THE ROYAL SOCIETY

Received 5 July 2001
Accepted 9 October 2001
Published online 1 February 2002

Generation of periodic waves by landscape features in cyclic predator–prey systems

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The vast majority of models for spatial dynamics of natural populations assume a homogeneous physical environment. However, in practice, dispersing organisms may encounter landscape features that significantly inhibit their movement. We use mathematical modelling to investigate the effect of such landscape features on cyclic predator–prey populations. We show that when appropriate boundary conditions are applied at the edge of the obstacle, a pattern of periodic travelling waves develops, moving out and away from the obstacle. Depending on the assumptions of the model, these waves can take the form of roughly circular 'target patterns' or spirals. This is, to our knowledge, a new mechanism for periodic-wave generation in ecological systems and our results suggest that it may apply quite generally not only to cyclic predator–prey interactions, but also to populations that oscillate for other reasons. In particular, we suggest that it may provide an explanation for the observed pattern of travelling waves in the densities of field voles (*Microtus agrestis*) in Kielder Forest (Scotland–England border) and of red grouse (*Lagopus lagopus scoticus*) on Kerloch Moor (northeast Scotland), which in both cases move orthogonally to any large-scale obstacles to movement. Moreover, given that such obstacles to movement are the rule rather than the exception in real-world environments, our results suggest that complex spatio-temporal patterns such as periodic travelling waves are likely to be much more common in the natural world than has previously been assumed.

Keywords: travelling wave; obstacle; reaction–diffusion; cyclic dynamics; field vole

1. INTRODUCTION

The vast majority of models for spatio-temporal dynamics of natural populations have assumed that populations are distributed in homogeneous environments. In particular, minimal attention has been given to the role of large-scale landscape features that will significantly inhibit the movement of dispersing organisms. Broadly speaking, such organisms can either find a route around such landscape features, refrain from moving altogether or simply attempt to traverse the obstacle. In this paper, we investigate for the first time, to our knowledge, the effects of these simple movement rules on the predicted overall spatio-temporal dynamics of cyclic predator–prey systems.

We begin our investigation using a reaction–diffusion-type model. This assumes that both predator and prey populations move continuously in space; and in the following we will discuss an alternative model that instead assumes that individuals occupy discrete but interconnected spatial sites. Throughout, we study predator–prey systems that are cyclic, meaning that in the absence of any spatial variation both prey and predator densities oscillate. Our model equations, detailed in Appendix A, are a standard model for this type of predator–prey system and we solve them on a two-dimensional domain with no-flux boundary conditions, meaning that individuals cannot enter or leave the domain. When the domain is homogeneous, randomly generated initial population densities rapidly even out, giving spatially uniform population cycles.

Our objective is to consider how large landscape features affect dynamical behaviour. To this end, we introduced into the domain a central obstacle, assuming either no-flux boundary conditions on the edge of the obstacle or that the population densities are always zero on the obstacle edge. The latter would correspond to individuals attempting to cross the obstacle, but always dying in the attempt. With no-flux boundary conditions, the obstacle has little effect on the population dynamics that quickly form uniform oscillations. However, when the population densities are zero around the obstacle, the behaviour is quite different (figure 1*a*; movie clips corresponding to this and other figures are available at http://www.ma.hw.ac.uk/~jas/supplements/obstacles/). The randomness of the initial conditions rapidly disappears, giving rise to periodic travelling waves moving out from the obstacle and through the domain. In these waves, there are again population cycles; however, the cycles are out of phase at different points in space and it is this that constitutes the travelling waves.

Spatio-temporal patterns resembling periodic travelling waves have been observed recently in several natural populations, including field voles (*Microtus agrestis*) (Lambin *et al.* 1998; MacKinnon *et al.* 2001) and red grouse (*Lagopus lagopus scoticus*) (Moss *et al.* 2000). In both of these cases, the underlying cause of these waves remains unknown. Previous modelling work has also shown that periodic waves are generated by invasions in cyclic populations (Sherratt *et al.* 1997, 2000), but there is no evidence for such an invasion in these two cases. We will show that the generation of periodic waves by

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