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Research article

Short-wave signal versus the indirect prey-taxis

Andrey Morgulis[1,2,*] **and Karrar Malal**[1]

[1] I.I. Vorovich Institute of Mathematics, Mechanics & Computer Science, Southern Federal University, Rostov-on-Don, Russia

[2] Southern Mathematical Institute of Vladikavkaz Scientific Center of Russian Academy of Science, Vladikavkaz, Russia

* **Correspondence:** Email: abmorgulis@sfedu.ru, morgulisandrey@gmail.com.

Abstract: We address short-wave asymptotics for one class of quasi-linear second-order PDE's systems involving the cross-diffusion described by the so-called Patlak-Keller–Segel law. It is common to employ these equations for modeling the predator–prey community with the prey–taxis, which is the interaction of two species of particles or cells through which the predator species is capable of moving directionally while searching for the prey species. However, we suppose the predators to be sensitive not to the prey density but to another cue field produced by the prey. Additionally, producing the cue is assumed to be sensitive to the intensity of an external field, which is independent from the community state and mimics the environmental inhomogeneity due to natural or artificial reasons. This is what we call the "external signal". We assume that the external signal takes a general short-wave form and construct a formal asymptotic expansion for the short-wave solutions with no restrictions on the spatial dimension or kinetics of inter- or intra-specific reactions modulo solving a hierarchy of the so-called slow systems. With no special assumption, we explicitly write down both the leading term in the asymptotics and the leading slow system, which governs the slow evolution of the amplitude of the leading term. Further, we apply the leading approximation to study the stability or instability induced by the external signal following Kapitza's theory for the upside-down pendulum. Applying the general results to some special classes of external signals, we construct examples of suppressing the taxical transport, examples of the robustness of the species equilibrium to the signal up to a very strong stabilization, and, oppositely, destabilization and blurring the borderline in the parametric space between the areas of stability and instability of this equilibrium.

Keywords: Patlak–Keller–Segel systems; prey–taxis; averaging; homogenization; short-wave asymptotics; induced stability
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1. Introduction and problem setting

This study examines the interactions of two different species, conditionally speaking, predators and prey, each composed of indistinguishable particles. Diffusion, as well as the ability of predators to generate a macroscopic mass flow while searching for prey, together determine the spatial distribution of species. The latter phenomenon is called "prey–taxis," following article [1], which arguably pioneered its study. A widely accepted (though not the only) model for taxis is the Patlak–Keller–Segel (PKS) model. It posits that tactic flow is parallel to the intensity gradient of a cue field that guides predators in their search for prey. Often (though not always), the cue is the prey concentration. The prey-taxis using a different cue is called indirect. In either case, adding the equation governing the cue field (if necessary) results in a system of second-order partial differential equations that describes the mass distribution of both species. It is also typical to consider the mass sources of both species, corresponding to the local kinetics of the system, driven by inter- and intra-specific responses. As a rule, such models are special cases of evolutionary systems considered by H. Amann [2].

Amann's work provides a general mathematical framework for studying the qualitative features of PKS systems, such as blow-up, the extinction of one or both species, or an emergency of a particular regime of their coexistence, sometimes revealing a rather complex spatiotemporal pattern; see [3–6]. A significant volume of research explores formation of such structures due to chains of bifurcations. In any case, the scenarios they describe typically begin with the instability of the simplest regime, such as the equilibrium of species with constant density (homogeneous equilibrium). In this context, the instability is the appearance or disappearance of exponentially growing modes of small perturbations caused by changing some parameters of the system. We will return to the discussion of this issue in Section 4.1.

Applying the bifurcation theory to systems with taxis seems to be pioneered by work [7] that addressed the traveling waves driven by an autotaxis. Next, [8–10] studied several scenarios of the onset of complex spatiotemporal patterns starting with the Poincare-Andronov-Hopf (PAH) bifurcation in the so-called slow taxis model; *cf.* Remark 1. Chakraborty et al. [11] continued studying the bifurcations in this kind of model with various kinetics, and, recently, it has been revisited [12]. The study [13] has addressed the direct PKS prey-taxis–that is, the one driven by the prey density. It has discovered the crucial dependence of the stability of the homogeneous equilibria on the system kinetics and the capability of prey-taxis for exerting the stabilizing effect. The instabilities followed by the emergency of complex spatio-temporal patterns nevertheless occur for certain kinetics; *cf.* [14,15]. It is worth mentioning that modeling more complex trophic chains also often uses PKS law for formalizing the interactions similar to prey-taxis. Several authors repeatedly emphasized their role in causing the instabilities and the heterogeneous pattern formation; e.g., [16, 17].

Tello & Wrozek [18] introduced the indirect prey-taxis model and studied the onset of the secondary steady regimes. Further studies [19, 20] continued exploring this kind of model and discovered a rich variety of the dynamical phenomena. Several articles treat allied models, which take into account the Alee effect [21], allow for more than one predator [22], or address the indirect pursuing-evading [23, 24]. In article [25], it has been noted that, under certain conditions, predator–prey systems with indirect and slow taxis are equivalent. In particular, this equivalence holds for the systems considered in [8, 9].

Most of the literature addresses the PKS systems possessing translational invariance with respect to time and space, although natural objects are always heterogeneous to some extent due to natural

or artificial causes. Of course, the influence of heterogeneity may be insignificant for the phenomena under consideration, but this is not always the case. For example, anthropogenic acoustic noise has a disorienting effect on marine mammals [26], thermal fronts and mesoscale ocean eddies affect the distribution of fish populations [27–29], and the emergence of an alternative food source can affect the dynamics of omnivorous animals [30].

When an inhomogeneity excites a process on a scale that differs sharply from the other characteristic scales of the system, an effective way to take it into account is to introduce a model with small parameters and then study it using asymptotic methods, as is done in the recent works *cf.* [31–35], which employ two different time scales. However, it is no less logical to consider distributed small-scale inhomogeneities defined as a known field [36–38]. In such a case, the issue naturally arises of the so-called induced stability or instability, or, in other words, of a change in the stability of the system as a result of an external influence under equal other conditions: For example, a comparison of the forced and free dynamics, all other things being equal, showing that one of them exhibits a stable regime, while the other does not. A classic example of induced stability is the inverted pendulum. The nonlinear theory of this phenomenon given by P. Kapitza is in fact based on the high-frequency asymptotics of nonlinear oscillations [39]. The approach of this theory has got a wide generalization, in particular, to the constrained dynamical systems [40, 41], and has repeatedly confirmed its effectiveness upon studying the thermogravitational convection [42, 43], the dynamics of interfaces and inclusions in fluid [44, 45], and the dynamics of elastic rods [46, 47]. However, its implementation for predator–prey systems with taxis and more general Amann–type systems with short-wave/high-frequency inhomogeneities has not received due attention, although such an analysis could be useful for assessing the influence of inhomogeneities on the change in the stability boundaries of the system and the transition to the formation of spatiotemporal patterns, and suitable asymptotics seem to be quite accessible to homogenization methods and multiple scales expansions; see, for example, [48]. To some extent, articles [36–38] contribute to filling this gap. Namely, articles [37, 38] study the induced stability in a system with direct predator–prey taxis, where the cues are the prey density and a short-wave external signal supplied independently of the system state. Article [36] addresses the same issue for a predator–prey system with the so-called "slow taxis", see Remark 1. In the present article, we consider a multidimensional problem with indirect taxis, general kinetics, and an arbitrary short-wave external signal. We suppose the cue to be not the prey density but the field induced by them, and the short-wave external signal to be influencing the cue induction as well. We construct a formal asymptotic expansion for the short-wave solutions modulo solving a hierarchy of the so-called slow systems; see the end of this section for additional details. Based on the leading term in the formal short-wave asymptotics, we examine the induced stability for this system and shed some light on the effects of the external signal on mass transfer and pattern formation.

Remark 1. In particular, the aforementioned equivalence of the slow and indirect taxis models holds true for the system considered in [36]. In this sense, the present paper generalizes the results of article [36], which addresses a model under rather strong restrictions; namely, only one spatial variable, a conservative predator, logistic prey, Lotka–Volterra kinetics of the species interactions, and the external signal in the form of a traveling wave

1.1. Formal set-up

The general predator–prey system with indirect taxis and an external signal has the form:

$$p_t + \operatorname{div}(\chi p \nabla s - \delta_1 \nabla p) = p f(p,q), \tag{1.1}$$

$$q_t - \operatorname{div}(\mu \nabla q) = q g(p,q), \tag{1.2}$$

$$s_t - \operatorname{div}(\delta_2 \nabla s) = \kappa_1 h + \kappa q - \nu s. \tag{1.3}$$

Here the distribution densities of predators and prey, $p = p(x,t) \geq 0$, $q = q(x,t) \geq 0$, are unknown functions of the spatiotemporal coordinates, $x \in \mathbb{R}^n$, $t > 0$. Given functions, f and g, determine the densities of the mass sources—that is, the local kinetics of the system. We assume them to be analytic in the cone $\{p > 0, q > 0\}$ and continuous up to its boundary, except for the origin. Within this cone, Eq (1.1) determines the predator balance through local kinetics, diffusion, and PKS taxis induced by a cue field of intensity $s = s(x,t)$, where the coefficient $\chi = \text{const} > 0$ measures the predator's sensing to the cue.

The additional equation (1.3) regards the cue field intensity. It shows that there is an external field, the intensity of which is determined by the known function $h = h(x,t)$, and this external signal influences the cue production by the prey. Hence, the external signal contributes to the PKS flow not directly, but through exerting an effect on the cue field induction. Additionally, the decay of the cue under the influence of the environment is taken into account. The coefficients $\nu = \text{const} > 0$, $\kappa = \text{const} > 0$ denote the rates of the cue decay and reproduction, respectively, and coefficient $\kappa_1 = \text{const} > 0$ measures the sensing of the cue reproduction to the external signal. The diffusion coefficients of predators, cue, and prey are denoted as $\delta_1 = \text{const} > 0$, $\delta_2 = \text{const} > 0$, and $\mu = \text{const} > 0$.

In the following discussion, we consider the system (1.1)–(1.3) as dimensionless and assume that the following equalities are satisfied:

$$\chi = 1,\ \kappa_1 = 1,\ \mu = 1, \tag{1.4}$$

$$g(0,q) \to 1,\ q \to +0, \quad g(0,1) = 0, \quad g_p(p,1) \to -1,\ p \to +0. \tag{1.5}$$

These assumptions are satisfied with appropriate scaling and therefore do not cause a loss in generality. In more detail: The transformation of the dimensional form of system (1.1)–(1.3) into a dimensionless form consists of the substitution

$$\check{x} = Lx,\ \check{t} = Tt,\ \check{p} = pP, \check{q} = qQ,\ s = \check{s}S,\ h = \check{h}H,$$

where $\check{z}$ denotes the dimensional version of variable z, and the positive quantities L, T, P, Q, S, H are the characteristic scales of the variables $\check{x}, \check{t}, \check{p}, \check{q}, \check{s}, \check{h}$ as yet undefined. Hence, the general dimensionless system (1.1)–(1.3) has the form

$$PT^{-1} p_t + PL^{-1} \operatorname{div}(\check{\chi} p S L^{-1} \nabla s - \check{\delta}_1 L^{-1} \nabla p) = P p \check{f}(Pp, Qq),$$

$$QT^{-1} q_t - QL^{-1} \operatorname{div}(\check{\mu} L^{-1} \nabla q) = Q q \check{g}(Pp, Qq),$$

$$T^{-1} S\, s_t - L^{-1} S \operatorname{div}(\check{\delta}_2 L^{-1} \nabla s) = \check{\kappa}_1 H h + \check{\kappa} Q q - \check{\nu} S\, s.$$

In applications, function g often reads as $g_0(q) - p g_1(p,q)/q$, where function g_0 is positive in a right neighborhood of zero including zero itself and changes sign exactly once; at this, $g_1(p,q) > 0$ for

$p > 0, q > 0$, $\lim\limits_{p\to+0} g_1(p,q) > 0\ \forall\, q > 0$, and $g_{1p}(p,q) = O(1)$, $p \to +0$, $\forall\, q > 0$; *cf.* [49] or, for more detail, [50]. Therefore, suppose that $\exists\, q_1 > q_0 > 0$, such that

$$\check{g}(0,q) > 0\ \forall q \in [0,q_0), \quad \check{g}(0,q_0) = 0,\ \check{g}(0,q) < 0\ \forall\, q \in (q_0,q_1), \quad \lim_{p\to+0} \check{g}_p(p,1) < 0.$$

Then, by choosing Q first, then T, and then P, we satisfy the following conditions:

$$\check{g}(0,Q) = 0, \quad T \lim_{q\to+0} \check{g}(0,Qq) = 1, \quad PT \lim_{p\to+0} (\partial\check{g}/\partial\check{p})(Pp,Q) \to -1.$$

In particular, for Lotka–Volterra kinetics with the logistic reproduction of prey, the dimensionless expression for the function g has the form $g = 1 - q - p$. Next, we choose L first, then S, and then H in a way that the following equalities hold:

$$\mu = L^{-2}T\check{\mu} = 1, \quad \chi = L^{-2}S\check{\chi} = 1,\ \kappa_1 = \check{\kappa}_1 TH/S = 1.$$

In accordance with the above-stated goal of the study, we assume that

$$h = h(x,t,x/\delta,t/\delta), \quad \delta_1 = \mu_1\delta, \quad \delta_2 = \mu_2\delta, \tag{1.6}$$

where the number $\delta > 0$ is small, and the function $h = h(x,t,\xi,\tau)$ is C^∞-smooth on $\mathbb{R}^{n+1} \times \mathbb{R}^{n+1}$ and periodic in the coordinates $\xi_1,\dots,\xi_n,\tau$ with periods $\ell_1,\dots\ell_n,\ell_0$. We seek for a formal expansion

$$(p,q,s) = \sum_{k=0}^{K-1} (p_k,q_k,s_k)(x,t,\xi,\eta)\delta^k + O(\delta^K),\ \delta \to +0,\ K \in \mathbb{N}, \tag{1.7}$$

where the order of approximation, K, can be as high as one wishes, and the coefficients, p_k, q_k, s_k, are periodic in fast coordinates, $\xi_1,\dots,\xi_n,\tau$, with periods $\ell_1,\dots\ell_n,\ell_0$. This periodicity entails that each term is one order smaller than the preceding one.

Based on the two-scale expansions method, we formulate an iterative procedure that allows for constructing arbitrarily many terms of expansion (1.7). As usual, each step of two-scale expansion requires solving a couple of PDE systems; one of them is in fast variables, ξ,τ, only, while the other one is in the slow variables, x,t, only. Moreover, the solution to the former system must satisfy the periodicity conditions stated above. We show that the fast system arising at each step has a solution possessing the required periodicity, provided the slow system of the previous step has a solution, and resolving the slow system completes evaluating the corresponding coefficient in the asymptotic expansion. However, we refrain from proving the existence of solutions to the whole chain of slow systems. Although we are quite optimistic regarding it, it evidently should be the subject of a separate paper.

At the same time, we state explicitly the leading term and the leading slow system that ensures the existence of the next term. We reveal a class of very simple explicit solutions to the leading slow system called quasi-equilibria, for which we address the issue of the induced stability and instability relying on this leading approximation only. In this regard, we follow the widely accepted procedure dating back to Kapitza's inverted pendulum theory, the outcomes of which get additional reliability thanks to the possibility for constructing the higher-order approximations.

The article is organized as follows. In Section 2, we introduce some notation and auxiliary tools. In Section 3, we expose the leading approximation of the asymptotics, derive the so-called leading

slow system governing the leading approximation on average, and address several adjacent issues. The higher asymptotic approximations are addressed in Appendix B. The rest of Section 3 covers the following: (i) discussing the terms in the leading slow system through which the external signal affects the slow dynamics and their explicit expressions for some particular classes of the external signals; (ii) a class of very simple asymptotic solutions called quasi-equilibria; (iii) the linearization of the leading slow system around a general quasi-equilibrium and the particular classes of the external signals, which allow for expressing explicitly the terms through which the external signal exerts its effect on the structure of the linearized leading slow system. In Section 4, we address the stability and instability induced by the external signal. We start with introducing some specific terminology and then perform the linear stability analysis using the so-called normal modes. Furhermore, we formulate some criteria for the stability and instability in terms of the control parameters of the model, including the ones depending on the signal only. Based on this, we reveal effects of stabilization and destabilization due to the external signal. Section 5 exposes several conclusive remarks. For better dynamics of the presentation, we supplied several assertions with the proofs' sketches only and moved the detailed proofs to Appendix A. Also, we set Appendix C that contains some details of the analysis presented in Section 4.

2. Auxiliaries

Let $D_{x,t} \stackrel{\text{def}}{=} \{(x,t) \in \mathbb{R}^{n+1} : \ x \in \Omega,\ t \in (t_0,t_1)\}$, where $t_0 \le 0 < t_1$ and Ω is a domain in $\mathbb{R}^n$ or an n-dimensional torus. In what follows, all considered functions of the variables (x,t,ξ,τ) are assumed to be periodic and square-summable in the fast coordinates $\xi_1,\dots,\xi_n,\tau$ with periods $\ell_1,\dots,\ell_n,\ell_0$ for arbitrarily fixed slow variables $(x,t) \in D_{x,t}$. Exceptions to this rule are stipulated separately. We define and denote the operations and operators of full and partial averaging as follows:

$$(Mf)(x,t) \stackrel{\text{def}}{=} \langle f\rangle(x,t) \stackrel{\text{def}}{=} \lim_{L\to\infty} \tfrac{1}{(2L)^{n+1}} \int\limits_{(-L,L)^{n+1}} f(x,t,\xi,\tau)\,d\xi d\tau, \tag{2.1}$$

$$(M^{\xi}f)(x,t,\tau) \stackrel{\text{def}}{=} \langle f\rangle^{\xi}(x,t,\tau) \stackrel{\text{def}}{=} \lim_{L\to\infty} \tfrac{1}{(2L)^{n}} \int\limits_{(-L,L)^{n}} f(x,t,\xi,\tau)\,d\xi, \tag{2.2}$$

$$(M^{\tau}f)(x,t,\xi) \stackrel{\text{def}}{=} \langle f\rangle^{\tau}(x,t,\xi) \stackrel{\text{def}}{=} \lim_{L\to\infty} \tfrac{1}{(2L)} \int\limits_{(-L,L)} f(x,t,\xi,\tau)\,d\tau. \tag{2.3}$$

Let $\mathbb{T}^{n+1}_{\xi,\tau}$ be the $n+1$-torus obtained by factorising $\mathbb{R}^{n+1}$ over the lattice $\mathbb{Z}^{n+1}_{\ell} \stackrel{\text{def}}{=} \ell_1\mathbb{Z}\times\ldots\times\ell_n\mathbb{Z}\times\ell_0\mathbb{Z}$. Taking into account the periodicity assumptions given above, we identify the fast coordinates ξ,τ with coordinates on the torus $\mathbb{T}^{n+1}_{\xi,\tau}$, and henceforth by a function of the variables (x,t,ξ,τ), we mean a function on $D_{x,t}\times\mathbb{T}^{n+1}_{\xi,\tau}$. Accordingly, the averaging operations introduced above allow for considering as operations over the functions on the torus and define operators M, M^{ξ}, M^{τ}, bounded in $\mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau})$, or more precisely, orthogonal projectors. In particular,

$$\operatorname{range}(\mathrm{I}-M) = \{u \in \mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau}) : \ \langle u\rangle = 0\} \stackrel{\text{def}}{=} \widetilde{\mathrm{L}}_2(\mathbb{T}^{n+1}_{\xi,\tau}).$$

Moreover, $M^{\xi}M^{\tau} = M^{\tau}M^{\xi} = M$ or, in other notation, $\langle\langle f\rangle^{\xi}\rangle^{\tau} = \langle\langle f\rangle^{\tau}\rangle^{\xi} = \langle f\rangle$.

For convenience of the subsequent presentation, we conformally change the standard metric in $\mathrm{L}_2(\mathbb{T})$, where $\mathbb{T}$ is a torus of arbitrary dimension; namely, we set $\|f\|_2 = \langle ff^*\rangle$, where the superscript * denotes complex conjugation and the angle brackets denote averaging over the torus.

Furthermore, the use of the notation for the fast variables as subscripts in the notation for a dependent variable indicates the partial derivative of this dependent variable with respect to the corresponding fast variables. Similarly, the use of the notation for fast variables as subscripts to denote a differential operation means that this operation must be performed by differentiating with respect to the fast variables while the slow variables are fixed. Differential operations with respect to the fast variables will also be denoted by a wide tilde above, for example, $\widetilde{\nabla}$.

Let $\epsilon > 0$. We set

$$\mathcal{H}_\epsilon \stackrel{\text{def}}{=} \partial_\tau - \epsilon\widetilde{\Delta}, \quad \mathcal{D} \stackrel{\text{def}}{=} (\widetilde{\nabla}\cdot\nabla + \nabla\cdot\widetilde{\nabla}); \tag{2.4}$$

$$\mathrm{H}^{s,2} \stackrel{\text{def}}{=} \{u \in \mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau}) : \sum(k^{2s}+m^4)|\hat{u}_{km}|^2 < \infty \quad (k,m) \in \mathbb{Z}^{n+1}_\ell\}; \tag{2.5}$$

$$\hat{u}_{k,m} = \langle u\mathrm{e}^*_{k,m}\rangle, \quad \mathrm{e}_{k,m} = \exp(i(k\tau + m\xi)), \quad (k,m) \in \mathbb{Z}^{n+1}_\ell.$$

Next, on the domain $\mathrm{H}^{1,2} \subset \mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau})$, we define the operator $\mathcal{H} = \mathcal{H}_\epsilon : \mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau}) \to \mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau})$ by expression (2.4). According to this definition, the operator $\mathcal{H}_\epsilon$ is densely defined and closed.

In what follows, by a spectral projector of an operator, we mean the projector onto the spectral subspace of this operator that commutes with it. The operator $\mathcal{H}_\epsilon$ is the heat operator on the torus; it is well-known that $\ker\mathcal{H}_\epsilon$ is its spectral subspace consisting of constant functions. In other words, no associated eigenfunctions correspond to the zero eigenvalue. The corresponding spectral projector is the averaging operator M. The right inverse operator $\mathcal{H}_\epsilon^{-1}$ is bounded from $\widetilde{\mathrm{L}}_2(\mathbb{T}^{n+1}_{\xi,\tau}) \to \widetilde{\mathrm{L}}_2(\mathbb{T}^{n+1}_{\xi,\tau})$. Thus, $\forall\, v \in \mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau}) : \langle v\rangle = 0$, the general solution to the equation $\mathcal{H}_\epsilon u = v$ on the torus $\mathbb{T}^{n+1}_{\xi,\tau}$ has the form: $u = \langle u\rangle + \mathcal{H}_\epsilon^{-1}v$, $\quad\langle\mathcal{H}_\epsilon^{-1}v\rangle = 0$, where $\langle u\rangle \in \ker\mathcal{H}_\epsilon$ is a free parameter.

Quite analogously to $\mathcal{H}_\epsilon$, the operators $\partial_\tau : \mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau}) \to \mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau})$ and $\widetilde{\Delta} : \mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau}) \to \mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau})$ are defined, and their right inverse operators, $\widetilde{\Delta}^{-1}v_1$ and $\widetilde{\partial_\tau}^{-1}v_1$, are bounded in the spaces $(\mathrm{I}-M^\xi)\mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau})$ and $(\mathrm{I}-M^\tau)\mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau})$, respectively. Thus, $\forall\, v_1 \in \mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau}) : M^\xi v_1 = 0$ and $\forall\, v_2 \in \mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau}) : M^\tau v_2 = 0$, the equations $\widetilde{\Delta}u_1 = v_1$, $\quad\partial_\tau u_2 = v_2$ have solutions, and any of them can be represented in the form $u_1 = M^\xi u_1 + \widetilde{\Delta}^{-1}v_1$, $u_2 = M^\tau u_2 + \partial_\tau{}^{-1}v_2$, where the functions $M^\xi u_1 \in \ker\widetilde{\Delta}^\xi$ and $M^\tau u_2 \in \ker\partial_\tau$ remain undetermined.

Definition 1. *For $\epsilon > 0$ and a vector function $\boldsymbol{w} \in \mathrm{C}^\infty\left(D_{x,t}\times\mathbb{T}^{n+1}_{\xi,\tau},\mathbb{R}^n\right)$, define the linear operator $\mathcal{L} = \mathcal{L}(\boldsymbol{w},\epsilon) : \mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau}) \to \mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau})$ acting on the domain $\mathrm{H}^{1,2}$ by mapping $u \mapsto \mathcal{H}_\epsilon u + \widetilde{\nabla}\cdot(u\boldsymbol{w})$.*

Lemma 1. *For all $(x,t) \in D_{x,t}$, the spectral projector P onto $\ker\mathcal{L}$ has the form*

$$P : u \mapsto \langle u\rangle\phi_*, \quad \phi_* \in \ker\mathcal{L}, \quad \langle\phi_*\rangle = 1.$$

Proof. Let $\mathcal{L}^*$ denote the operator adjoint to $\mathcal{L}$ and let $\mathcal{J} : \mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau}) \to \mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau})$ be the action of the inversion $(\xi,\tau) \mapsto (-\xi,-\tau)$. We set $\breve{\mathcal{L}}^* \stackrel{\text{def}}{=} \mathcal{J}\mathcal{L}^*\mathcal{J}$. Then $\ker\breve{\mathcal{L}}^* = \ker\mathcal{L}^*$ and

$$\breve{\mathcal{L}}^* : \varphi \mapsto (\partial_\tau + \boldsymbol{w}\widetilde{\nabla})\varphi - \epsilon\widetilde{\Delta}\varphi, \quad \forall\varphi \in \mathrm{H}^{1,2}.$$

Since the resolvents of the operators $\breve{\mathcal{L}}^*$, $\mathcal{L}^*$ and $\mathcal{L}$ are compact, their spectra are discrete and the solvability of the equations $\mathcal{L}^*u = f$ and $\mathcal{L}u = f$ obeys the Fredholm alternative. Therefore, $\dim\ker\mathcal{L} = \dim\ker\mathcal{L}^*$ and $\dim\operatorname{range}P = \dim\operatorname{range}P^*$, that is, the dimensions of the spectral subspaces also coincide.

The equation $(\partial_\tau + \boldsymbol{w}\widetilde{\nabla})\varphi - \epsilon\widetilde{\Delta}\varphi = 0$ is subject to the strong maximum and minimum principles (see, e.g., [51, 52]). Therefore any solution to it on the torus is constant. Thus,

$$\ker \breve{\mathcal{L}}^* = \ker \mathcal{L}^* = \{\varphi = \text{const}\}.$$

Suppose there is an associated eigenfunction to the zero eigenvalue of operator $\mathcal{L}^*$. Then there exists a solution to the equation on the torus $\mathcal{L}^*\psi = 1$, but this contradicts the one-sided minimum principle. Hence, dim range $P = 1$. Moreover, the assumption that $\langle u\rangle = 0$ for some $u \in \operatorname{Ker}\mathcal{L} \setminus \{0\}$ would imply the existence of a solution to the equation $\mathcal{L}^*\psi = 1 \neq 0$, which would contradict what we have proved above. Furthermore, directly by definition,

$$P^2 u = \langle Pu\rangle\phi_* = \langle u\rangle\langle\phi_*\rangle\phi_* = Pu$$

and $\mathcal{L}P = P\mathcal{L} = 0$. □

Remark 2. A useful by-product of Lemma 1 is the implicit mapping

$$\Phi(\cdot, \epsilon) : \boldsymbol{w} \mapsto \phi_*, \quad \phi_* \in \ker \mathcal{L}(\boldsymbol{w}, \epsilon), \quad \langle\phi_*\rangle = 1. \tag{2.6}$$

In view of Lemma 1, the right inverse operator $\mathcal{L}^{-1}(\boldsymbol{w}, \epsilon) : \widetilde{\mathrm{L}}_2(\mathbb{T}^{n+1}_{\xi,\tau}) \to \widetilde{\mathrm{L}}_2(\mathbb{T}^{n+1}_{\xi,\tau})$ is defined, and $\forall\, f \in \widetilde{\mathrm{L}}_2(\mathbb{T}^{n+1}_{\xi,\tau})$, the general solution to the equation $\mathcal{L}(\boldsymbol{w}, \epsilon)u = f$ has the form $u = \bar{u}\phi_* + \mathcal{L}^{-1}(\boldsymbol{w}, \epsilon)f$. Moreover $\langle u\rangle = \bar{u}$.

3. Asymptotics

Here we return to the system consisting of Eqs (1.1)–(1.3) with a general short-wave external signal (1.6). We discuss the leading term of the asymptotics (1.7) (it is of zero order in the small parameter), address the terms of orders 1 and 2, and clarify the conditions under which they do exist. As a result, we derive the so-called leading slow system, which governs the leading term on average. For addressing the higher-order terms, see Appendix II. To focus our considerations more precisely, we additionally assume that $\langle h\rangle = 0$.

Let f be some function in $D_{x,t} \times \mathbb{T}^{n+1}_{\xi,\tau}$, for example, one of the coefficients in expansion (1.7). We adopt the brief notation $\overline{f} = \langle f\rangle = Mf$, $\widetilde{f} = (\mathrm{I} - M)f$; in particular, $\tilde{h} = h$, $\bar{h} = 0$.

After introducing fast variables ξ, τ and taking into account convention (1.4), system (1.1)–(1.3) takes the following form:

$$\delta\left(\mathcal{H}_{\mu_1} p + \nabla \cdot (p\widetilde{\nabla}s) + \widetilde{\nabla}\cdot(p\nabla s)\right) + \widetilde{\nabla}\cdot(p\widetilde{\nabla}s) =$$
$$\delta^2\left(pf(p,q) - (\partial_t - \mu_1\mathcal{D})p - \nabla\cdot(p\nabla s) + \delta\mu_1\Delta p\right), \tag{3.1}$$
$$\left(-\widetilde{\Delta} + \delta\left(\partial_\tau - \mathcal{D}\right)\right)q = \delta^2\left(qg(p,q) - (\partial_t - \Delta)q\right), \tag{3.2}$$
$$(\mathcal{H}_{\mu_2} + \delta(\partial_t - \mu_2\mathcal{D}))s = \delta\left(\tilde{h} + \kappa q - \nu s + \delta\mu_2\Delta s\right). \tag{3.3}$$

Substitution of expansion (1.7) into Eqs (3.1)–(3.3) and grouping terms of order $k = 0, 1, 2, \ldots$ leads to a chain of equations for the coefficients of this expansion, which must be solved on $D_{x,t} \times \mathbb{T}^{n+1}_{\xi,\tau}$. To start with, we write down the systems of equations corresponding to $k = 0, 1, 2$.

For $k = 0$:

$$\widetilde{\nabla}\cdot(p_0\widetilde{\nabla}q_0)=0,\quad \widetilde{\Delta}q_0=0,\quad \mathcal{H}_{\mu_2}s_0=0. \tag{3.4}$$

For $k=1$:

$$\mathcal{L}(\boldsymbol{w}_0,\mu_1)p_0+\widetilde{\nabla}\cdot(p_1\widetilde{\nabla}s_0)=0,\quad \text{where } \boldsymbol{w}_0=\nabla s_0+\widetilde{\nabla}s_1, \tag{3.5}$$

$$\widetilde{\Delta}q_1=(\partial_\tau-\mathcal{D})\,q_0, \tag{3.6}$$

$$\mathcal{H}_{\mu_2}s_1=\tilde{h}+\kappa q_0-\nu s_0-(\partial_t-\mu_2\mathcal{D})s_0. \tag{3.7}$$

For $k=2$:

$$\mathcal{L}(\boldsymbol{w}_0,\mu_1)p_1+\widetilde{\nabla}\cdot(p_2\widetilde{\nabla}s_0)=\Psi,\ \text{where} \tag{3.8}$$

$$\Psi=p_0f_0-(\partial_t-\mu_1\mathcal{D})p_0-\nabla\cdot(p_0\boldsymbol{w}_0)-\widetilde{\nabla}\cdot(p_0\boldsymbol{w}_1),$$

$$\boldsymbol{w}_1=\widetilde{\nabla}s_2+\nabla s_1,\ f_0=f(p_0,q_0),$$

$$-\widetilde{\Delta}q_2=q_0g_0-(\partial_\tau-\mathcal{D})\,q_1-(\partial_t-\Delta)q_0,\ g_0=g(p_0,f_0), \tag{3.9}$$

$$\mathcal{H}_{\mu_2}s_2=\kappa q_1-\nu s_1-(\partial_t-\mu_2\mathcal{D})s_1+\mu_2\Delta s_0. \tag{3.10}$$

3.1. Leading approximation

Solutions to Eq (3.4) have the form:

$$s_0=\bar{s}(x,t),\quad q_0=\overline{q}_0^{\xi}(x,t,\tau) \tag{3.11}$$

while the function p_0 remains completely unknown.

In view of equalities (3.11), Eq (3.5) takes the form $\mathcal{L}(\boldsymbol{w}_0,\mu_1)p_0=0$. By Lemma 1,

$$p_0=\bar{p}\Phi(\boldsymbol{w}_0,\mu_1),\quad \bar{p}=\bar{p}(x,t), \tag{3.12}$$

where the map Φ was introduced by Remark 2. The function $\bar{p}$ plays the role of a constant of integration. The compatibility condition of Eq (3.6) has the form $\partial_\tau\overline{q}_0^{\xi}=0$, and therefore $q_0=\bar{q}$, that is, function $\bar{q}=\bar{q}(x,t)$ is another "constant of integration". The compatibility condition for Eq (3.7) reads

$$\bar{s}_t+\nu\bar{s}=\kappa\bar{q}. \tag{3.13}$$

If $q_0=\bar{q}$ and $s_0=\bar{s}$, where $\bar{s}$ is a solution to Eq (3.13), then system (3.6)–(3.7) has the solution

$$q_1=\overline{q}_1^{\xi}(x,t,\tau),\quad s_1=\tilde{s}_1+\bar{s}_1,\quad \tilde{s}_1=\mathcal{H}_{\mu_2}^{-1}\tilde{h}, \tag{3.14}$$

where functions $\bar{s}_1$ and $\overline{q}_1^{\xi}$ remain unknown.

Thus, in the leading approximation, the predators respond to the short-wave external signal by a short-wave parcel (3.12). Its slow amplitude, $\bar{p}=\bar{p}(x,t)$, represents the mean density of predators—that is, $\langle p_0\rangle=\bar{p}$. This parcel undergoes a twofold slow modulation by altering both the amplitude, $\bar{p}$, and the transport velocity field, $\boldsymbol{w}_0=\nabla\bar{s}+\widetilde{\nabla}\tilde{s}_1$. While its fast component, $\widetilde{\nabla}\tilde{s}_1$, is completely determined by the external signal, Eq (3.13) links the slow one, $\nabla\bar{s}$, to the leading approximation of the prey density, $\bar{q}$, which is not yet determined.

The system governing the slow modulation of the leading approximation follows from the compatibility conditions of system (3.8)–(3.10). Taking into account the identities $\widetilde{\nabla}s_0=0$ and $\widetilde{\nabla}q_1=0$, see (3.11) and (3.14), we write these conditions as

$$\bar{p}_t+\nabla\cdot\Big(\bar{p}\left(\nabla\bar{s}+\bar{\mathrm{V}}(\nabla\bar{s})\right)\Big)=\bar{p}\bar{f}(\bar{p},\bar{q},\nabla\bar{s}),\quad \text{where}\quad \bar{f}(\bar{p},\bar{q},\nabla\bar{s})\stackrel{\text{def}}{=}\langle\phi_*f(\phi_*\bar{p},\bar{q})\rangle, \tag{3.15}$$

$$\bar{\nabla}(\nabla\bar{s}) \stackrel{\text{def}}{=} \langle\phi_*\widetilde{\nabla}\tilde{s}_1\rangle, \quad \phi_* \stackrel{\text{def}}{=} \Phi(\nabla\bar{s}+\widetilde{\nabla}\tilde{s}_1,\mu_1), \quad \tilde{s}_1 = \mathcal{H}_{\mu_2}^{-1}\tilde{h}, \tag{3.16}$$

$$\overline{q}_{1\tau}^{\xi} = M^{\xi}\left(\bar{q}g_0 - (\partial_t-\Delta)\bar{q}\right), \tag{3.17}$$

$$\bar{s}_{1t} + \nu\bar{s}_1 = \kappa\bar{q}_1 + \mu_2\Delta\bar{s}, \text{ where } \bar{q}_1 = \langle q_1\rangle,\ \bar{s}_1 = \langle s_1\rangle, \tag{3.18}$$

where g_0 is defined in (3.9). Equation (3.17) is compatible under the condition

$$(\partial_t-\Delta)\bar{q} = \bar{q}\bar{g}(\bar{p},\bar{q},\nabla\bar{s}), \quad \text{where} \quad \bar{g}(\bar{p},\bar{q},\nabla\bar{s}) = \langle g(\phi_*\bar{p},\bar{q})\rangle. \tag{3.19}$$

Definition 2. *By the leading slow system, we mean the system of Eqs* (3.13)*,* (3.15)*,* (3.16)*, and* (3.19) *with respect to the mean values of the leading approximation,* $\bar{p} = \bar{p}(x,t)$*,* $\bar{q} = \bar{q}(x,t)$*, and* $\bar{s} = \bar{s}(x,t)$*.*

Remark 3. The external signal influences the leading slow system, changing both the kinetics and the tactical transport of predators—that is, transforming $f \to \bar{f}, g \to \bar{g}$ and adding the drift term, $\nabla\cdot(\bar{p}\bar{\nabla}(\nabla\bar{s}))$, to the predator mass balance. Hence, both the averaged transport and the kinetics are nonlocal. A notable exception is p-linear kinetics, that is, where the functions $pf(p,q)$, $qg(p,q)$ are linear (not necessarily homogeneous) in p. Then they are preserved under homogenization, so that $\bar{f} = f(p,q)$ and $\bar{g} = g(p,q)$. In particular, Lotka–Volterra kinetics is p-linear, as are a number of other classical models of interspecies reactions, *cf.*, [49].

The following theorem summarizes the above analysis.

Theorem 1. *Let the mean values of the leading approximation,* $\bar{p} = \bar{p}(x,t), \bar{q} = \bar{q}(x,t)$*,* $\bar{s} = \bar{s}(x,t)$*, give a solution to the leading slow system. Then the systems of Eqs* (3.4)–(3.7) *completely determine the coefficients* p_0, q_0, s_0*, as well as the coefficients* q_1, s_1 *up to their mean values,* $\langle q_1\rangle$ *and* $\langle s_1\rangle$*. More precisely,* $p_0 = \bar{p}\phi_*$*,* $s_0 = \bar{s}$*,* $q_0 = \bar{q}$*,* $q_1 = \overline{q}_1^{\xi} = \tilde{q}_1 + \bar{q}_1$*,* $\tilde{q}_1 = \partial_\tau^{-1}(M^{\xi}-M)g_0$*,* $s_1 = \tilde{s}_1 + \bar{s}_1$*,* $\tilde{s}_1 = \mathcal{H}_{\mu_2}^{-1}\tilde{h}$*. Moreover, Eqs* (3.8) *and* (3.9) *become compatible, and their solutions,* p_1 *and* q_2*, have the form* $q_2 = \overline{q}_2^{\xi} - \bar{q}\widetilde{\Delta}^{-1}(I-M^{\xi})g_0$*,* $p_1 = \bar{p}_1\phi_* + \mathcal{L}^{-1}(\boldsymbol{w}_0,\mu_1)\widetilde{\Psi}$*. Also,* $\tilde{s}_2 = \mathcal{H}_{\mu_2}^{-1}\left(\kappa\tilde{q}_1 - \nu\tilde{s}_1 - (\partial_t - \mu_2\mathcal{D})\tilde{s}_1\right)$*, provided that Eq* (3.18) *holds true. The projections* $\overline{q}_2^{\xi} = M^{\xi}q_2$*,* $\bar{s}_2$*,* $\bar{q}_1$*,* $\bar{s}_1$*, and* $\bar{p}_1$ *remain undetermined in any case.*

3.1.1. Drift and stationary signal

Within this subsubsection, the notation of $\widetilde{s}$ replaces the notation $\tilde{s}_1 = \mathcal{H}_{\mu_2}^{-1}\tilde{h}$, where $\tilde{h}$ is the external signal (see formulae (2.4) and (3.14)). Here, the signal may depend on slow variables too. We do not indicate this explicitly to simplify the notation.

We set

$$\mathfrak{e} \stackrel{\text{def}}{=} \exp(\tilde{s}/\mu_1), \quad \mathfrak{e}_* \stackrel{\text{def}}{=} \mathfrak{e}\langle\mathfrak{e}\rangle^{-1}. \tag{3.20}$$

Finding $\phi_* = \Phi(\bar{\boldsymbol{u}} + \widetilde{\nabla}\tilde{s},\mu_1)$ consists of solving the stationary equation

$$\widetilde{\nabla}\cdot(\phi_*(\widetilde{\nabla}\tilde{s}+\bar{\boldsymbol{u}}) - \mu_1\widetilde{\nabla}\phi_*) = 0. \tag{3.21}$$

The substitution $\phi_* = \mathfrak{e}\psi\langle\mathfrak{e}\psi\rangle^{-1}$ reduces it to the equation:

$$\widetilde{\nabla}\cdot(\mathfrak{e}(\psi\bar{\boldsymbol{u}} - \mu_1\widetilde{\nabla}\psi)) = 0. \tag{3.22}$$

For $\bar{\boldsymbol{u}} = 0$, this equation is solved explicitly, and we conclude that $\phi_* = \mathrm{e}_*$. Then $\bar{\mathrm{V}}(0) = \langle \mathrm{e}_* \widetilde{\nabla} \tilde{s} \rangle = \mu_1 \langle \widetilde{\nabla} \mathrm{e}_* \rangle = 0$. Thus, $\bar{\mathrm{V}}(0) = 0$ under the condition that the external signal is stationary and the cue intensity is everywhere constant. (In the general case, this is not so, even if the cue intensity is constant, see Section 3.3.2).

There exists a class of external signals allowing one to explicitly express the field $\bar{\mathrm{V}}$; namely,

$$\tilde{h} = \tilde{h}_1(\xi_1) + \ldots + \tilde{h}_n(\xi_n) \Rightarrow \tilde{s} = \tilde{s}_1(\xi_1) + \ldots + \tilde{s}_n(\xi_n), \quad \langle \tilde{h}_j \rangle = \langle \tilde{s}_j \rangle = 0, \ j = 1...n. \tag{3.23}$$

Let the external signal have the form of (3.23). Then the solution to Eq (3.22) reads

$$\psi = \psi_1(\xi_1) \ldots \psi_n(\xi_n), \quad \psi_i(y) = (\bar{u}_i - \mu_1 \partial_y)^{-1} \mathrm{e}_i^{-1}(y), \quad \mathrm{e}_i(y) = \exp(\tilde{s}_i(y)/\mu_1), \ y \in \mathbb{R}. \tag{3.24}$$

Further, $\langle \mathrm{e}\psi \rangle \bar{\mathrm{V}}(\bar{\boldsymbol{u}}) = \langle \mathrm{e}\psi \widetilde{\nabla} \tilde{s} \rangle = \mu_1 \langle \psi \widetilde{\nabla} \mathrm{e} \rangle$ by the definition of this field and the function $\tilde{s}$. Hence

$$\bar{\mathrm{V}}(\bar{\boldsymbol{u}}) = -\tfrac{\mu_1 \langle \mathrm{e} \widetilde{\nabla} \psi \rangle}{\langle \mathrm{e}\psi \rangle}, \text{ that is,} \quad \bar{\mathrm{V}}_i(\bar{\boldsymbol{u}}) = \bar{\mathrm{V}}_i(u_i) = -\tfrac{\mu_1 \langle \mathrm{e}_i \partial_i \psi_i \rangle}{\langle \psi_i \mathrm{e}_i \rangle}, \quad \text{where } \partial_i \stackrel{\text{def}}{=} \partial_{\xi_i}, \ i = 1...n. \tag{3.25}$$

We simplify this as follows $-\mu_1 \langle \mathrm{e}_j \partial_j \psi_j \rangle = \langle \mathrm{e}_j (\mathrm{e}_j^{-1} - \bar{u}_j \psi_j) \rangle$. Hence,

$$\bar{\mathrm{V}}_j(\bar{\boldsymbol{u}}) = \frac{1}{\langle \mathrm{e}_j \psi_j \rangle} - \bar{u}_j, \quad j = 1...n. \tag{3.26}$$

In view of formulae (3.26), Eq (3.15) takes the following form:

$$\bar{p}_t + \nabla \cdot (\bar{p}\bar{\boldsymbol{v}}) = \bar{p} \bar{f}(\bar{p}, \bar{q}, \nabla \bar{s}), \ \bar{v}_j = \frac{1}{\langle \mathrm{e}_j (\bar{s}_{x_j} - \mu_1 \partial_{\xi_j})^{-1} \mathrm{e}^{-1} \rangle}. \tag{3.27}$$

Remark 4. For each, $j = 1...n$ the right-hand side of formula (3.26) admits an analytic continuation from the real axis of the plane $\bar{u}_j$ to some strip covering it, and moreover $\bar{V}_j(\bar{u}_j) = O(\bar{u}_j)$, $\bar{u}_j \to +0$. This follows from the fact that zero is a simple pole of the resolvent of the operator $\partial : \mathrm{L}_2(\mathbb{S}) \to \mathrm{L}_2(\mathbb{S})$, where the notation of $\mathbb{S}$ is for the circumference. The corresponding spectral projector is $f \mapsto \langle f \rangle 1$, where the angle brackets denote averaging over $\mathbb{S}$. Hence, $\lambda \langle \mathrm{e}_j (\lambda - \mu_1 \partial_{\xi_j})^{-1} \mathrm{e}_j^{-1} \rangle \to \langle \mathrm{e}_j \rangle \langle \mathrm{e}_j^{-1} \rangle$, $\lambda \to 0$, where $\langle \mathrm{e}_j \rangle \langle \mathrm{e}_j^{-1} \rangle > 1$ by virtue of the convexity of the exponent function. From this and from formulae (3.27), there follow the inequalities $\bar{v}_j / \bar{s}_{x_j} < 1$ for small $\bar{s}_{x_j}$, $j = 1...n$. This indicates the possibility for suppression of tactical transport since, in the original system, the speed of tactical transfer is *equal* to $\nabla \bar{s}$ (see (1.1) and (1.4)).

Remark 5. We set $h_i(\xi) = A_{0i} h_{0i}(\xi)$ for some $i = 1...n$, where $\langle h_{0i}^2 \rangle = 1$. Then it is logical to regard the quantity $A_i \stackrel{\text{def}}{=} A_{0i}/\mu_2$ as the effective amplitude of the i-th term in the external signal given by equality (3.23). The Laplace asymptotics of the integrals expressing the mean values $\langle \mathrm{e}_i \rangle$ and $\langle \mathrm{e}_i^{-1} \rangle$ show exponential growth of each of them as $A_i \to \infty$, so that the above-mentioned suppression of tactic transport is strengthened exponentially as the amplitude of the external signal grows.

3.2. Quasi-equilibria

By the equilibria of system (1.1)–(1.3), we mean particular solutions such that both the species densities and the cue intensity are identically constant — that is,

$$s = s_e \equiv \text{const}, \quad q = q_e \equiv \text{const}, \quad p = p_e \equiv \text{const}. \tag{3.28}$$

For the existence of equilibria, the external signal must be constant. Then the equilibrium species densities p_e, q_e and the cue intensity s_e satisfy the equations:

$$p_e f(p_e, q_e) = 0, \quad q_e g(p_e, q_e) = 0, \quad h + \kappa q_e - \nu s_e = 0, \quad h = \text{const}\,. \tag{3.29}$$

If a system possesses a complete translational invariance, then the possibility for its equilibrium is expected, and this is not the case otherwise. However, if a small-scale inhomogeneity does not undergo modulation on the basic and greater scales, it is natural to consider the so-called quasi-equilibria—that is, the short waves that do not undergo slow modulation.

In order to exclude a slow modulation of the external signal, we adopt the condition

$$\tilde{h} = \tilde{h}(\xi, \tau), \ \nabla\tilde{h} = \partial_t\tilde{h} \equiv 0. \tag{3.30}$$

In the leading approximation, every quasi-equilibrium corresponds to a suitable equilibrium (understood in the usual sense) of the leading slow system. Indeed, the existence of a quasi-equilibrium entails the equalities

$$\bar{s} = \bar{s}_e \equiv \text{const}, \quad \bar{q} = \bar{q}_e \equiv \text{const}, \quad \bar{p} = \bar{p}_e \equiv \text{const}, \ \phi_* = \phi_*(\xi, \tau) \tag{3.31}$$

(this follows from the expressions of the leading approximation by formulae (3.11)–(3.12)). Thus, these densities have to satisfy the following equations:

$$\bar{p}_e \bar{f}_e(\bar{p}_e, \bar{q}_e) = 0, \quad \bar{q}_e \bar{g}_e(\bar{p}_e, \bar{q}_e) = 0, \quad \nu\bar{s}_e - \kappa\bar{q}_e = 0, \tag{3.32}$$

$$\bar{f}_e(\bar{p}, \bar{q}) \stackrel{\text{def}}{=} \bar{f}(\bar{p}, \bar{q}, \nabla\bar{s})\big|_{\nabla\bar{s}=0}, \quad \bar{g}_e(\bar{p}, \bar{q}) \stackrel{\text{def}}{=} \bar{g}(\bar{p}, \bar{q}, \nabla\bar{s})|_{\nabla\bar{s}=0}\,. \tag{3.33}$$

The possibility of equilibrium of the leading slow system does not contradict the possibility of drift in view of condition (3.30), owing to which the drift field in Eq (3.15) is constant.

Remark 6. In the general case, the equations of quasi-equilibria—that is, Eq (3.32)—differ from the equations of equilibria—that is, Eq (3.29)—since the functions $\bar{f}_e$ and $\bar{g}_e$ do not coincide with functions f and g given originally. However, they coincide in the case of p-linearity (see also Remark 3). Thus, for p-linear kinetics, every quasi-equilibrium corresponds to an equilibrium of the original system with no signal and vice versa—that is, $\bar{s}_e = s_e$, $\bar{q}_e = q_e$, and $\bar{p}_e = p_e$.

3.3. Linearization

Define a pair of linear functions $\bar{a}_i^e : \mathbb{R}^2 \to \mathbb{R}$, $i = 1, 2$, and a pair of vector fields $\bar{\boldsymbol{b}}_i^e$, $i = 1, 2$, by setting

$$\bar{a}_i^e(\zeta_1, \zeta_2) = \langle a_i(\phi_*\zeta_1, \zeta_2)\rangle, \ \ i = 1, 2, \tag{3.34}$$

$$\boldsymbol{b}_i^e\nabla\bar{\psi} = \langle a_i(\mathcal{L}^{-1}(\widetilde{\nabla}\tilde{s}_1, \mu_1)\widetilde{\nabla}\cdot(\phi_*\nabla\bar{\psi}), 0)\rangle, \ i = 1, 2, \tag{3.35}$$

for an arbitrary smooth test function $\psi = \psi(x, t)$. Here, functions a_i have the form

$$a_1(\zeta_1, \zeta_2) = d(pf(p, q))(\zeta_1, \zeta_2)\big|_{p=p_0, q=q_0}, \quad a_2(\zeta_1, \zeta_2) = d(qg(p, q))(\zeta_1, \zeta_2)\big|_{p=p_0, q=q_0}, \tag{3.36}$$

$$\text{where} \quad p_0 = \bar{p}_e\phi_*, q_0 = \bar{q}_e.$$

Lemma 2. *The linearization of the leading slow system near its equilibrium* $(\bar p_e, \bar q_e, \bar s_e)$ *has the form*

$$p_t + \nabla\cdot(p\boldsymbol{c}^e + \bar p_e\mathcal{T}\nabla s) + \bar p_e\bar{\boldsymbol{b}}_1^e\nabla s = \bar a_1^e(p,q), \tag{3.37}$$

$$(\partial_t - \Delta)q + \bar p_e\bar{\boldsymbol{b}}_2^e\nabla s = \bar a_2^e(p,q), \tag{3.38}$$

$$s_t + \nu s = \kappa q, \ \textit{where} \tag{3.39}$$

$$\boldsymbol{c}^e = \bar{\mathrm{V}}(0), \quad \mathcal{T}_{i,j} = \delta_{ij} - \left\langle \phi_{*i}\tilde s_{1\xi_j}\right\rangle, \ i,j = 1...n, \quad \tilde s_1 = \mathcal{H}_{\mu_2}^{-1}\tilde h, \quad \bar p_e\boldsymbol{b}_i^e = \bar{\boldsymbol{b}}_i, \tag{3.40}$$

$$\phi_{*i} = \mathcal{L}^{-1}(\widetilde{\nabla}\tilde s_1, \mu_1)\phi_{*\xi_i}, \ \langle\phi_{*i}\rangle = 0, \quad i = 1...n, \tag{3.41}$$

where $\bar a_i^e$ *are the linear functions* (3.34) *and* $\boldsymbol{b}_i^e$ *are the vector fields* (3.35).

Proof. The key point is the differentiation of the mapping $\check\Phi : y \mapsto \Phi(\boldsymbol{y} + \widetilde{\nabla}\tilde s_1, \mu_1)$, where $y \in \mathbb{R}^n$, the map Φ is defined by formula (2.6), and the differentiation is performed at $y = 0$, while we identify the element y and the constant vector field $\boldsymbol{y}$ on the torus $\mathrm{T}^{n+1}_{\xi,\tau}$. At the formal level it is fairly obvious that $d\check\Phi(v) = -v_i\phi_{*i}$. A more rigorous and detailed study of this differentiation can be found in Appendix A. Let us also dwell on the computation of the sensing tensor, $\mathcal{T}$. Let $\bar{\boldsymbol{g}} : (x,t) \mapsto \bar{\boldsymbol{g}}(x,t) \in \mathbb{R}^n$. In view of formula (3.16), we have $\bar{\mathrm{V}}(\bar{\boldsymbol{g}})\nabla\bar\psi = \langle(\check\Phi\circ\bar{\boldsymbol{g}})\widetilde{\nabla}\tilde s_1\nabla\bar\psi\rangle$, where $\bar\psi$ is a test function of the slow variables. Hence, $\nabla\bar\psi\bar{\mathrm{V}}'\bar{\boldsymbol{v}} = \langle d\check\Phi(\bar{\boldsymbol{v}})\widetilde{\nabla}\tilde s_1\nabla\bar\psi\rangle$, where $\bar{\mathrm{V}}'$ denotes the differential of the map $\bar{\mathrm{V}}$. Thus, differentiation of the map $\bar{\mathrm{V}}$ leads to a tensor field with components $-\left\langle\phi_{*i}\tilde s_{1\xi_i}\right\rangle$. The terms involving the linear functions a_i^e and the vector functions $\boldsymbol{b}_i^e$ are obtained analogously, upon linearization of the maps $F_1 : (\bar p,\bar q,\bar s) \mapsto \bar p\bar f(\bar p,\bar q,\nabla\bar s)$, $\quad F_2 : (\bar p,\bar q,\bar s) \mapsto \bar q\bar g(\bar p,\bar q,\nabla\bar s)$. □

Remark 7. Since the external signal, by assumption, does not undergo slow modulation–that is, equalities (3.30) hold–the linearized system (3.37)–(3.39) possesses translational invariance. Indeed, it turns out that $\mathcal{T} = \text{const}$, $\boldsymbol{c}^e = \text{const}$, $\boldsymbol{b}_i^e = \text{const}$, $i = 1,2$.

Remark 8. For p-linear kinetics, $\boldsymbol{b}_i^e = 0$. Indeed, let v be an arbitrary function on the torus of fast variables. In view of p-linearity, $\langle a_i(v\zeta_1,0)\rangle = \langle v\rangle a_i(\zeta_1,0)$, $i = 1,2$. Hence, the mean values are zero in formula (3.35). A similar argument shows that $\bar a_i^e = a_i^e$, $i = 1,2$, where a_i^e are the linear functions (3.36) at $p_0 = \bar p_e$, $q_0 = \bar q_e$; *cf.*, Remark 6.

3.3.1. Stationary signal

From here on, the notation of $\tilde s$ replaces $\tilde s_1 = \mathcal{H}_{\mu_2}^{-1}\tilde h$ unless cancelling this convention is proclaimed. This should be kept in mind upon operating functions $\mathfrak{e}$ and $\mathfrak{e}_*$, *cf.,* equalities (3.20).

In this subsection, we supplement assumption (3.30) by the following one:

$$h = \tilde h(\xi) \Rightarrow \tilde s = \tilde s(\xi).$$

Let such a signal be fixed. Then the components $\mathcal{T}_{ij}$ are computed by averaging over the torus $\mathbb{T}^n_\xi$ and the operator $\mathcal{L} = \mathcal{L}(\widetilde{\nabla}\tilde s, \mu_1)$ is replaced by its stationary version $w \mapsto \widetilde{\nabla}\cdot(w\widetilde{\nabla}\tilde s - \mu_1\widetilde{\nabla}w)$, acting in $\mathrm{L}_2(\mathbb{T}^n_\xi) \to \mathrm{L}_2(\mathbb{T}^n_\xi)$, with the previous notation preserved. Lemma 1 remains valid in this case and under its conditions, $\phi_* = \mathfrak{e}_*$ (see Section 3.1.1 concerning the last equality). Accordingly, the right inverse $\mathcal{L}^{-1}(\boldsymbol{w},\epsilon) : \widetilde{\mathrm{L}}_2\left(\mathbb{T}^n_\xi\right) \to \widetilde{\mathrm{L}}_2\left(\mathbb{T}^n_\xi\right)$ is defined, where the tilde above indicates the subspace of functions with zero mean in L_2.

By assumption, $\boldsymbol{c}^e = \bar{\mathrm{V}}(0) = 0$ (see Section 3.1.1). However, the sensing tensor cannot be computed explicitly with no additional assumptions. Therefore, we restrict ourselves to the class of external

signals (3.23). Then $\mathfrak{e} = \mathfrak{e}_1(\xi_1)\mathfrak{e}_2(\xi_2)...\mathfrak{e}_n(\xi_n)$, $\mathfrak{e}_i = \mathrm{e}^{\frac{\tilde{s}_i}{\mu_1}}$, and the substitution $\phi_{*i} = \psi_i\mathfrak{e}_*, \quad \psi_i = \psi_i(\xi_i)$, reduces equation $\mathcal{L}(\widetilde{\nabla}\tilde{s}, \mu_1)\phi_{*i} = \phi_{*\xi_i}$ to the equations $\mu_1\psi_{i\xi_i} = \frac{1}{\mathfrak{e}_i\langle\mathfrak{e}_i^{-1}\rangle} - 1,\ i = 1...n$. Each of them has a unique solution such that $\langle\phi_{*i}\rangle = 0$, where $\phi_{*i} = \psi_i\mathfrak{e}_*$. Further,

$$\mathcal{T}_{j,k} = \delta_{j,k} - \langle\phi_{*j}\tilde{s}_{\xi_k}\rangle = \delta_{j,k} + \mu_1\langle\psi_{j\xi_k}\mathfrak{e}_*\rangle = \delta_{j,k} + \delta_{j,k}\left\langle\left(\frac{1}{\mathfrak{e}_j\langle\mathfrak{e}_j^{-1}\rangle} - 1\right)\mathfrak{e}_*\right\rangle \Rightarrow \tag{3.42}$$

$$\mathcal{T}_{j,k} = \frac{\delta_{j,k}}{\langle\mathfrak{e}_j\rangle\langle\mathfrak{e}_j^{-1}\rangle}, \quad j,k = 1\ldots n. \tag{3.43}$$

Remark 9. *One can deduce the result in [36] pertaining to the effect of a stationary signal from expressions* (3.43) *in the particular case of* $n = 1$.

Remark 10. Another way to derive expressions (3.43) consists in linearizing expression (3.26) for the drift velocity. One way or another, these expressions agree with Remark 5 in the sense that they reveal the suppression of tactic transport in the direction of the axis Ox_j with exponential sharpness as the amplitude A_j of the component h_j of the external signal (3.23) grows.

Consider the case of a general stationary signal free from restriction (3.23).

Lemma 3. *Let* $h = h(\xi)$. *Then the sensing tensor* $\mathcal{T}$ *is symmetric and its eigenvalues belong to the semi-interval* $(0, 1]$.

Proof. Let $\bar{\boldsymbol{u}} = (u_1, .., u_n)$ be a vector field on the torus associated with a constant vector in $\mathbb{R}^n$. The keynote in the proof is that the quadratic form $u_iu_j\mathcal{T}_{ij}$ allows for evaluating using the quadratic form of some projector, which acts in Hilbert's space of vector fields on the torus with a specially selected metric; see Appendix A for details.

Remark 11. The maximum eigenvalue of the sensing tensor can reach unity provided that the external signal, $\tilde{h}$, is invariant with respect to translations along some subspace in $\mathbb{R}^n_\xi$, which in this case is the eigen-subspace of the unity. However, a generic stationary signal generates a sensing tensor such that each of its eigenvalues is strictly less than unity—that is, the tactic transport is suppressed to some extent; *cf.* Remark 18. In this sense, the effect of a generic stationary signal is analogous to that produced by signal (3.23), although we cannot yet assert exponential decay of the eigenvalues of the sensing tensor matrix as generic external signal intensity grows.

3.3.2. Traveling waves

In this subsection, we supplement assumption (3.30) with the following one:

$$h = \tilde{h}(\eta),\ \eta = (\eta_1, \ldots, \eta_n), \quad \eta_i = \xi_i - \omega_i\tau, \quad |\omega_i|\ell_0 = \ell_i,\ i = 1...n,$$

or, possibly, $\omega_i = 0$. The function $\tilde{h}$ is assumed ℓ_i-periodic in each of the self-similar variables, while the restrictions on the wave speeds, ω_i, entail time periodicity with a given period, ℓ_0. With these self-similar variables, we associate all functions and differential operations considered in this section. In particular, the operator $\mathcal{L}(\widetilde{\nabla}\tilde{s}, \mu_1)$ is replaced by its self-similar version:

$$\mathcal{L}(\widetilde{\nabla}\tilde{s}, \mu_1) : w \mapsto \nabla\cdot(w(\widetilde{\nabla}\tilde{s} - \bar{\boldsymbol{\omega}}) - \mu_1\widetilde{\nabla}\phi_*), \quad \bar{\boldsymbol{\omega}} = (\omega_1, \ldots, \omega_n).$$

Then the equation for the function ϕ_* coincides with Eq (3.21) up to the replacement of $\bar{\boldsymbol{u}}$ by $-\bar{\boldsymbol{\omega}}$. To use the explicit solution to the latter presented in Section 3.1.1, assume the external signal is a sum of simple traveling waves:

$$\tilde{h} = \tilde{h}(\eta) = \tilde{h}_1(\eta_1) + \ldots + \tilde{h}_n(\eta_n), \quad \langle\tilde{h}\rangle = \langle\tilde{h}_j\rangle = 0, \ j = 1...n, \tag{3.44}$$

where the means are computed over the torus $\mathbb{T}^n_\eta$, as in all subsequent formulae of this section. Then $\tilde{s} = \tilde{s}_1(\eta_1) + \ldots + \tilde{s}_n(\eta_n)$, where $\tilde{s}_j = -(\omega_j + \mu_2\partial_j)^{-1}\partial_j^{-1}\tilde{h}_j$, $\langle\tilde{s}_j\rangle = 0$, and $\partial_j = \partial_{\eta_j}$, $j = 1...n$.

Remark 12. Useful information about the behavior of the functions $\tilde{s}_j$ as $\omega_j \to 0$ and $\omega_j \to \infty$ is given by their a priori estimates $\omega^2\langle(\partial_j^\ell\tilde{s}_j)^2\rangle \le \langle(\partial^{\ell-1}\tilde{h}_j)^2\rangle$, $\ell = 1, 2, ...$, as well as $\langle(\partial_j^\ell(\tilde{s}_j - \tilde{S}_j))^2\rangle \le \omega^2\langle(\partial^\ell\tilde{S}_j)^2\rangle$, where $S_j = -\partial_j^{-2}\tilde{h}_j/\mu_2$.

Consider the residual drift, $\boldsymbol{c}^e = \langle\phi_*\nabla\tilde{s}\rangle$ (see (3.16) and (3.40)) for a fixed external signal in the form (3.44). Then

$$\boldsymbol{c}^e = (c_1, \ldots, c_n), \quad c_j = \omega_j - \frac{1}{\langle \mathfrak{e}_j\psi_j\rangle}, \tag{3.45}$$

where the functions ψ_j and $\mathfrak{e}_j$ are expressed by formulae (3.24), up to the replacement of $\bar{u}_i$ by $-\omega_i$, ψ_j by $-\psi_j$, and ξ_j by η_j. Thus, $\boldsymbol{c}^e \neq 0$, generally speaking. Hence, a nonzero drift with uniform cue distribution is the generic case in the class of external signals (3.44), in contrast to the class of stationary external signals.

Remark 13. It turns out that $c_j = O(\langle(\partial_j s_j)^2\rangle/\omega_j)$, $\omega_j \to \infty$, $j = 1...n$ for a fixed signal h in the form (3.44). These estimates follow from the equalities

$$\mu_1\langle \mathfrak{e}_j\psi_j\rangle = \operatorname{sgn}(\omega_j)\int\limits_{\eta>0} \mathrm{e}^{-\frac{|\omega_j|\eta}{\mu_1}}\langle\mathfrak{e}\sigma_{j,\eta}\mathfrak{e}^{-1}\rangle d\eta, \text{ where } (\sigma_{j,\eta}\mathfrak{e})(t) = \mathfrak{e}(t - \eta\operatorname{sgn}(\omega_j)), \ j = 1...n, \tag{3.46}$$

which follow directly from the definition of the functions ψ_j. In addition,

$$c_j = \omega_j\left(1 - \left(\langle\mathfrak{e}_j\rangle\langle\mathfrak{e}_j^{-1}\rangle\right)^{-1} + O(\omega_j)\right), \ \omega_j \to 0, \ \ j = 1...n,$$

where $\langle\mathfrak{e}_j\rangle\langle\mathfrak{e}_j^{-1}\rangle > 1$, *cf.* Remarks 4 and 5.

Let us compute the sensing tensor. We start with the solution to the equations $\mathcal{L}\phi_{*j} = \phi_{*\eta_j}$, $\langle\phi_{*\eta_j}\rangle = 0$, $j = 1...n$, where $\mathcal{L} = \mathcal{L}(\widetilde{\nabla}\tilde{s}, \mu_1)$. The solutions have the form: $\phi_{*j} = \mathfrak{e}\check{\psi}_j(C_j\psi_j - \theta_j)\langle\mathfrak{e}\psi\rangle^{-1}$, where $\theta_j = (\omega_j + \mu_1\partial_j)^{-1}\psi_j$, $\check{\psi}_j = \psi_1\ldots\psi_n\psi_j^{-1}$, and we set $C_j = \langle\mathfrak{e}_j\theta_j\rangle\langle\mathfrak{e}_j\psi_j\rangle^{-1}$ to obey the condition $\langle\phi_{*j}\rangle = 0$, where the denominator is nonzero by virtue of equality (3.46). Further, $\mathcal{T}_{jk} = \delta_{jk} - \langle\phi_{*j}\partial_k\tilde{s}_k\rangle$. Proceeding with the computations, we arrive at the equalities

$$\mathcal{T}_{ij} = \delta_{ij}\langle\mathfrak{e}_j\theta_j\rangle\langle\mathfrak{e}_j\psi_j\rangle^{-2}, \quad i, j = 1...n. \tag{3.47}$$

Remark 14. By definition of the functions θ_j, $j = 1...n$,

$$\mu_1{}^2\langle\mathfrak{e}_j\theta_j\rangle = \int\limits_{\eta>0}\eta\mathrm{e}^{-\frac{|\omega_j|\eta}{\mu_1}}\langle\mathfrak{e}\sigma_{j,\eta}\mathfrak{e}^{-1}\rangle d\eta, \text{ where } (\sigma_{j,\eta}\mathfrak{e})(t) = \mathfrak{e}(t - \eta\operatorname{sgn}(\omega_j)), \ j = 1...n, \tag{3.48}$$

and these equalities entail the inequalities $\mathcal{T}_{ii} > 0$, $i = 1...n$, as well as the estimates

$$\mathcal{T}_{ij} = \delta_{ij}\left(\left(\langle \mathrm{e}_j\rangle\langle \mathrm{e}_j^{-1}\rangle\right)^{-1} + O(\omega_j)\right),\ \omega_j \to +0,\ i, j = 1...n, \tag{3.49}$$

$$\mathcal{T}_{ij} = \delta_{ij}\left(1 + \langle(\partial_j s_j)^2\rangle\omega_j^{-2}(1 + O(\omega_j^{-1}))\right),\ \omega_j \to \infty,\ i, j = 1...n. \tag{3.50}$$

Remark 15. Equalities (3.49) indicate the possibility of *suppression* of tactic transport in the direction of propagation of each of the waves constituting the signal (3.44). Indeed, without the signal, $\mathcal{T}_{ij} = \delta_{ij}$, but $\mathcal{T}_{jj} < 1$ for a nonzero amplitude of the wave h_j and a sufficiently small speed of its propagation, ω_i. Moreover, the leading term in estimate (3.49) can be arbitrarily small for a sufficiently large amplitude A_j of the wave h_j, and this effect is exponential; *cf.*, Remark 5. At the same time, equalities (3.50) show that $\mathcal{T}_{jj} > 1$ for large ω_j. Therefore, an increase in the propagation speed of the wave that is a component of the external signal (3.49) *strengthens* the tactic transport in the direction of propagation of this wave.

4. Induced stability and instability

In this section, we compare the stability of equilibria and quasi-equilibria, using the leading slow system to study the latter ones. We assume the coexistence of species—that is, there exists both an equilibrium and a quasi-equilibrium—and the following inequalities hold true:

$$p_e > 0, \quad q_e > 0,\ \bar{p}_e > 0, \quad \bar{q}_e > 0. \tag{4.1}$$

4.1. Terminology

The linear stability analysis of systems possessing translational invariance (see Remark 7) uses the so-called *normal modes* of perturbations, which have the following form:

$$\hat{a}\exp(\lambda t + i\hat{x}x), \quad \hat{a} \in \mathbb{C}^\ell, \quad \lambda \in \mathbb{C}, \quad \hat{x} \in \mathbb{R}^n, \tag{4.2}$$

where ℓ is the number of unknowns in the linearized system, $\hat{a} = \hat{a}(\hat{x})$ is the unknown amplitude, and $\lambda = \lambda(\hat{x})$ is the eigenvalue of the corresponding spectral stability problem, which for each particular wave vector, $\hat{x}$, reduces to an algebraic eigenvalue problem owing to the separation of variables. A normal mode is called *stable (unstable, neutral)* if the real part of the corresponding eigenvalue λ is negative (positive, equal to zero). It is also customary to say that an *equilibrium is stable (unstable, neutral)* if each of its eigenmodes is stable (there exists an unstable (neutral) mode).

Let the system together with its equilibrium depend smoothly on N parameters. Then the spectral stability problem depends on the same parameters, and, hence, each normal mode depends on them, as well as on the wave vector $\hat{x}$. The subset of the $n + N$-dimensional parameter space on which neutral modes exist is called *neutral*. The boundary of the projection of this set along the $\hat{x}$-subspace onto the subspace of the remaining N parameters forms a *critical set* separating the stability region from the instability region in the N-dimensional parameter space of the family of equilibria.

The neutral set of parameters, as a rule, is a union of smooth strata of various dimensions. If a parameter point belongs to a stratum of maximal dimension $N + n - 1$, then there exists either a simple pair of complex conjugate modes with $\mathrm{Re}\,\lambda = 0$, $\mathrm{Im}\,\lambda \neq 0$, or a simple real mode with $\lambda = 0$. Points

of the first and second types form two types of disjoint $N + n - 1$-dimensional strata. Strata of the first (second) type are called oscillatory (monotone). The sections of the monotone and oscillatory strata by 2D planes spanned by various couples of the parameters are widely known as the neutral curves.

Figure 1 illustrates a possible shape of the neutral set of a one-parameter family ($n = N = 1$). (The figure has no relation to any particular stability problem.) It shows 4 neutral strata of maximal dimension 1, and their junction point—a stratum of zero dimension. The red strata are, say, monotone, and the blue ones are oscillatory. The critical set consists of a single value of the parameter, denoted by A_{cr}. The instability region in the one-dimensional parameter space is given by the inequality $A > A_{cr}$.

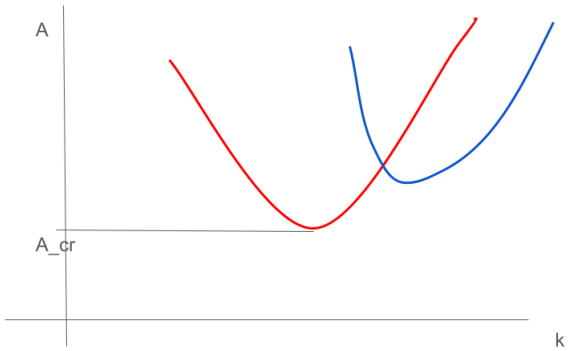

Figure 1. Scheme of the neutral set in the case of $N = n = 1$, where the parameter is A, and the wave number is k.

If a smooth path transversally intersects a neutral stratum of maximal dimension, then a stable eigenmode becomes unstable, or vice versa. This phenomenon is called the "onset of instability," and we speak of oscillatory (monotone) instability if the intersection occurs with an oscillatory (monotone) stratum. The onset of instability is an important indicator of local bifurcations: Oscillatory instability is a precursor of the excitation of self-oscillations according to the Andronov–Hopf bifurcation scenario, and monotone instability is a precursor of branching off the secondary stationary regimes, perhaps inhomogeneous, from the equilibrium. All these transitions are of considerable interest, in particular, in connection with the study of pattern formation in the dynamics of cells or populations, see the articles cited in the Introduction.

4.2. Normal modes

In what follows, we omit those proofs, the reductions of which to elementary computations are obvious. In any case, they are quite accessible using computer algebra, *e.g.*, *Maple*. However, for the sake of transparency, we put several key expressions in Appendix C.

Consider a quasi-equilibrium satisfying condition (4.1), the corresponding linearization of the leading slow system (3.37)–(3.39), and its normal modes (4.2). Let us introduce artificial diffusion terms into the corresponding spectral stability problem for addressing possible effects of small diffusion of the predator and the cue (see the original system (1.1)–(1.3)). As a result, for each wave vector $\hat{x}$,

there arises the eigenvalue problem

$$\begin{pmatrix} \lambda + \mathrm{i}kc + k^2\delta_1 - a_{11} & -a_{12} & \mathrm{i}kp_e b_1 - \check{\chi} p_e k^2 \\ -a_{21} & \lambda - a_{22} + k^2 & \mathrm{i}kp_e b_2 \\ 0 & -\kappa & \lambda + \nu + k^2\delta_2 \end{pmatrix} \begin{pmatrix} \hat{p} \\ \hat{q} \\ \hat{s} \end{pmatrix} = 0, \tag{4.3}$$

where $(\hat{p}, \hat{q}, \hat{s}) = \hat{a}$ is the unknown amplitude of the normal mode, $k = |\hat{x}|$, $c \stackrel{\text{def}}{=} \boldsymbol{c}^e \cdot \hat{\boldsymbol{x}}/k$, $b_i \stackrel{\text{def}}{=} \bar{\boldsymbol{b}}_i^e \cdot \hat{\boldsymbol{x}}/k$, $i = 1, 2$, $\check{\chi} \stackrel{\text{def}}{=} \hat{\boldsymbol{x}} \cdot \mathcal{T}\hat{\boldsymbol{x}}/k^2$. Furthermore, a_{ij}, $i, j = 1..2$, are the coefficients of the linear functions $\bar{a}_i^e$ which, together with the vectors $\bar{\boldsymbol{b}}_i^e$, $\boldsymbol{c}^e$ and the tensor $\mathcal{T}$, were introduced by equalities (3.34)–(3.36) and (3.40)–(3.41), and $\bar{p}_e$ denotes the predator density at the equilibrium of the leading slow system.

Remark 16. In problem (4.3), the coefficients $\delta_1 \geq 0$ and $\delta_2 \geq 0$ are responsible for the artificial diffusion. The case $\delta_1 = \delta_2 = 0$ corresponds exactly to the spectral stability problem for the linearized leading slow system (3.37)–(3.39). All assertions of this and the subsequent sections are valid for all sufficiently small nonnegative values of δ_1 and δ_2, including zero.

For $k \neq 0$, each eigenvalue $\lambda = \lambda(\hat{x})$ of problem (4.3) has a complex conjugate pair, $\lambda^* = \lambda(-\hat{x})$. Each such pair generates a two-dimensional subspace of real-valued solutions to the linearized system, whose elements have the form:

$$\mathrm{Re}\,(\hat{a}(\hat{x}) \exp(\lambda(\hat{x})t + i\hat{x} \cdot x)). \tag{4.4}$$

Hence, any real eigenvalue, if it exists, has multiplicity of at least two, with the exception of the eigenmode corresponding to $k = 0$. In particular, the dimension of a monotone stratum cannot be maximal, despite the realness of the original linearized system.

Spatially homogeneous modes (corresponding to $k = 0$) are stable under the conditions $a_{11} + a_{22} < 0$ and $a_{11}a_{22} - a_{12}a_{21} > 0$. Additionally, we assume that $a_{12} > 0$, $a_{21} < 0$, since the prey (predator) density is naturally regarded as a factor enhancing (suppressing) the reproduction of the predator (prey).

The explicit computation of coefficients a_{ij} and b_i in full generality appears to be too cumbersome. For simplicity, we assume p-linearity regarding the kinetics of system (1.1)–(1.3). Then the coefficients a_{ij} are determined by equalities (3.36), where $p_0 = p_e = \bar{p}_e$, $q_0 = q_e = \bar{q}_e$, $p_e > 0$, and $q_e > 0$ are the equilibrium species densities in the original system (1.1)–(1.3); then, a direct check shows that $a_{11} = 0$. Moreover, $b_1 = b_2 = 0$ (*cf.* Remarks 6 and 8).

Thus, the external signal controls only the coefficients c and $\check{\chi}$. They also depend on the point of the unit sphere in the space of wave vectors, but for now, we shall regard them as additional independent parameters and assume that $\check{\chi} > 0$. This inequality has not been proved in the general case, but it holds in all explicit examples at our disposal.

So, in the remaining part of the article, we assume

$$\check{\chi} > 0,\ \delta_1 \geq 0,\ \delta_2 \geq 0,\ \kappa > 0, \nu > 0,\ a_{12} > 0,\ a_{21} < 0,\ a_{22} < 0,\ b_1 = b_2 = a_{11} = 0. \tag{4.5}$$

These inequalities, in particular, entail the stability of the homogeneous mode, and also exclude monotone instability even for $c = 0$. Although matrix (4.3) is real for $c = 0$, its determinant is positive.

We fix the kinetic terms of system (1.1)–(1.3) consistent with assumptions (4.5) and (4.1), and all the other conditions adopted above. Thereby we also fix the coexistence equilibrium (which coincides with

the quasi-equilibrium by virtue of the assumed p-linearity) and the coefficients a_{ij}. In particular, the Lotka–Volterra kinetics with a logistic law of prey reproduction and under the condition of coexistence of species is suitable. In this case (with the normalization stated above), $f = \gamma q - \beta$, $g = 1 - p - q$, where $\gamma > \beta > 0$.

Consider the tuples of values of parameters $\delta_1, \delta_2, \kappa, \nu$ ordered accordingly in this sequence. In this set, define the subset $\mathcal{A}$ uniting those tuples that consist of the parameters values obeying conditions (4.5). Additionally, consider the extended tuples $\widetilde{\Pi} \stackrel{\text{def}}{=} (\Pi, c, \check{\chi}, k)$, where $\Pi \in \mathcal{A}$, and define $\widetilde{\mathcal{A}} = \mathcal{A} \times \mathbb{R} \times (0, \infty)^2$. The compactness of a set of the parameter tuples (extended or not) is understood in the sense of the standard topology of $\mathbb{R}^m$.

According to one of the theorems of matrix theory [53], ch. XV, given a *complex* polynomial of order N, there is an algorithmic procedure to construct a $2N \times 2N$ *real* matrix such that the number of sign changes in the chain of its main minors of orders $0, 2, 4, \ldots, 2N$ is equal to the number of roots of this polynomial in the open right semi-plane. (The zero-order minor is equal to unity by definition.) Hence, given wave vector $\hat{x}$, the number of corresponding unstable modes is equal to the number of sign changes in the chain of Hankel minors $1, \Delta_2, \Delta_4, \Delta_6$ associated to the characteristic polynomial of matrix (4.3), where the subscripts are equal to the orders of the Hankel minors. Hence, the neutral strata of maximal dimension (necessarily oscillatory, as proved) consist of nondegenerate solutions to exactly one of the equations $\Delta_i(\widetilde{\Pi}) = 0$, $\widetilde{\Pi} \in \widetilde{\mathcal{A}}$, where the determinants Δ_i, $i = 2, 4, 6$ are real polynomials in the members of the tuple $\widetilde{\Pi}$. They are expressed explicitly; *cf.* Appendix C. It is noteworthy that $\Delta_2 > 0$ everywhere on $\widetilde{\mathcal{A}}$, while Δ_4 and Δ_6 contain only even powers of the parameter c.

Proposition 1. *Let $C \subset \mathcal{A}$ be a compact set; given $c_* \in [0, \infty)$, set*

$$\widetilde{C} \stackrel{\text{def}}{=} C \times [-c_*, c_*] \times [0, \chi_*] \times (0, \infty).$$

Then (i) set $\{\Delta_4 = 0\}$ is the graph of rational function $\check{\chi} = \chi_4(\Pi, c, k) = \chi_{40}(\Pi, k) + c^2 \chi_{42}(\Pi, k)$, defined everywhere on the set $\{(\Pi, c, k) \in \mathcal{A} \times \mathbb{R} \times (0, \infty)\}$, where the function χ_{40} is everywhere positive, and the function χ_{42} is nonnegative. Moreover, $\forall\, \Pi \in \mathcal{A}$, $\exists\,! \, k = k_4(\Pi) > 0 : \inf\limits_{k>0} \chi_{40}(\Pi, c, k) = \chi_{40}(\Pi, k_4(\Pi))$.

(ii) $\inf\limits_{\{\Delta_4 = 0\} \cap \widetilde{C}} \check{\chi} = \inf\limits_{\{\Delta_4 = 0\} \cap \{c = 0\} \cap \widetilde{C}} \check{\chi} = \chi_{40}(\Pi, k_4(\Pi)) \stackrel{\text{def}}{=} \chi_4^*(C) > 0$, *and it is attained on a compact subset of the set $\widetilde{C} \cap \{c = 0\}$.*

(iii) either $\inf\limits_{\{\Delta_6 = 0\} \cap \widetilde{C}} \check{\chi} \stackrel{\text{def}}{=} \chi_6^*(C, c_*) > 0$ *or* $\inf\limits_{\widetilde{C}} \Delta_6 > 0$ *provided that $c_* > 0$ is small sufficiently.*

(iv) $\forall\, C$, $\exists\, c_* > 0 : \min(\chi_4^*(C), \chi_6^*(C, c_*)) > 0$, and $\forall\, \Pi \in C$ and $\forall\, c \in (-c_*, c_*)$, the equilibrium is stable for $0 \le \chi < \chi_{cr}^*(C, c_*) \stackrel{\text{def}}{=} \min(\chi_4^*(C), \chi_6^*(C, c_*))$.

Proof. Assertion (i) follows by a direct check, and (ii) follows from (i). We pass to assertion (iii). From the explicit expression of the determinant Δ_6, it follows that for a sufficiently small c_*, $|c| < c_*$ and for $\Pi \in \mathcal{A}$, $\exists\,! \, m \in N : \lim\limits_{k \to \infty} k^{-m} \Delta_6(\Pi, c, k) = a(\Pi, c)$ and $\inf_{\Pi \in C,\, |c| < c_*} a(\Pi, c) > 0$. This observation entails compactness for the set $\{\Delta_6 = 0\} \cap \widetilde{C}$. Let it be nonempty, and then it contains a tuple $\widetilde{\Pi}_6^*$ such that its projection onto the $\check{\chi}$ axis (along the hyperplane of the other parameters) coincides with χ_6^*. The positivity of χ_6^* follows from the positivity of the polynomial Δ_6 everywhere on the projection of the set $\widetilde{C}$ along the $\check{\chi}$-axis onto the hyperplane of the other parameters. Item (iv) is a consequence of (iii) and (ii). □

Remark 17. The determinant Δ_4 does not depend on c for $\delta_1 = \delta_2 = 0$, that is, in this particular case, $\chi_{42} = 0$ and $\chi_4 = \chi_{40}$ does not depend on c. The noted feature does not affect the conclusions of this and the next sections. It is also worth noting that the coefficient a introduced in the proof of Proposition 1 can indeed become negative for sufficiently large c. In that case, $\chi_6^* = 0$ and normal modes with wave vectors filling unbounded subdomains lying outside some ball may turn out to be unstable. However, the inequalities $\delta_1 > 0$ and $\delta_2 > 0$ entail $a > 0$, so that this short-wave instability is probably suppressed for arbitrarily small diffusions of the predator and the cue.

The determinant Δ_6 is a third-order polynomial in $\check{\chi}$, positive for $\check{\chi} = 0$ and for $\check{\chi} \to \infty$ (for an arbitrarily fixed collection of the remaining parameters). Thus, either there are no positive zeros, or there are exactly two of them, counting multiplicities. Moreover, simple positive zeros (if any) determine the functions $\check{\chi} = \chi_6^{\pm}$, $\chi_6^+ > \chi_6^- \geq 0$, on certain domains contained in the projection of the set $\widetilde{\mathcal{A}}$ along the χ-axis onto the hyperplane of the other parameters, and $\chi_6^+ = \chi_6^-$, or $\chi_6^- = 0$, on the boundary of every such domain.

A multiple root $\chi_6^+ = \chi_6^-$ occurs when $c = 0$, and here the matrix of problem (4.3) is real. In more detail: If $c = 0$, then the determinant Δ_2 is a divisor of Δ_4, and the square of their ratio, $(\Delta_4/\Delta_2)^2$, is a divisor of Δ_6. Moreover, $(\Delta_6\Delta_2^2/\Delta_4^2)$ is an everywhere positive polynomial. Hence, χ_{40} is a double root of the equation $\Delta_6|_{c=0} = 0$. This is an expected effect, since when a pair of complex conjugate unstable eigenvalues of a real matrix arises, the distribution of signs along the Hankel chain must change as follows:

$$+\,+\,{+}{+}\,+ \;\mapsto\; +\,+\,-\,+\,. \tag{4.6}$$

It is precisely such a change of sign that occurs when the parameter $\check{\chi}$ passes the threshold value, χ_{40}, by virtue of the divisibility and multiplicity indicated above. Moreover, the complex conjugate pair of neutral modes is double, in view of the mirror symmetry in $\hat{x}$. At the same time, the simultaneous fulfillment of the conditions $c = 0$ and $\check{\chi} < \chi_4^*$ entails the stability of the equilibrium.

The substitution $\check{\chi} = \chi_{40} + \epsilon c$ transforms the equation $\Delta_6 = 0$ to the form $c^2\Delta_6^\sharp(c, \epsilon) = 0$, where

$$\Delta_6^\sharp = -\Delta_{602} + \Delta_{620}\epsilon^2 + c(\Delta_{630}\epsilon^3 + \Delta_{612}\epsilon + c(\Delta_{622}\epsilon^2 + \Delta_{604} + c(\Delta_{614}\epsilon + c\Delta_{606}))),$$

and $\Delta_{602} > 0$, $\Delta_{620} > 0$ for each collection of the remaining parameters. Hence, the equation $\Delta_6^\sharp(c, \epsilon) = 0$ has solutions $(0, \pm\sqrt{\Delta_{602}/\Delta_{620}})$ satisfying the conditions of the implicit function theorem with respect to the expression $\epsilon = \epsilon(c)$. Thus, there exist a couple of functions $\epsilon^\pm(c)$ analytic for small c, and such that their graphs pass through the points $(0, \pm\sqrt{\Delta_{602}/\Delta_{620}})$, and the equation $\Delta_6 = 0$ for small $c \neq 0$ has two distinct solutions $\chi_6^\pm(c) = \chi_{40} + \epsilon^\pm(c)c$. Moreover $\chi_6^\pm(c) = \chi_{40} \pm c\sqrt{\Delta_{602}/\Delta_{620}} + O(c^2)$, $c \to 0$.

Thus, the parts of the oscillatory strata of maximal dimension adjacent to the hyperplane $c = 0$ are the graphs of the functions $\check{\chi} = \chi_6^\pm$ for $c \neq 0$. The intersection with the plane $c = 0$ of the union of the closures of these parts is a separate stratum of lower dimension lying on the graph of the function $\check{\chi} = \chi_{40}$. We introduce the functions $\chi_{nt}^- = \chi_6^\pm$ for $\mp c > 0$ and $\check{\chi} = \chi_{nt}^+$, $\chi_{nt}^+ = \chi^\pm$ for $\pm c > 0$. In view of what has been said, for a suitable smallness of $c \neq 0$, we have $\chi_{nt}^- < \chi_{nt}^+$, and the distribution of signs along the Hankel chain with a gradual increase of $\check{\chi}$ changes as follows:

$$+\,+\,+\,+ \overset{\check{\chi}=\chi_{nt}^-}{\mapsto} +\,+\,+\,- \overset{\check{\chi}=\chi_4}{\mapsto} +\,+\,-\,- \overset{\check{\chi}=\chi_{nt}^+}{\mapsto} +\,+\,-\,+\,.$$

According to this diagram, for an arbitrarily fixed nonzero wave vector $\hat{x}$ and for sufficiently small $c \neq 0$, there are no unstable modes for $\check{\chi} < \chi_{nt}^{-}$, there exists exactly one unstable mode for $\chi_{nt}^{-} < \check{\chi} < \chi_{nt}^{+}$, there exist exactly two unstable modes for $\chi_{nt}^{+} < \check{\chi}$, and nothing happens when the value χ_4 is passed through.

In fact, there are smooth extensions for functions $\chi_{nt}^{\pm}$ to a wider interval of parameter c that keep parameterising the null set of minor Δ_6 and preserve inequality $\chi_{nt}^{-} < \chi_4 < \chi_{nt}^{+}$. To see this, observe that $\Delta_6|_{\check{\chi}=\chi_4} < 0$ for every $c \neq 0$ and for every collection of the other parameters. Hence, equation $\Delta_6 = 0$ to be solved in $\check{\chi}$ has one positive root to the left of χ_4 and another root to the right for every collection of the other parameters such that $c \neq 0$.

Thus, the above analysis and Proposition 1 entails the following:

Proposition 2. *Under the conditions of Proposition 1, (i)* $\chi_{cr}(C, 0) = \chi_4^*(C)$*; (ii)* $\forall\, C,\ \exists\, c_* > 0 :$ $\{\Delta_6 = 0\} \cap \widetilde{C} \neq \varnothing$ *and* $0 < \chi_{cr}(C, c_*) = \chi_6^*(C, c_*) < \chi_4^*(C)$.

Proof. Indeed, $\exists\ \Pi_4 \in C :\ \chi_{40}(\Pi_4, k_4(\Pi_4)) = \chi_4^*(C)$, and at the same time, $\chi_{40}(\Pi_4, k_4(\Pi_4)) > \chi_{nt}^{-}(\Pi_4, c, k_4(\Pi_4)) \geq \chi_{cr}(C, c_*)\ \forall\, c :\ |c| < c_*$, if c_* is sufficiently small. □

4.3. Effect of the external signal

In this section, we give examples of inducing stability and instability of the coexistence equilibria by an external signal. Let $k > 0$ and $\hat{y} \in \mathbb{R}^n :\ |\hat{y}| = 1$, and consider the normal mode associated with the wave vector $\hat{x} = k\hat{y}$. The corresponding problem (4.3) depends on the sensing coefficient and the drift coefficient, $\check{\chi} = \hat{y}\mathcal{T}\hat{y}$ and $c = \hat{y} \cdot \boldsymbol{c}^e$. We set $\chi_* \stackrel{\text{def}}{=} \sup \hat{y}\mathcal{T}\hat{y} \geq \check{\chi}$, $c_* = |\boldsymbol{c}_e| \geq |c|$.

Without an external signal, the drift vanishes and the sensing tensor becomes trivial—that is, $\bar{\mathrm{V}}(\bar{\boldsymbol{w}}) = 0\ \forall\, \bar{\boldsymbol{w}}$, and therefore $\mathcal{T} = E$, $\boldsymbol{c}^e = 0$, and hence, $c_* = c = 0$, $\chi_* = \check{\chi} = 1$; see (3.16) and (3.40). We set $\mathcal{A}_{cr}^0 \stackrel{\text{def}}{=} \{\Pi \in \mathcal{A} :\ \inf_{k>0} \chi_{40}(\Pi, k) = 1\}$. This set is nonempty generically, and also in the case of Lotka–Volterra kinetics, for example. Further, let $C_{cr}^0 \subset \mathcal{A}_{cr}^0$ be a compact set, and then $\chi_4^*(C_{cr}^0) = 1 = \chi_{cr}(C_{cr}^0, 0)$; see Proposition 2. Thus, without a signal, set $\mathcal{A}_{cr}^0$ is a subset of the critical set of the equilibrium separating the regions of its stability and instability; see Section 4.1.

Suppose an external signal is supplied such that $c_* = 0$, for example, a stationary one (see Section 3.3.1), and let $\chi_* > 1$. Then $\forall\, \Pi \in \mathcal{A}_{cr}^0,\ \exists\, \hat{y}$ and $k > 0$, such that the wave vector $\hat{x} = k\hat{y}$ corresponds to an unstable mode, that is, the quasi-equilibrium is unstable. If, however, $\chi_* < 1$, then the quasi-equilibrium is stable.

In the case of a generic stationary signal, all eigenvalues of the matrix of the corresponding tensor $\mathcal{T}$ belong to the interval (0,1) (in view of Lemma 3 and Remark 11). Then $\chi_* < 1 = \chi_{cr} = \chi_{40}^*$. Hence, the quasi-equilibrium for a generic stationary signal is stable, while the corresponding equilibrium without a signal is critical in the sense of stability. Thus, a stationary signal has, generally speaking, a stabilizing effect. It manifests itself brightly if the external signal satisfies condition (3.23). Then the sensing tensor is diagonal, and its diagonal elements tend to zero exponentially as $A_0 \to \infty$, where A_0 is the characteristic value of the effective amplitudes of the additive components of the signal, $h_j = h_j(\xi_j)$; see formula (3.43) and Remark 10.

Now, let the external signal be defined by formula (3.44). Then it is an additive superposition of plane traveling waves propagating along the coordinate axes with velocities ω_j, $j = 1...n$. Let their effective amplitudes be tied to the characteristic value A_0. Here formula (3.45) determines the residual drift, and formulae (3.47) determine the sensing tensor, which is moreover diagonal. We fix $\epsilon > 0$ and

choose $A_0 > 0$ and $\omega_* > 0$ so that $\chi_* < 1 - \epsilon$ when $\sup_j \omega_j < \omega_*$. The possibility of such a choice follows from Remark 15, which also implies that there is a threshold $\omega^* > 0$ such that the inequality $\omega_j > \omega^*$ for at least one $j = 1...n$ entails the inequality $\chi_* > 1$. Let, for definiteness, $\omega_n > \omega^*$ and $\hat{y} = e_n$, and then $\boldsymbol{c}^e\hat{\boldsymbol{y}} > 0 = c_n = c$. Without loss of generality, we assume $c > 0$ and $e_n\mathcal{T}e_n = \chi_*$.

Further, in view of Remark 13, $c_j = O(\omega_j^{-1})$, $j = 1...n$, both as $\omega_n \to +0$ and as $\omega_n \to \infty$. We choose ω_* and ω^* so that for $\inf_j \omega_j > \omega^*$ or for $\sup_j \omega_j < \omega_*$, the quantity c_* is so small that both Propositions 1 and 2 hold. Then, having increased, if necessary, ω_*, we shall have $0 \neq |c| = |c_n| < c_*$ and $\chi_{cr}(C^0_{cr}, c_*) = \inf_{k>0,|c|<c_*,\Pi\in C^0_{cr}} \chi^-_{nt}(\Pi, c, k) < \chi^*_4(C^0_{cr}) = 1 < \chi_* \ \forall\, \Pi \in C^0_{cr}$.

At the same time, having decreased, if necessary, ω_*, $\forall\ \omega :\ \sup_j \omega_j < \omega_*$, we shall have

$$0 \neq |c| = |c| < c_* \text{ and } \chi^*_4(C^0_{cr}) = 1 > \chi_{cr}(C^0_{cr}, c_*) = \inf_{k>0,|c|<c_*,\Pi\in C^0_{cr}} \chi^-_{nt}(\Pi, c, k) > 1 - \epsilon = \chi_*.$$

Thus, we arrive at the following assertion. Choose a tuple of parameters Π on the critical set of the coexistence equilibrium of the system without an external signal, and let the signal have the form (3.44). The characteristic amplitude of such a signal can be chosen so that the coexistence quasi-equilibrium is stable when all the waves constituting the signal propagate with sufficiently small velocities and unstable when the propagation velocity of at least one of them is sufficiently large. Moreover, the threshold propagation velocities can be chosen the same for each compact subset of the critical set of the coexistence equilibrium of the system without an external signal.

Let us illustrate what has been said with a concrete example; see Figure 2. Consider a system with two spatial variables and with Lotka–Volterra kinetics, so that $x = (x_1, x_2)$, $\xi = (\xi_1, \xi_2)$, $\eta = (\eta_1, \eta_2)$, $f = \gamma q - \beta, \beta < \gamma$, $g = 1 - q - p$. Then $\exists\, \kappa = \kappa^0_{cr}(\gamma, \beta, \nu) > 0 : \mathcal{A}^0_{cr} \supset \{\delta_1 = 0, \delta_2 = 0, \kappa^0_{cr}(\gamma, \beta, \nu), \nu\}$. We set $k^0_{cr} = k_4(\Pi^0_{cr})$, where $\Pi^0_{cr} = (0, 0, \gamma, \beta, \kappa^0_{cr}, \nu)$. We fix $\gamma = 4/3, \beta = 1/3$. For C^0_{cr}, we choose one point of the parameter space with coordinates $\delta_1 = 0, \delta_2 = 0, \nu = 1, \kappa = \kappa^0_{cr}(4/3, 1/3, 1)$. This choice uniquely defines the magnitude of k^0_{cr}. Thus, without a signal, the parameters of the system are on the critical set of the equilibrium. For a stationary signal, the inequality $\chi_* > 1$ ($\chi_* < 1$) entails instability (stability) of the quasi-equilibrium. We choose the signal in the form (3.44), where $n = 2$, $h_1(\eta) = h_2(\eta) = \sin\eta$, and let $\omega_1 = 0$, $\omega_2 = \omega > 0$. For $\omega = 0$, we have $\mathcal{T}_{11} = \mathcal{T}_{22} = I_0(1)^{-2} < 0.7 < 1$ (I_0 is the modified Bessel function of the first kind), so that the quasi-equilibrium is stable. Let $\omega \neq 0$, consider the mode with wave vector $k^0_{cr}e_2$, where e_2 is the unit vector of the axis Ox_2. Now the quantity χ^-_{nt} is expressed as a function of c only, and c is a function of ω only. The quantity $\mathcal{T}_{22}$ also depends only on ω. The graphs of the functions $\chi^-_{nt}(\omega)$ and $\mathcal{T}_{22}(\omega)$ are shown in Figure 2 in red and blue, respectively. The mode with wave vector $k^0_{cr}e_2$ is unstable (stable) for the values of ω lying to the right (left) of the projection of the intersection point of these graphs onto the abscissa axis. It is worth noticing that the graphs' behavior for relatively small and relatively high values of the signal wave speed, ω, qualitatively matches what we have been saying above.

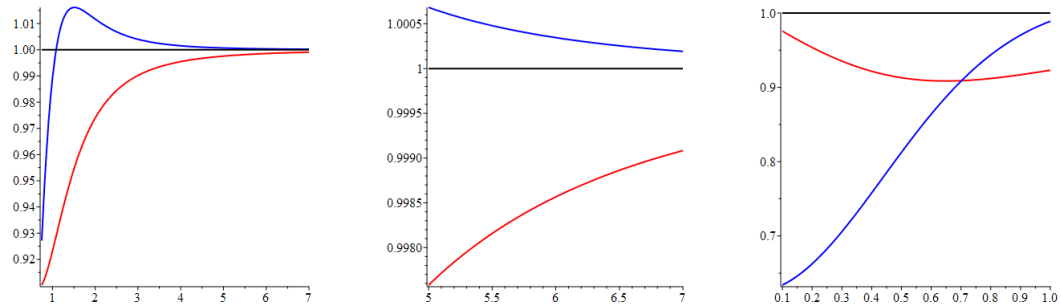

Figure 2. Three fragments of the graphs $\chi_{nt}^{-} = \chi_{nt}^{-}(\omega)$ (red) and $\mathcal{T}_{22} = \mathcal{T}_{22}(\omega)$ (blue). The black line corresponds to the critical value χ_* for a stationary signal.

5. Discussion and conclusions

We have addressed a spatial "predator–prey" system in multiple dimensions with indirect Patlak–Keller–Segel taxis driven by the cue field induced by the prey while assuming the cue field induction to be additionally influenced by a short-wave external signal. For this system, we have proposed a procedure for constructing asymptotics of arbitrarily high approximation order while assuming no special forms of the signal or of solutions or system kinetics. So, we have generalized the previous result [36] substantially.

The leading term of this asymptotics has the form of a short-wave parcel. Its amplitude undergoes slow modulation, which, in turn, is governed by the leading slow system, written in explicit form. The latter, in comparison with the original system without a signal, exhibits two main features caused only by the external signal: predator drift and modification of the kinetics of the system. By "drift" we mean the deviation of the advection velocity of predators from the cue gradient. We present a particular class of signals that allows for expressing the drift explicitly. The interesting question for further investigations is whether the long-term evolution of the aforementioned package brings it into a soliton-like form.

The kinetics of the system is not modified if it is p-linear—that is, the kinetic terms $pf(p,q)$ and $qg(p,q)$ are linear in p. Interestingly, this type of kinetics is widely recognized in population dynamics; *cf.* article [49] and monograph [50] for more information on the subject.

Since the original system without a signal possesses translational invariance, the leading slow system inherits it under the condition that the external signal does not undergo slow modulation. This case allows one to identify quasi-equilibria—that is, short-wave solutions not subject to slow modulation—with homogeneous equilibria of the leading slow system and to consider the induced stability by analogy with the theory of the inverted pendulum of P. Kapitza. The external signal influences the stability of these equilibria through three types of control parameters depending only on the signal, namely, the components of the residual drift velocity of the predators, $\boldsymbol{c}^e$, the components of the sensing tensor, $\mathcal{T}$, and the components of the two cue drift velocity vectors, $\boldsymbol{b}_i^e$, $i = 1, 2$, arising upon the linearization of the modified kinetics. Furthemore, $\boldsymbol{c}^e = 0$ in the case of stationary external signals and $\boldsymbol{b}_i^e = 0$, $i = 1, 2$, in the case of p-linear kinetics.

The sensing tensor measures the anisotropy of the sensing of predators to the cue. A typical stationary external signal generates a sensing tensor indicating that the sensing is to some extent suppressed in any direction. Moreover, there exists a class of stationary signals for which the sensing

tensor is computed explicitly, and on this basis, we have discovered the examples of exponential decay of the sensing along one or several spatial coordinate axes as the intensity of the external signal grows. At the same time, a nonstationary external signal can enhance the sensing and tactic transport in certain directions. In particular, we have observed the inversion of the effect of the external signal having the form of a superposition of waves of fixed profiles traveling along different coordinate axes. Namely, such a signal destabilizes the quasi-equilibrium when the propagation velocity of at least one wave is sufficiently large and stabilizes it when the velocities of all waves are sufficiently small. This destabilization can be described as a kind of blurring of the boundary between the stability and instability regions existing in the parameter space of the system without a signal. We are not aware of examples of a "predator–prey" system with taxis, direct or indirect, that admits destabilization of the coexistence equilibrium solely due to the external signal, in the sense that the equilibrium becomes stable for any set of parameters of the system when the external signal is off.

The stability of an individual mode depends substantially on the direction of the wave vector $\hat{\boldsymbol{x}}$. Among the modes corresponding to the same $|\hat{\boldsymbol{x}}|$, the choice of the most dangerous one (in the sense of instability) depends on the relations between $\boldsymbol{c}^e \cdot \hat{\boldsymbol{x}}$ and $\hat{\boldsymbol{x}} \cdot \mathcal{T}\hat{\boldsymbol{x}}$. In view of this, questions naturally arise concerning the control and optimization of the residual drift and the sensing tensor, and the same can be asked about the nonlinear drift, $\bar{\mathrm{V}}$. This remains for future research.

Although the leading term of the asymptotics gives us a summary of the most essential information about the solution, higher-order terms (*cf.* Appendix B) may play an important role in justifying the asymptotic approximation. We are optimistic about the possibility of solving this issue in the future, since there is considerable positive experience in similar problems [54–59].

In conclusion, we note that the homogenization of the response to a short-wave external signal proposed in this article reduces to solving linear parabolic equations to evaluate the drift, which is anyway feasible using numeric techniques. Hence, there exists a relatively simple possibility of predicting the behavior of predator–prey-type systems with taxis in short-wave external fields and controlling them by means of artificially created external signals.

Author contributions

A. Morgulis: Conceptualization, methodology, writing—review and editing, supervision; K. Malal: Formal analysis, investigation, writing—original draft preparation. All authors have read and agreed to the published version of the manuscript.

Use of Generative-AI tools declaration

The authors declare they have not used Artificial Intelligence (AI) tools in the creation of this article.

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Conflict of interest

The authors declare no conflicts of interests.

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Appendices

A. Appendix A. Details of the proofs

A.1. Differentiability of $\check{\Phi}$

Recall the differential operator $\mathcal{L} = \mathcal{L}(\boldsymbol{w}, \epsilon) : \mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau}) \to \mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau})$ and its right inverse $\mathcal{L}^{-1}(\boldsymbol{w}, \epsilon) : \widetilde{\mathrm{L}}_2(\mathbb{T}^{n+1}_{\xi,\tau}) \to \widetilde{\mathrm{L}}_2(\mathbb{T}^{n+1}_{\xi,\tau})$ introduced by Definition 1 and Remark 2, together with the mapping $\Phi : \boldsymbol{w} \to \Phi(\boldsymbol{w}, \epsilon)$. Here the wide-tilde notation specifies range$(I - M)$-subspace, where M is the averaging operator over the torus.

Lemma 4. *Given* $\boldsymbol{w} \in \mathrm{C}^\infty(\mathbb{T}^{n+1}_{\xi,\tau}, \mathbb{R}^n)$ *and* $\epsilon > 0$*, the mapping* $\check{\Phi} : y \mapsto \Phi(\boldsymbol{y} + \boldsymbol{w}, \epsilon)$*, where* $y \in \mathbb{R}^n$ *and* $\boldsymbol{y}$ *is the vector field on the torus that corresponds to* y*, is* L_2*-differentiable at the origin and*

$$d\check{\Phi}(v)\,|_{y=0} = -v_i\phi_{*i},\ i = 1...n, \quad \phi_{*i} = \mathcal{L}^{-1}(\boldsymbol{w}, \epsilon)\partial_{\xi_i}\check{\Phi}(0),$$

where the summation convention is in effect.

Proof. Consider the operator family $y \to \mathcal{L}(\boldsymbol{y} + \widetilde{\nabla}\tilde{s}_1, \mu_1)$ consisting of the operators specified by Definition 1. Given this family member, Lemma 1 describes its spectral projector, P. The well-known results in the perturbation theory for the linear operators imply that the operator-valued function, P, is analytic in y in some neighborhood of the origin. Then the conjugated function, P^* is analytic too, and its differential, $P^*_1 : v \to P^*_1 v$, satisfies the limit identity $\rho^{-1}(P^*_1(\rho y) - P^*_1(0)) \to P^*_1 y$, $\rho \to 0$, relative to the uniform operator topology. Hence, by the definition of projector $P(y)$,

$$\rho^{-1}\langle\psi_1(\check{\Phi}(\rho y) - \check{\Phi}(0))\rangle\langle\psi_2\rangle = \rho^{-1}\langle\psi_1(P(\rho y) - P(0))\psi_2\rangle \to \langle\psi_1(P_1 y)\psi_2\rangle\ \forall\ \psi_1, \psi_2 \in \mathrm{L}_2 \Rightarrow \quad \text{(A.1)}$$
$$\langle\psi_1(P_1 y)\psi_2\rangle = 0\ \forall\ \psi_2 :\ \langle\psi_2\rangle = 0,$$

and this, in turn, entails the following assertion:

$$\exists\,\{\phi_{*i},\ i = 1...n\} \subset \mathrm{L}_2 : \langle\phi_{*i}\rangle = 0,\ (P_1 v)\psi = \langle\psi\rangle\phi_{*i}v_i,$$

where the summation agreement is in effect. The constraints imposed here on functions ϕ_{*i} are necessary to obey the condition $PP_1 + P_1P = P_1$, which, in turn, follows from the projector-valuedness of function P. Moreover, by limit identity (A.1) (written for $\psi_2 = 1$), $\forall\,\delta > 0$, $\exists\rho > 0$:

$$\langle\psi_1(\rho^{-1}(\check{\Phi}(\rho y) - \check{\Phi}(0)) - \phi_{*i}y_i)\rangle \le \delta\|\psi_1\|,$$

and this is the L_2-differentiability of the mapping $y \mapsto \phi_* = \check{\Phi}(y) = P(y)1$ at the origin. For calculating the corresponding differential, let us note that $\langle(P(y)1)\check{\mathcal{L}}^*(y)\psi\rangle = 0\ \forall\psi$, where $\check{\mathcal{L}}(y) = \mathcal{L}(\boldsymbol{w} + \boldsymbol{y}, \epsilon)$ and $\check{\mathcal{L}}(y) = \mathcal{L}^*(0) - \boldsymbol{y}\widetilde{\nabla}$. Hence,

$$0 = d(y \mapsto \langle\check{\Phi}(y)\check{\mathcal{L}}^*(y)\psi\rangle)\Big|_{y=0}(v) = (\langle\phi_{*i}\check{\mathcal{L}}^*(0)\psi\rangle - \langle\phi_*\psi_{\xi_i}\rangle)v_i,\ \text{where } \phi_* = \check{\Phi}(0).$$

These identities (valid for every test function ψ (in the fast variables) and every $v \in \mathbb{R}^n$) give the weak formulations to the following equations:

$$\check{\mathcal{L}}(0)\phi_{*i} = -\phi_{*\xi_i},\ \langle\phi_{*i}\rangle = 0, \quad i = 1...n. \quad \text{(A.2)}$$

Additional constrains, $\langle\phi_{*i}\rangle = 0$, arise once again from differentiating the constraint $\langle P\check{\Phi}(y)\rangle = 1\ \forall\, y$. However, they get satisfied by the construction of the right inverse to $\mathcal{L}$; see Remark 2. Hence, we arrive at what the lemma claims. □

A.2. Proof of Lemma 3

Define the Hilbert space $\mathrm{L}_{2,\mathfrak{e}}$ as the vector space of L_2-summable real vector fields on the torus $\mathbb{T}^n_\xi$, equipped with the metric

$$\|\boldsymbol{w}\|^2_{\mathfrak{e}} = \langle \mathfrak{e}\boldsymbol{w}^2\rangle.$$

Let $\bar{\boldsymbol{u}} = (u_1, .., u_n)$ and $\bar{\boldsymbol{v}} = (v_1, .., v_n)$ be a pair of vector fields on the torus of fast variables, associated with constant vectors in $\mathbb{R}^n$, and $\mathcal{L} = \mathcal{L}(\widetilde{\nabla}\tilde{s}, \mu_1)$. Since $\widetilde{\nabla}\tilde{s} = -\mu_1 \mathfrak{e}\widetilde{\nabla}\mathfrak{e}^{-1}$, we have $\mathcal{L}u = -\mu_1\widetilde{\nabla}\cdot(\mathfrak{e}\widetilde{\nabla}(\mathfrak{e}^{-1}u))$. Further,

$$u_j v_k \langle \mathfrak{e}\rangle\langle \phi_{*j}\tilde{s}_{\xi_k}\rangle = \mu_1\langle(\bar{\boldsymbol{v}}\widetilde{\nabla}\tilde{s})\mathcal{L}^{-1}(\bar{\boldsymbol{u}}\widetilde{\nabla}\mathfrak{e})\rangle = -\mu_1\langle \bar{\boldsymbol{v}}\mathfrak{e}\widetilde{\nabla}\mathfrak{e}^{-1}\mathcal{L}^{-1}\widetilde{\nabla}\cdot(\mathfrak{e}\bar{\boldsymbol{u}})\rangle.$$

We continue the right-hand side of the last equality in a natural way to a bilinear form on the space $\mathrm{L}_{2,\mathfrak{e}}$, which we transform as follows (we omit the coefficient μ_1):

$$-\langle \boldsymbol{v}\mathfrak{e}\widetilde{\nabla}\mathfrak{e}^{-1}\mathcal{L}^{-1}\widetilde{\nabla}\cdot(\mathfrak{e}\boldsymbol{u})\rangle = \langle\widetilde{\nabla}\cdot(\mathfrak{e}\boldsymbol{v})\mathfrak{e}^{-1}\mathcal{L}^{-1}\widetilde{\nabla}\cdot(\mathfrak{e}\boldsymbol{u})\rangle = \langle\widetilde{\nabla}\cdot(\mathfrak{e}\boldsymbol{v})\Big((I-M)(\mathfrak{e}^{-1}\mathcal{L}^{-1})\Big)\widetilde{\nabla}\cdot(\mathfrak{e}\boldsymbol{u})\rangle. \tag{A.3}$$

Here it is useful to note that $\langle f, Mg\rangle = 0$ if $\langle g\rangle\langle f\rangle = 0$. Recall that the space $\widetilde{\mathrm{L}_2}$ consists of square-summable scalar functions on the torus with zero mean and is equipped with the metric $|f|^2 = \langle ff^*\rangle$. Define the operator $\mathcal{L}_{\mathfrak{e}} : \widetilde{\mathrm{L}_2} \to \widetilde{\mathrm{L}_2}$ by the mapping $\mathcal{L}_{\mathfrak{e}} : \eta \mapsto -\mu_1\widetilde{\nabla}\cdot(\mathfrak{e}\widetilde{\nabla}\eta)$. It is symmetric and has a bounded right inverse $(I-M)\mathfrak{e}^{-1}\mathcal{L}^{-1} : \widetilde{\mathrm{L}_2} \to \widetilde{\mathrm{L}_2}$, which, hence, is symmetric. Therefore the bilinear forms forming the chain (A.3) are symmetric. Thus, there arises a symmetric bounded operator $Q : \mathrm{L}_{2,\mathfrak{e}} \to \mathrm{L}_{2,\mathfrak{e}}$, $Q : \boldsymbol{u} \mapsto -\mu_1\widetilde{\nabla}\Big((I-M)(\mathfrak{e}^{-1}\mathcal{L}^{-1})\Big)\widetilde{\nabla}\cdot(\mathfrak{e}\boldsymbol{u})$, where the factor $(I-M)$ can be omitted. Moreover, the operator Q is a projector and an orthogonal projector (since it is symmetric). Indeed,

$$Q^2\boldsymbol{u} = \mu_1^2\widetilde{\nabla}\mathfrak{e}^{-1}\mathcal{L}^{-1}\widetilde{\nabla}\cdot(\mathfrak{e}\widetilde{\nabla}(\mathfrak{e}^{-1}\mathcal{L}^{-1}\widetilde{\nabla}\cdot(\mathfrak{e}\boldsymbol{u}))) = -\mu_1\widetilde{\nabla}\mathfrak{e}^{-1}\mathcal{L}^{-1}\widetilde{\nabla}\cdot(\mathfrak{e}\boldsymbol{u}) = Q\boldsymbol{u}.$$

Hence,

$$u_j u_k\langle\mathfrak{e}\rangle\langle\phi_{*j}\tilde{s}_{1\xi_k}\rangle = (\bar{\boldsymbol{u}}, Q\bar{\boldsymbol{u}})_{\mathfrak{e}} \geq 0 \quad \text{and} \quad u_j u_k\langle\mathfrak{e}\rangle\langle\phi_{*j}\tilde{s}_{1\xi_k}\rangle \leq \|\bar{\boldsymbol{u}}\|^2_{\mathfrak{e}} = \langle\mathfrak{e}\rangle\sum_i u_i^2.$$

Suppose that $Q\bar{\boldsymbol{u}} = \bar{\boldsymbol{u}}$. Then $\bar{\boldsymbol{u}} = \widetilde{\nabla}\phi$, which is false for a function on the torus. This completes the proof, since $\bar{\boldsymbol{u}}\mathcal{T}\bar{\boldsymbol{u}} = \bar{\boldsymbol{u}}^2 - (\bar{\boldsymbol{u}}, Q\bar{\boldsymbol{u}})_{\mathfrak{e}}\langle\mathfrak{e}\rangle^{-1}$. □

Remark 18. Let the external signal $\tilde{h} = \tilde{h}(\xi)$ be invariant with respect to translations along some subspace in $\mathbb{R}^n_\xi$. Then there exists vector $\bar{\boldsymbol{w}}$ such that $\bar{\boldsymbol{w}}\widetilde{\nabla}\mathfrak{e} = 0 = \widetilde{\nabla}\cdot(\mathfrak{e}\bar{\boldsymbol{w}})$, and hence $Q\bar{\boldsymbol{w}} = 0$. The converse is also true. Hence, a generic stationary signal generates a sensing tensor such that each of its eigenvalues is strictly less than unity.

B. Appendix B. Higher approximations

Here we address the chain of equation arising for the terms of order $k \geq 3$ of expansion (1.7). Bearing in mind what we already know about the terms of lowest orders, we write these equations as follows

$$\mathcal{L}(\boldsymbol{w}_0, \mu_1)p_{k-1} = \mu_1\Delta p_{k-3} - (\partial_t - \mu_1\mathcal{D})p_{k-2}$$

$$+\sum_{j=0..k-2}(p_j f_{k-2-j}-\nabla\cdot(p_j\boldsymbol{w}_{k-2-j})-\widetilde{\nabla}\cdot(p_j\boldsymbol{w}_{k-1-j})), \tag{B.1}$$

$$\text{where}\quad \boldsymbol{w}_m=(\nabla s_m+\widetilde{\nabla}s_{m+1}),\ m=0,1,\dots,$$

$$-\widetilde{\Delta}q_k=\sum_{j=0..k-2}q_j g_{k-2-j}-(\partial_\tau-\mathcal{D})\,q_{k-1}-(\partial_t-\Delta)q_{k-2}, \tag{B.2}$$

$$\mathcal{H}_{\mu_2}s_k=\kappa q_{k-1}-\nu s_{k-1}-(\partial_t-\mu_2\mathcal{D})s_{k-1}+\mu_2\Delta s_{k-2}, \tag{B.3}$$

where coefficients f_k, g_k result from expanding the reaction terms as follows

$$f(p,q)=\sum_{m=0}f_m\delta^m,\ f_0=f(p_0,q_0),\quad g(p,s)=\sum_{m=0}g_m\delta^m,\ g_0=g(p_0,q_0). \tag{B.4}$$

We have omitted the explicit expressions here for the exposition's compactness.

In this appendix, we have to deal with the projection of various functions arising from the decompositions of the space $\mathrm{L}_2(\mathbb{T}^{n+1}_{\xi,\tau})$ due to the actions of projective operators M, M^τ, M^ξ, P; see Section 2 for their definitions. For convenience, we set the notations for these as follows. Given a function f, define

$$\bar f=\langle f\rangle=Mf,\ \widetilde{f}=(I-M)f,\quad \overline{f}^{\xi}=M^\xi f,\ \widetilde{f}^{\xi}=(I-M^\xi)f,\quad \overline{f}^{\tau}=M^\tau f,\ \widetilde{f}^{\tau}=(I-M^\tau)f,$$
$$\widetilde{f}^{\sharp}=(M^\xi-M)f,\quad f^\bullet=Pf=\langle f\rangle\phi_*,\ f^\circ=(I-P)f,$$

so that $f=\bar f+\tilde f=f^\bullet+f^\circ,\quad f=\bar f+\widetilde{f}^{\sharp}+\widetilde{f}^{\xi},\quad \tilde f=\widetilde{f}^{\xi}+\widetilde{f}^{\sharp}$.

We recall that each equation in the chain of Eqs (B.1)–(B.3) has to be solved on the torus $\mathbb{T}^{n+1}_{\xi,\tau}$. For the subsequent analysis, it is substantial to see the triangle form of system (B.1)–(B.3). Indeed, the system allows for isolating unknowns s_k and q_k from the third and second equations correspondingly and then isolating p_{k-1} from the first one, provided all these equations are compatible. It turns out that the compatibility of every separate equation in system (B.1)–(B.3) makes it compatible as a whole.

We restore the notation $\tilde s_1$ in accordance with Eq (3.14). For the compactness of the layout, we will use the notation Op_m, $m=1,2,3,\dots$, for every operation (possibly differential or non-local) on only those coefficients p_k, q_k, s_k that are indexed by $k\le m$. For instance,

$$\sum_{j=0..m}p_j f_{m-j}-a_1(p_m,q_m)=\sum_{j=1..m-1}p_j f_{m-j}=Op_{m-1},$$
$$\sum_{j=0..m}q_j g_{m-j}-a_2(p_m,q_m)=\sum_{j=1..m-1}q_j g_{m-j}=Op_{m-1},$$

where linear functions a_i are to be evaluated by formulae (3.36) using coefficients p_0 and q_0 taken from the leading term in the asymptotics. Besides, it follows from Eqs (B.2) and (B.3) that

$$\tilde s_m=Op_{m-1},\quad \widetilde{q}^{\xi}_m=Op_{m-1},\ \widetilde{q}^{\tau}_m=Op_{m-1},\tilde q_m=\widetilde{q}^{\xi}_m+\widetilde{q}^{\tau}_m=Op_{m-1}. \tag{B.5}$$

At the same time,

$$p^\circ_m=\bar p\mathcal{L}^{-1}(\boldsymbol{w}_0,\mu_1)\widetilde{\nabla}\phi_*\nabla\bar s_m+Op_{m-1}.$$

Indeed, it is obvious that

$$p^\circ_m=\mathcal{L}^{-1}(\boldsymbol{w}_0,\mu_1)((\bar p\widetilde{\nabla}\phi_*\nabla\bar s_m)+\widetilde{\nabla}\cdot(p_0\widetilde{\nabla}\tilde s_{m+1}))+Op_{m-1}, \tag{B.6}$$

and the second summand can also be identified with an Op_{m-1} expression, since

$$\tilde{s}_{m+1} = \mathcal{H}_{\mu_2}^{-1}(\kappa\tilde{q}_m - \nu\tilde{s}_m + \mu_2\Delta\tilde{s}_{m-1} - (\partial_t - \mu_2\mathcal{D})\tilde{s}_m) = Op_{m-1}.$$

Additionally, we define a pair of functions, $\bar{a}_i : \mathbb{R}^2 \to \mathbb{R}$, $i = 1, 2$, and a pair of vector fields, $\boldsymbol{b}_i$, $i = 1, 2$, by formulae (3.34)–(3.36) for $p_0 = \bar{p}\phi_*$, $q_0 = \bar{q}$, where $\bar{p}$, $\bar{q}$ are the solutions to the leading slow system that determine the leading term in the asymptotics.

Definition 3. *By the slow system of order $\ell = 1, 2, \ldots$, we mean the system of equations for the unknown functions $\bar{p}_\ell, \bar{q}_\ell, \bar{s}_\ell$ in the slow variables x, t, which reads*

$$\bar{p}_{\ell,t} + \nabla\cdot(\bar{p}_\ell\bar{\boldsymbol{v}} + \bar{p}\nabla\bar{s}_\ell) - \bar{\boldsymbol{b}}_1\nabla\bar{s}_\ell - \bar{a}_1(\bar{p}_\ell, \bar{q}_\ell) = \mu_1\Delta\bar{p}_{\ell-1} + \langle a_1(r_\ell, \tilde{q}_\ell) - \nabla\cdot(p_0\tilde{\boldsymbol{w}}_\ell)\rangle + \sum_{j=1..\ell-1}\left\langle p_j f_{\ell-j} - \nabla\cdot(p_j\boldsymbol{w}_{\ell-j})\right\rangle, \tag{B.7}$$

$$(\partial_t - \Delta)\bar{q}_\ell - \bar{\boldsymbol{b}}_2\nabla\bar{s}_\ell - \bar{a}_2(\bar{p}_\ell, \bar{q}_\ell) = \left\langle a_2(r_\ell, \tilde{q}_\ell) + \sum_{j=1..\ell-1} q_j g_{\ell-j}\right\rangle, \tag{B.8}$$

$$\bar{s}_{\ell,t} + \nu\bar{s}_\ell - \kappa\bar{q}_\ell = \mu_2\Delta\bar{s}_{\ell-1}, \tag{B.9}$$

where $\bar{\boldsymbol{v}} = \nabla\bar{s} + \bar{\nabla}(\nabla\bar{s})$, $\boldsymbol{w}_m = \nabla s_m + \widetilde{\nabla}s_{m+1}$, $r_\ell = p_\ell^\circ - \mathcal{L}^{-1}(\boldsymbol{w}_0, \mu_1)\widetilde{\nabla}\phi_*\nabla\bar{s}_\ell$.

Remark 19. The right-hand sides in the equations of the slow system of order ℓ are $Op_{\ell-1}$-expressions.

Theorem 2. *Let $\ell > 0$, and suppose that for every $m = 0...\ell - 1$, the triad of coefficients p_m, q_m, s_m in expansion* (1.7) *is known and is such that (a) the triad of their mean values, $\bar{p}_m, \bar{q}_m, \bar{s}_m$, yields a solution to the slow system of order m (where $m = 0$ corresponds to the leading slow system); (b) the triad p_{m-1}, q_m, s_m satisfies the system of Eqs* (B.1)–(B.3) *with $k = m$. Finally, assume that the slow system of order ℓ admits a solution $\bar{p}_\ell, \bar{q}_\ell, \bar{s}_\ell$. Then the coefficients p_ℓ, q_ℓ, s_ℓ are determined completely and in such a way that*
(i) the triad $p_{\ell-1}, q_\ell, s_\ell$ solves the system of Eqs (B.1)–(B.3) *for $k = \ell$, and*

$$p_{\ell-1} = \bar{p}_{\ell-1}\phi_* + \bar{p}\mathcal{L}^{-1}(\boldsymbol{w}_0, \mu_1)\widetilde{\nabla}\cdot(\phi_*\nabla\bar{s}_{\ell-1}) + Op_{\ell-2}, \quad q_\ell = \bar{q}_\ell + Op_{\ell-2}, \quad s_\ell = \bar{s}_\ell + Op_{\ell-2};$$

(ii) for $k = \ell + 1$, the system of Eqs (B.1)–(B.3) *admits a solution $p_\ell, q_{\ell+1}, s_{\ell+1}$, such that*

$$p_\ell = \bar{p}_\ell\phi_* + \bar{p}\mathcal{L}^{-1}(\boldsymbol{w}_0, \mu_1)\widetilde{\nabla}\cdot(\phi_*\nabla\bar{s}_\ell) + Op_{\ell-1}, \quad q_{\ell+1} = \bar{q}_{\ell+1} + Op_{\ell-1}, \quad s_{\ell+1} = \bar{s}_{\ell+1} + Op_{\ell-1},$$

where the mean values $\bar{q}_{\ell+1}, \bar{s}_{\ell+1}$ of coefficients $q_{\ell+1}, s_{\ell+1}$ remain undetermined;
(iii) for $k = \ell + 2$, the Eqs (B.1) *and* (B.2) *allow one to isolate the following unknowns:*

$$p_{\ell+1} = \bar{p}_{\ell+1}\phi_* + \bar{p}\mathcal{L}^{-1}(\boldsymbol{w}_0, \mu_1)\widetilde{\nabla}\cdot(\phi_*\nabla\bar{s}_{\ell+1}) + Op_\ell, \quad q_{\ell+2} = \bar{q}_{\ell+2} + Op_\ell,$$

where the mean values $\bar{q}_{\ell+2}$, $\bar{s}_{\ell+1}$, and $\bar{p}_{\ell+1}$ remain undetermined.

Proof. The compatibility conditions for Eqs (B.1)–(B.3) are equivalent to the orthogonality of their right-hand sides to the kernels of the operators adjoint to those staying in their left-hand sides (see Section 2). This observations leads to the following equalities:

$$\bar{p}_{k-2,t} + \nabla\cdot\langle p_{k-2}\boldsymbol{w}_0 + p_0\boldsymbol{w}_{k-2}\rangle = \mu_1\Delta\overline{p}_{k-3} + \tag{B.10}$$

$$\left\langle a_1(p_{k-2}, q_{k-2}) + \sum_{j=1..k-3} p_j f_{m-j} \right\rangle, \quad \text{where} \quad \boldsymbol{w}_m = \nabla s_m + \widetilde{\nabla} s_{m+1},$$

$$\partial_\tau \overline{q}^{\xi}_{k-1} = M^{\xi}\left((\Delta - \partial_t)\overline{q}^{\xi}_{k-2} + a_2(p_{k-2}, q_{k-2}) + \sum_{j=1..k-3} q_j g_{k-2-j}\right), \tag{B.11}$$

$$\bar{s}_{k-1,t} + \nu \bar{s}_{k-1} = \kappa \bar{q}_{k-1} + \mu_2 \Delta \bar{s}_{k-2}. \tag{B.12}$$

Comparing this system with its predecessors shows that Eq (B.10) in fact coincides with Eq (B.7) of the slow system of order $\ell = k-2$, the compatibility condition for Eq (B.11) coincides with Eq (B.8) of the slow system of order $\ell = k-2$, and Eq (B.12) coincides with Eq (B.9) of order $\ell = k-1$. Hence, resolving the slow system of order ℓ enables us to isolate the unknown $q_{\ell+2}$ from Eq (B.2) with $k = \ell+2$, then $s_{\ell+1}$ from (B.3) with $k = \ell+1$, and finally $p_{\ell+1}$ from (B.1) with $k = \ell+2$. This gives us

$$p_{\ell+1} = p^{\bullet}_{\ell+1} + \mathcal{L}^{-1}(\boldsymbol{w}_0, \mu_1)(\mu_1 \Delta p_{\ell-1} - (\partial_t - \mu_1 \mathcal{D}) p_\ell + \sum_{j=0..\ell} (p_j f_{\ell-j} - \nabla \cdot (p_j \boldsymbol{w}_{\ell-j}) - \widetilde{\nabla} \cdot (p_j \boldsymbol{w}_{\ell+1-j}))), \tag{B.13}$$

$$\text{where} \quad \boldsymbol{w}_m = \nabla s_m + \widetilde{\nabla} s_{m+1}, \; p^{\bullet}_{\ell+1} = \bar{p}_{\ell+1} \Phi(\nabla \bar{s} + \widetilde{\nabla} \tilde{s}_1, \mu_1),$$

$$q_{\ell+2} = \bar{q}_{\ell+2} + \partial_\tau^{-1} M^{\xi}\left((\Delta - \partial_t) q_\ell + \sum_{j=0..\ell} q_j g_{\ell-j}\right) + \tag{B.14}$$

$$\widetilde{\Delta}^{-1}\left((\partial_\tau - \mathcal{D}) q_{\ell+1} - (\Delta - \partial_t) q_\ell - \sum_{j=0..\ell} q_j g_{\ell-j}\right),$$

$$s_{\ell+1} = \bar{s}_{\ell+1} + \mathcal{H}^{-1}_{\mu_2}\left(\kappa q_\ell - \nu s_\ell + \mu_2 \Delta s_{\ell-1} - (\partial_t - \mu_2 \mathcal{D}) s_\ell\right). \tag{B.15}$$

From Eqs (B.13)–(B.15), it follows that

$$p_{\ell+1} = \bar{p}_{\ell+1} \phi_* + \bar{p} \mathcal{L}^{-1}(\boldsymbol{w}_0, \mu_1) \widetilde{\nabla} \cdot (\phi_* \nabla \bar{s}_{\ell+1}) + O p_\ell, \tag{B.16}$$

$$q_{\ell+2} = \bar{q}_{\ell+2} + O p_\ell, \tag{B.17}$$

$$s_{\ell+1} = \bar{s}_{\ell+1} + O p_{\ell-1}. \tag{B.18}$$

From equalities (B.16)–(B.18) written for the index ℓ shifted down by 2, it follows that $p_{\ell-1}$ and q_ℓ are completely determined under the assumptions of the theorem. Similarly, shifting the same index down by 1 leads to the unknowns s_ℓ and p_ℓ being determined completely. Also, $q_{\ell+1}$ is determined up to its mean value. Finally, without shifting the index, we see that $q_{\ell+2}$ and $s_{\ell+1}$ can be determined up to their mean values, and $p_{\ell+1}$ admits the representation (B.16) (where the first two terms remain undetermined). Hence, all the assertions of Theorem 2 hold true under the assumptions stated therein. □

Remark 20. For an arbitrarily specified approximation order, the asymptotic solution (1.7) is attainable by an iterative process consisting of successively solving the slow systems and systems (B.1)–(B.3). These are linear systems, except for the leading slow one. Of course, constructing the whole sequence of approximations includes solving the whole sequence of the slow systems. Exploring their solvability is beyond the scope of this study. At the same time, this is likely not a very hard problem, as there are significant advances in exploring the solvability of so-called parabolic-hyperbolic models of tactic motions, which are obviously close relatives to our slow systems; *cf.* articles [60,61] and the references therein. Anyway, we leave this issue for future work.

C. Appendix C. Hankel's determinants

This appendix contains several explicit expressions involving Hankel's determinants. We assume the parameters to satisfy restrictions (4.1) and (4.5). For avoiding too-bulky expressions, we set $\delta_1 = \delta_2 = 0$, that is, we remove the artificial diffusivity and get back to the eigenvalue problem arising directly from the linearized leading slow system. For the same purpose, we use the following notation:

$$a_{12} = a^2, \quad -a_{22} = F^2, \quad a^2 a_{2,1} = -G^2, \quad z = k^2.$$

Also, all the notations of Sections 4.2 and 4.3 remain valid. In particular, $p_e > 0$ denotes the equilibrium density, which is also the quasi-equilibrium one by the assumed p-linearity.

Thus, $\Delta_2 = F^2 + \nu + z$,

$$\Delta_4 = \left(\nu^2 + \left(F^2 + z\right)\nu + G^2\right)\left(F^2 + z\right)\left(F^2 + \nu + z\right) - \check{\chi} G^2 p_e\, z\,\kappa\, \left(F^2 + \nu + z\right)a^{-2},$$

$$\chi_{40}(\Pi, k) = \tfrac{\left(F^2+z\right)\left(\nu^2+\left(F^2+z\right)\nu+G^2\right)a^2}{G^2 p_e\, z\,\kappa},$$

$$k_4^2(\Pi) = \nu^{-1} FR,\ R = \sqrt{\nu(F^2\nu + G^2 + \nu^2)},$$

$$\chi_4^*(\Pi) = \inf \chi_{40}(\Pi, k) = \tfrac{a^2\left(\nu F^2+FR+G^2+\nu^2\right)(\nu F+R)}{\kappa p_e G^2 R}.$$

Obviously, the equation $\chi_4^*(\Pi) = 0$ allows for isolating the variable κ and this determines a smooth function $\kappa = \kappa_4$. So, $\mathcal{A}_0 \neq \varnothing$. Further,

$$\Delta_6 = \left(a^{-2} z p_e \kappa G^2 \check{\chi}\right)^3 -$$
$$2(a^{-2}\check{\chi} z\kappa p_e G^2)^2 \left(\left(F^2 + z\right)\nu^2 + \left(F^4 + 2\,zF^2 - G^2/2 + z^2\right)\nu + G^2\left(F^2 + z\right)\right)$$
$$+ a^{-2}\check{\chi} z\kappa\, p_e (F^2 + z) G^2 \left\{\left(F^2 + z\right)\nu^4 +\right.$$
$$\left(2\,z^2 + \left(4\,F^2 - c^2\right)z + 2\,F^4 - 2\,G^2\right)\nu^3 +$$
$$\left(F^2 + z\right)\left(z^2 + \left(2\,F^2 - 2\,c^2\right)z + F^4\right)\nu^2 +$$
$$\left(-c^2 z^3 + \left(-2\,F^2 c^2 + 2\,G^2\right)z^2 + \left(-F^4 c^2 + 4\,F^2 G^2\right)z + 2\,G^2 F^4 - 2\,G^4\right)\nu + G^4\left(F^2 + z\right)\Big\}$$
$$+ \nu\left(F^2 + z\right)^2 G^2 \left\{\nu^4 + \left(2\,F^2 + 2\,z\right)\nu^3 + \left(z^2 + \left(2\,F^2 + c^2\right)z + F^4 + 2\,G^2\right)\nu^2 +\right.$$
$$\left. 2\left(c^2 z + G^2\right)\left(F^2 + z\right)\nu + F^4 c^2 z + 2\,F^2 c^2 z^2 + c^2 z^3 + G^4\right\}.$$

By this expression, it follows that determinant Δ_6 is a third-order polynomial in $\check{\chi}$, positive for $\check{\chi} = 0$ and $\check{\chi} \to \infty$ (for an arbitrarily fixed collection of the remaining parameters) as we have claimed in Section 4.2. Furthermore,

$$\Delta_6|_{c=0}\Delta_2^2\Delta_4^{-2} = (\check{\chi} p_e z\kappa + a^2\nu)G^2/a^2$$

as we have claimed in Section 4.2. At the same time,

$$\tfrac{\partial_z^5 \Delta_6}{5!} = \tfrac{\left(p_e \check{\chi}\,\kappa\left(\nu - c^2\right) + c^2 a^2\right)\nu G^2}{a^2}.$$

Hence, the leading term in Δ_6 remains positive as $k \to +\infty$ provided that c is small enough; say, $c^2 < \nu$. This is exactly what we have claimed in Section 4.2. Finally, substituting $\check{\chi} = \chi_{40} + \epsilon c$ transforms the equation $\Delta_6 = 0$ to the form $c^2\Delta_6^\sharp(c, \epsilon) = 0$, where

$$\Delta_6^\sharp/z = -\nu^2\left(F^2+z\right)^2\left(F^2+\nu+z\right)^3 a^6 - c\varepsilon\, p_e z\nu\kappa G^2\left(F^2+z\right)\left(F^2+\nu+z\right)^2 a^4 + \varepsilon^2 z p^2\kappa^2 a^2 G^4\left(F^2+\nu+z\right)\left(\left(F^2+z\right)\nu+G^2\right) + c\varepsilon^3 z^2 p_e^3\kappa^3 G^6.$$

From this expression, it follows that

$$\Delta_6^\sharp = -\Delta_{602} + \epsilon^2\Delta_{620} + \ldots, \text{ where}$$
$$\Delta_{602} = \nu^2 z\left(F^2+z\right)^2\left(F^2+\nu+z\right)^3 a^6 > 0,$$
$$\Delta_{620} = z^2\left(F^2+\nu+z\right)G^4 p^2\left(\left(F^2+z\right)\nu+G^2\right)\varkappa^2 a^2.$$

This is exactly what we have claimed in Section 4.2.



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