

The Role of Prey Taxis in Biological Control: A Spatial Theoretical Model

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Submitted January 16, 2002; Accepted October 22, 2002;
Electronically published June 27, 2003

ABSTRACT: We study a reaction-diffusion-advection model for the dynamics of populations under biological control. A control agent is assumed to be a predator species that has the ability to perceive the heterogeneity of pest distribution. The advection term represents the predator density movement according to a basic prey taxis assumption: acceleration of predators is proportional to the prey density gradient. The prey population reproduces logistically, and the local population interactions follow the Holling Type II trophic function. On the scale of the population, our spatially explicit approach subdivides the predation process into random movement represented by diffusion, directed movement described by prey taxis, local prey encounters, and consumption modeled by the trophic function. Thus, our model allows studying the effects of large-scale predator spatial activity on population dynamics. We show under which conditions spatial patterns are generated by prey taxis and how this affects the predator ability to maintain the pest population below some economic threshold. In particular, intermediate taxis activity can stabilize predator-pest populations at a very low level of pest density, ensuring successful biological control. However, very intensive prey taxis destroys the stability, leading to chaotic dynamics with pronounced outbreaks of pest density.

Keywords: predator-prey model, reaction-diffusion-advection, trophic function, spatial heterogeneity.

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The aims of biological control are to depress the pest density and to maintain it durably under some economic threshold through the importation and establishment of a natural enemy. The efficiency of a biological control program can be characterized by the ratio between the equilibrium population size of the pest in the presence and in the absence of the natural enemy (Beddington et al. 1975). Calculating the ratio for different field observations, Beddington et al. (1978) have shown that, in many successful cases, this ratio does not exceed 2.5%. Obviously, an adequate mathematical model for a pest-enemy system must exhibit persistent dynamics at such low pest density. It is not necessary for the model dynamics to be an equilibrium. Pest extinction or fluctuations that do not exceed the economic threshold all or most of the time are also compatible with satisfactory control (Murdoch et al. 1985). Therefore, for the mathematical assessment of population stability, it is appropriate to use the Lagrange definition: boundedness of fluctuating population abundance (Svirezhev and Logofet 1983).

In this article, we consider biological control by predators. The trophic function g representing the consumption rate of a single predator is the fundamental character of the predator-prey interaction. If N is the prey population density, then the classical expression of this function is prey dependent: $g = g(N)$, which corresponds to the assumption that predators encounter prey at random. The hypothesis is known to be valid for homogeneous systems (Gause 1935; Holling 1959; Luckinbill 1973; Bohannan and Lenski 1997, 1999; Haydon and Lloyd 1999). However, simple predator-prey models resting on a prey-dependent expression fail to describe the dynamics of pest-enemy systems: in those cases where control is successful, the pest is depressed more than can be predicted by simple models (Beddington et al. 1978). This raises a paradox for biological control (Luck 1990; Arditi and Berryman 1991; Berryman 1999): prey-dependent, spatially homogeneous models predict that one cannot both reduce the pest density and obtain a highly stable interaction. In fact, the paradox implies that predator-prey models should be modified to include processes that allow pests and natural

enemies to persist in stable interactions at a low level of pest density.

A large body of theoretical ecology has developed with the purpose of understanding how the natural enemy is able to keep the temporal variability of pest density low enough to avoid outbreaks above the acceptable threshold. The major conclusion is that nonrandom search, that is, the tendency of predators to aggregate where prey are abundant, can contribute to stability (Hassell and May 1973, 1974; Hassell 1976, 1978; Free et al. 1977; May 1978; Chesson and Murdoch 1986). Other explanations for successful biological control are different forms of pest refuges (Beddington et al. 1975, 1978; Hawkins et al. 1993; Lynch et al. 1998), mutual interference among predators (Hassell and Varley 1969; Beddington et al. 1975; DeAngelis et al. 1975), and local pest extinctions (Murdoch et al. 1985; Hastings 1990; Luck 1990).

There are two ways to incorporate spatial structure into models and to describe spatial population interactions. The first is to represent space explicitly by either continuous spatial coordinates or discrete localities. The second is implicit in the sense that it does not address topographic space explicitly, but assumptions regarding a certain spatial structure of the biotic interactions are hidden in its postulates (Czárán 1998). For instance, the role of various kinds of heterogeneities can be included implicitly into the trophic function by accounting for predator dependence: $g = g(N, P)$ (e.g., Hassell and Varley 1969; Hassell and May 1974; Beddington 1975; DeAngelis et al. 1975). With the same idea, Arditi and Ginzburg (1989) suggested that the spatial behavior of predators in heterogeneous environment leads to the dependence of the trophic function on the ratio of prey to predator abundances: $g = g(N/P)$. This conjecture was later confirmed by the spatially explicit, mechanistic models of Poggiale et al. (1998), Cosner et al. (1999), and Arditi et al. (2001) and also experimentally by Arditi and Saïah (1992). The parsimonious, spatially implicit ratio-dependent model resolves the biological control paradox (Arditi and Berryman 1991). However, like the other predator-dependent models cited above, this model is phenomenological. Even though they exhibit realistic dynamics, these models do not explain the spatial mechanisms that promote the persistence of the interacting populations.

Here we present an explicit manner to model the predator-prey system that accounts for a sequence of closely intertwined phenomena: foraging behavior \rightarrow aggregation \rightarrow local extinction \rightarrow spatial heterogeneity \rightarrow partial refuges. We consider that the movement of predators is induced by the heterogeneity in the prey distribution and that predators tend to aggregate in regions of high prey density. This pattern of movement, so-called prey taxis (Kareiva and Odell 1987; Turchin 1998), is as-

sumed to be the only source of the phenomena listed above, with all environmental factors assumed to be homogeneous and constant.

Our mathematical setting is based on a reaction-diffusion-advection type of partial differential equations. Since the articles of Fisher (1937) and Kolmogorov et al. (1937), the use of such systems for representing species interactions has been carried forward (e.g., Keller and Segel 1971; Levin and Segel 1976; Levin 1977; Mimura and Murray 1978; Mimura and Kawasaki 1980; Okubo 1980; Mimura and Yamaguti 1982; Edelstein-Keshet 1988; Murray 1993; Turchin 1998). In conventional prey taxis models, the directed movement of predator density is due to the advective velocity, which is assumed to be proportional to the gradient of prey density (Czárán 1998; Grünbaum 1998; Turchin 1998; Berezovskaya and Karev 1999; Berezovskaya et al. 1999). Our approach differs by the general assumption concerning taxis: we assume that the directed movement is not determined by the velocity itself but by the velocity variation (i.e., the acceleration), which is proportional to the prey density gradient (or, in general, to the gradient of some stimulus; see Govorukhin et al. 1999, 2000; Sapoukhina and Tyutyunov 2000; Arditi et al. 2001). There are many observations of the dependence of individual acceleration on the stimulus gradient, and this assumption has become a foundation of individual-based models. For example, Okubo and Chiang (1974) and Okubo et al. (1977) analyzed trajectories of swarming midges. They showed that individual acceleration is zero at the center of the swarm, where the density of midges is maximum and the density gradient is zero by definition, and increases with distance from the center, being maximum on the edge where the density is minimum and the gradient is maximum. Schooling fish demonstrate a similar response to their own density gradient: at the center of the school, where the density gradient is zero, individual motion loses the directional component and becomes random (Parrish and Turchin 1997). Observations of another schooling fish have allowed Flierl et al. (1999) to conclude that the probability of changing the direction of individual movement (velocity variation) depends on the difference between ambient and preferred temperatures. Analyzing herbivore movement, Kareiva (1982) detected that insects modify their migratory impulse, that is, accelerate, in response to the quality of the food patch.

For large-scale, long-term predator-prey systems spanning many generations, there are no data that would allow us to confirm or to contradict the hypothesis of the dependence of taxis acceleration on the stimulus gradient. However, existing field-scale studies of the spatiotemporal predator-pest dynamics provide evidence of a strong aggregative response by the predator population to pest clusters, manifested by movements of dynamically coupled

species patches (e.g., Dixon 2000; Winder et al. 2001). Winder et al. (2001) have found that the increase of predator activity is related positively to the degree of aphid clustering into patches, independent of the aphid abundance. Taking into account the phenomenon of accelerated predator movement along the prey density gradient at the individual level, we can assume that this phenomenon takes place at the level of population density as well. Modeling prey taxis by the acceleration accounts both for the dependence of taxis velocity on the prey density gradient and for the inertial component of the directional movement. The latter is a main difference between the proposed model and conventional taxis models. At the large spatio-temporal scale, the inertial movement of the population is determined not only by mechanical laws but also by behavioral and social effects. For example, ladybirds are attracted not only to the sites where aphids are but also to those where they have recently been present (Dixon 2000). Such spatial behavior requires memory and learning, and it is known in various species (see, e.g., McFarland 1985).

On a long timescale, the directed population movements result both from predator detection of prey patches and from their life cycle processes (Kindlmann and Dixon 1993; Dixon 2000; Winder et al. 2001). On this scale, our spatially explicit approach subdivides the predation process into random movement represented by diffusion, directed movement described by prey taxis, local prey encounters, and consumption modeled by the trophic function. Thus, our model allows studying the effects of large-scale predator spatial activity on population dynamics. We will first find the conditions of the emergence of spatial patterns. Next, we will show how two coupled phenomena (prey taxis and spatial heterogeneity) drive the dynamic properties of the predator-pest community. Our analysis highlights the role of predator-directed movement in its ability to maintain the pest population under some economic threshold. We will show that the proposed explicit model provides a realistic description of the population dynamics under biological control: it can produce stable pest-enemy interactions at a very low pest density. Finally, interpreting the modeling results and comparing them with observations, we will discuss the possibilities of applying the proposed approach to the study of real biological control dynamic systems.

The Model

Let us consider a one-dimensional domain $[0, L]$ in which the predator is able to perceive the local heterogeneity of pest density. The directed component of the predator movement is described according to the following prey

taxis assumption: the acceleration is proportional to the gradient of pest density,

$$\frac{\partial v}{\partial t} = \kappa \frac{\partial N}{\partial x} + \delta_v \frac{\partial^2 v}{\partial x^2}, \quad (1)$$

where $N(x, t)$ is the pest density at the position $x \in [0, L]$ at time t , $v(x, t)$ is the velocity of the predators, κ is the taxis coefficient of the predator, which represents the sensitivity of predators to heterogeneity of the pest density distribution, and δ_v is the diffusion of velocity. This diffusion term in equation (1) is interpreted as an effect of social behavior: arrayal forces equalize speeds and directions of neighbors (Flierl et al. 1999). Note that since v is the instantaneous velocity of predator density movement defined at each spatial coordinate, equation (1) is used to describe the gradual speeding up of the directed movement when a prey aggregate is being approached.

The local dynamics (reproduction, pest consumption, and predator mortality) are modeled as processes acting in infinitely small and, hence, homogeneous elementary segments of the considered domain. Thus, according to the suggestion of Arditi and Ginzburg (1989) about the applicability of prey-dependent trophic functions to homogeneous systems, we will describe the local predator-prey interactions by the Holling Type II function (1959). Under these assumptions, population dynamics obey the following model:

$$\begin{aligned} \frac{\partial N}{\partial t} &= rN \left(1 - \frac{N}{K}\right) - \frac{aNP}{1 + ahN} + \delta_N \frac{\partial^2 N}{\partial x^2}, \\ \frac{\partial P}{\partial t} &= e \frac{aNP}{1 + ahN} - \mu P - \frac{\partial(Pv)}{\partial x} + \delta_P \frac{\partial^2 P}{\partial x^2}, \end{aligned} \quad (2)$$

where $P(x, t)$ is the predator density, r is the pest reproduction rate, K is the pest carrying capacity, a is the searching efficiency, h is the handling time, e is the conversion efficiency, μ is the predator mortality, and δ_N and δ_P are the pest and predator diffusions, respectively. All parameters are positive constants. Note that the nonspatial analogue of model (1)-(2) is simply the well-known Rosenzweig-MacArthur model.

The trophic function implicitly includes the small-scale rapid movements of individuals due to the local searching behavior of predators, while the advective term, in which the prey taxis velocity v follows equation (1), describes explicitly the directed movement of the population density on the larger and slower spatiotemporal scale. Both population life cycles are assumed to occur on similar scales, and both population densities vary in time. Thus, model (1)-(2) differs from an earlier study (Arditi et al. 2001) in

which the predator demography was assumed to be so much slower than the prey's that the total predator population was assumed to be constant. That simpler preliminary model could not apply to situations of biological control of insect pests by insect enemies.

Let us perform a nondimensionalization to reduce the number of parameters in model (1)-(2). Choosing the variables $\tilde{t} = rt$, $\tilde{N} = N/K$, $\tilde{P} = P/eK$, and $\tilde{v} = v/r$; setting the parameters $\tilde{a} = aeK/r$, $\tilde{h} = rh/e$, $\tilde{\mu} = \mu/r$, $\tilde{\kappa} = K\kappa/r^2$, $\tilde{\delta}_N = \delta_N/r$, $\tilde{\delta}_P = \delta_P/r$, and $\tilde{\delta}_v = \delta_v/r$; and dropping \sim for notational convenience, we find that the system (1)-(2) takes the form

$$\begin{aligned}\frac{\partial N}{\partial t} &= N(1-N) - \frac{aNP}{1+ahN} + \delta_N \frac{\partial^2 N}{\partial x^2}, \\ \frac{\partial P}{\partial t} &= \frac{aNP}{1+ahN} - \mu P - \frac{\partial(Pv)}{\partial x} + \delta_P \frac{\partial^2 P}{\partial x^2}, \\ \frac{\partial v}{\partial t} &= \kappa \frac{\partial N}{\partial x} + \delta_v \frac{\partial^2 v}{\partial x^2}.\end{aligned}\quad (3)$$

We assume zero flux boundary conditions:

$$v \Big|_{x=0,L} = \frac{\partial N}{\partial x} \Big|_{x=0,L} = \frac{\partial P}{\partial x} \Big|_{x=0,L} = 0. \quad (4)$$

The analysis of a two-dimensional generalization of this model in a closed rectangular habitat has shown that the conclusions regarding the role of prey taxis in the emergence of spatially heterogeneous dynamics remain valid (Sapoukhina 2002). For this reason, we only treat here the one-dimensional case.

Analysis and Results

The spatially homogeneous dynamic regimes of model (3)-(4) correspond to those of the Rosenzweig-MacArthur model. There are three spatially homogeneous equilibria (see appendix), and we are interested in the nontrivial uniform equilibrium

$$(N_2^*, P_2^*, v_2^*) = \left[\frac{\mu}{a(1-\mu h)}, \frac{a(1-\mu h) - \mu}{a^2(1-\mu h)^2}, 0 \right], \quad (5)$$

which corresponds to coexistence of prey and predators in the absence of predator active movements. If there are no spatial effects, that is, perturbations are homogeneous, the stability condition for equilibrium (5) reduces to the well-known expression

$$\frac{\mu}{1-\mu h} < a < \frac{1+\mu h}{h(1-\mu h)}. \quad (6)$$

Otherwise, the steady state (5) loses its stability; for smaller values of parameter a , it becomes negative, and for larger values, a homogeneous limit cycle C_0 arises around equilibrium (5). In order to clarify the effect of predator active movement, we will first study how the taxis coefficient κ makes spatial patterns arise from the initially stable uniform equilibrium (5) and then how spatial patterns also arise from the initially stable uniform limit cycle C_0 .

Stability of the Homogeneous Nontrivial Equilibrium

A local stability analysis has been performed using standard techniques (see, e.g., Murray 1993) adapted to the above system (for details, see appendix). We study the stability of equilibrium (5) with respect to spatially heterogeneous perturbations; hence, we consider parameter values satisfying inequality (6).

For the uniform solution (5) to be stable with respect to a spatial perturbation with wave number $k = n\pi/L$ ($n = \pm 1, \pm 2, \dots$), the general stability condition

$$\begin{aligned}0 \leq \kappa < \frac{1}{P_2^* \mu} \left(\delta_N + \delta_P - \frac{a_{11}}{k^2} \right) \\ \times \left\{ (\delta_v + \delta_P) [(\delta_N + \delta_v)k^2 - a_{11}] + \frac{\mu a_{21}}{k^2} \right\}\end{aligned}\quad (7)$$

should be satisfied (see appendix). Here $a_{11} < 0$ and $a_{21} > 0$ are the elements of the Jacobian matrix at the equilibrium.

It is easily seen from inequality (7) that, if $\kappa = 0$ (in other words, if predators encounter prey at random), the uniform steady state is stable for all admissible parameter values. When active movement is allowed (i.e., $\kappa > 0$), there is a bifurcation value of the taxis coefficient κ^* such that inequality (7) is violated for $\kappa > \kappa^*$. In this case, equilibrium (5) loses its stability oscillatorily, and a spatially inhomogeneous solution arises in the vicinity of equilibrium (5). Obviously, the establishment of heterogeneous dynamics depends on the relation between directed and random predator movements: the higher the diffusion values, the higher the bifurcation value κ^* of the taxis coefficient.

For illustration, let us fix the parameters to $L = 5$, $h = 10$, $\mu = 0.01$, $\delta_N = 0.01$, $\delta_P = 0.6$, and $\delta_v = 0.001$. With these values, figure 1a shows the parameter portrait of the critical condition (7). According to stability condition (6), we consider the domain $a \in (0.01; 0.12)$ in which the equilibrium is stable in the absence of spatial

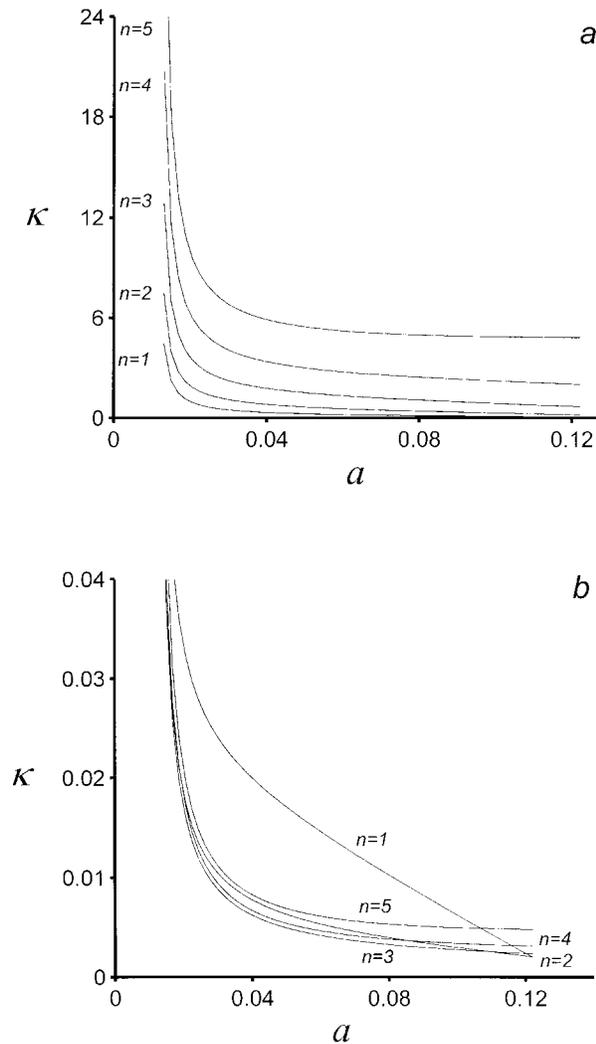


Figure 1: Critical curves of the oscillatory instability of the spatially homogeneous positive equilibrium (N_2^*, P_2^*, v_2^*) for $n = 1 \dots 5$, computed for two different values of predator diffusion: (a) $\delta_p = 0.6$; (b) $\delta_p = 0.01$.

effects. For a fixed mode n , values of κ and a situated under the critical curve (7) correspond to stability of equilibrium (5) with respect to the perturbation with wave number $k = n\pi/L$. The values of κ and a situated over the critical curve determine the instability domain of the mode n . When $\kappa = 0$, equilibrium (5) is stable with respect to any spatial perturbations, even if diffusion exists. Let us fix a value of a and increase κ gradually. It is easy to see from figure 1a that $n = 1$ is the first mode to become unstable. This means that the uniform equilibrium (5) loses its stability with spatiotemporal oscillations, and the arising spatially heterogeneous dynamic has a maximum

spatial extension: its half-period is the size of habitat L . With further increase of the taxis coefficient, the higher modes are excited successively, with the result that spatial heterogeneity becomes more pronounced.

Figure 1b illustrates the critical curves (7) for the same parameter values, with the difference that predator diffusion is $\delta_p = 0.01$. This decrease of diffusion leads to the decrease of κ^* . Furthermore, the succession of modes changes. The uniform steady state (5) becomes unstable by the excitation of higher modes than in the previous case (fig. 1a). For instance, for $a = 0.06$, the first excited mode is $n = 3$. Thus, the half-period of the arising heterogeneous dynamics is $L/3$; that is, spatial complexity is higher.

The local dynamics of the heterogeneous regimes for supercritical values of the taxis coefficient are illustrated by numerical simulations for $a = 0.06$ (fig. 2). We see that the higher the value of κ , the higher the frequency and the amplitude of the local density oscillations.

To summarize, we have obtained the analytical condition (7) for the generation of spatial patterns by prey taxis. Active movement drives the oscillatory instability: the homogeneous equilibrium becomes unstable and inhomogeneous spatial solutions appear. With increase of κ , the dynamics becomes more complex and more distant from the original equilibrium (see fig. 2). The same effects of the taxis activity may be expected on the homogeneous limit cycle of the model (3)-(4).

Stability of the Homogeneous Limit Cycle

As already mentioned, in the absence of spatial effects, exceeding the upper critical value (6) of the searching efficiency leads to the emergence of a homogeneous limit cycle C_0 , while equilibrium (5) becomes unstable. Such high values of a lead to large oscillations that periodically bring the pest population to values close to its carrying capacity. Furthermore, the higher a , the larger the amplitude of the oscillations. Therefore, in this case, the model does not describe successful biological control in which the pest should be depressed below some economic threshold (Luck 1990; Arditi and Berryman 1991). We show here that prey taxis changes this situation.

As an example, we study the influence of κ on the stability of the homogeneous cycle C_0 that exists for $L = 5$, $a = 0.2$, $h = 10$, $\mu = 0.01$, $\delta_N = 0.01$, $\delta_p = 0.6$, and $\delta_v = 0.001$. The method (for details, see, e.g., Kuznetsov 1998) consists in studying modifications of the phase curve family in the vicinity of C_0 according to the taxis coefficient κ . A cross section orthogonal to the vector field at a certain point of the cycle is taken, and the Poincaré map is constructed. Then, eigenvalues (multipliers) of the Jacobian matrix of this map at the fixed point are derived numer-

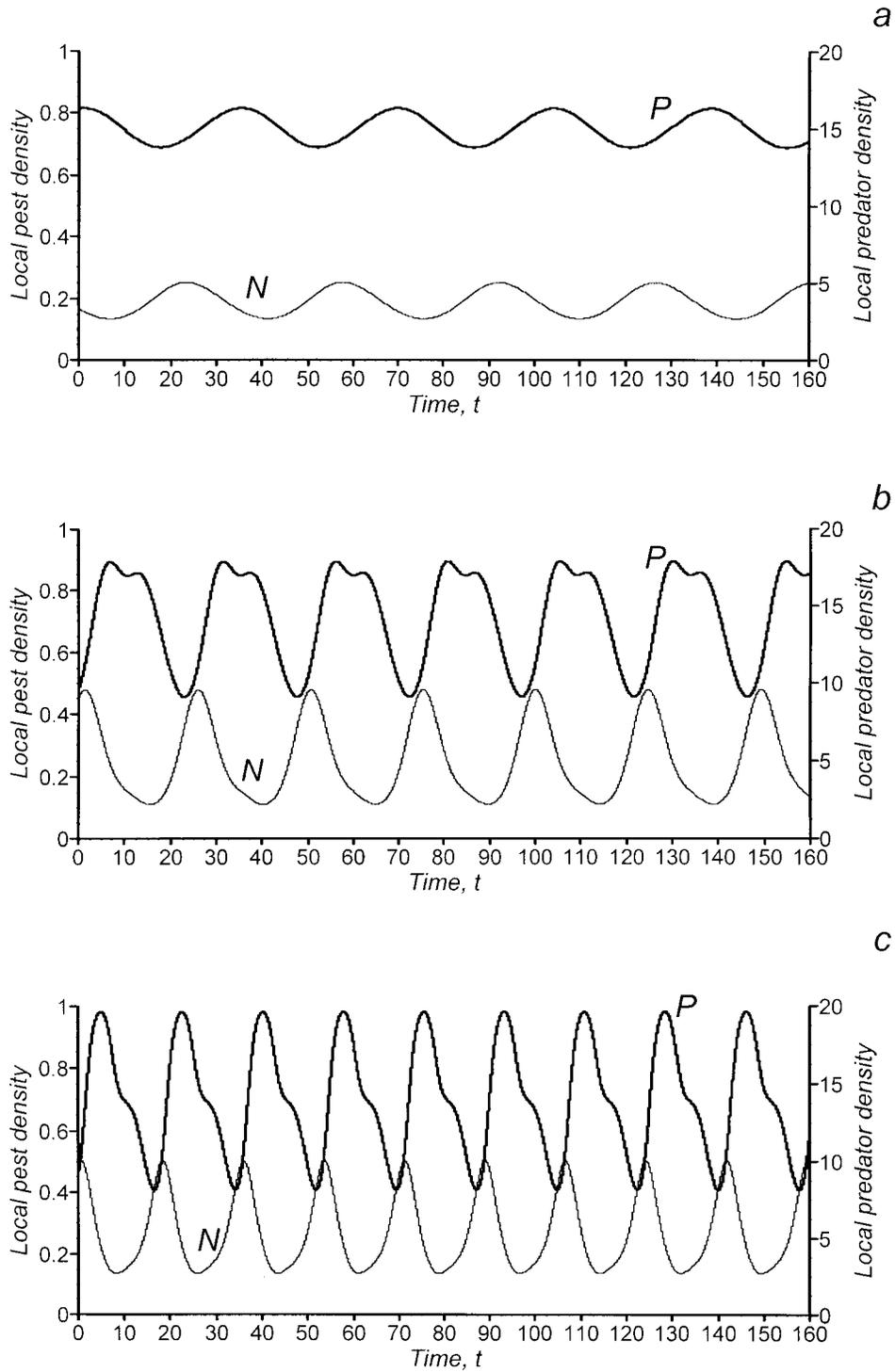


Figure 2: Local oscillations of pest and predator densities (at point $x = 1.7$) for the heterogeneous dynamics arising from the oscillatory instability of the homogeneous positive equilibrium $(N_2^*, P_2^*, v_2^*) = (0.185, 15.089, 0)$. Temporal dynamics are shown for different supercritical values of the taxis coefficient: (a) $\kappa = 0.2$; (b) $\kappa = 0.6$; (c) $\kappa = 1.4$.

ically. The positions of the multipliers associated with C_0 with respect to the unit circle in the complex plane describe qualitatively the bifurcations occurring in response to variations of κ .

If predators disperse randomly, that is, $\kappa = 0$, all multipliers are located within the unit circle, except for the multiplier that equals 1 (fig. 3a), which means that the cycle C_0 is stable. We increase the taxis coefficient gradually. When $\kappa = \kappa_1 \approx 0.0095$, one of the multipliers goes out of the unit circle through -1 (fig. 3b). This implies that the homogeneous cycle C_0 loses its stability oscillatorily via period doubling, and a stable spatially heterogeneous periodic regime appears in the vicinity of C_0 . When the taxis coefficient attains a second critical value $\kappa = \kappa_2 \approx 0.047$, all multipliers get back into the unit circle (fig. 3c); the heterogeneity disappears and becomes stable again. At $\kappa = \kappa_3 \approx 0.062$, one of the multipliers goes out of the unit circle through 1 (fig. 3d); that is, the homogenous cycle

C_0 loses its stability monotonically, and new stable spatially inhomogeneous oscillations R_κ arise.

The characteristics of the dynamics R_κ arising from destabilization of C_0 are summarized in figure 4, where the amplitudes of the spatially averaged population densities

$$\langle N \rangle = \frac{1}{L} \int_0^L N(x, t) dx,$$

$$\langle P \rangle = \frac{1}{L} \int_0^L P(x, t) dx,$$

are presented. For values of the taxis coefficient $\kappa \in [0; 0.0095] \cup [0.047; 0.062]$, C_0 is the only attractor of the system; therefore, such κ do not generate spatial patterns.

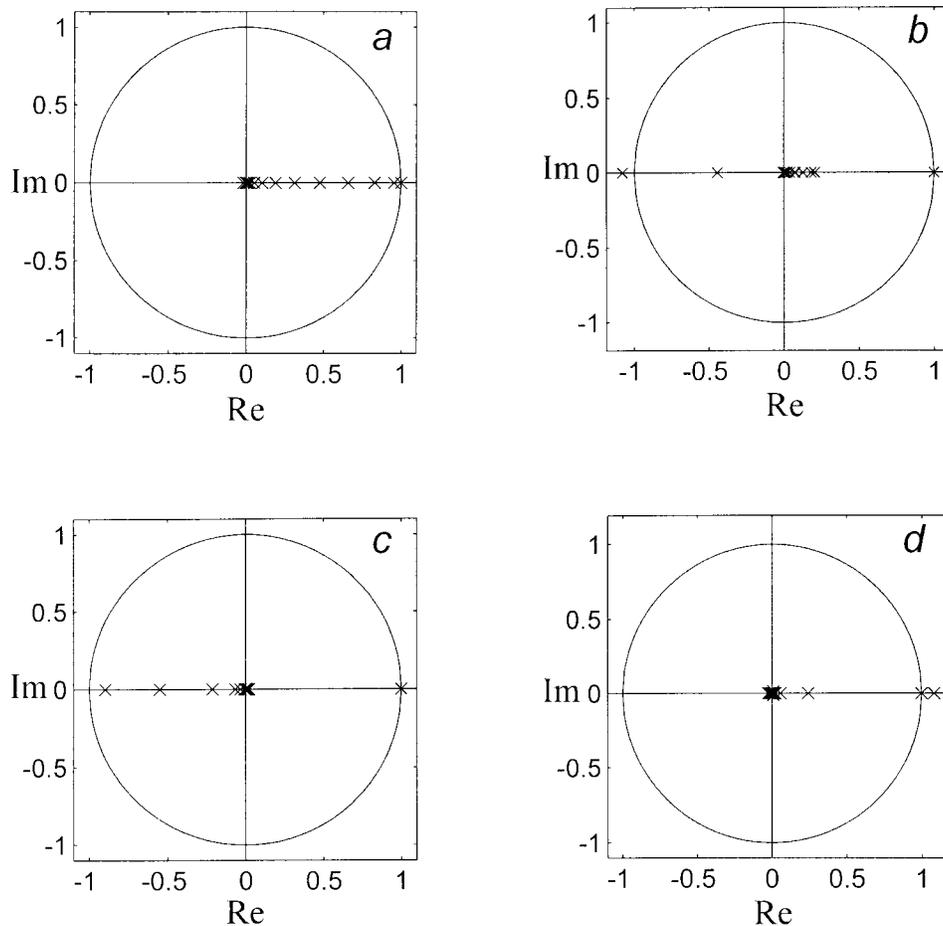


Figure 3: Positions on the complex plane of multipliers computed for the homogeneous oscillations C_0 for different values of the taxis coefficient: (a) $\kappa = 0$; (b) $\kappa = 0.0095$; (c) $\kappa = 0.047$; (d) $\kappa = 0.062$.

For $\kappa \geq 0.062$, model (3)-(4) exhibits stable heterogeneous dynamics R_κ becoming more distant from the original homogeneous cycle C_0 (dashed lines in fig. 4) with the increase of κ . The variations of spatially aggregated densities $\langle N \rangle$ and $\langle P \rangle$ of R_κ are much smaller than in C_0 in the relatively wide range $\kappa \in [0.1; 0.6]$. For higher values of the taxis coefficient ($\kappa > 0.6$), density amplitudes grow somewhat. Moreover, there is a slight growing trend of the densities when averaged over space and time:

$$\langle\langle N \rangle\rangle = \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T \langle N \rangle dt,$$

$$\langle\langle P \rangle\rangle = \lim_{T \rightarrow \infty} \frac{1}{T} \int_0^T \langle P \rangle dt.$$

Regarding the biological control paradox, let us study the case of a very voracious predator. Keeping the other parameters unchanged, we set $a = 0.7$ and $h = 2.857$. When the spatial movement is a random process, that is, $\kappa = 0$, there are a low but unstable pest equilibrium and a stable homogeneous limit cycle C_0 with large amplitude, a typical illustration of the paradox. For a sufficiently high value of the taxis coefficient, C_0 becomes unstable and spatial patterns arise. Figure 5 shows the cycle C_0 and the arising heterogeneous dynamics R_κ for $\kappa = 0.5$. The variations of the spatially averaged population densities in R_κ are dramatically smaller than those of the original cycle. To further illustrate the properties of the heterogeneous dynamics, let us compare in figure 6 the regimes R_κ for various values of the taxis coefficient, plotting the local dynamics as well. Figures 6*b* and 6*d* show that the amplitude of local fluctuations of the heterogeneous regimes R_κ is much lower than for the homogeneous regime C_0 . In other words, the example shows that the predator-prey system is stabilized at both the global and local spatial scales. In comparison with the original cycle C_0 , the pest density fluctuates with a very small amplitude about average values that are lower than 2.5% of the pest carrying capacity $K = 1$ (fig. 6*a*–6*d*). The higher the values of κ , the more complex the stabilized dynamics (i.e., with pronounced patchiness; fig. 6*c*). Further increase of the taxis coefficient leads to growth of average densities of both species and of the fluctuation amplitudes. A very intense taxis results in chaotic spatiotemporal dynamics with significant nonperiodic outbreaks of the pest population density (fig. 6*e*, 6*f*).

The properties of model (3)-(4) allow us to conclude that high searching efficiency, short handling time, and directed movement are desirable attributes of a biocontrol

agent. While high values of a and low values of h lead to low pest density, the predator's taxis activity can stabilize the dynamics. The coefficient κ should be high enough to generate spatial patterns but not too high in order to avoid chaotic dynamics.

Discussion

The spatiotemporal heterogeneity of predator-prey systems can arise in many ways, for example, from temporal asynchronies between prey and predators or from phenotypic variability in the susceptibility of individual prey to predation (Hassell and Anderson 1989). It may be caused directly by the environmental inhomogeneity across a landscape, for example, geological processes and climate (Huston 1994). A central theme of our study is the demonstration that spatial patchiness can result from an intrinsic source, that is, prey taxis. This is shown by the mathematical analysis of the dynamic model presented here (eqq. [3], [4]), extending the findings of earlier models (Sapoukhina and Tyutyunov 2000; Arditi et al. 2001; Tyutyunov et al. 2001).

In our model, the spatial dynamics of the interacting populations display constantly moving density patches, which agrees with field observations (e.g., Winder et al. 2001). Predators respond to the heterogeneity of the prey density by accelerating toward the localities where prey are abundant, resulting in predator aggregation (see spatial patterns in fig. 7). When reaching a local maximum of prey concentration, predators decelerate because the prey gradient reverses. Predator aggregations lead to local prey extinctions, while patches with low predator densities play the role of partial refuges where prey densities grow (fig. 7). Then predators move actively to the newly formed prey clusters. In sum, this spatially explicit model is able to capture various kinds of heterogeneity that are liable to promote the persistence of predator-prey interactions (see, e.g., Hassell and Anderson 1989).

Stability is known to be often bought at the expense of increased pest density (Briggs et al. 1999). For instance, a diffusion-limited mechanism decreasing reproduction and predation rates because of limited individual mobility reduces the magnitude of oscillations of population densities, while the prey density tends to its carrying capacity (Cuddington and Yodzis 2000). Statistical stabilization is known to be another phenomenon that can reduce the oscillations. A weak diffusion can cause oscillatory instability of the homogeneous cycle C_0 and emergence of heterogeneous dynamics that show some tendency to large-scale stabilization of the system (see, e.g., the recent articles of Petrovskii and Malchow 1999, 2001; Malchow 2000). A similar effect was obtained with a cellular automaton model by Basset et al. (1997), who showed that, with cer-

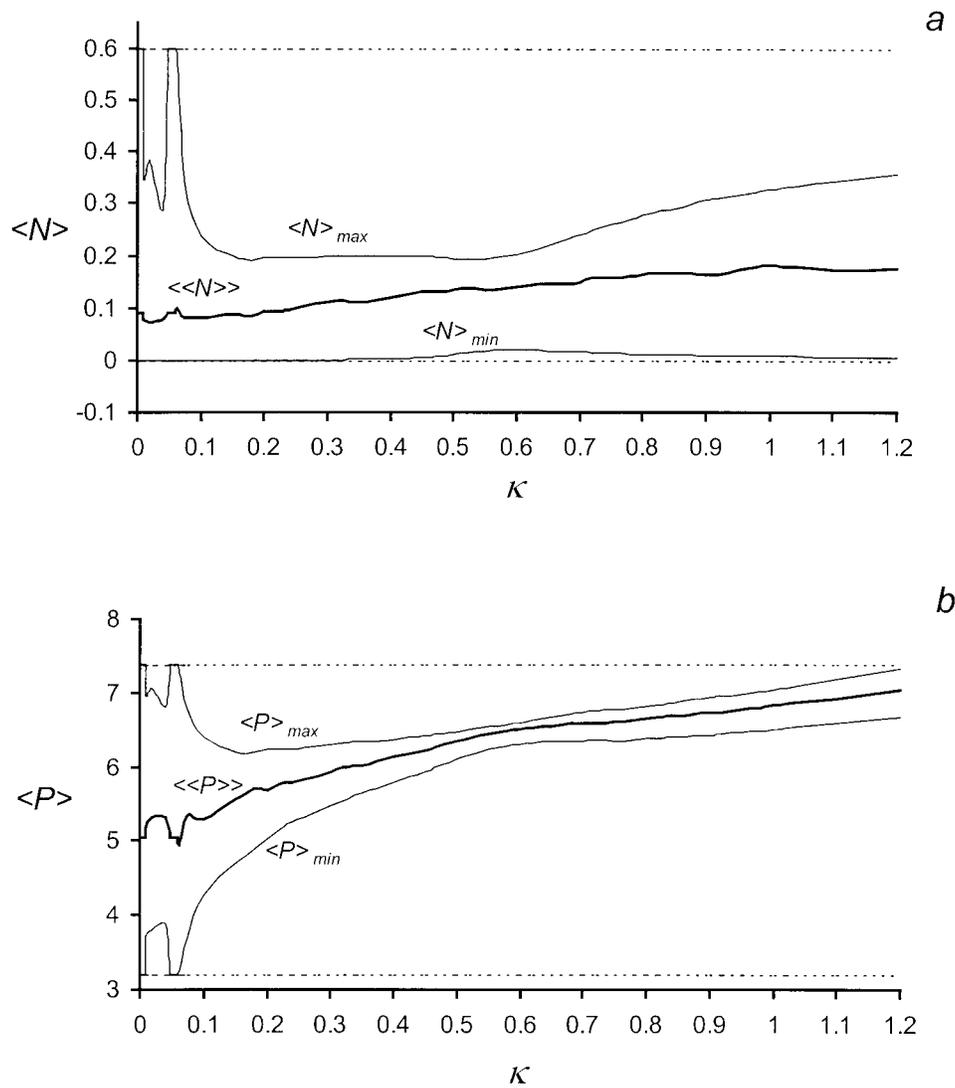


Figure 4: Characteristics of the heterogeneous dynamics R_κ of the spatially averaged densities $\langle N \rangle$ and $\langle P \rangle$ versus taxis coefficient κ : minimum, maximum, and temporally averaged values of the variables. The dashed lines depict the amplitude of the homogeneous cycle C_0 .

tain assumptions concerning the movement of grazers, the large-scale dynamics of a grass-grazer system could be stable even though the local interaction was unstable. Studying a multipatch Rosenzweig-MacArthur model, Jansen and de Roos (2000) also demonstrated some reduction of spatially averaged density oscillations. In all these models, the reduction of the cycle amplitude is caused by spatial desynchronization of local predator-prey oscillations, and a significant suppression of the pest density without local outbreaks cannot be achieved.

In contrast to these models, in our model, the homogeneous cycle C_0 loses its stability monotonically for sufficiently high values of the taxis coefficient. The new het-

erogeneous regime R_κ that appears as a result of this bifurcation moves away from C_0 with further increase of κ (see fig. 4). Reduction of predator-prey cycles is obtained on both global and local scales (fig. 6a–6d). Thus, the heterogeneous dynamics reproduce the patterns of populations in a situation of successful biological control. Because of the way of introducing prey taxis, our model can easily maintain the pest density under the 2.5% threshold proposed by Beddington et al. (1978) as a criterion of model adequacy (fig. 6a–6d).

Let us recall that, among spatially independent models, the ratio-dependent approach resolves the biocontrol paradox (Arditi and Berryman 1991). Previous work with a

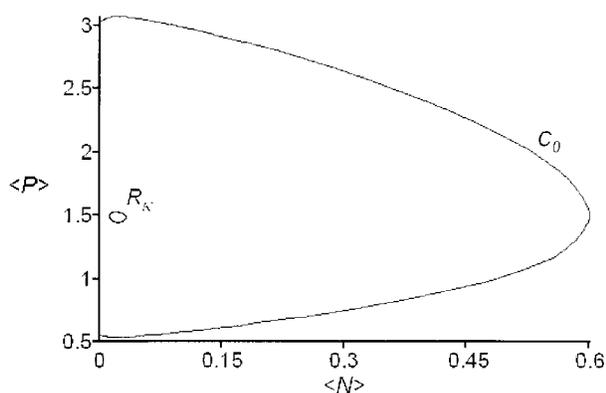


Figure 5: Unstable homogeneous cycle C_0 and stable heterogeneous dynamics R_κ generated by $\kappa = 0.5$, presented on the plane of spatially averaged population densities.

different spatially explicit model had shown that a predator-prey system based on the same prey taxis mechanism as here generated ratio-dependence on a large scale, although the local interactions were modeled with simple prey-dependent trophic functions either of the Lotka-Volterra type (Arditi et al. 2001) or of Holling Type II (Sapoukhina 2002). These earlier results, together with the fact that our present prey-dependent spatially explicit model also resolves the paradox, corroborates the conjecture of Arditi and Ginzburg (1989) that the ratio-dependent model is a means of representing heterogeneity in an implicit way.

The proposed model overcomes an existing controversy in the interpretation of the role of spatial activity of natural enemies in pest population depression and regulation. On the one hand, the model demonstrates that a natural enemy with a pronounced aggregated attack depresses the pest density to a very low level on which, furthermore, it can persist because of the emergence of a spatially heterogeneous regime (fig. 6a–6d). This confirms the major conclusion that aggregation is the key to stability and successful control (Hassell and May 1973, 1974; May 1978). On the other hand, Murdoch and Stewart-Oaten (1989) had pointed out that the stabilizing effect of aggregation largely disappeared when the natural enemy was allowed to redistribute within a generation. They concluded that aggregation is typically a destabilizing process. Also, studying the effect of habitat fragmentation on the stability of predator-prey interactions, Kareiva (1987) emphasized that patchiness promoted aphid outbreaks because it interfered with the nonrandom searching behavior of ladybird predators. We have shown in turn how the degree of depression of pest abundance depends on the taxis coefficient of a potential control agent. A low sensitivity of

predators to the heterogeneity of pest density does not affect the dynamics qualitatively, but if it exceeds a certain bifurcation value, it promotes persistence of the interacting populations, which is observed in a rather wide range of the taxis coefficient (fig. 4). Further increase of κ is followed by a slight growth of both pest and predator population densities. Moreover, after $\kappa \approx 0.6$, the amplitude of pest fluctuations increases (fig. 4a) because of the development of chaotic dynamics with pronounced outbreaks (see example in fig. 6e, 6f). This implies that a very high taxis coefficient destroys the stability of pest-predator interactions. In conclusion, the different model properties in different ranges of the taxis coefficient reconcile divergent theoretical statements and field observations of various authors (see also Hawkins et al. 1993; Lynch et al. 1998).

Regarding the ability to move actively, it is interesting to note that most biological control practitioners consider it to be one of the most important attributes of an effective natural enemy (Nechols and Obrycki 1989). The success of biological control is known to depend on the behavioral responses of the natural enemy to prey density variations—first of all, on those that are related to active movement (Viktorov 1975; Hassell and Godfray 1992; Waage and Mills 1992). The proposed model shows that the effectiveness of a predator depends on its power to follow prey dispersal. The model suggests that a certain degree of predator nonrandom mobility is necessary to stabilize the pest density at a desirably low level. However, with increasing taxis coefficient, a growth of pest abundance is observed (fig. 4). This is also confirmed by the practice of classical biological control. A successful natural enemy should remain in the pest colony until almost complete pest eradication (Bondarenko and Asiakin 1975; Waage and Mills 1992). If it is an extremely active migrant, the predator easily leaves the locations of low pest density, saving the pest from local extinction (Gurianova 1984; Murdoch et al. 1985). Therefore, a too high migration activity is considered as an undesirable attribute of a potential biological control agent (Izhevsky 1990; Crawley 1997). The observed increase of both species abundances with an increase of the taxis coefficient (fig. 4) means that predators, reacting faster to prey concentrations, increase their individual ration and fecundity and at the same time preserve the prey. The influence of predator movement activity on the ability to overcome prey scarcity is also discussed by Basset et al. (1997), Govorukhin et al. (1999, 2000), Sapoukhina and Tyutyunov (2000), and Arditi et al. (2001). In the context of biological control, these results imply that there is an optimal interval for the intensity of directed movement: both too low and too high values of the taxis coefficient diminish predator efficiency at controlling the pest.

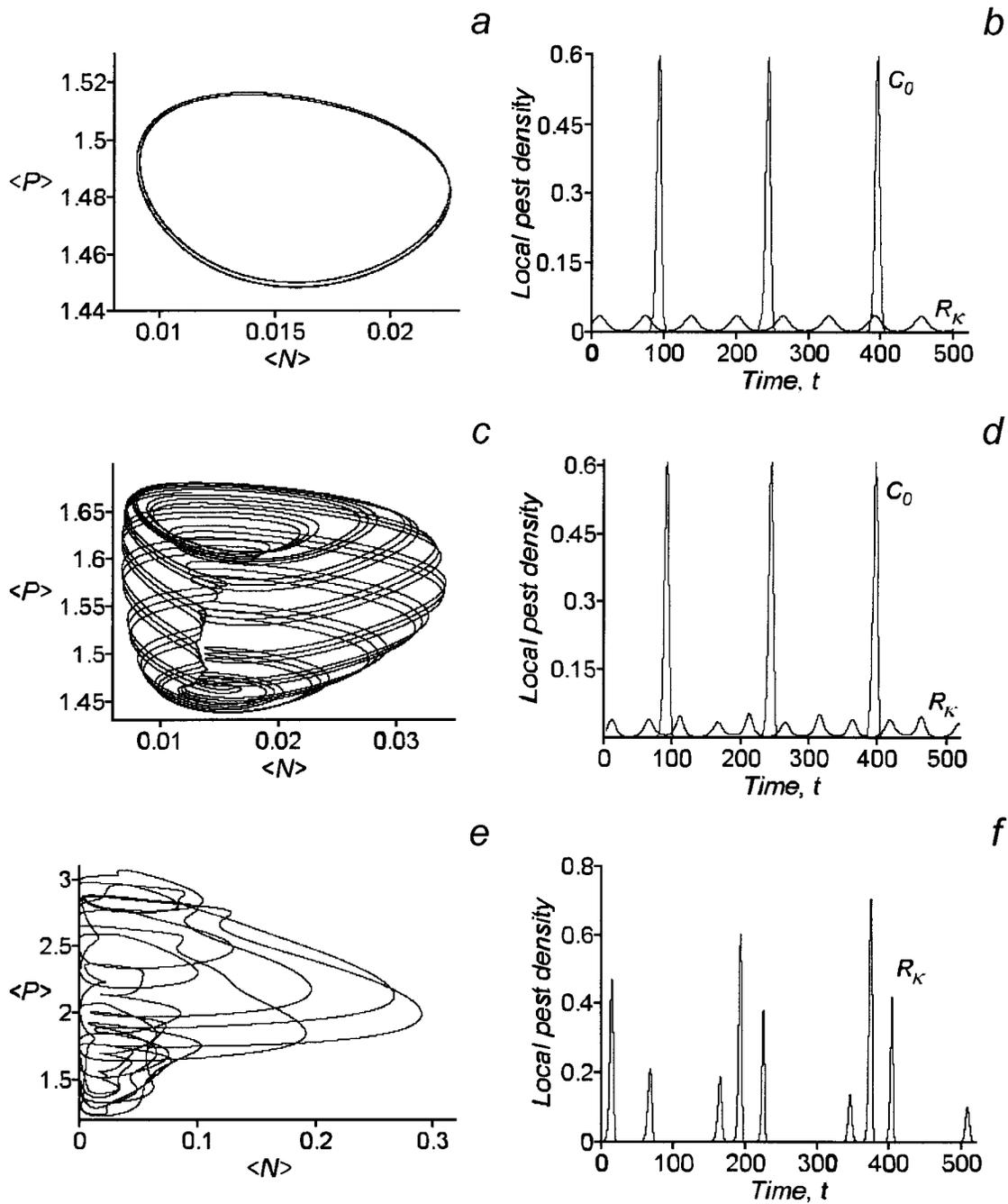


Figure 6: Phase trajectories of the spatially heterogeneous dynamics R_κ , presented on the $(\langle N \rangle, \langle P \rangle)$ plane, and local fluctuations (at point $x = 1.7$) of the pest density in R_κ in comparison with the homogeneous dynamics C_0 ; (a, b) $\kappa = 0.5$, R_κ is periodic; (c, d) $\kappa = 1$, R_κ is quasi-periodic; (e, f) $\kappa = 1.5$, R_κ is chaotic.

The proposed approach might be applicable to cases of biological control where the response of a natural enemy to the gradient of pest density is marked (e.g., an aphid-ladybird system). Observed at the level of the population,

this pattern of movement is known to be mediated at the level of the individual (Flierl et al. 1999). There are various possible mechanisms directing the long-term movements of predator density toward locations of increased resource

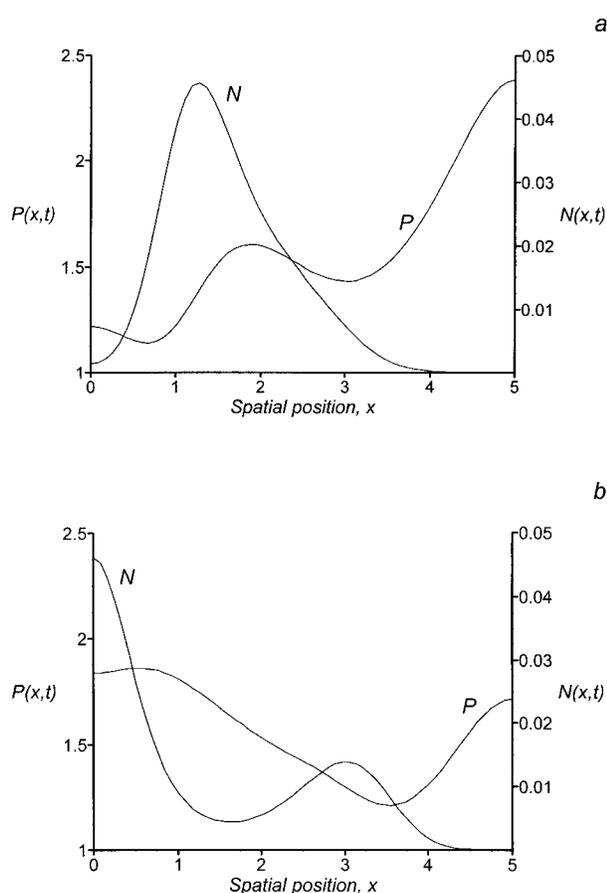


Figure 7: Examples of spatial patterns generated by prey taxis, shown at two different instants: (a) $t = 20$; (b) $t = 90$. Parameters are $\kappa = 1$, $L = 5$, $a = 0.7$, $h = 2.857$, $\mu = 0.01$, $\delta_N = 0.01$, $\delta_p = 0.6$, and $\delta_e = 0.001$.

availability that can be classified as follows (Flierl et al. 1999): a direct response to the gradient of prey distribution, which can be determined by various cues (Rotheray 1979; Godfray 1994; Dixon 2000); adaptive probing allowing to gain the information on the larger scale (Berg and Brown 1972); some forms of social behavior that involve sharing the information about neighboring localities; and area-restricted search. Studying the detailed quantification of the individual-level movements of the ladybird *Coccinella septempunctata* preying on the goldenrod aphid (*Urolencon nigroturbeculatum*), Kareiva and Odell (1987) and the later modeling developments by Grünbaum (1997, 1998) have shown that area-restricted search of individual predators determined by the turning rate depending on predator satiety leads to prey taxis of the ladybird swarm. Even though at the individual level the ladybird response to heterogeneity of aphid density is extremely weak, the

cumulative effect of many individuals produces strong aggregation in areas of high prey density (Ives et al. 1993).

The obtained results on the effects of prey taxis on the predator-prey dynamics agree well with known dynamical properties of aphid-ladybird systems. Considering a slow-fast continuum in the life-history parameters of coccidophagous and aphidophagous ladybirds, Dixon (2000) indicates that coccidophagous ladybirds have been more successful biological control agents than aphidophagous species, which have much faster rates of all life-history processes, including movement activity characteristics. Numerous observations have shown that, although being potentially effective biocontrol agents, ladybirds often fail to depress the pest population because of their very active nonrandom searching behavior (Kareiva 1987; Dixon 2000). Regarding this problem, a clear example in which the controlling efficiency of ladybirds has been improved by reducing the spatial activity is provided by Ferran et al. (1998), who have obtained a flightless strain of the ladybird *Harmonia axyridis*, which is now produced commercially as a biocontrol agent.

In summary, the proposed approach for modeling prey taxis provides an adequate description and explains successful cases of biological control. The explicit representation of spatiotemporal dynamics helps understand how the natural enemy is able to keep the temporal and local variability of the pest low enough to avoid economically damageable outbreaks. Beyond biological control, the model is potentially relevant to many systems since it accounts for various stabilizing mechanisms (aggregative response, local extinctions, spatial heterogeneity, and partial refuges). In fact, it provides an explanation for predators and prey to be able to coexist stably at “any” density for reasons other than prey self-limitation. In other words, it can demonstrate stable top-down control in trophic systems.

Acknowledgments

We are grateful for the thoughtful comments of anonymous reviewers. The research was partially supported by the Russian Foundation for Basic Research (grants 98-01-00908 and 00-01-00725), the U.S. Civilian Research and Development Foundation (grant REC-004), and the French Ministry of Agriculture. This work is a contribution of the French COREV research network.

APPENDIX

Local Stability Analysis

There are three spatially homogeneous equilibria in model (3)-(4):

$$(N_0^*, P_0^*, v_0^*) = (0, 0, 0), \quad (\text{A1})$$

corresponding to extinction of both populations;

$$(N_1^*, P_1^*, v_1^*) = (1, 0, 0), \quad (\text{A2})$$

corresponding to predator extinction; and

$$(N_2^*, P_2^*, v_2^*) = \left[\frac{\mu}{a(1-\mu h)}, \frac{a(1-\mu h) - \mu}{a^2(1-\mu h)^2}, 0 \right], \quad (\text{A3})$$

positive for $a > \mu/(1-\mu h) > 0$, corresponding to coexistence of prey and predators. Because of the boundary conditions (4) and the well-known dynamic properties of the corresponding nonspatial model, one can conclude that the trivial equilibrium (A1) is a saddle point and that equilibrium (A2) is stable for $a \leq \mu/(1-\mu h)$.

Linearizing system (3) about equilibrium (A3), we obtain

$$\begin{aligned} \frac{\partial n}{\partial t} &= a_{11}n + a_{12}p + \delta_N \frac{\partial^2 n}{\partial x^2}, \\ \frac{\partial p}{\partial t} &= a_{21}n - P_2^* \frac{\partial v}{\partial x} + \delta_P \frac{\partial^2 p}{\partial x^2}, \\ \frac{\partial v}{\partial t} &= \kappa \frac{\partial n}{\partial x} + \delta_v \frac{\partial^2 v}{\partial x^2}, \end{aligned} \quad (\text{A4})$$

where $n(x, t)$, $p(x, t)$, and $v(x, t)$ are small spatial perturbations of equilibrium (A3); a_{ij} ($i, j = 1, 2$) are the elements of the Jacobian matrix \mathbf{J} at the equilibrium:

$$\mathbf{J} \Big|_{N_2^*, P_2^*} = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} = \begin{bmatrix} \mu h - \frac{\mu(1+\mu h)}{a(1-\mu h)} & -\mu \\ 1 - \mu h - \frac{\mu}{a} & 0 \end{bmatrix}.$$

We look for a Fourier series solution of equilibrium (A4):

$$\begin{aligned} n(x, t) &= \sum_k n_k e^{\lambda t} \cos kx, \\ p(x, t) &= \sum_k p_k e^{\lambda t} \cos kx, \\ v(x, t) &= \sum_k v_k e^{\lambda t} \sin kx, \end{aligned} \quad (\text{A5})$$

where $k = n\pi/L$ is the wave number for the mode $n = 0, \pm 1, \pm 2, \dots$. Obviously, solution (A5) of system (A4) satisfies the boundary conditions (4). Substituting perturbations (A5) into system (A4) and canceling $e^{\lambda t}$, we obtain the eigenvalues $\lambda(k)$ as functions of the wave number k as the roots of

$$\lambda^3 + p(k^2)\lambda^2 + q(k^2)\lambda + r(k^2) = 0,$$

where

$$p(k^2) = k^2(\delta_N + \delta_P + \delta_v) - a_{11},$$

$$q(k^2) = k^4(\delta_v\delta_N + \delta_P\delta_N + \delta_v\delta_P) - k^2 a_{11}(\delta_P + \delta_v) + a_{21}\mu,$$

$$r(k^2) = k^4\delta_v\delta_P(k^2\delta_N - a_{11}) + \mu k^2(a_{21}\delta_v + P_2^*\kappa).$$

Let us impose the constraint that equilibrium (A3) is stable in the absence of diffusion and advection, that is, $\text{Re}\lambda(k^2 = 0) < 0$. In this case, the eigenvalues are the solutions of

$$\lambda^2 - a_{11}\lambda + a_{21}\mu = 0,$$

and linear stability of equilibrium (A3) is guaranteed if $a_{11} < 0$ and $a_{21} > 0$, that is,

$$\frac{\mu}{1-\mu h} < a < \frac{1+\mu h}{h(1-\mu h)}. \quad (\text{A6})$$

Otherwise, the steady state (A3) loses its stability: for smaller values of parameter a , the trivial equilibrium (A1) becomes stable, and for larger values, a homogeneous limit cycle arises around (A3).

Hence, analyzing the stability of the nontrivial equilibrium (A3) with respect to spatial perturbations, we further consider the parameter values satisfying equilibrium (A6). For the uniform solution (A3) to be stable with respect to spatial perturbations, we require $\text{Re}\lambda(k^2) < 0, \forall k^2 > 0$. The necessary and sufficient conditions for this to hold are the Routh-Hurwitz conditions:

$$\begin{cases} p(k^2) > 0, \\ r(k^2) > 0, \\ p(k^2)q(k^2) - r(k^2) > 0. \end{cases}$$

Note that $p(k^2)$ and $r(k^2)$ are positive if equilibrium (A6) is satisfied. Hence, $\forall k^2 > 0, \text{Re}\lambda(k^2) < 0 \Leftrightarrow p(k^2)q(k^2) - r(k^2) > 0$. Thus, the stability condition for the steady state (A3) is

$$\begin{aligned} 0 \leq \kappa < \frac{1}{P_2^*\mu} \left(\delta_N + \delta_P - \frac{a_{11}}{k^2} \right) \\ \times \left[(\delta_v + \delta_P)[(\delta_N + \delta_v)k^2 - a_{11}] + \frac{\mu a_{21}}{k^2} \right], \\ \forall k^2 > 0. \end{aligned}$$

This is condition (7). See the main text for interpretation.

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