Quasisoliton 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 a 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]. Here we demonstrate solitonlike behavior in a class of waves, which can exist in population dynamics models as a consequence of taxis.

Spatiotemporal dynamics of interacting populations are often described in terms of reaction-diffusion systems that take into account local dynamics and 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. The importance of taxis 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*, and dynamics of planktonic communities and of insect populations [2–10].

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, as well as random motion of both species (diffusion). In this Letter we consider the problem in one spatial dimension, x, using the equations

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

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, $\frac{\partial}{\partial x}(P\frac{\partial Z}{\partial x})$ and $\frac{\partial}{\partial x}(Z\frac{\partial P}{\partial x})$ are taxis terms [7], h_- is the coefficient of negative taxis of P on the gradient of Z, and 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:

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

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 "intelligent" taxis have been studied before, by means of individual-based Monte Carlo simulations [13] and by using partial differential equations [14–16], our objective here is 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 Eqs. (1) and (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].

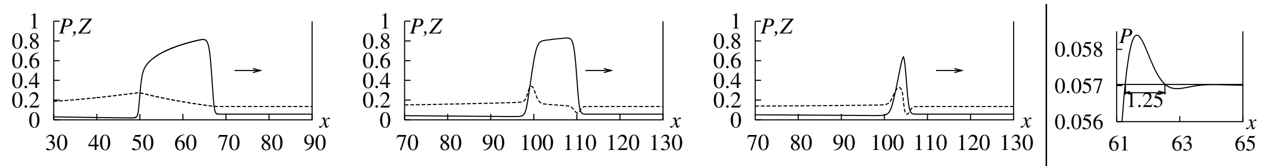
Three finite difference schemes were used, differing in their approximation of the taxis terms $\mathcal{L}u = \frac{\partial}{\partial x} u(x, t) \frac{\partial S(x,t)}{\partial x}$: scheme A, the central implicit scheme [17]; scheme B, an "upwind" explicit scheme; and scheme C, an upwind implicit scheme (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. 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.—Figure 1 shows the stationary profiles of population waves in a purely reaction-diffusion case 1(a) and with addition of taxis terms 1(b)–1(f). The taxis terms significantly change the shape of the profiles. The value of the pursuit coefficient h_+ has a much more pronounced effect than the value of the evasion coefficient h_-. With 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., nonmonotonic 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. 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 an influx of predators, and the same sequence of events occurs progressively at each point in the spatial (x) direction, constituting a traveling wave. This requires only taxis, but not diffusion terms, in Eq. (1). The excitable kinetics of Eq. (2) strongly magnify a localized increase of the prey population, through the prey-escape mechanism (prey multiply faster than predators). This, of course, is also essential for waves in purely diffusive systems.

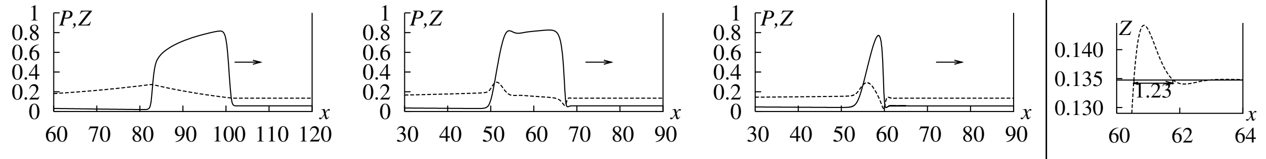
Taxis waves may have unusual spatially oscillatory nonmonotonic, constant-speed fronts; see Figs. 1(g) and 1(h). Since these oscillations are small, they can be described by linearized theory. In a steadily propagating wave with speed c, variables P and Z depend on $\xi = x - ct$ and satisfy

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

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 $(P, Z)(\xi) \approx (P_0, Z_0) + \mathrm{Re}[(P_1, Z_1)e^{\lambda\xi}]$, $|P_1, Z_1| \ll |P_0, Z_0|$, with $\lambda_{1,2} \approx 1.9925 + 2.5014i$. This predicts the half length of oscillations along the ξ coordinate of $\pi/\mathrm{Im}(\lambda_{1,2}) \approx 1.256$, in good agreement with the observed shape; see Figs. 1(g) and 1(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 exponentially decaying amplitude.

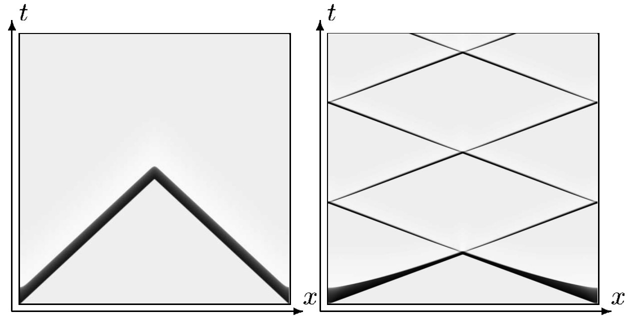


(a) $h_- = h_+ = 0$ (b) $h_- = 0, h_+ = 0.5$ (c) $h_- = 0, h_+ = 0.9$ (g) $h_- = h_+ = 1$



(d) $h_- = 1, h_+ = 0$ (e) $h_- = 1, h_+ = 0.5$ (f) $h_- = h_+ = 1$ (h) $h_- = h_+ = 1$

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 evidence of the different propagation mechanisms involved. Note the oscillatory onset of the pulse front when both $h_+ > 0$ and $h_- > 0$. (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 $1.256\ldots$.



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

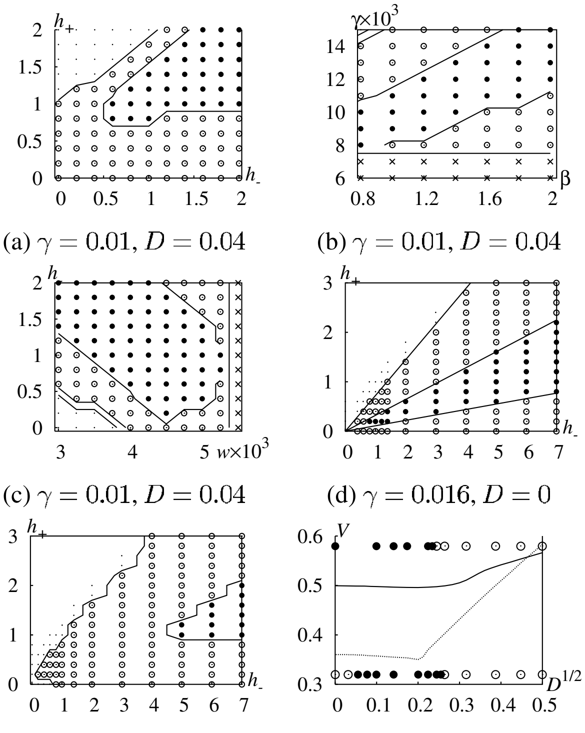
FIG. 2. Space-time density plots showing interaction of waves in (a) purely diffusive and (b) taxis cases. In both panels, the length of the interval $L = 300$, and the time scale $t \in [0, 2200]$. Black corresponds to $P = 0.9$, and white to $P = 0$.

Solitary taxis waves, after a transient, adopt the same shape amplitude and speed regardless of the details of the initial conditions. In this they are similar to reaction-diffusion waves and different from solitons in conservative systems.

Quasisoliton interaction of pulses.—We have found that the system (1) and (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). Figure 2 shows results of simulations in an interval of length L with no-flux boundaries $\frac{\partial P}{\partial x}|_{x=0,L} = 0$ 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, Fig. 2(a), the waves annihilate at the collision. With the taxis terms included, Fig. 2(b), the waves penetrate through each other on collision, and are then reflected from the boundaries.

Solitonlike 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, Figs. 3(a)–3(e) show regions in the parameter space corresponding to different regimes of interaction and propagation of taxis waves described by Eqs. (1) and (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 solitonlike 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, quasisoliton behavior requires both h_+ and h_-. Figures 3(d) and 3(e) provide further evidence of a completely different mechanism of propagation of taxis waves. Figure 3(d) shows that annihilating and reflecting waves exist in absence of diffusion. Figure 3(e) shows an example when propagating waves do not exist in a purely diffusive medium, but only taxis makes the propagation possible. Figure 3(f) shows dependence of the wave propagation velocity on the diffusion coefficient D. It is clearly different from the $\propto D^{1/2}$ 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 more evidence of a different mechanism of taxis waves, especially of quasisolitons.



(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: quasisolitons. Hollow circles: annihilating pulses. Dots: there is no stable propagation of pulses. Crosses: oscillatory local kinetics. (f) Wave propagation velocity as a 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.

Figure 4 explains the reflection of two colliding taxis waves (reflection of a single wave from a nonflux boundary is equivalent to a half of this picture). Predators are low ahead of the prey wave, as they 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 attracts

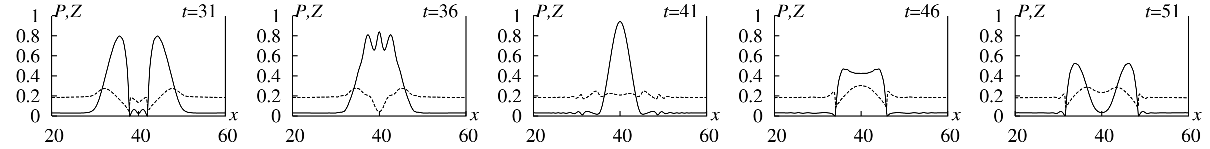


FIG. 4. Mechanism of reflection of two taxis waves. Solid lines: P, dashed lines: Z; $\gamma = 0.016$, $D = 0$, $h_+ = 1$, $h_- = 5$.

predators, which abandon the margins of the collision zone ($t = 36, \ldots, 41$). Prey escapes from the center of the collision zone towards the margins abandoned by the predators. These events invert the gradients of the populations and recreate front structures on the margins of the collision zone ($t = 41, \ldots, 46$), which then generate two new, "reflected" taxis waves ($t = 51$). They subsequently restore their normal amplitude (not shown). Reflection is stipulated by interaction of both the pursuit and evasion taxis terms, forming a positive feedback loop. This explains why the quasisoliton regions are bounded away from the coordinate axes on Figs. 3(a), 3(d), and 3(e).

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

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

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 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.

In conclusion, we have shown that the inclusion, in a predator-prey model, of terms representing taxis of each species on the gradient of the other can have a significant effect on the mechanism, structure, and speed of propagating waves in the system. Taxis terms can change the character of interactions between waves, allowing them to penetrate/reflect, rather than annihilate. Some experimental evidence of this has been observed in bacterial populations [26]. Though our motivation has been predator-prey systems, the existence of these waves, whose character is quite different from the more widely studied nonlinear waves in "simple" reaction-diffusion systems, may be expected to have significance for other physical systems.

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[1] R. K. Dodd, J. C. Eilbeck, J. D. Gibbon, and H. C. Morris, *Solitons and Nonlinear Waves Equations* (Academic Press, London, 1984).

[2] G. R. Ivanitskii, A. B. Medvinskii, and M. A. Tsyganov, Usp. Fiz. Nauk **161**, 13 (1991).

[3] T. J. Pedley and J. O. Kessler, J. Fluid Mech. **212**, 155 (1990).

[4] T. Hofer, J. A. Sherratt, and P. K. Maini, Physica (Amsterdam) **85D**, 425 (1995).

[5] A. B. Medvinsky, S. V. Petrovskii, I. A. Tikhonova, H. Malchow, and B. L. Li, SIAM Rev. **44**, 311 (2002).

[6] J. Adler, Science **153**, 708 (1966).

[7] E. F. Keller and L. A. Segel, J. Theor. Biol. **30**, 225 (1971).

[8] B. N. Vasiev, P. Hogeweg, and A. V. Panfilov, Phys. Rev. Lett. **73**, 3173 (1994).

[9] F. S. Berezovskaya and G. P. Karev, Usp. Fiz. Nauk **169**, 1011 (1999).

[10] J. A. Sherratt, Proc. R. Soc. London, Ser. A **456**, 2365 (2000).

[11] J. E. Truscott and J. Brindley, Philos. Trans. R. Soc. London, Ser. A **347**, 703 (1994).

[12] L. Matthews and J. Brindley, Dyn. Stab. Syst. **12**, 39 (1997).

[13] A. Rozenfeld and E. Albano, Physica (Amsterdam) **266A**, 322 (1999).

[14] J. D. Murray and J. E. R. Cohen, SIAM J Appl. Math. **43**, 66 (1983).

[15] J. Murray, *Mathematical Biology* (Springer-Verlag, Berlin, 1989).

[16] G. J. Pettet, D. L. S. McElwanin, and J. Norbury, IMA J. Appl. Math. **17**, 395 (2000).

[17] A. Samarskii and A. Goolin, *Numerical Methods* (Nauka, Moscow, 1989).

[18] K. W. Morton and D. F. Mayers, *Numerical Solution of Partial Differential Equations* (Cambridge University Press, Cambridge, 1989).

[19] R. Kobayashi, T. Ohta, and Y. Hayase, Phys. Rev. E **50**, R3291 (1994).

[20] V. Petrov, S. K. Scott, and K. Showalter, Philos. Trans. R. Soc. London, Ser. A **347**, 631 (1994).

[21] J. Kozek and M. Marek, Phys. Rev. Lett. **74**, 2134 (1995).

[22] O. V. Aslanidi and O. A. Mornev, JETP Lett. **65**, 579 (1997).

[23] O. V. Aslanidi and O. A. Mornev, J. Biol. Phys. **25**, 149 (1999).

[24] A. von Oertzen, A. S. Mikhailov, H. H. Rotermund, and G. Ertl, J. Phys. Chem. B **102**, 4966 (1998).

[25] H. H. Rotermund, S. Jakubith, A. von Oertzen, and G. Ertl, Phys. Rev. Lett. **66**, 3083 (1991).

[26] M. A. Tsyganov, I. B. Kresteva, A. B. Medvinskii, and G. R. Ivanitskii, Dokl. Akad. Nauk **333**, 532 (1993).