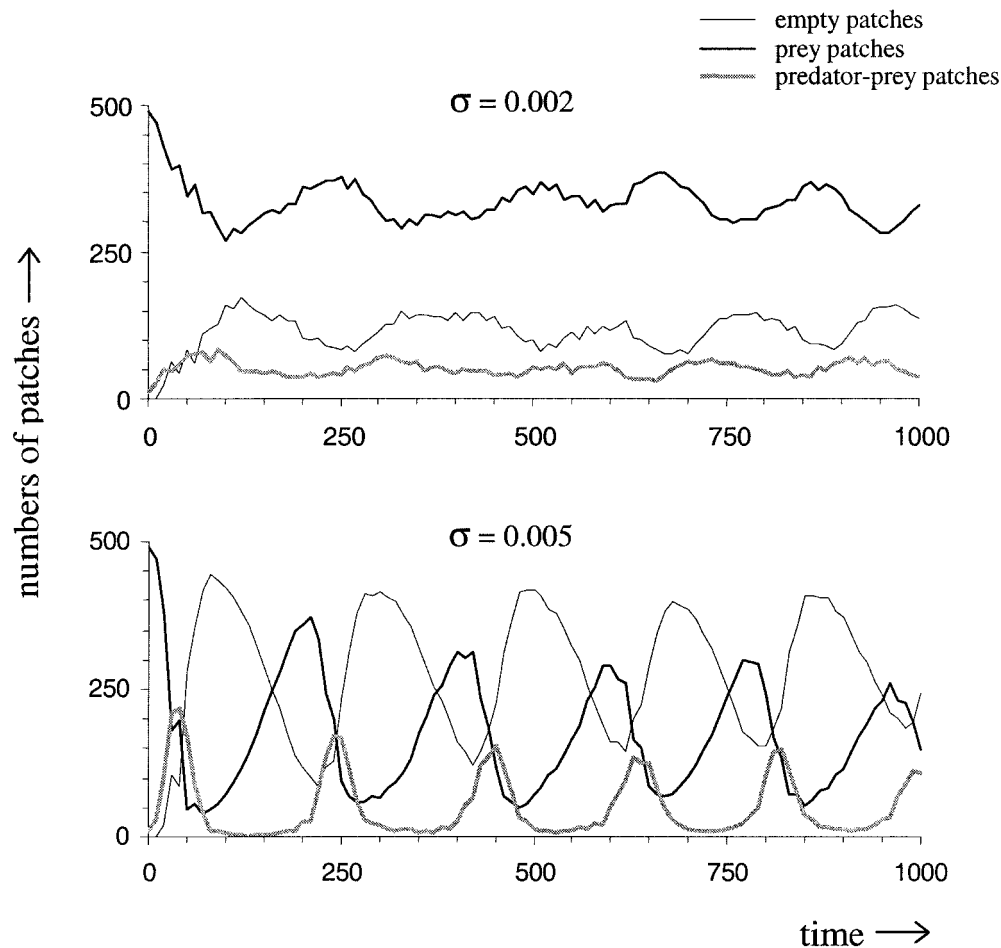


Figure 2: Simulated dynamics of the number of empty patches, prey patches, and predator-prey patches for two values of predator survival during migration: $\sigma_p = 0.002$ and $\sigma_p = 0.005$. For higher values, the populations become extinct.

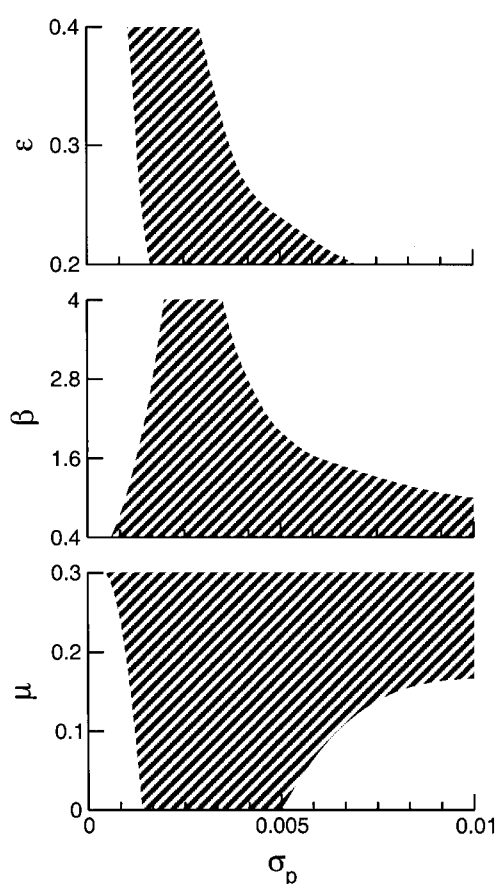


Figure 3: Regions of parameter space (ϵ , β , and μ vs. σ_p) for which the predator-prey metapopulation persists (shaded area) or becomes extinct (open area).

shared among different predator types in proportion to the product of their per capita consumption rate and their number in the patch. We studied invasibility and long-term competition for a range of values of predator survival during migration.

Invasibility

We assessed the invasion success of a rare mutant in an environment set by a resident to construct a pairwise invasibility plot (van Tienderen and De Jong 1986; Metz et al. 1992). As a measure for the fitness of each strategy, we used the average number of newborn migrants that result from the local colony founded by a newborn migrant, R_m , as proposed by Metz and Gyllenberg (2001) for metapopulations for which the dynamics converge to a point attractor. The variable R_m relates to fitness in the same manner, as does R_0 in classic population dynamics (Mylius

and Diekmann 1995). Mutants differed from residents in one of the three evolutionary variables (ϵ , β , or μ), with the other two set to their default values (table 1). To assess whether the mutant will invade the system ($R_m > 1$) or die out ($R_m < 1$), simulations were carried out, as follows. First, the residents were allowed to establish a metapopulation. After 2,000 d, a mutant was released in a randomly selected patch, and the mutants that migrated during the interaction with prey, or after overexploitation, were recorded and then removed. The mean number of mutant migrants in 4,000 of these invasion trials, multiplied by the probability to survive migration (σ_p), gives an estimate of R_m . At the diagonal of the pairwise invasibility plot, resident types invade their own resident population and hence should have an R_m value equal to unity. For all other mutant-resident combinations in the plot, $R_m > 1$ (indicated by an "X" in fig. 4) is where the mutant invades the resident population, and $R_m < 1$ (indicated by the absence of an "X" in fig. 4) is where the mutant will die out. Assuming the time scale of the process from invasion to fixation can be uncoupled from the population dynamical time scale, the pairwise invasibility plot can be used to predict the evolutionary dynamics of the exploitation strategy (van Tienderen and De Jong 1986; Metz et al. 1992).

The areas where mutants invade (fig. 4) have irregular contours as a result of stochasticity and as a result of discrete time and discrete population densities, but the general patterns can be readily recognized. Mutants with a higher prey-to-predator conversion efficiency (ϵ) than the resident can always invade, irrespective of σ_p . This does not hold for mutants of β and μ , as there is an optimum for either β or μ , the value of which depends on σ_p . When σ_p decreases, the ESS (evolutionarily stable strategy) shifts to lower optima for β and to higher optima for μ . This implies a shift to lower population growth rates, and therefore prudent predators will evolve.

To pinpoint the areas where two strategy types can invade each other's population or resist each other's invasion, so-called mutual invasibility plots can be constructed by mirroring the pairwise invasibility plots around the diagonal and outlining the areas where both the original and mirror image R_m values are larger than 1 (mutual invasibility) or smaller than 1 (mutual exclusion; Metz et al. 1996a, 1996b; Geritz et al. 1998). In figure 4, we have mirrored the pairwise invasibility plots for the case of $\sigma_p = 0.003$. For ϵ , this plot does not show possibilities for mutual invasibility, but for β and μ , they do. In the latter case, voracious predators (large β or small μ) and prudent predators (small β or large μ) can coexist, but—according to long-term simulations shown in figure 5—such populations with mixed strategies are vulnerable to invasion by intermediate strategies. Given the form of the pairwise invasibility plots for β and μ (fig. 4), the existence of such

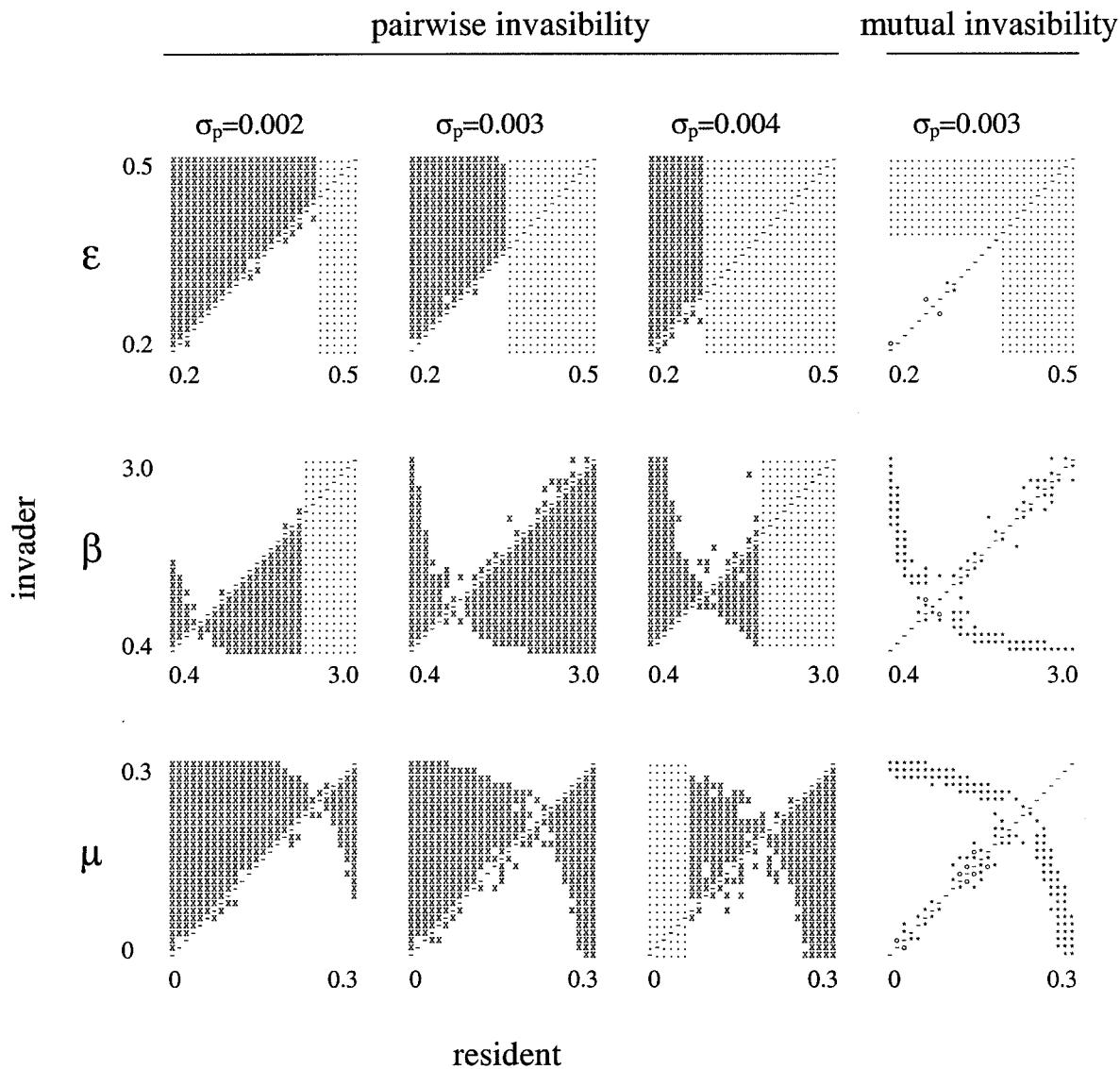


Figure 4: Pairwise and mutual invasibility plots for invaders that differ from the resident with respect to ε , β , and μ . Within each plot, the resident strategy is denoted at the horizontal axis, the invader at the vertical axis. Both axes express the same range of values. Simulation results are provided for different values of σ_p . The invader-resident coordinates are indicated by an “X” if $R_m > 1$ (i.e., predator y can invade resident x), by a dash at the diagonal (i.e., invader is of the same type as the resident), and by a dot if the resident does not persist. In the mutual invasibility plots, an asterisk indicates that the two strategies can invade each other’s resident population, and an open circle indicates that the two strategies resist each other’s invasion when resident.

an intermediate strategy that is both convergence stable and evolutionarily stable can already be predicted on the basis of the general theory regarding these plots (Geritz et al. 1998), even though mutual invasibility areas do occur.

Long-Term Simulations

For a mutant to reach fixation, $R_m > 1$ is a necessary but not sufficient condition. For example, the system may en-

ter into evolutionary cycles (Dieckmann et al. 1995; Doebeli 1998) or “the resident may strike back” after a mutant successfully invaded (Dieckmann et al. 1999). To check whether invasion implies fixation, a series of long-term simulations was carried out, where two mutants arise from the current resident, one with a slightly higher and one with a slightly lower value of either ε , β , or μ . For example, when ε is the trait under mutation, mutants were of type $(\varepsilon - \delta, \beta, \mu)$ and $(\varepsilon + \delta, \beta, \mu)$. First, the resident was re-

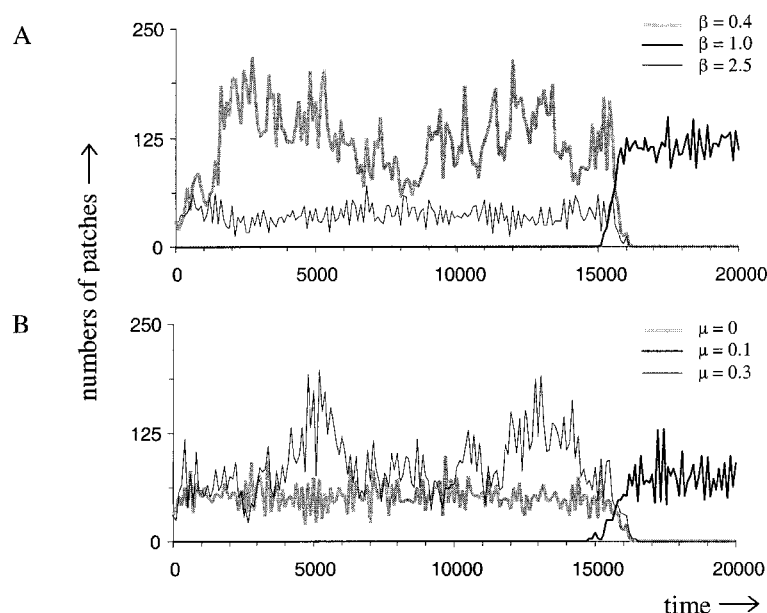


Figure 5: Simulations showing that two predator types differing in either β (A) or μ (B) can coexist. The numbers of patches in which the types occur—either alone or together with the other—are plotted at 100-d intervals. Near day 15,000, some predators of an intermediate type are introduced, and they appear to replace the two coexisting residents.

leased and its dynamics were simulated over 2,000 d. Thereafter, the two mutants were released in two randomly selected patches and the simulation was continued for another 50 d. After this period of competitive interaction, the overall population sizes of the resident and the mutants were evaluated. When a mutant went extinct during the 50 d, it was introduced again. Then, the simulation was continued for another 50 d, and so on. When mutants had outcompeted the resident, the simulation was continued until just one of the mutant types was left over, which was then assigned the status of new resident. After the reintroduction of a plus and a minus mutant, the simulation procedure started all over again. Successive exclusions of residents, followed by assignments of new residents, cause the exploitation strategy of the resident to shift along a fitness gradient until it reaches a fixed point. To test whether this is a unique singular strategy (i.e., values for ε , β , or μ for which the local fitness gradient is 0) or whether there are more, the simulations were repeated with different initial conditions.

The simulations of evolutionary change showed that β as well as μ reach a unique fixed end point, the position of which depends on σ_p (fig. 6). The ε , however, does not reach a fixed point but evolved to higher and higher values until the system went extinct. The same occurred for β when σ_p was large, but otherwise β evolved to a fixed point at which the system persisted, and its value decreased with

decreasing σ_p . For μ , there was always selection for migration during the interaction ($\mu > 0$), given the range of σ_p tested and the default values for ε and β . Selection for $\mu = 0$ occurred only when β is low and σ_p is high, for example, when $\beta \leq 1$ and $\sigma_p \geq 0.004$ (fig. 6D).

We conclude that long-term simulations confirm the predictions derived from the pairwise invasibility plots in figure 4 and provide no evidence for protected polymorphisms, evolutionary cycling, and “resident strikes back” scenarios in our simulations.

Multiple Predator Invasion and Minimization of Prey Density

For the interpretation of the evolutionary outcomes, it is important to stress that our metapopulation model incorporates competition and selection processes within patches (individual selection) and between patches (group selection). With respect to individual selection, Lotka-Volterra competition models predict the winning consumer type to be the one that can sustain its population at the lowest level of the resource (MacArthur and Levins 1967). In patch-state metapopulation models, this prediction translates into the winning predator type keeping the number of prey patches at a minimum (Anderson and May 1982). However, prudent exploitation strategies may evolve as a result of group selection if the frequency of

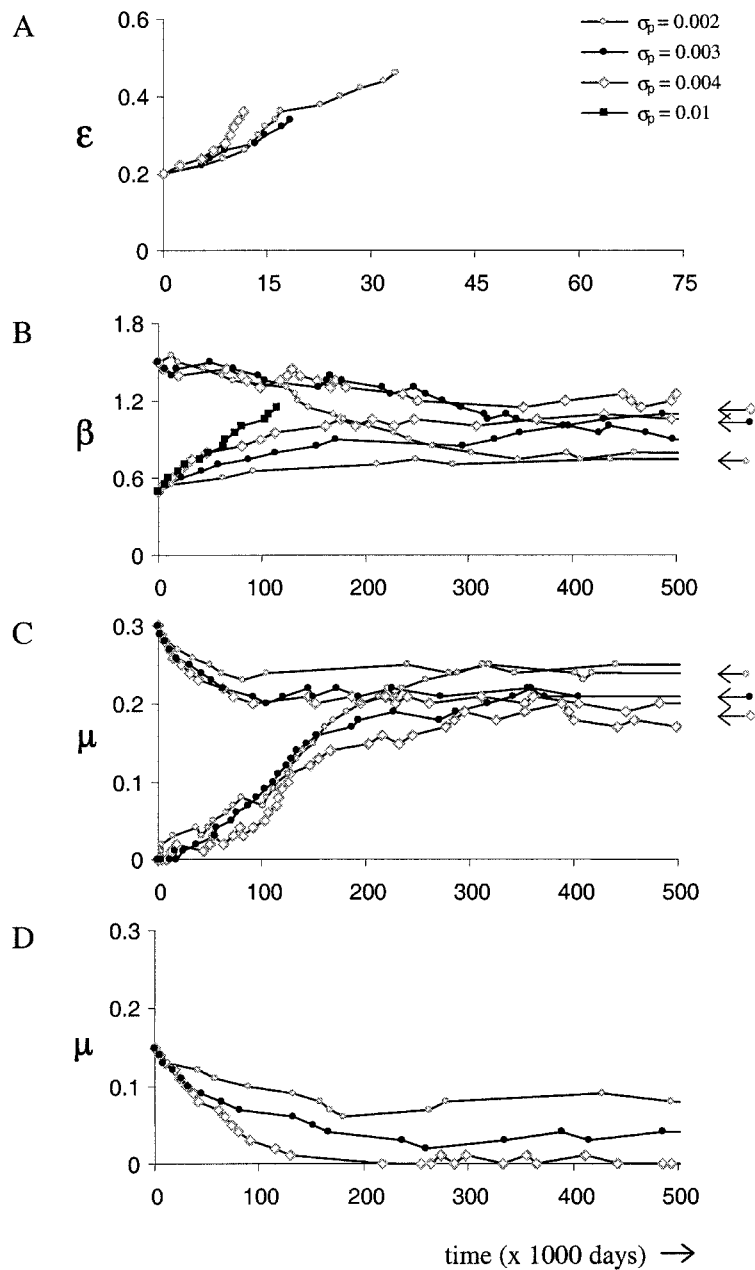


Figure 6: Evolutionary dynamics of a resident and two mutant predator types (in ϵ , β , or μ) for several values of predator survival during migration (σ_p). The graphs show the change in the resident parameter (strategy) over time. As soon as a mutant type eliminates both the resident and the other mutant, it becomes the new resident. These takeover events are indicated by the symbols in the curve against time. All parameters other than the ones subject to evolution were set at their default values (except in the bottom graph; see below). When populations failed to persist, the simulations were stopped (see A for competition among ϵ types and B for competition among β types when $\sigma_p = 0.01$). Otherwise, the resident's evolutionary variable stabilizes after a period of gradual change. The final value depends on predator survival during migration and is reached irrespective of initial conditions. These final values can be compared with the predictions of the pairwise invasibility analysis (see arrows at the right side of B and C). The bottom graph (D) shows an extra set of simulations of evolution in μ for a nondefault value of β ($\beta = 1$) to show conditions where selection favors $\mu = 0$ instead of $\mu > 0$.

invasions per local population is low. Similarly, the invasion history of a local population has been shown to lead to increased virulence in host-pathogen systems (Nowak and May 1994; van Baalen and Sabelis 1995a; Mosquera and Adler 1998). The balance between the individual and group selection process is set by the frequency of invasions per patch (Eshel 1977; Wade and McCauley 1988; Harrison and Hastings 1996). To assess this balance, we therefore investigate whether the predator-prey system settles at a point where, first, overall prey density is minimized or not and, second, multiple invasions are frequent or not. To this end, we measured the overall number of prey in the migration pool and the frequency at which predators arrive in predator-prey patches, as a function of ε , β , and μ . The frequency of co-invasion was quantified as the mean number of predators arriving after the first predator invaded a prey patch. For single invasions, this measure equals 0, and it is 1 when the second invader on average arrives by the time the prey in the patch is on average overexploited. A frequency of co-invasion smaller than unity therefore means that the probability of single invasions is larger than the probability of multiple invasions, whereas a value larger than unity implies the opposite.

The simulation results in figure 7 show that there exists a minimum prey density for intermediate values of β and μ , whereas for increasing values of ε prey density ultimately reaches its minimum at 0. The predators reach a maximum density where ε causes predator and prey to become extinct, but they do not where β and μ minimize prey density. Instead, predator density has no extremum but continually decreases with β and increases with μ . The frequency of co-invasion remains always lower than unity for all ε tested, whereas it is close to but always slightly smaller than unity where β and μ minimize prey density. This latter conclusion follows from the data in table 2, where—for different α and σ_p —the values of β and μ are given for which the frequency of co-invasion equals unity, and separately the values of β and μ for which prey density is at its minimum. Table 2 also shows that the winning strategy in terms of β and μ is always at the “prudent side” of the β and μ that would give rise to the minimum prey density. Moreover, the winning strategy is bounded by the parameter combinations for which $P_{co} = 1$ and those for which the global prey density is minimized.

The Likely “Face” of Prudence

Prudent strategies may be manifested by a lower prey-to-predator conversion efficiency (ε), a lower consumption rate (β), and a higher emigration rate (μ). To get some first insight into which of these different strategies are more likely to be targeted by selection, we rescaled the X-axes

of figure 7A into the impact of ε , β , and μ on the growth rate of the local predator population and considered how proportional changes in ε , β , and μ contribute to minimize overall prey density. This shows that prey density decreases at the fastest rate for proportional increases in ε , followed by proportional increases in μ and then by proportional decreases in β (fig. 8). Note that increases in ε cause evolution to more virulent strategies, whereas the other two imply evolution to avirulent or prudent strategies. Thus, assuming the traits have similar genetic architectures and mutation rates, we predict that—provided there are upper constraints on conversion—evolution is more likely to target emigration than predation. Simulations (not shown) in which both the emigration and the predation rate were allowed to evolve confirmed that changes in the emigration rate were indeed more rapid and more likely to occur.

Discussion

Evolution of Prudent Predators

Our simulations show that competitive exclusion leads to virulence in terms of the conversion efficiency (ε) but prudence in terms of the per capita consumption rate (β) and the per capita emigration rate (μ). Apparently, there are different ways to change the predator's productivity per local prey population while the overall prey density is close to its minimum. It all depends on the balance between the duration of the local predator-prey interaction period and the local population growth rate of the predator. If we assume upper constraints on conversion efficiency, then the prediction is that evolution will lead to prudent predators. At first sight this seems to contradict the conclusions of van Baalen and Sabelis (1995b), who predicted that killer-type strategies would evolve under a much larger range of initial within-patch predator-prey densities than milker-type strategies. Van Baalen and Sabelis based their analysis on similar assumptions regarding the local interactions (except for the carrying capacity for the prey population, but note that its inclusion would give predators less control over the interaction period, which in turn selects against prudent predators). Scrutiny of the assumptions shows three possible causes for why the predictions from our simulations differ from those of van Baalen and Sabelis (1995b): only the subset of persisting predator-prey populations are considered, predator-prey feedback causes single infections to prevail, and the colonization process of the predators is stochastic, thereby allowing part of the predators to monopolize exploitation of local prey populations. In our simulation model, feedback on the prey population causes the overall prey density to be minimized, and by its impact on the predator pop-

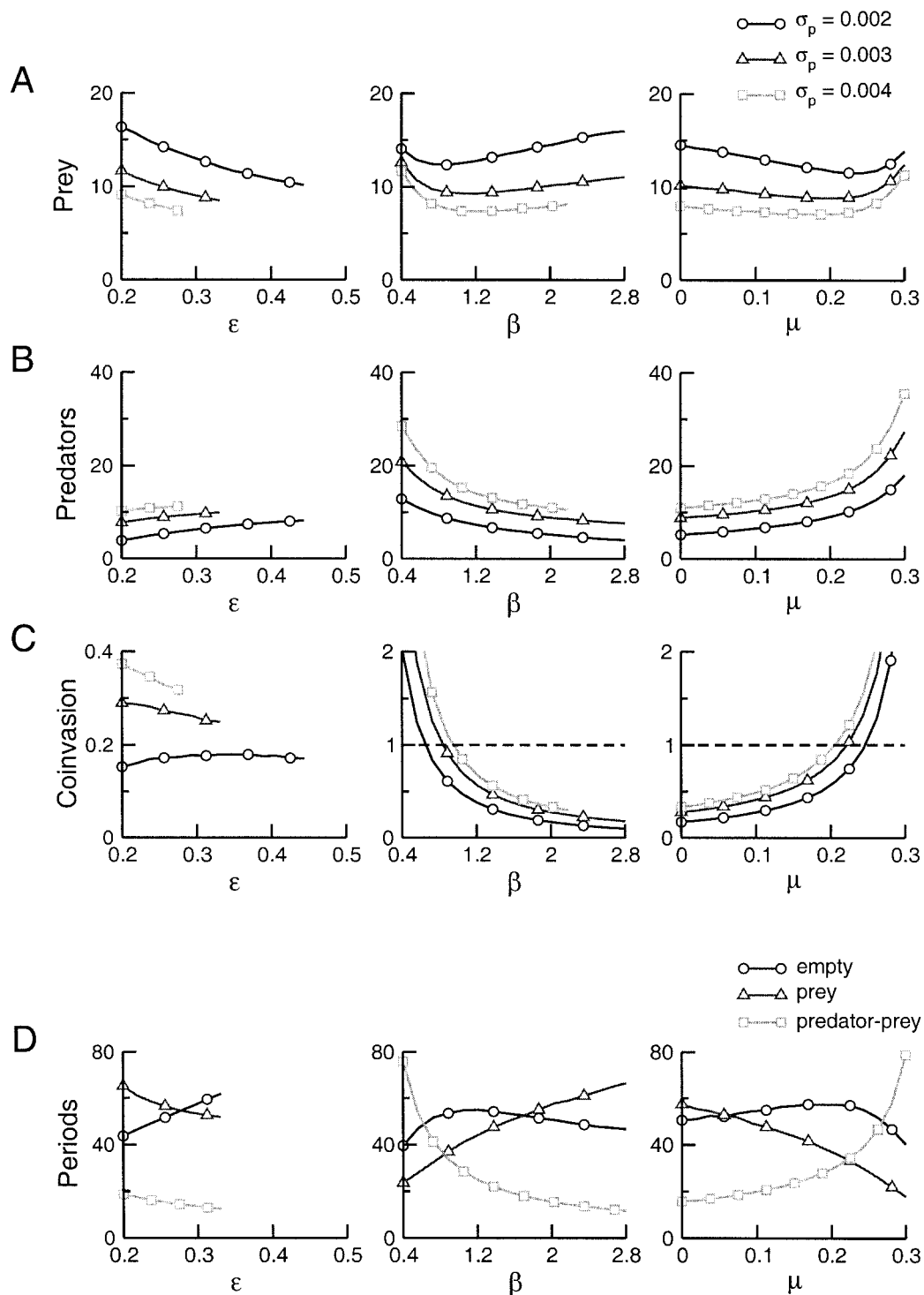


Figure 7: Mean numbers of prey (A) and predators (B) in the migration pool and the mean number of invading predators in predator-prey patches (C) plotted against ϵ , β , and μ for several values of predator survival during migration (σ_p). Means were calculated over intervals of 20,000 d (after a transient of 2,000 d). When populations do not persist, as in the ϵ and β plots, the curves are discontinued. The minima in the prey curves (A) correspond closely to the breaking points between single and multiple invasion (C). Note that the overall number of predators is not optimized when prey is minimized. The three bottom graphs (D) show mean periods in days wherein a patch is empty, occupied by prey, or occupied by prey and predators ($\sigma_p = 0.003$). These show that the minima in the prey curves also correspond closely to the point at which prey periods and predator-prey periods are equal in length.

Table 2: Numerical simulation data

Variable	α	σ_p	Simulation results in terms of β or μ values			
			Invasion analysis	Long-term competition	For which $P_{co} = 1$	For which N is minimized
β	.15	.002	.35	.34	.3	.4
β	.15	.003	.45	.46	.4	.5
β	.15	.004	.5	.52	.4	.6
β	.5	.002	.75	.80	.65	.9
β	.5	.003	1.0–1.1	1.00	.85	1.2
β	.5	.004	1.1–1.2	1.15	.95	1.15
μ	.15	.002	.29–.30	.30	.3	.3
μ	.15	.003	.28–.29	.29	.3	.28
μ	.15	.004	.27–.28	.28	.29	.27
μ	.5	.002	.23–.25	.24	.25	.24
μ	.5	.003	.20–.22	.21	.22	.2
μ	.5	.004	.17–.20	.19	.21	.18

Note: These data illustrate that the ESS β or μ (obtained either via pairwise invasibility analysis or via long-term competition involving 12 replicates per experiment) settles at values close to (but not exactly at) the β or μ values for which the frequency of co-invasion equals unity as well as β or μ values for which the prey density (N) is minimized. The simulations were carried out for different values of the prey growth rate (α) and predator survival during migration (σ_p).

ulation increases the probability of single invasions as well as the role of stochastic colonization by predators.

While our simulations contradict predictions from another model, they also contradict empirical observations. In a recent study, Pels and Sabelis (1999) measured em-

igration rates of several field-collected strains of predatory mites, *Phytoseiulus persimilis*, from leaves that were infested with spider mites, *Tetranychus urticae*. Predatory mites can actively disperse within a patch (typically a plant or group of plants) but depend on passive aerial transport by wind currents for migration among patches. Pels and Sabelis (1999) found several “killer” strains of predatory mites that suppressed aerial migration until the local prey population was eliminated and only one “milker”-like strain that initiated emigration some days before the moment of prey elimination (thus they left when there were still prey available). The killer strains originated from a population near the coastline of Sicily, where many populations of *P. persimilis* occurred, whereas the milker type was collected farther inland, where the predators are scarce. These results agree with our simulations in that the relatively more prudent strains are found where the probability of migration and colonization is relatively low, but they do not in that killers are found more frequently than milkers. We think these contrasts between predictions and observations arise from a variety of factors that cause predators to lose control over the local exploitation of prey. For example, one may think of environmental disasters (heavy rain, wind, or fire), overexploitation of plants by herbivores, exploitation competition with other predator species, or diseases.

Another class of mechanisms that may explain the difference between simulations and empirical data arises from the responses of predatory mites to odors from plants infested by herbivorous prey mites (Sabelis et al. 1984; Sabelis and Van der Weel 1993; Sabelis and Afman 1994;

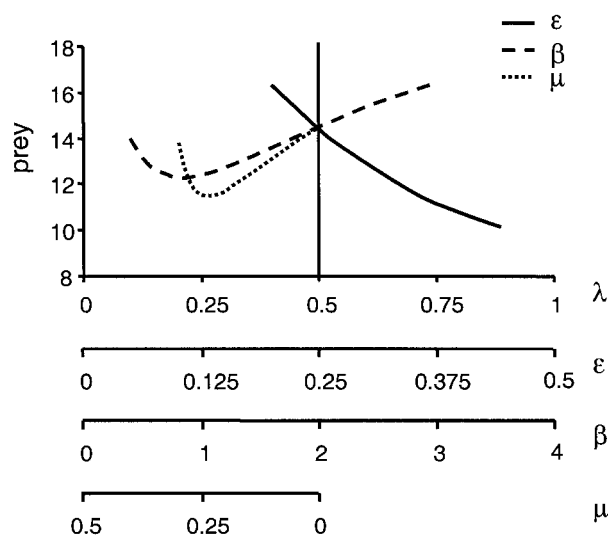


Figure 8: Average number of prey in the migration pool as a function of λ , ϵ , β , and μ , where $\lambda = \epsilon\beta - \mu$. The X-axes are scaled such that a shift over the ϵ , β , or μ axis translates into a uniform effect on the local predator growth rate (λ). The overall prey density declines at the fastest rate when λ is increased through ϵ . For fixed ϵ , the overall prey density changes faster through μ than through β . Parameters as in table 1; $\sigma_p = 0.002$.

Janssen 1999). These responses will increase the probability of multiple invasion and therefore favor the evolution of killers (Nowak and May 1994; van Baalen and Sabelis 1995b). However, predatory mites also avoid plants with herbivorous prey mites if occupied by other predators that are potential competitors (Janssen et al. 1997). The avoidance probably occurs in response to the alarm pheromones released by the prey mites, and this will decrease the probability of multiple invasion. Thus, whether aggregative responses to prey patches contribute to multiple invasion and thereby to the evolution of killers remains to be elucidated.

Competitive Exclusion and Multiple Invasion

Our simulations concerning the evolution of β and μ show that the system evolves to a state where (1) the overall prey density is close but not equal to its minimum, (2) the likelihood that predators exploit a patch alone is larger than the likelihood they have to share it with a competitor, and (3) the exploitation strategies favored by selection were more prudent than the ones that would exactly minimize prey density. A prey density close to its minimum superficially resembles the outcome of Lotka-Volterra competition models of well-mixed populations, which pertains to the selection process at the level of local populations (group selection). However, the likelihood of patch sharing being larger or smaller than single exploitations pertains to the selection within local populations, that is, at the individual level. The complex feedback loops in the model studied in this article prevent the evolutionary outcome to be governed by a simple minimization argument (Mylius and Diekmann 1995), and therefore neither of the two conditions, a minimum prey density or an equal likelihood of single and co-invasion, are realized in our evolutionary simulations (cf. characteristics 1 and 2 above). Nonetheless, a comparison of the model results with the minimum prey density and the likelihood of co-invasion is instructive as these quantities represent the opposing selective forces operating in the metapopulation and can hence be expected to put bounds to the evolutionary outcome in our simulation model. Indeed, in our long-term evolution simulations, the predator strategy always evolves to a parameter within these bounds.

Intuitively, one might expect that the number of prey dispersers produced over the entire lifetime of a prey-predator patch is lower than the number of dispersing prey produced before predators invade the patch. In our simulations, the opposite is true: most of the dispersing prey originate from predator-prey patches because the mean number of prey in the predator-free period is smaller than the mean number of prey during the period of predator-prey interaction. The analysis of a phenomenological

Levins-type model without local dynamics (see appendix) suggests that this larger number of dispersing prey, which is produced after predator invasion, is crucial for the observed evolutionary outcome. Assume that the range of possible evolutionary outcomes is bounded by the strategy that minimizes the global prey density and the strategy for which the chance that a predator can exploit a prey patch alone equals the chance that it has to share the patch with a competitor. As argued above, these bounds would correspond to individual selection and group selection dominating the evolutionary outcome, respectively. The analysis of the Levins model (see appendix) shows that the second bound occurs for a more prudent strategy than the one that minimizes global prey density if the contribution of prey-predator patches to the pool of prey dispersers is larger than the contribution by prey patches. Under these conditions the range of possible outcomes thus resides at the prudent side of the strategy that minimizes global prey density. Conversely, the range of possible outcomes is at the less prudent side of the strategy for which global prey density attains a minimum if the contribution of prey-predator patches to the pool of prey dispersers is smaller than the contribution by prey patches. These predictions of the Levins-type model therefore agree with our finding that selection favors more prudent strategies than those that would minimize prey density (characteristic 3 above). In addition, the predictions point to the hypothesis that less prudent strategies, as those expected on the basis of Lotka-Volterra competition models, are expected to evolve if the within-patch model dynamics is such that a prey patch on average contributes more to the prey disperser pool than a prey-predator patch.

Evolution and Persistence

To explain why predator-prey systems persist in nature despite selection on predators, two hypotheses have been put forward: first, the evolution of superpredators is prevented by constraints on the predators (MacArthur and Levins 1967), and, second, the evolution of superpredators is counteracted by the evolution of antipredator traits in the prey (Red Queen hypothesis; Van Valen 1973). Our simulations provide insight into how selection influences the various predator traits (ε , β , and μ) and how these traits promote or diminish the probability of persistence. On the one hand, conversion efficiency tends to evolve to ever higher values, thereby ultimately causing the predator-prey system to crash, but on the other hand, emigration and consumption evolve so as to promote predator-prey persistence. Thus, the system cannot persist without constraints on the conversion efficiency, and one may ask whether such constraints are likely to be met. Calow (1977) argued that the maximum energy conversion efficiency for

heterotrophic organisms has an upper bound somewhere between 70% and 80% as a result of maintenance and biomass synthesis. Such high values may hold for sit-and-wait predators but not for predators that search. Moreover, predators usually do not consume their prey completely and our parameter ε also includes the conversion processes involved in producing eggs.

Persistence of predator-prey systems thus hinges on constraints imposed by conversion physiology in a model setting with imposed environmental structure and global mixing among the migrants. Which combinations of ε , β , and μ evolve when there is no global mixing among the migrants is an open question for future research.

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APPENDIX

The Levins-Type Model

Consider the following Levins type predator-prey model, consisting of a fraction of prey patches n_1 , a fraction of predator-prey patches n_2 , and a complementary fraction of empty patches $n_0 = 1 - n_1 - n_2$. Empty patches turn into prey patches at a rate proportional to the fraction of empty patches and to the number of dispersing prey. Prey patches turn into predator-prey patches at a rate proportional to the fraction of prey patches and to the number of dispersing predators. Predator-prey patches turn into empty patches at a fixed turnover rate ω . Prey migrate from prey patches at rate φ_1 , and from predator-prey

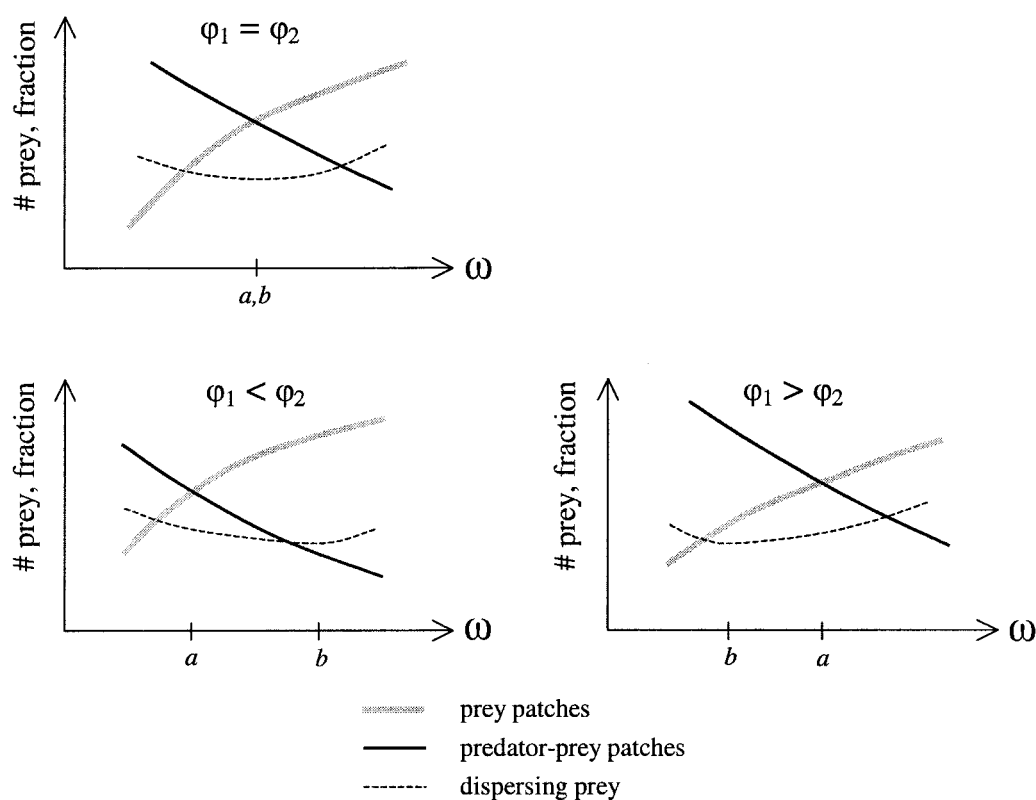


Figure A1: Equilibria in a Levins-type predator-prey metapopulation for prey patches (\bar{n}_1) and predator-prey patches (\bar{n}_2), and the number of dispersing prey ($\varphi_1 \bar{n}_1 + \varphi_2 \bar{n}_2$), as a function of the turnover rate (ω) of predator-prey patches. When the number of dispersing prey per prey patch (φ_1) is equal to the number of dispersing prey per predator-prey patch (φ_2 ; $\varphi_1 = \varphi_2$), the fractions of prey patches and predator-prey patches are equal at the same point (indicated by a), where the number of dispersing prey is minimized (indicated by b). When fewer prey migrate from prey patches than from predator-prey patches ($\varphi_1 < \varphi_2$), the minimum number of dispersing prey occur at the right-hand side of a , whereas they occur at the left-hand side when more prey migrate from prey patches than from predator-prey patches ($\varphi_1 > \varphi_2$).

patches at rate φ_2 , whereas predators migrate from predator-prey patches at rate v . The dynamics of the patches can be represented by the following equations (Holt 1997):

$$\begin{aligned}\frac{dn_1}{dt} &= (\varphi_1 n_1 + \varphi_2 n_2)(1 - n_1 - n_2) - v n_1 n_2, \\ \frac{dn_2}{dt} &= v n_1 n_2 - \omega n_2.\end{aligned}$$

Let $\varphi_1 = \varphi_2 = \varphi$ and let the equilibrium values of empty, prey, and predator patches be denoted by \bar{n}_0 , \bar{n}_1 , and \bar{n}_2 . From $dn_2/dt = 0$, it then follows that $\bar{n}_1 = \omega v^{-1}$. Rewriting the equation of dn_1/dt using the equilibrium values \bar{n}_0 , \bar{n}_1 , and \bar{n}_2 yields

$$H(\omega, \bar{n}_0) = \frac{dn_1}{dt} = \varphi(1 - \bar{n}_0)\bar{n}_0 - \omega(1 - \omega v^{-1} - \bar{n}_0).$$

By applying the implicit function theorem, we can derive for $\bar{n}_0(\omega)$:

$$\frac{d\bar{n}_0(\omega)}{d\omega} = -\frac{\partial H(\omega, \bar{n}_0)/\partial \omega}{\partial H(\omega, \bar{n}_0)/\partial \bar{n}_0}.$$

Thus for $d\bar{n}_0(\omega)/d\omega = 0$, it is required that

$$\frac{\partial H(\omega, \bar{n}_0)}{\partial \omega} = -1 + \frac{2\omega}{v} + \bar{n}_0 = 0.$$

The latter condition implies that $1 - \bar{n}_0 = 2\omega v^{-1} = 2\bar{n}_1$ and, together with $\bar{n}_0 + \bar{n}_1 + \bar{n}_2 = 1$, that $\bar{n}_1 = \bar{n}_2$.

Thus, if $\varphi_1 = \varphi_2$, the number of empty patches in equilibrium reaches a maximum at a value for ω for which the fraction of prey patches is precisely equal to the fraction of predator-prey patches, $\bar{n}_1 = \bar{n}_2$. Coinciding with this maximum, the overall prey density and the number of prey in the migration pool, that is $\varphi(\bar{n}_1 + \bar{n}_2)$, is minimized, as is the number of occupied patches (fig. A1). An equal fraction of prey and predator-prey patches implies that the average lifetime of a prey patch is equal to the average lifetime of a predator-prey patch (i.e., they have the same per-patch turnover rates). Because a prey patch turns into a predator-prey patch as soon as the first predator arrives, it can be argued that on average the next predator arrives after an equal amount of time. Thus, the second invader is expected by the time the prey is driven to extinction. In other words, the likelihood of single invasions equals the likelihood of co-invasions.

Hence, if the contribution to the prey disperser pool by prey patches equals the contribution by predator-prey patches ($\varphi_1 = \varphi_2$), prey minimization and equal likelihood

of single and co-invasion occurs for the same exploitation strategy ω . From figure A1 it can now readily be seen that for $\varphi_1 < \varphi_2$ (i.e., a larger contribution to the prey disperser pool by predator-prey patches) an equal likelihood of single and co-invasion occurs at a value of ω that is lower (i.e., more prudent) than would minimize the number of dispersing prey, while for $\varphi_1 > \varphi_2$ (i.e., a larger contribution to the prey disperser pool by prey patches) the opposite holds.

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