Quasi-soliton interaction of pursuit-evasion waves in a predator-prey system

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We consider a system of partial differential equations describing two spatially distributed populations in a "predator-prey" interaction with each other. The spatial evolution is governed by three processes, positive taxis of predators up the gradient of prey (pursuit), negative taxis of prey down the gradient of predators (evasion) and diffusion resulting from random motion of both species. We demonstrate a new type of propagating wave in this system. The mechanism of propagation of these waves essentially depends on the taxis and is entirely different from waves in reaction-diffusion system. Unlike typical reaction-diffusion waves, which annihilate on collision, these "taxis" waves can often penetrate through each other and reflect from impermeable boundaries.

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Behavior in the form of solitary propagating waves is typical for many spatially extended nonlinear dissipative systems. Solitary waves that remain unchanged after collision with each other are less typical and are known only for a rather narrow class of nonlinear dissipative media [1]. In this respect, such waves are analogous to the solitons in conservative systems, whose study, as stable particle-like waves of nonlinear systems, remain a key interdisciplinary topic of modern mathematical physics. In the present paper we demonstrate soliton-like behavior in a class of waves, which can exist in population dynamics models as a consequence of taxis.

Spatio-temporal dynamics of interacting populations are often described in terms of reaction-diffusion systems, that take into account local dynamics, including growth and interaction of the species, and their undirected spread in space, e.g. resulting from individual random motions. However, one characteristic feature of living systems is their ability to react to changes of the environment, and to move towards, or away from, an environmental stimulus, behavior known as taxis. Examples are chemotaxis, phototaxis, thermotaxis and gyrotaxis [2, 3]. Many models of spatial dynamics of populations take taxis into account, and its importance has been recognized in modeling various biological and ecological processes, including propagation of epidemics, bacterial population waves, aggregation in the cellular slime mold *Dictyostelium discoideum*, dynamics of planktonic communities and of insect populations. [2, 4, 5]. The existence of traveling waves, and also stationary spatially-inhomogeneous structures, in interacting populations with taxis has been demonstrated experimentally and theoretically [6–10].

Here we consider a system of partial differential equations describing two spatially distributed populations in a "predator-prey" relationship with each other. The spatial evolution is governed by three processes, positive taxis of predators up the gradient of prey (pursuit) and negative taxis of prey down the gradient of predators (evasion), yielding nonlinear "cross-diffusion" terms, and random motion of both species (diffusion). In this paper we consider the problem in one spatial dimension, x, using the equations

$$\begin{aligned} \frac{\partial P}{\partial t} &= f(P,Z) + D\frac{\partial^2 P}{\partial x^2} + h_-\frac{\partial}{\partial x}P\frac{\partial Z}{\partial x}, \\ \frac{\partial Z}{\partial t} &= g(P,Z) + D\frac{\partial^2 Z}{\partial x^2} - h_+\frac{\partial}{\partial x}Z\frac{\partial P}{\partial x}, \end{aligned} \tag{1}$$

where P is the density of the prey population, Z is the density of the predator population, D is their diffusion coefficients, for simplicity considered constant, uniform and equal for both species, $\frac{\partial}{\partial x}\left(P\frac{\partial Z}{\partial x}\right)$ and $\frac{\partial}{\partial x}\left(Z\frac{\partial P}{\partial x}\right)$ are taxis terms [7], h_- is the coefficient of negative taxis of P on the gradient of Z, h_+ is the coefficient of positive taxis of Z on the gradient of P.

We choose as local kinetics functions $f(P,Z)$ and $g(P,Z)$ the Holling type III form used by Truscott and Brindley [11] to describe the population dynamics of phytoplankton, P, and zooplankton, Z:

$$\begin{aligned} f(P,Z) &= \beta P(1-P) - ZP^2/(P^2+\nu^2), \\ g(P,Z) &= \gamma ZP^2/(P^2+\nu^2) - wZ. \end{aligned} \tag{2}$$

It is known that these kinetics demonstrate "excitable" behavior, and the reaction-diffusion system (1), $h_\pm = 0$, with these terms has propagating solitary wave solutions [11, 12]. We now show how inclusion of the taxis terms can alter the properties of such solutions.

Though predator-prey systems, with one or both populations demonstrating "intelligent" taxis have been studied before, by means of individual-based Monte-Carlo simulations

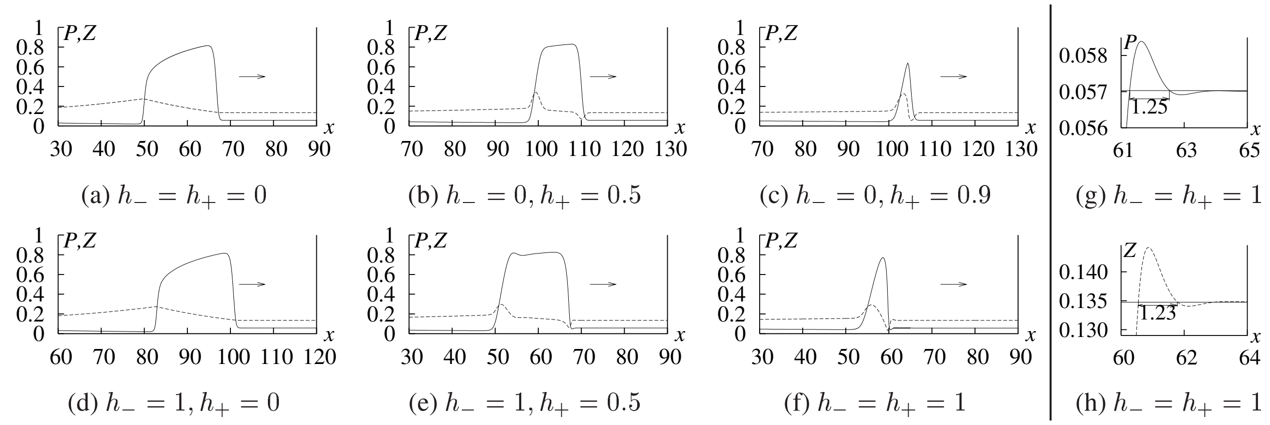


FIG. 1: (a–f) The profiles of waves with $D = 0.04$ and different taxis coefficients $h_\pm$ (at $h_- = 0$, $h_+ = 1$ solitary wave solutions do not exist). The different shape of the profiles is an evidence of different propagation mechanisms involved. Note the oscillatory onset of the pulse front when both $h_+ > 0$, $h_- > 0$. (g,h) The oscillatory onset of the front of the pulse of (f), magnified. The horizontal lines are at the steady state levels, (P_0, Z_0). The theoretical value for the oscillation half-length is $1.256\ldots$.

[13] and by using partial differential equations [14–16], our objective here to isolate and identify the specific role of the taxis terms in creating novel behavior.

Details of the model and numerical methods Unless specified otherwise, we have calculated solutions to equations (1,2) with the following parameter values: $D = 0.04$, $\nu = 0.07$, $\beta = 1$, $\gamma = 0.01$, $w = 0.004$, $h_+ = 1$ and $h_- = 1$. The ranges of values of β, γ, w were based on those in [12].

Three finite difference schemes were used, differing in their approximation of the taxis terms $Lu = \frac{\partial}{\partial x} u(x,t) \frac{\partial S(x,t)}{\partial x}$: scheme A: the central implicit scheme [17]; scheme B: an "upwind" explicit scheme, and scheme C: an "upwind" implicit scheme (see e.g. [18] for the discussion of upwind schemes).

The majority of calculations were based on scheme C with discretization steps $\delta x = 0.1$, $\delta t = 5 \times 10^{-3}$ for most figures or scheme B with $\delta x = 0.5$ and $\delta t = 0.01$ for large-scale parametric studies fig. 3(a–e). Selected control calculations used scheme B with smaller steps, down to $\delta x = 0.01$, $\delta t = 4 \times 10^{-6}$, and schemes A and C with $\delta x = 0.01$, $\delta t = 10^{-3}$.

Different mechanisms of wave propagation Fig. 1 shows the stationary profiles of population waves in a purely reaction-diffusion case (a) and with addition of taxis terms (b-f). The taxis terms significantly change the shape of the profiles. The value of the pursuit coefficient h_+ has much more pronounced effect than the value of the evasion coefficient h_-. If only evasion ($h_- > 0$) but no pursuit ($h_+ = 0$) added, waves tend to retain the same shape as purely diffusive waves, with long and smooth plateaus. The addition of pursuit ($h_+ > 0$) adds distinctive features, e.g. non-monotonic behavior of predators around the front and/or the back of the wave. Here we suggest a qualitative explanation of wave shape change in terms of the pursuit term (h_+) only. Ahead of the wave, the system is at its stable equilibrium. Consider the effect of a local increase of the prey density P above the equilibrium. The resulting flux of predators to the area, described by the taxis term with the coefficient h_+, will deplete the density of predators in surrounding areas, and the conditions of equilibrium will be violated. Decreased density of predators will temporarily encourage growth of prey, followed by influx of predators, and the same sequence of events occurs progressively at each point in the spatial (x) direction, constituting a traveling wave in the population pattern. Note that no diffusion of either prey or predators is required; the phenomenon requires only the presence of taxis terms in equation (1).

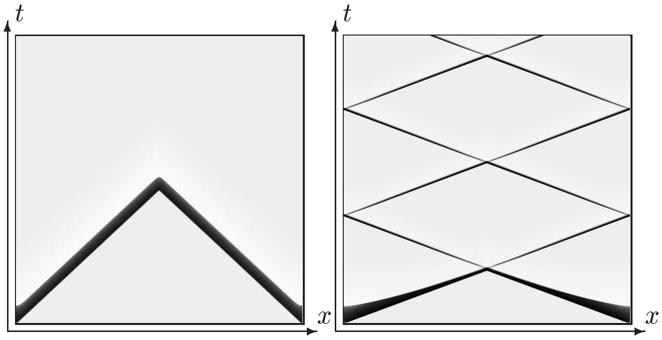
The "excitable" character of the kinetics in (2) leads to a strong magnification of the localized increase of the prey population, through the prey-escape mechanism (prey multiply faster than predators). This feature, of course, is also essential for solitary waves in purely diffusive systems.

An unusual feature of taxis waves is the oscillatory character of the front, see fig. 1(g,h): spatial non-monotonicity of wavefront, which, however, propagates with a constant speed'. Since these oscillations have a small amplitude, they can be described by linearized theory. Indeed, in a steadily propagating wave with speed c, variables P and Z depend only on the combination $\xi = x - ct$, and satisfy the "automodel" system

$$\begin{aligned} f(P,Z) + D\frac{\mathrm{d}^2 P}{\mathrm{d}\xi^2} + h_- \frac{\mathrm{d}}{\mathrm{d}\xi} P \frac{\mathrm{d}Z}{\mathrm{d}\xi} + c\frac{\mathrm{d}P}{\mathrm{d}\xi} &= 0, \\ g(P,Z) + D\frac{\mathrm{d}^2 Z}{\mathrm{d}\xi^2} - h_+ \frac{\mathrm{d}}{\mathrm{d}\xi} Z \frac{\mathrm{d}P}{\mathrm{d}\xi} + c\frac{\mathrm{d}Z}{\mathrm{d}\xi} &= 0. \end{aligned} \quad (3)$$

The speed of the wave in fig. 1(f) is $c = 0.3535$, and the steady-state values of the variables are $P_0 = 0.05703$, $Z_0 = 0.13480$. With these parameters, a straightforward calculation gives solutions in the form $(P,Z)(\xi) \approx (P_0, Z_0) + \mathrm{Re}\left[(P_1, Z_1)e^{\lambda\xi}\right]$, $|P_1, Z_1| \ll |P_0, Z_0|$, with $\lambda_{1,2} \approx 1.9925 + 2.5014i$. This predicts the half-length of oscillations along ξ coordinate of $\pi/\mathrm{Im}(\lambda_{1,2}) \approx 1.256$, in a good agreement with the observed shape, see fig. 1(g,h). This means that these oscillations are not a numerical artifact. Note that in an ideal stationary profile there will be an infinite number of oscillations, of explonentially decaying amplitude.

An important feature of solitary taxis waves is the uniformity of their shape, amplitude and speed: after a transient, these are the same, regardless of the details of the initial conditions. In this they are similar to reaction-diffusion excitation waves and different from solitons in conservative systems.



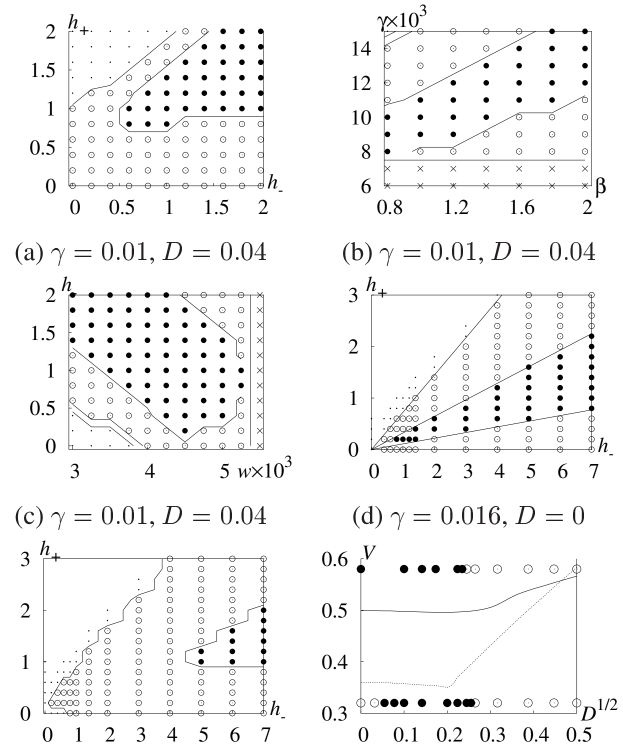
(a) $h_- = h_+ = 0$ (b) $h_- = h_+ = 1$

FIG. 2: Space-time density plots showing interaction of waves in (a) purely diffusive and (b) taxis cases. On both panels, the length of the interval $L = 300$, the time scale $t \in [0, 2200]$. Black corresponds to $P = 0.9$, white to $P = 0$.

Quasi-soliton interaction of pulses We have found that the system (1,2) has a region of parameters where solitary waves interact as solitons. That is, they do not annihilate, as reaction-diffusion pulses usually do, but penetrate through, or reflect from, each other (since the waves are indistinguishable, these two terms mean the same thing). Fig. 2 shows results of simulations in an interval of finite length L with no-flux boundary conditions $\frac{\partial P}{\partial x}|_{x=0,L} = 0$ and $\frac{\partial Z}{\partial x}|_{x=0,L} = 0$. Two waves were initiated simultaneously, one at each end of the interval; the results are shown as density plots. In the purely diffusive case, panel (a), the waves annihilate at the collision. With the taxis terms included, panel (b), the waves penetrate through each other on collision, and are then reflected from the boundaries.

Soliton-like interactions of solitary waves have been observed in some reaction-diffusion systems with excitable kinetics, both in numerics [19–24] and in experiments [24, 25]. Such interactions are always limited to narrow parameter ranges close to the boundaries between excitable and oscillatory (limit cycle) regimes of the reaction kinetics.

In contrast, fig. 3(a–e) shows regions in the parameter space corresponding to different regimes of interaction and propagation of taxis waves described by equations (1,2). Both the existence of steady propagating pulses and their ability to penetrate/reflect have a complex relationship with the kinetic and propagation parameters. However, it is quite clear that the ranges of parameters providing soliton-like behavior are not in any sense narrow, and do not require proximity to the oscillatory kinetics. Although large enough h_+ is typically sufficient for propagation of waves, quasi-soliton behavior requires both h_+ and h_-. Figs. 3(d,e) provide further evidence of a completely different mechanism of propagation of taxis



(a) $\gamma = 0.01, D = 0.04$ (b) $\gamma = 0.01, D = 0.04$

(c) $\gamma = 0.01, D = 0.04$ (d) $\gamma = 0.016, D = 0$

(e) $\gamma = 0.016, D = 0.04$ (f) (see caption)

FIG. 3: (a–e) Parametric regions corresponding to different regimes of taxis waves. Solid circles: quasi-solitons. Hollow circles: annihilating pulses. Dots: there is no stable propagation of pulses. Crosses: oscillatory local kinetics. (f) Wave propagation velocity as function of the square root of the diffusion coefficient. Solid line and the upper row of symbols: $\gamma = 0.016$, $h_+ = 1$, $h_- = 5$. Dotted line and the lower row: standard parameter values. In reaction-diffusion systems, this dependence is always a straight line.

waves. Fig. 3d shows that annihilating and reflecting waves exist in absence of diffusion. Fig. 3e shows an example that propagating waves do not exist in a purely diffusive medium, but only taxis makes the propagation possible.

Fig. 3(f) shows dependence of the wave propagation velocity on the diffusion coefficient D. This dependence is clearly different from $\propto D^{1/2}$ law obeyed by reaction-diffusion waves. There is a marked change of this dependence near the transition between annihilating and reflecting waves, which is yet another evidence of different mechanism of taxis waves, especially of quasi-solitons.

Fig. 4 illustrates the mechanism of reflection of two colliding taxis waves (reflection of a single wave from a non-flux boundary is mathematically equivalent to a half of this picture). As noted above, a feature of taxis waves is low level of predators ahead of the prey wave, as the predators are attracted backwards by the prey density gradient. This backward gradient of predators encourages the forward movement of prey (see $t = 31$). The meeting of two prey waves creates a high peak of prey density ($t = 31 \ldots 41$). This higher local density of prey attracts predators, which abandon the mar-

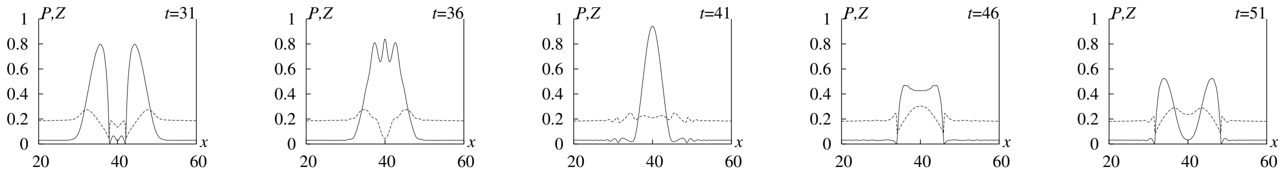


FIG. 4: Mechanism of reflection of two taxis waves. Solid lines: P, dashed lines: Z; $\gamma = 0.016$, $D = 0$, $h_+ = 1$, $h_- = 5$.

gins of the collision zone ($t = 36 \ldots 41$). The local growth of predators causes escape of the prey from the center of the collision zone towards the margins abandoned by the predators. These events inverse the gradients of the populations and re-create front structures on the margins of the collision zone ($t = 41 \ldots 46$), which then cause generation of two new, "reflected" taxis waves ($t = 51$), which subsequently restore their normal amplitude (not shown on figure). So, the phenomenon of reflection is stipulated by interaction of both the pursuit and evasion taxis terms, forming a positive feedback loop. This explains why the quasi-soliton regions are bounded away from the coordinate axes on fig. 3(a,d,e).

The interplay and positive feedback between the two taxis terms can also be elucidated by considering a simple linear analogue of equations (1):

$$\frac{\partial P}{\partial t} = h_- \frac{\partial^2 Z}{\partial x^2}, \qquad \frac{\partial Z}{\partial t} = -h_+ \frac{\partial^2 P}{\partial x^2}, \tag{4}$$

which are obtained from (1) by putting $f_{1,2} = D = 0$ and removing nonlinearity from the taxis terms. System (4) is equivalent to a Schrödinger equation for $\psi = h_+^{1/2} P + i h_-^{1/2} Z$. This is consistent with oscillatory fronts of taxis waves and their ability to reflect from each other. The role of nonlinearities appears to be in selecting a unique amplitude and shape of propagating waves, and restricting, compared to (4), values of $h_\pm$ that allow reflection. Adding diffusion in (4) destroys propagating waves, but not necessarily in (1) where its dissipative effect may be compensated by the nonlinear kinetics.

Conclusions. We have studied a spatially distributed predator-prey system of equations, in which, in addition to or instead of diffusion terms, we have included terms describing taxis of the species on each other's gradient: predators pursuing prey, and prey escaping predators. We have found that the taxis terms change the shape of the propagating waves and increase the propagation speed, which is an evidence of a different mechanism of propagation of these waves. In this change the major role is played by the pursuit terms. Also, the taxis terms can change the interaction between propagating waves, i.e. make them penetrate/reflect, rather than annihilate. For this effect, both pursuit and evasion terms are essential.

Quasi-soliton interaction of taxis waves has some experimental evidence. In [26], such interaction of bacterial population taxis waves was observed in vitro, where colliding waves continued to propagate after collision without delay.

Though our results are motivated by predator-prey systems, they illustrate the possible dramatic consequences of the inclusion of taxis terms in the model. The waves demonstrated here are, for sufficiently strong taxis, totally different in character and mechanism from the much more widely studied waves in "simple" reaction-diffusion systems.

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