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Quasi-one-dimensional waves in rodent populations in heterogeneous habitats: A consequence of elevational gradients on spatio-temporal dynamics

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HIGHLIGHTS

- We study a quasi-one-dimensional population that expands and contracts.
- We build a mathematical model of the dynamics and show that the observed features require an Allee effect in the description.
- We find good qualitative agreement between the model and the field studies.

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ABSTRACT

Wave propagation can be clearly discerned in data collected on mouse populations in the Cibola National Forest (New Mexico, USA) related to seasonal changes. During an exploration of the construction of a methodology for investigations of the spread of the Hantavirus epidemic in mice we have built a system of interacting reaction diffusion equations of the Fisher–Kolmogorov–Petrovskii–Piskunov type. Although that approach has met with clear success recently in explaining Hantavirus refugia and other spatiotemporal correlations, we have discovered that certain observed features of the wave propagation observed in the data we mention are impossible to explain unless modifications are made. However, we have found that it is possible to provide a tentative explanation/description of the observations on the basis of an assumed Allee effect proposed to exist in the dynamics. Such incorporation of the Allee effect has been found useful in several of our recent investigations both of population dynamics and pattern formation and appears to be natural to the observed system. We report on our investigation of the observations with our extended theory.

1. Introduction and summary of field observations

The abundance and distribution of animal populations on the landscape is determined by the availability of suitable habitat, including shelter and food resources. In heterogeneous environments (e.g., steep elevational gradients with changes in climate and vegetation), the distribution of animal populations may be more tightly constrained by concomitant gradients in limiting resources. However, biotic resources also fluctuate in space and time, allowing normally unsuitable (suboptimal) adjacent habitat to periodically become more hospitable for short time periods (i.e., resource pulses). During favorable conditions in optimal habitat, a species' population will often rise in number with favorable reproduction and survival, and the resulting increase in population density may ultimately lead to dispersal of some individuals from the optimal habitat to nearby suboptimal habitats. When environmental conditions return to normal, the suboptimal habitat becomes inhospitable, and the dispersing individuals must either return to their habitat of origin, continue dispersing further in hopes of finding suitable habitat, or perish in the inhospitable habitat. Viewed from a landscape level over many years, these dynamics appear as a series of waves of a species' population emanating from and retreating to regions of optimal habitat. Given this conceptual dynamic pattern, the

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purpose of this report is to develop the mathematical basis of this phenomenon, and parameterize the model with data from a small mammal landscape study in New Mexico.

In a field study Tinnin (2003) assessed the abundance and distribution of rodent populations along a habitat gradient, as part of an effort to characterize and understand the dynamics of the temporal and spatial dynamics of Hantavirus (Mills et al., 1999; Yates et al., 2002). The study was carried out in one of the major (unnamed) canyons on the west slope of the Sandía Mountains, Cibola National Forest (New Mexico, USA). The canyon extends from an elevation of 1820 m to 2165 m. The upper end is closed by a sheer cliff face of the Sandía Mountains, while the lower one lies on the alluvial fan southwest of Placitas. Along this canyon, 14 lines of Sherman traps were set every 200 m, perpendicular to the main direction of the canyon. Fig. 1 shows a schematic representation of the geometry of the system.

A variety of habitats are found at different elevations. Approximately the upper half of the canyon is covered by a forest of conifers (piñón and ponderosa pines, and Douglas fir) and oak. This habitat is the optimal and preferred one for the deer mouse (*Peromyscus maniculatus*) and the brush mouse (*P. boylii*), as a result of production of major food items, acorns and pine nuts. The lower elevations are suboptimal, being covered mainly by juniper, shrubs and grasses. As observed during the study (Tinnin, 2003), certain environmental and demographic conditions may force the rodents to invade and retract from the suboptimal habitat.

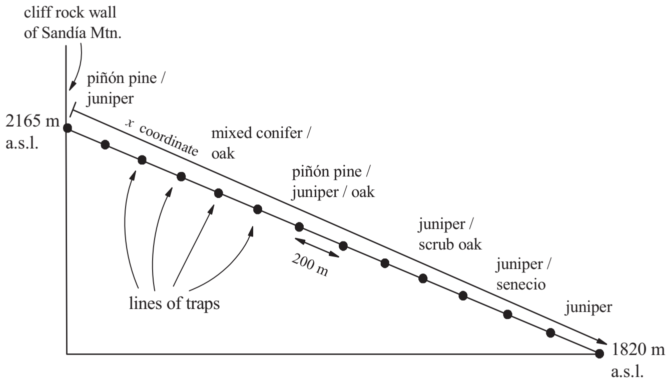

Fig. 1. Schematic representation of the site of the study by Tinnin (2003). Heights are measured above sea level (a.s.l).

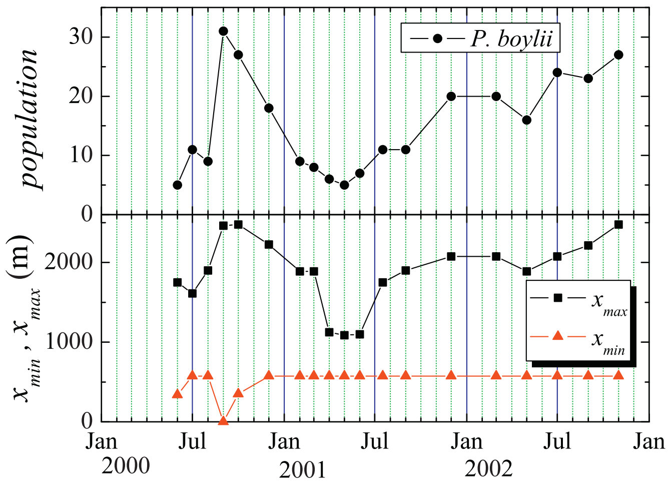

Fig. 2. Temporal evolution of the observed population of *P. boylii*. The top panel shows the number of captured animals (minimum number known alive). The bottom panel shows the evolution of the range (maximum and minimum positions of captured animals). x_{min} is the position closer to the high altitude rock wall boundary of the canyon. x_{max} is the one at lower altitude.

Fig. 2 (top) shows the temporal evolution of the observed population (usually called *minimum number known alive*, which is a proxy for total population) of *P. boylii* (brush mouse), one of the common species present and a host for Hantavirus. Three regimes of population growth are observed, around the summer months (which carry the most precipitation during the monsoon season, July–September), followed by a decline in winter. The two declines observed are very different from each other: the first is very visible and drives the population to very low levels during the first months of 2001. The second one is very mild, with only one observation of population drop just before the summer increase in 2002.

A similar pattern is observed in the range of the population. Let us choose a single coordinate along the canyon as the distance from its top. In Fig. 2 (bottom) we show the upper and lower bounds of the population of *P. boylii* as a function of time. The position of the high elevation border of the population, x_{min}, remains almost constant in time (and close to the rock wall closing the canyon from above), except during months of very high population. The only movement of the border to higher altitude corresponds to the very large population peak following the summer of 2000. Very different is the behavior of the lower border, x_{max}, which also oscillates similarly to the measured population number shown in the top panel. Observe that, during the periods of high population, the range of *P. boylii* extends over almost the whole canyon, while during the periods of low population it reduced to about the upper half.

The correspondence between the temporal features of population number and range suggests that the population may be expanding and contracting with almost constant density. Even though the field measurements do not allow an absolute assessment of animal density along the canyon, let us assume for simplicity in the formulation of the model that this is the case. A plot of the population number as a function of the population range $x_{max}-x_{min}$ is shown in Fig. 3. Most of the observations (with the exceptions of those three with smallest range) appear forming a cloud of almost linear behavior. This corresponds to an average (along the canyon) linear density of 18 ± 3 animals/km, which we assume represents the population density of the system.

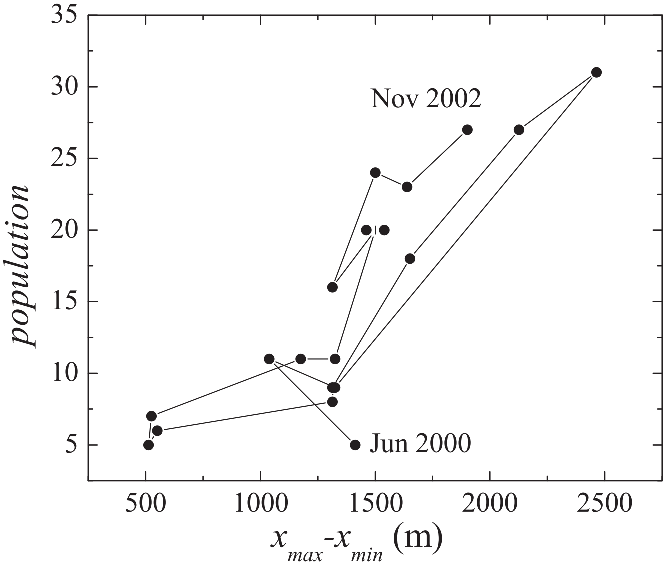

Fig. 3. Relation between population number and population range of *P. boylii*. Discarding the three measurements that lie far from the almost linear cloud (those with ranges close to 500 m) the linear density is 18 ± 3 animals/km.

Why do the measurements that correspond to the smallest observed populations, and smallest range, lie far from the linear density regime? While we cannot discard the possibility that the observations at such low density are plagued by an artifact of measurement, we take the point of view in the present analysis that this behavior reflects an important feature about the demographics of the system. We suggest that the behavior arises from variations in social structure when resources are scarce. Observations of *P. boylii* in New Mexico (Kalcounis-Rüppel and Ribble, 2007; Ribble and Stanley, 1998) has indicated that at low density *P. boylii* becomes territorial. In such a scenario, it is not clear how waves of population invasion would proceed given that individuals would strongly interact and exclude one another (Giuggioli et al., 2011). We explore the possibility that an Allee effect, to be explained below, is the source of the interesting observations for the linear regime of Fig. 3.

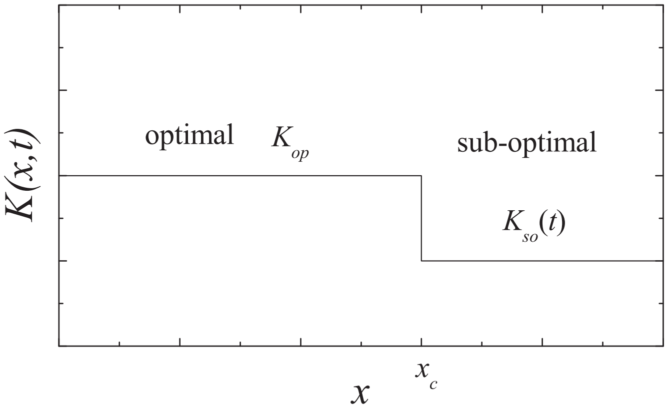

Fig. 4. Simplified habitats along the one-dimensional canyon.

2. Formulation of the model

Summarizing the main observations of the discussion above, we see that we have here a quasi-one-dimensional system with a population subject to a habitat gradient and temporal variations. The population is seen to oscillate seasonally in number and in range, maintaining a fairly constant linear density along the relevant dimension. Moreover, the population has a well defined footprint, or range, with one border almost fixed at high altitude, and a lower border (a front) that moves downwards and upwards.

We notice that the system is functionally almost one-dimensional, restricted to the canyon, and with the population expanding and contracting along it. Certainly, the sides of the canyon do not constitute an insurmountable barrier to the mice, and in principle the population can also spread perpendicularly to the main direction of the canyon. But lacking observations in this regard, and given that the habitat gradient is in the direction of the canyon, we construct our model to be one-dimensional . Furthermore, since the cliff wall of the Sandía Mountains indeed may constitute a barrier for mice propagation, our model will have a reflecting boundary at $x=0$.

Secondly, as a first step in the analysis, we will consider a single population, without distinctions of gender, age or infectious state, representing an idealized population of *P. boylii*. We will consider that this population is subject to purely diffusive transport (Abramson et al., 2006; Giuggioli et al., 2006), and will attempt to reproduce the qualitative behavior of the front along the canyon. A general model for this population is (Abramson and Kenkre, 2002; Abramson et al., 2003; Kenkre et al., 2007) the following reaction–diffusion equation:

$$\frac{\partial u}{\partial t}=f[u(x,t)]+D\frac{\partial^2 u}{\partial x^2}, \tag{1}$$

where $u(x,t)$ represents the mice density, f is a function of it (and of the parameters that characterize the habitat) and D is the diffusion coefficient. Perhaps the simplest model for $f(u)$ is a logistic one, in which case Eq. (1) becomes a one-dimensional heterogeneous Fisher–Kolmogorov–Petrovskii–Piskunov (FKPP) equation:

$$\frac{\partial u}{\partial t}=ru\left(1-\frac{u}{K(x,t)}\right)+D\frac{\partial^2 u}{\partial t^2}, \tag{2}$$

with a space and time dependent environmental parameter $K(x,t)$ modeling the diversity of habitats, which can be taken into account as follows. Since the habitats can be roughly classified as optimal (the conifers/oak) and suboptimal (the juniper/shrubs/grass), we can model them using piecewise spatially uniform environmental parameters (see Fig. 4). A possible time dependence of $K(x,t)$ could be an oscillating $x_c(t)$, which would produce a corresponding oscillation in the ranges of the high and low density populations. This choice, however, does not seem to be the best. This is so because x_c represents the transition from the forest to the grassland, and this does not oscillate seasonally. What might be expected to vary sensibly in the course of the year is the value of K itself. A plausible choice would be

$$K(x,t)=\begin{cases}K_{op} & \text{if } x\le x_c,\\ K_{so}(t) & \text{if } x>x_c.\end{cases} \tag{3}$$

An equation such as (2), together with (3) and with initial condition in the optimal habitat, is expected to have solutions in the form of a propagating front, connecting a region of high population on the left to a region of low population on the right, such as the simpler situations where K is uniform and constant. However, the traveling wave solutions of FKPP's equation propagate in either one direction or the other, depending on the slope of the front connecting the asymptotic equilibria to the left and to the right. In our present scenario, with the optimal habitat on the left, this means that the waves will propagate always toward the right (with a speed that may be affected by the oscillating $K_{so}(t)$ on the right). Such a model would be unable to reproduce, even qualitatively, the observed pattern of expansion and retraction of the population. It is interesting that, even if the oscillating $K_{so}(t)$ approaches zero during its minima, this situation persists: the negligible population in the suboptimal habitat recovers immediately when $K_{so}(t)$ increases again, and the front continues towards the right. This is a drawback of all the models involving a logistic term: the zero population state is always unstable, a situation that may be far from reality, especially for rather small populations such as the rodent ones observed in the region.

In a number of recent investigations (Kenkre, 2003; Kenkre and Kuperman, 2003; Clerc et al., 2005, 2010; Kumar et al., 2009) we have explored consequences on epidemics spread and general pattern formation when equations of the FKPP type are generalized to include the so-called Allee effect (Allee, 1931, 1938; Perthame, 2008). This effect, or feature, is present in many population systems and means that the nature of the reaction in the reaction diffusion scenario is such that the population suffers extinction if it starts out at sufficiently low levels of population density, that its growth overwhelms this tendency to extinction if the density exceeds a critical level, and that at sufficiently high levels a saturation effect sets in counteracting the Malthusian explosion. The nonlinearity term that corresponds to this situation is cubic in the population density (unlike quadratic as in the FKPP equation). The representative generalization of the FKPP equation, termed sometimes (Murray, 1993) the “reduced Nagumo equation”, has been used by us in our previous work (Kenkre, 2003; Kenkre and Kuperman, 2003; Clerc et al., 2005, 2010; Kumar et al., 2009) to address ecological and pattern formation phenomena. We will use that generalization in the analysis below.

The function $f(u)$ we use here has the state $u=0$ as stable, with a threshold a below which the population is attracted to this state. The equations are, in their simplest form,

$$\frac{\partial u}{\partial t} = ru(u-a(x,t))\left(1-\frac{u}{K(x,t)}\right)+D\frac{\partial^2 u}{\partial x^2}. \tag{4}$$

As explained in detail elsewhere (Kenkre, 2003; Kenkre and Kuperman, 2003; Clerc et al., 2005, 2010; Kumar et al., 2009) the reaction part of Eq. (4) has three equilibria: $u=0$ (stable), $u=a$ (unstable) and $u=K$ (stable). The reduction of the growth rate at low densities constitutes a usual mathematical model for the Allee effect (Stephens et al., 1999; Courchamp et al., 1999). The dynamics of small populations and their increased risk of extinction is a problem of considerable importance for invading populations and other systems with heterogeneous or changing habitats, and it has been studied both theoretically and in the field (Courchamp et al., 1999; Taylor and Hastings, 2005; Kokko and Sutherland, 2001; Tobin et al., 2011). In the present case of *P. boylii*, Tinnin observed (Tinnin, 2003) some evidence supporting the increased instability of small populations. On the one hand, the mass of the captured mice was smaller in the lower range, an indicator of younger animals. Besides, the invaders do not find an empty landscape but a resident population of *P. leucopus*, their competitors for food and shelter resources. These observations, together with the need to add stability to the equilibrium $u=0$ to support backward propagating fronts, contribute to the evidence of an Allee effect at play in the system.

Eq. (4) has many interesting solutions in the form of traveling waves, and for a wide region of parameters they represent expanding and contracting populations. In the next section we explore a variety of examples of these.

3. Traveling waves, expansion and contraction

We have undertaken an exploration of different behaviors displayed by Eq. (4), both in scenarios that mimic the spatio-temporal one found in the Sandía study and in other possibly interesting cases.

Let us assume that the external driving of the system, through $K(t)$ and $a(t)$, is sufficiently slow to ensure an adiabatic regime in which the traveling front tracks them with a time dependent velocity and a time dependent steepness, which has been shown to occur for certain reaction–diffusion systems (Giuggioli et al., 2008) when a traveling front possesses the same qualitative shape although quantitatively different to the one in the asymptotic regime. Under such a condition, the usual transformation of variables to a moving system of reference in which the front is stationary can be made: $x \to x-c(\tau)t$, where τ represents the slow time scale of the adiabatic approximation. Furthermore, with the boundaries $u(z\to-\infty)=1$ and $u(z\to\infty)=0$, and with $K(t)$ and $a(t)$ kept piecewise uniform below and above x_c, Eq. (4) has traveling wave solutions with velocity (Murray, 1993):

$$c(\tau)=\sqrt{\frac{rD}{2K(\tau)}}(K(\tau)-2a(\tau)). \tag{5}$$

It is clear that the sign of the velocity depends on the sign of $K-2a$ in Eq. (5), so there is a possibility of fronts propagating in both directions. Let us now specify the temporal variation of the suboptimal environment and threshold parameters. We expect that during the favorable season (the one with best food and water resources, for example) the environmental parameter would be highest and the Allee effect would be weakest, with the smallest Nagumo threshold. In this context we can model these parameters as opposite-phase harmonic oscillations:

$$K_{so}(t)=k_0+k_1\sin(2\pi t/T), \tag{6}$$

$$a_{so}(t)=a_0+a_1\sin(2\pi t/T+\pi), \tag{7}$$

where T is the period of the oscillation. The average velocity of the front can be found integrating Eq. (5) along a period:

$$\langle c\rangle=\frac{1}{T}\int_0^T c(\tau)\,d\tau = \frac{\sqrt{2rD}}{\pi}\frac{\kappa(2a_1+k_1)\mathcal{E}\left(\frac{2k_1}{\kappa}\right)-2(a_0k_1+a_1k_0)\mathcal{K}\left(\frac{2k_1}{\kappa}\right)}{k_1\sqrt{\kappa}}, \tag{8}$$

where $\kappa=k_0+k_1$, and $\mathcal{E}(x)$ and $\mathcal{K}(x)$ are complete elliptic integrals of the second and first kinds, respectively (note that we use calligraphic symbols for these, to avoid confusion with our environmental parameter K). Fig. 5 shows this average speed as a function of the mean values of the oscillating parameters, a_0 and k_0. One of the contours in this plot is thicker than the others, and it corresponds to stationary fronts with $\langle c\rangle=0$. The region above this line corresponds to fronts propagating away towards the right in the canyon. The region below it corresponds to fronts propagating towards the interface at x_c, where they get stabilized by the density diffusing from the optimal habitat.

3.1. Representation of seasonal changes by oscillating parameters

For the sake of simplicity let us fix some of the parameters to arbitrary values, and present examples of the behavior of the solutions when only some of them change. In the following, we shall keep constant the growth rate, $r=0.2$, the diffusion coefficient, $D=1$, the value of the optimal environmental parameter $K_o=1$, and the optimal value of the threshold $a_o=0.1$ which, in relation to K_o, represents a *weak* Allee effect in the optimal habitat.

Figs. 6 and 7 show the behavior of the total population, $U(t)=\int u(x,t)\,dx$, integrated over the whole system. Both figures show a case with K_{so} and a_{so} oscillating with opposite phases. I

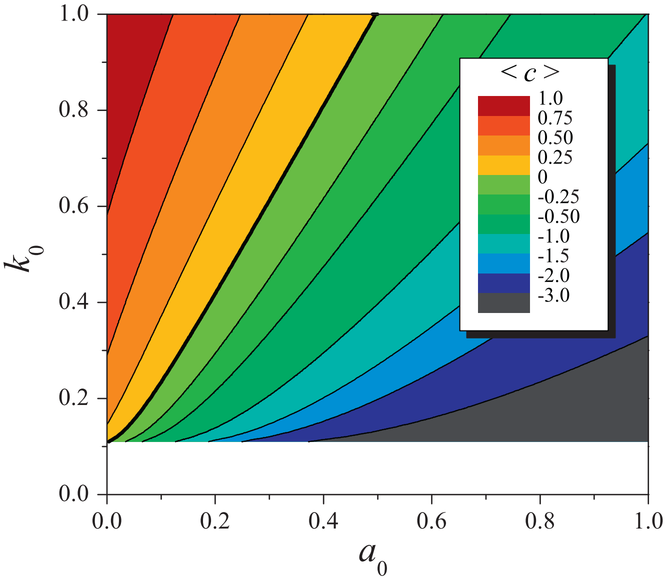

Fig. 5. Contour plot showing the average velocity (color coded as shown in the legend) of the front propagating in the suboptimal habitat. The thick line shows the level $\langle c\rangle=0$. Both parameters oscillate with $a_1=k_1=0.1$. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)

corresponds to a case with strong Allee effect in the suboptimal habitat, which is necessary to have a front moving towards the left (see Eq. (5)). When it comes close to the transition at x_c it stabilizes into an oscillating stationary state that moves forward and backward with a period equal to that of the driving force. Otherwise—if the Allee effect is not strong enough—the front moves away unboundly towards the right, just as in the FKPP equation case.

Fig. 6 shows that the amplitude of the oscillation depends on the period T without any critical feature (compare to a case where the adiabatic approximation breaks down, see below). Fig. 7 shows the correlation between the population and the range, and it is the model equivalent to the field observation of Fig. 3. Time is a parameter in this representation. The case corresponding to the parameters used in Fig. 6 is the narrow loop shown with a thick line. The population moves along this loop in the stationary state. The correlation is linear enough to agree well with the available observations. The width of the loop originates in the different rates of growth, r, and spread, D, of the population. So this width can be controlled by these parameters. Also, setting $k_1 = 0$ (no environmental parameter oscillation) makes the loop very narrow, almost one-dimensional . In the same Fig. 7 (thin full line) we see that suppressing the oscillation of the threshold also eliminates the population oscillation.

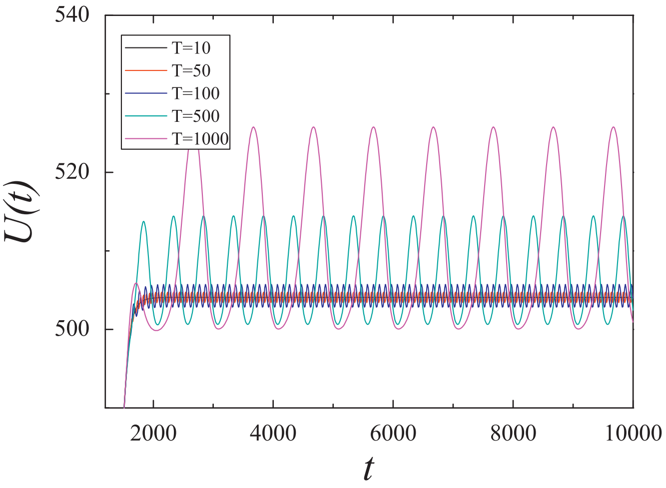

Fig. 6. Population as a function of time, subject to periodic environment and threshold parameters, characterized by their period T, indicated for each curve. $U(t)$ denotes the total population in the system.

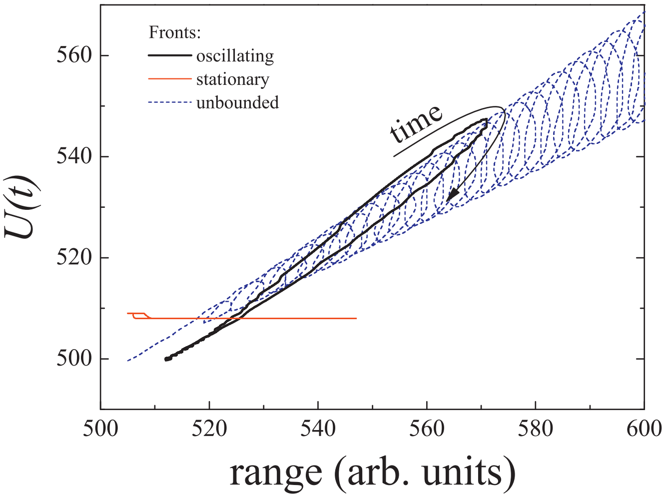

Fig. 7. Population versus range in the model defined by Eq. (4). Thick line: the case displayed in Fig. 6, with driving period T=2000. Compare to Fig. 3. The stationary oscillation moves along the loop. Red line: a stationary front with constant population, corresponding to the same parameters but $a_1 = 0$ (no oscillation in the threshold). Dashed blue line: a case showing the breakdown of the adiabatic approximation, with k_0=0.6, k_1=0.15, a_0=0.29 and a_1=0.15, and driven with a “fast” T=200. This same set of parameters, but with a slower driving (a larger T) shows a stationary oscillating front with a behavior similar to the one shown by the thick line. (For interpretation of the references to color in this figure caption, the reader is referred to the web version of this article.)

3.2. Breakdown of the adiabatic approximation

Eq. (8) (see also Fig. 5) allows fronts propagating with negative velocity even if the Allee effect is not so strong, $a_0 < k_0/2$, provided that the amplitudes of the oscillation are the right ones. However, for non-oscillating K_{so} and a_{so}, this situation is unstable, with a front propagating unboundly towards the right. Fig. 7 shows one such case with a spiralling dashed line. So, a transition is expected as the period of the parameters grows from 0, illustrating the validity of the adiabatic approximation performed to calculate the average speed in Eq. (8). Fig. 8 shows this: even though Eq. (8) predicts a stationary situation for this set of parameters, a fast oscillation of the driving force gives a front moving away with a positive average velocity. That is, if the parameters $K_{so}(t)$ and $a_{so}(t)$ oscillate much faster than the typical timescale of the population dynamics, the population feels their varying effect averaged over multiple oscillations. In this case, a *sudden* approximation performs better, by setting $K_{so}(t)$ and $a_{so}(t)$ at their mean values, and these predict a positive velocity. The relevance of these regimes in natural systems, in particular in the field study carried out at the Sandía Mountain, cannot be assessed at the present stage.

4. Remarks

Although reaction diffusion systems have been used extensively to understand invasion dynamics in animal populations (for a highly readable partial review of this wide topic see, e.g., Volpert and Petrovskii, 2009), applications of this kind of studies in heterogeneous environment are not straightforward. Although there is ample evidence that the invasion dynamics of an animal population are crucially dependent on the characteristics of the environment (Tilman and Kareiva, 1997), it is not always obvious how to quantify its spatio-temporal features. To test the

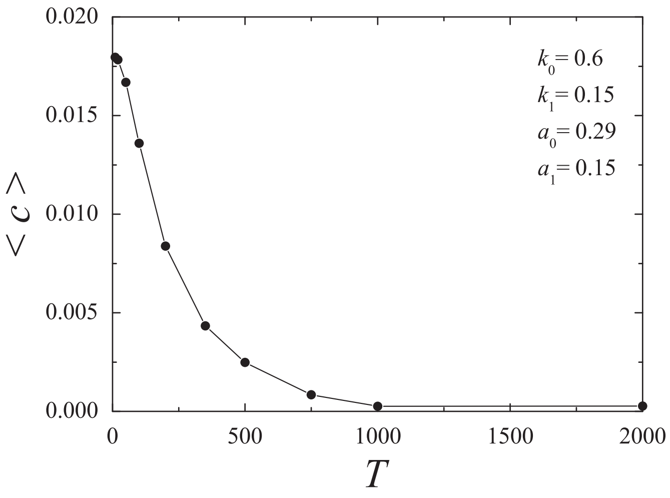

Fig. 8. Breakdown of the adiabatic approximation. Even though Eq. (8) predicts a stationary situation for this set of parameters, a fast oscillation of the driving force gives a front moving away with a positive average velocity.

applicability of reaction diffusion predictions in an environment with varying spatio-temporal characteristics, we have analyzed an experimental data set of an expanding and contracting *P. boylii* mouse population along a steep canyon of the Sandía Mountain in New Mexico, which has allowed to simplify the analysis reducing the system to an effective one-dimensional model. By using a reduced Nagumo equation (Murray, 1993), as done in our recent studies of pattern formation and population dynamics (Kenkre, 2003; Kenkre and Kuperman, 2003; Clerc et al., 2005, 2010; Kumar et al., 2009), it has been possible to link the spatio-temporal oscillations observed in the mouse population along the canyon to the spatio-temporal seasonal forcing in the environment.

The model analyzed in detail in Section 3 has two parameters that oscillate in time, representing seasonal changes in the environment and their effect in the biological system. These are K_{so} and a_{so}, the environmental parameter and the threshold of extinction, respectively, that characterize the Nagumo equation. The functional dependence we postulated for them in Eqs. (6) and (7), with a phase difference of half a period, is rooted in the meaning of the parameters and the interpretation of their seasonal dependence. Our choice of an out-of-phase oscillation is a realistic one, but it is certainly possible that in some circumstances the maximum threshold lags behind the minimum of $K_{so}(t)$. However, a small departure from the phase difference of half a period that we have used in the present analysis does not affect the dynamics observed or its interpretation that we have presented.

The role of the cubic term in Eq. (4) is twofold in the population dynamics. On the one hand, the stability of the $u=0$ equilibrium and the existence of a threshold effectively provides a *negative* growth rate in the vicinity of the null population. This corresponds to the observed *sub*-optimal nature of part of the habitat, with increased rates of winter kill, predation, scarceness of resources, etc. On the other hand, the convex shape of the cubic beyond the threshold provides global stability to the population—this is just as in the case of a regular logistic term. The temporal variation of K_{so} and a_{so}, as explained above, ensures a smooth transition between the seasons, providing growing and shrinking basins of attraction.

As we said in the Introduction, the present knowledge of the system does not allow a quantitative characterization of the population density. Nevertheless, we suggest that the present analysis provides a good qualitative account of the population dynamics and the effects observed in the field, as well as an indirect support for the existence of a relatively strong Allee effect with a seasonal dependence.

Acknowledgments

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References

Abramson, G., Kenkre, V.M., 2002. Spatio-temporal patterns in the Hantavirus infection. Phys. Rev. E 66, 011912-1–011912-5.
Abramson, G., Kenkre, V.M., Yates, T.L., Parmenter, R.R., 2003. Traveling waves of infection in the Hantavirus epidemics. Bull. Math. Biol. 65, 519–534.
Abramson, G., Giuggioli, L., Kenkre, V.M., Dragoo, J.W., Parmenter, R.R., Parmenter, C.A., Yates, T.L., 2006. Diffusion and home range parameters of rodents: *Peromyscus maniculatus* in New Mexico. Ecol. Complex. 3, 64–70.
Allee, W.C., 1931. Animal Aggregations: A Study in General Sociology. University of Chicago Press, Chicago, IL.
Allee, W.C., 1938. The Social Life of Animals. Beacon Press, Boston.
Clerc, M.G., Escaff, D., Kenkre, V.M., 2005. Patterns and localized structures in population dynamics. Phys. Rev. E 72, 056217.
Clerc, M.G., Escaff, D., Kenkre, V.M., 2010. Analytical studies of fronts, colonies, and patterns: combination of the Allee effect and nonlocal competition interactions. Phys. Rev. E 82, 036210.
Courchamp, F., Clutton-Brock, T., Grenfell, B., 1999. Inverse density dependence and the Allee effect. TREE 14, 405–410.
Giuggioli, L., Abramson, G., Kenkre, V.M., Parmenter, C., Yates, T., 2006. Theory of home range estimation from displacement measurements of animal populations. J. Theor. Biol. 240, 126–135.
Giuggioli, L., Kalay, Z., Kenkre, V.M., 2008. Study of transients in the propagation of nonlinear waves in some reaction diffusion systems. Eur. Phys. J. B 62, 341–348.
Giuggioli, L., Potts, J.R., Harris, S., 2011. Animal interactions and the emergence of territoriality. PLoS Comput. Biol. 7, e1002008, pp. 1–9.
Kalcounis-Rüppel, C., Ribble, D.O., 2007. A phylogenetic analysis of the breeding systems of Neotomine–Peromyscine rodents. In: Wolff, J., Sherman, P.W. (Eds.), Rodent Societies: An Ecological and Evolutionary Perspective. University of Chicago Press, Chicago, IL, pp. 68–85.
Kenkre, V.M., 2003. Memory formalism, nonlinear techniques, and kinetic equation approaches. In: Kenkre, V.M., Lindenberg, K. (Eds.), Modern Challenges in Statistical Mechanics, Patterns, Noise, and the Interplay of Nonlinearity and Complexity, AIP Conference Proceedings, vol. 658, American Institute of Physics, Melville, NY, USA.
Kenkre, V.M., Kuperman, M., 2003. Applicability of the Fisher equation to bacterial population dynamics. Phys. Rev. E 67, 051921.
Kenkre, V.M., Giuggioli, L., Abramson, G., Camelo-Neto, G., 2007. Theory of Hantavirus infection spread incorporating localized adult and itinerant juvenile mice. Eur. Phys. J. B 55, 461–470.
Kokko, H., Sutherland, W.J., 2001. Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. Evol. Ecol. Res. 3, 537–551.
Kumar, Niraj, Kuperman, M.N., Kenkre, V.M., 2009. Theory of possible effects of the Allee phenomenon on the population of an epidemic reservoir. Phys. Rev. E 79, 041902.
Mills, J.N., Ksiazek, T.G., Peters, C.J., Childs, J.E., 1999. Long-term studies of Hantavirus reservoir populations in the southwestern United States, a synthesis. Emerg. Infect. Dis. 5 (1), 135–142.
Murray, J.D., 1993. Mathematical Biology, second ed. Springer, New York, USA.
Perthame, B., 2008. Transport Equations in Biology, Frontiers in Mathematics Series. Springer-Verlag, New York.
Ribble, D.O., Stanley, S., 1998. Home ranges and social organization of syntopic *Peromyscus boylii* and *P. truei*. J. Mammal. 79, 932–941.
Stephens, P.A., Sutherland, W.J., Freckleto, R.P., 1999. What is the Allee effect? Oikos 87, 185–190.
Taylor, C.M., Hastings, A., 2005. Allee effects in biological invasions. Ecol. Lett. 8, 895–908.
Tilman, D., Kareiva, P. (Eds.), 1997. Spatial Ecology. Princeton University Press.
Tinnin, D.S., 2003. Testing the Refugia Hypothesis: Population Dynamics of *Peromyscus* and Hantavirus seroprevalence across an Elevational Gradient. Thesis of Master of Science in Biology, University of New Mexico, Albuquerque, NM.
Tobin, P.C., Berec, L., Liebhold, A.M., 2011. Exploiting Allee effects for managing biological invasions. Ecol. Lett. 14, 615–624.
Volpert, V., Petrovskii, S., 2009. Reaction–diffusion waves in biology. Phys. Life Rev. 6, 267–310.
Yates, T.L., Mills, J.N., Parmenter, C.A., Ksiazek, T.G., Parmenter, R.R., Vande Castle, J.R., Calisher, C.H., Nichol, S.T., Abbott, K.D., Young, J.C., Morrison, M.L., Beaty, B.J., Dunnum, J.L., Baker, R.J., Salazar-Bravo, J., Peters, C.J., 2002. The ecology and evolutionary history of an emergent disease, Hantavirus Pulmonary Syndrome. Bioscience 52, 989–998.