Unexpected spatial patterns in an insect outbreak match a predator diffusion model

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SUMMARY

An outbreak of the western tussock moth (*Orgyia vetusta*) with a sharp spatial boundary has been hypothesized to be the result of an interaction with mobile parasitoids. We report here a striking correspondence between the qualitative prediction of a general model for a mobile predator and a sessile prey and initial observations of the outbreak of western tussock moth. The model makes the counter-intuitive prediction that the prey species will have its highest population density at the edge of an outbreak, which corresponds to observations made of the western tussock moth. This is a striking pattern that should be looked for in other population systems.

1. INTRODUCTION

Although reaction-diffusion equations and the patterns they generate have occupied an important place in the literature of theoretical ecology, correspondence between theory and field observation has been limited; in part because much of the theoretical focus has been on solutions exhibiting small variability over space (Kareiva 1990; Kareiva & Wennergren 1995), rather than on using the models as a tool to look for confirming or rejecting hypotheses for mechanisms controlling the spatial distribution of species. Here we report how sharply varying (in space) solutions with large variation in prey densities, obtained by a previous singular-perturbation analysis (Fife 1976; Mimura *et al.* 1980; Conway 1984) of a reaction-diffusion predator-prey model correspond closely to field observations of the spatial distribution of the western tussock moth (*Orgyia vetusta*) and its major parasitoids, in agreement with a hypothesis based on parasitoid or predator diffusion. The model makes the striking counter-intuitive prediction that for small enough herbivore movement rates the highest population densities of the herbivore occur just at the edge of the outbreak patch, a prediction that is consistent with data from an outbreak of tussock moths. The prediction is a qualitative one, depending only on the functional response of the predator being saturating, and an essentially immobile prey. This is one of the clearest demonstrations of a correspondence between the theory of reaction-diffusion equations and observations of spatial pattern in a natural system.

2. MODEL AND ANALYSIS

We begin with a general continuous time spatial predator-prey or host-parasitoid model on a one-

dimensional interval. The spatial location is x , with $0 < x < L$, so L is the length of the interval. Let $h(x, t)$ and $p(x, t)$ be the density of the host and the parasitoid at location x at time t , respectively. The dynamics, and boundary conditions expressing the fact that individuals do not leave the region of interest, are given by

$$\frac{\partial h}{\partial t} = hf(h, p) + D_h \frac{\partial^2 h}{\partial x^2} \quad (1)$$

$$\frac{\partial p}{\partial t} = pg(h, p) + D_p \frac{\partial^2 p}{\partial x^2} \quad (2)$$

$$\left. \frac{\partial h}{\partial x} \right|_{x=0} = \left. \frac{\partial p}{\partial x} \right|_{x=0} = \left. \frac{\partial h}{\partial x} \right|_{x=L} = \left. \frac{\partial p}{\partial x} \right|_{x=L} = 0 \quad (3)$$

where the local per capita growth rate of the host is given by $f(h, p)$, the per capita growth rate of the parasitoid is given by $g(h, p)$, and movement is random with the diffusion coefficients D_h and D_p describing the rate of movement of the herbivore and the parasitoid, respectively. The usual form of analysis of the generation of spatial patterns in these equations in the ecological literature has been to focus on the existence of small amplitude patterns (Turing 1952; Levin 1974; Kareiva 1990), which arise out of different rates of movement and a type II functional response of the predator. However, relating these solutions to field observations of pattern is problematical because the theory only considers small-amplitude solutions, while observations can be made only of solutions that exhibit large variations in population density over space.

Although the dynamics of large amplitude solutions of this model are too complex to study in general, substantial progress has been made in the past (Fife 1976; Mimura *et al.* 1980; Conway 1984) in finding approximate solutions where the movement of the prey is small enough. We will not attempt to repeat the

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development of this elegant theory here, but will instead present a very heuristic discussion of the theory using a new graphical representation, and emphasize the very striking qualitative predictions of this theory not previously emphasized that can be examined within the context of field and experimental systems.

Note that if the prey does not move, then at equilibrium, at each spatial location,

$$hf(h, p) = 0. \quad (4)$$

As illustrated in figure 1, if the predator has a type II (or possibly a type III) functional response, there will be a range of predator levels for which there are three prey equilibria. If the predator population is fixed, two of these equilibria are stable ($h = 0$ and the larger solution of $f(h, p) = 0$), and one is unstable (the smaller solution of $f(h, p) = 0$). The theory (Fife 1976; Mimura *et al.* 1980; Conway 1984) shows that there can be a solution which satisfies the boundary conditions at each end of the suitable habitat and 'jumps' between these two population levels—there will be a narrow region (whose width will scale like the movement rate of the herbivore) over which the equilibrium population level of the herbivore changes from the upper equilibrium to zero (see figures 1 and 2). (The singular perturbation method is used to construct the solution that is approximated by the one that has the 'jump'—as the movement rate of the prey approaches zero, the solution approaches one that is discontinuous.) A similar result can also arise in an alternative model incorporating an Allee effect in the prey and a linear functional response (Mimura & Murray 1978).

Our major focus is on the second striking qualitative result (figures 1 and 2), which is independent of the particular population model chosen (although dependent on the presence of the type II or III functional response), that the highest population levels of the prey must occur at the edge of the region occupied by the prey. Not surprisingly, for sufficiently high prey mobility, the highest prey population levels are no longer found at the edge of the 'outbreak', as illustrated in numerical solutions given by Mimura & Murray (1978) for a related model with linear functional response and an Allee effect in the prey. However, in the tussock moth system, the prey (host) mobility is so low that the highest prey population levels would certainly be expected to occur at the edge of the region occupied by the prey. The heuristic explanation is that if the prey is immobile and the predator diffuses randomly, then the per herbivore predation/parasitism rates are lower at the edge of the outbreak than in the interior of the outbreak.

Both these predictions are expected to hold under the predator diffusion hypothesis for the generation of spatial pattern in the host population, but an explanation based on host plant quality should not lead to the highest density of herbivores at the edge of the outbreak patch (Harrison 1995, 1997). Thus, the theory presented here provides an example of a case where one can distinguish process from pattern. Both predictions will need to be examined in a variety of ecological systems, but we present here evidence from a study of tussock

Figure 1. Phase plane for herbivore–predator/parasitoid system with a spatial solution, corresponding to the case of a completely immobile herbivore, on a one-dimensional habitat of length L illustrated by the heavy line. The x values along the heavy line correspond to spatial locations (see figure 2 for the same solution drawn as population levels as a function of spatial location). In this figure, the isoclines for the herbivore, h , and predator/parasitoid, p , populations are drawn, where a type II functional response is assumed. Since the movement of the herbivore is assumed to be very limited, at any point in space the equilibrium herbivore population will either lie on the isocline or on the line $h = 0$. As indicated by the arrows on the figure, for a fixed level of the predator/parasitoid, the herbivore population will approach its isocline to the right of the 'hump', and move away from the isocline to the left of the 'hump'. The spatial location $x = b$, at which the 'jump' in the herbivore population occurs, and the population levels of both species at $x = 0$ and $x = L$ (where the heavy line ends), are uniquely determined by the boundary conditions specifying that no organisms leave the habitat under consideration. Since the population within the outbreak must lie on the 'stable' part of the herbivore isocline, as the predator population declines (in space), the herbivore population must go up, so the highest herbivore population has to lie at the edge of the patch.

moths and their parasitoids which is compatible with the qualitative predictions of the qualitative analysis of the predator diffusion hypothesis.

3. TUSOCK MOTH OUTBREAKS

The western tussock moth *Orgyia vetusta* (Lymantriidae) forms localized outbreaks within stands of shrubby lupines (*Lupinus arboreus* and *L. chamissonis*) in coastal California. Outbreaks may cause defoliation of hundreds of contiguous bushes, and may last for more than 10 years at a given site. Despite being food-limited, these few dense populations show very little tendency to spread, and the moth remains consistently sparse or absent on vast areas of its host plant (Harrison 1994). Experimental evidence shows this is not caused by spatial variation in host plant quality or predator abundance (Harrison 1994, 1995, 1997; Harrison & Wilcox 1995). Instead, low mobility is a contributing factor; adult female moths are flightless, larvae show low rates of passive aerial dispersal (ballooning), and experimentally created outbreaks spread a median of

Figure 2. Singular solution corresponding to a completely immobile herbivore of the spatial herbivore–predator or host–parasitoid system corresponding to the phase plane in figure 1. Within a one-dimensional habitat of length L , the predator population level as a function of spatial location is given by a dashed line, and the herbivore population by a solid line. Note that the highest herbivore levels occur at the edge of the outbreak. For a herbivore that has very low movement rates there will be a solution close to the one illustrated, and if the movement rates of the herbivore are still higher, then the highest herbivore levels will no longer be found at the edge of the outbreak. Solutions with several outbreak patches also exist.

only 2 m in a year (Harrison 1994, 1995, 1997). In contrast, some of the major natural enemies at the study site are highly mobile; they include the wasp *Teleonomus californicus* (Ashmead), which parasitizes eggs, and the tachinid flies *Tachinomyia similis* (Williston), *Patelloa pluriseriata* or *P. fuscimacula* (Aldrich & Webber), and *Protodejeania echinata* (Townsend), which attack larvae and emerge from pupae.

Very low prey and high parasitoid mobility provide the essential conditions for the predator diffusion hypothesis analysed above. Brodmann *et al.* (1997) tested predictions of this hypothesis at the Bodega Marine Reserve (University of California, Sonoma Co., CA), where they created an approximately straight-line transect leading 200 m through a tussock moth outbreak (distances -200 to 0 in figure 3) and 500 m through an adjacent non-outbreak area (distances 0 – 500 in figure 3). In 1994, 21 lupine bushes were randomly chosen along the transect, 7 inside and 14 outside the outbreak area, and 4 egg masses were placed on each bush to assay egg parasitism. In 1995, 60 bushes were chosen along the transect, 20 inside and 40 outside the outbreak area; each was enclosed with a fence and inoculated with 15 or 60 larvae to assay larval parasitism. In 1995, Brodmann *et al.* (1997) counted the number of naturally occurring tussock moth larvae on the three nearest neighbours of

Figure 3. Densities of tussock moth larvae with distance from the edge of the outbreak at two sampling dates (A, 24 June 1995; B, 10 July 1995)—data from Brodmann *et al.* (1997). Densities are measured as number of larvae within one 0.25 m^2 quadrat on the surface of three bushes (randomly selected). The choice of the edge of the outbreak is arbitrary. The spatial distribution of densities of moth larvae is strikingly similar to figure 2. In particular, the highest densities of tussock moth are clearly found at the edge of the outbreak.

each experimental bush. They also measured densities of adult parasitoids using sticky cards.

In both years, rates of parasitism by each species were significantly higher outside than inside the outbreak area, and increased either monotonically or unimodally with distance from the outbreak area (Brodmann *et al.* 1997). This result confirmed one key, non-obvious, prediction of the predator diffusion hypothesis. Here we report the confirmation of the second prediction outlined above, one which was not apparent until the singular perturbation analysis described above was performed. As figure 3 shows, densities of larval tussock moths in 1995 were substantially higher at the edge of the outbreak area (near distance 0) than within the outbreak (distances -200 – 0 m). This was true for both dates on which larvae were sampled, even though larval densities declined considerably during this time.

4. CONCLUSIONS

An ideal test of the predator diffusion model would be a fully experimental one, in which the movement of parasitoids from outbreak to non-outbreak areas was prevented, which should result in the spread of the outbreak (Turchin 1987). However, in many cases such an approach is not practical. We believe that the combination of theoretical development leading to the prediction of non-obvious patterns, and empirical demonstration of these patterns, has made this one of the best-documented cases of spatial pattern formation in a predator–prey system (Kareiva & Odell 1987; Turchin & Kareiva 1989). We recognize that other biological processes, such as predator (or parasitoid) aggregation, may also play a role and will require further investigation. We are continuing our modelling study of this system looking at more detailed models, using both explicit simulation approaches and analytic discrete spatial models.

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