=========================== **MATHEMATICS** ===========================

# Slow Taxis in a Predator–Prey Model

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Partial differential equations were first applied to the analysis of biological community dynamics in [3], and this approach has been widely developed [8, 9, 12]. For example, one of the possible predator–prey models can be reduced by suitable scaling to the following system of reaction–advection–diffusion equations:

$$\partial_t p + \text{div}\,[(p + P_e)\mathbf{v}] = \delta_p \Delta p, \quad \int_D p\,dx = 0; \quad (1)$$

$$\partial_t N = N(N_e - p - N) + \delta_N \Delta N. \quad (2)$$

Here, $\delta_p$ and $\delta_N$ are positive diffusion coefficients, $P_e > 0$ is the average predator density viewed as a parameter, $N_e = 1 - P_e$, $p$ is the predator density fluctuation, $P = P_e + p \geq 0$, and $N \geq 0$ is the prey density. The polynomial nonlinearity in (2) is taken from the classical Lotka–Volterra model: it describes local reproduction and mortality in the prey, while, for the predator, the contribution of these processes on the time scales under consideration is assumed to be negligible.

System (1), (2) is considered in a domain $\{(x, t): x \in D, t > 0\}$, where $D \in R^m$ ($m = 1, 2, 3$) is a bounded simply connected domain. On the boundary of $D$, we set the boundary conditions

$$\mathbf{n}\nabla N = \mathbf{n}\nabla p = \mathbf{n} \cdot \mathbf{v} = 0, \quad x \in \partial D, \quad (3)$$

which mean that the community habitat is closed.

The velocity $\mathbf{v}$ of predator advection depends on the migration mechanisms taken into account. One of such mechanisms is taxis, i.e., the orientation of individuals depending on the environmental properties, which are observed and estimated by them as benefits or threats (see, e.g., [2, 4]).

In a conventional taxis model, the advective velocity of migrants is expressed as a weighed sum of the gradients of the stimuli taken into account [1, 12]. For example, we may set in (1)

$$\mathbf{v} = \kappa\nabla N, \quad \kappa = \text{const} > 0. \quad (4)$$

The hypothesis (4) assumes an instantaneous orientation of predators (fast taxis), which restricts the range of its applicability. It is natural to expect that, in the general case, the stimuli distribution determines the acceleration rather than the velocity of advection (slow taxis). Such a model was formulated in [5]. However, it was not analyzed, and the author made use of approximation (4) at once.

We consider a simplified model of slow taxis, assuming that the environmental resistance to motion and the convective acceleration are small. Thus, we deal with problem (1)–(3) supplemented with the following equations and boundary conditions:

$$\partial_t \mathbf{v} = \kappa\nabla N + \delta_v \Delta \mathbf{v}, \quad \mathbf{n} \times \text{rot}\mathbf{v} = 0, \quad x \in \partial D. \quad (5)$$

The term $\delta_v \Delta \mathbf{v}$ ($\delta_v > 0$) describes the matching of velocities caused, for example, by shoaling effects.

Let FT denote problem (1)–(4) and ST denote the problem defined by (1)–(3) and (5). In the ST model, the environmental resistance to the motion of predators can be taken into account by adding the term $-\nu\mathbf{v}$ ($\nu > 0$) to the right-hand side of (5). The fast-taxis equation (4) arises in the principal asymptotic approximation of the FT problem as $\kappa \to \infty$ and $\nu \to \infty$, so that $\kappa/\nu$ remains bounded.

Both the FT and ST problems have two homogeneous equilibrium regimes, denoted by $E$ and $E_0$:

$$E: \mathbf{v} \equiv p \equiv 0, \; N \equiv N_e; \quad E_0: N \equiv \mathbf{v} \equiv p \equiv 0.$$

A homogeneous equilibrium in the community (i.e., a situation when the equilibrium value of $N$ is positive) is possible as long as $P_e < 1$. The equilibrium regime $E_0$ corresponds to prey population extinction caused by predation, i.e., to community collapse.

In both the FT and ST problems, the equilibrium $E$ collides with $E_0$ when $P_e = 1$. In this case, $E_0$ becomes stable and preserves this property for all $P_e > 1$. However, $E$ is stable for all $P_e < 1$ in the FT problem, while

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this is not true for the ST problem. Specifically, on the interval $(0, 1)$, a positive single-valued function $\kappa^*(P_e)$ is defined such that the equilibrium $E$ is stable if $\kappa < \kappa^*(P_e)$ $[P_e \in (0, 1)]$ and is unstable otherwise. The neutral curve $\Gamma = \{\kappa = \kappa^*(P_e)\}$ corresponds to oscillatory instability: one conjugate pair of resolvent's simple poles lies on the imaginary axis; here, the ranks of the corresponding spectral projectors are equal to the multiplicity of the minimum nonzero eigenvalue of the Neumann problem for the Laplace operator in $D$.

The function $\kappa^*(P_e)$ is bounded from below by a positive number $\kappa_*^*$ and is unbounded from above: $\kappa^*(P_e) \to \infty$ as $P_e \to 1$ or $P_e \to 0$. The inverse $P_e^*(\kappa)$ of $\kappa^*$ is two-valued: $P_e^*(\kappa) = (P_u, P_s)$, where $0 < P_u < P_s < 1$ and $\kappa > \kappa_*^*$.

Thus, if $\kappa > \kappa_*^*$ and the parameter $P_e$ increases through the critical value $P_u$, then, under the well-known nondegeneracy conditions, a limit cycle $C$ bifurcates from $E$. The corresponding periodic solutions to the ST problem are the velocity and density waves of the maximum spatial scale. In particular, if $D$ is a parallelepiped in $R^3$, then the cycle $C$ bifurcates on the invariant subspace of triplets $(\mathbf{v}, p, N)$ depending only on one coordinate $x_j$; moreover, the $Ox_j$ direction is parallel to the largest side of $D$, and the cycle $C$ is associated with the nonlinear traveling waves of maximum length.

The extension of $C$ in the parameter $P_e$ to the region where $P_e > P_u$ and subsequent transitions in the one-dimensional ST problem have been studied numerically. We employed the Galerkin method (10 and 20 harmonics) and the method of lines (the spatial derivatives were approximated by central differences on a 50-point grid). The computations were continued until stabilization of the regime. Both methods produced similar results.

The transition scenario was found to become more complex with increasing $\kappa/\delta$, where $\delta$ is the characteristic value of the diffusion coefficients. The most complex scenario observed was as follows (see Fig. 1): the equilibrium $E \to$ periodic regime $C \to$ doubled periodic regime $\to$ quasi-periodic regime $\to$ chaotic regime $\to$ quasi-periodic regime $\to$ periodic regime $\to$ the equilibrium $E_0$. As $\kappa/\delta$ decreases, the transition scenarios became simpler down to the most primitive: $E \to E_0$.

Furthermore, for large enough $\kappa/\delta$, a stable nonequilibrium regime was observed for all $P_e \in (P_u, P_s^*)$, where $P_s^* > 1$ (see Fig. 2). The curves presented in the figure were obtained from fixed initial data. Figure 2 shows that a nonequilibrium regime is preferable to equilibrium for both species if the resource deficiency is sufficiently great (i.e., $P_e$ is close to or greater than 1): both the average prey population size $\langle\langle N\rangle\rangle$ and the
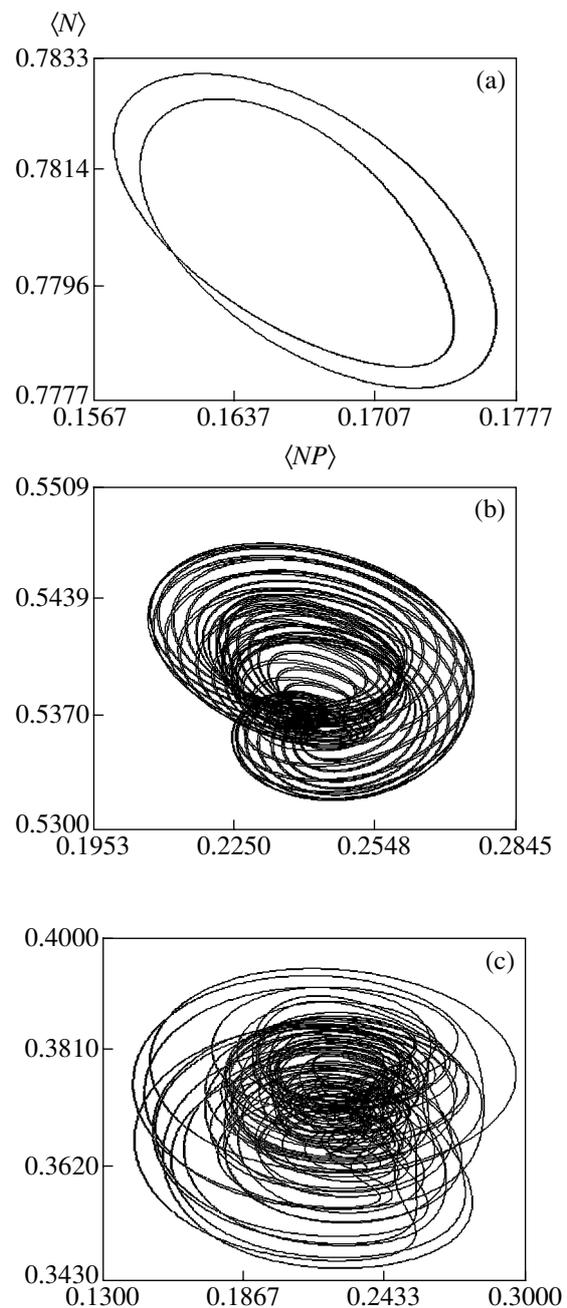
**Fig. 1.** Projections of the phase trajectory onto the plane $(\langle NP\rangle, \langle N\rangle)$, where $P = P_e + p$. Angular brackets denote spatial averaging: $\langle f\rangle = |D|^{-1}\int_D f\,dx$. The parameter values are $\kappa = 6$, $\delta_v = 0.00001$, $\delta_p = 0.2$, and $\delta_N = 0.05$. (a) Doubled periodic regime with $P_e = 0.22$, (b) quasi-periodic regime with $P_e = 0.47$, and (c) chaotic regime with $P_e = 0.65$.

average prey consumption by predators $\langle\langle NP\rangle\rangle$ are greater than their equilibrium values.

Thus, we conclude that inhomogeneity of a trophic community may arise and develop in a homogeneous environment dynamically, under the control of taxis
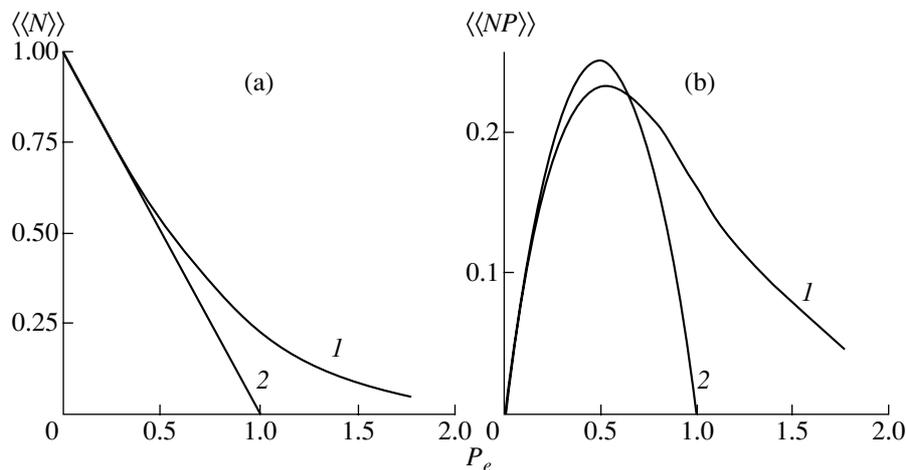
**Fig. 2.** Spatiotemporal averages (a) $\langle\langle N\rangle\rangle$ and (b) $\langle\langle NP\rangle\rangle$ as functions of $P_e$. Here, $\langle\langle f\rangle\rangle = \lim \frac{1}{T}\int_0^T \langle f\rangle dt$ as $T \to \infty$; *1*, observed averages, *2*, averages in homogeneous equilibrium. The parameter values are $\kappa = 2$, $\delta_v = 0.00001$, $\delta_p = 0.05$, and $\delta_N = 0.05$.

and/or other behavioral mechanisms. An adaptive role of the inhomogeneity was observed in experiments (see, e.g., [6, 10, 11]) and in the analysis of mathematical models based on other principles (see, e.g., a recent paper [7]). However, the model defined by (1)–(3) and (5) does not require the hypothesis of global knowledge that was introduced in [7].

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