THEORETICAL POPULATION BIOLOGY 34, 169–176 (1988)

Overall Population Stability Despite Local Extinction: The Stabilizing Influence of Prey Dispersal from Predator-Invaded Patches

M. W. SABELIS*

Department of Population Biology, University of Leiden, P.O. Box 9516, 2300 RA Leiden, The Netherlands

AND

O. DIEKMANN

Centre for Mathematics and Computer Science, Kruislaan 413, 1098 SJ Amsterdam, and Institute of Theoretical Biology, Groenhovenstraat 5, 2311 BT Leiden, The Netherlands

Received October 1, 1987

INTRODUCTION

Extinction of local populations in the field is not easily assessed. Important confounding factors are the subjective criteria used to define the term "local population", to select the scale of spatial heterogeneity under consideration and to infer local population extinction from population samples. Yet there exists a wealth of studies suggesting that local population extinction is not a rare phenomenon. In two recent papers Murdoch *et al.* (1984, 1985) argued that local populations of scale insects in California (Olive Scale, Red Scale, and Cottony-Cushion Scale) and Larch sawflies in Manitoba were driven to extinction by parasitoids. Similar phenomena have been reported for herbivore–plant systems, such as Ragwort and a moth (Van der Meijden, 1979; Van der Meijden *et al.*, 1985), and for predator–prey systems, such as backswimmers, waterbugs and mosquitofish feeding on mosquito larvae (Murdoch *et al.*, 1985), and phytoseiid mites feeding on spider mites (Huffaker, 1958; Huffaker *et al.*, 1963; Takafuji *et al.*, 1983; Sabelis and Van der Meer, 1986).

Even when local populations exhibit unstable dynamical behaviour, one may still observe population persistence at a larger spatial scale. Indeed,

* Present address: Department of Pure and Applied Ecology, University of Amsterdam, Kruislaan 302, 1098 SM Amsterdam, The Netherlands.

0040-5809/88 $3.00

local predator–prey cycles may proceed out of phase and consequently the predators will not wipe out their prey everywhere at the same time. Spatial heterogeneity thus creates the possibility of a "hide and seek" game and, at least in principle, global persistence may occur despite local extinctions (Maynard Smith, 1974; Roff, 1974; Hilborn, 1975; Zeigler, 1977; Hastings, 1977; Gurney and Nisbet, 1978; Crowley, 1978, 1981; Hogeweg and Hesper, 1981; Chesson, 1982).

Two important questions still await a detailed and complete answer (see also Hassell and Sabelis, 1987):

(1) How can asynchrony of local predator–prey cycles be maintained, given the many and varied ways in which the environment, the predators, and the prey can all have a synchronizing effect on local interactions?

(2) Can asynchrony between local cycles indeed produce a prey refuge in space *and* time whose net effect acts as a stabilizing mechanism analogous to that of "genuine" refuges in classic predator–prey models?

In order to answer these questions many factors have to be considered. For instance, a variable predator–prey interaction period may enhance asynchrony. In addition, small prey colonies may be more or less "invulnerable" (since they are not easily detected by predators) and hence constitute a temporary refuge in much the same way as invulnerable juvenile stages of hosts are in the context of parasitoid–host interactions (Murdoch *et al.*, 1987). Similarly, the class of prey searching for a suitable patch to found a new colony (prey "aireal plankton") is invulnerable to predation. We intend to investigate systematically the influence of such factors in future work, exploiting the framework of structured population models (Metz and Diekmann, 1986) to build detailed and, hopefully, more realistic models. The sole aim of this paper is to call attention to a less direct (and therefore easily overlooked) factor which diminishes the effects of synchrony: the founding of new prey colonies by prey which leave a predator-invaded patch during the interaction period. By analyzing some (over)simplified models we will show that this dispersal process has a strong stabilizing influence.

Two Simplified Versions of Hastings' Predator–Prey Patch Model

We will concentrate on two simple predator–prey patch models which are essentially due to Hastings (1977). Both models apply to a situation in which patches can belong to three possible categories and where there is just one transition possible from each category, viz., empty patches → prey (invaded) patches → predator (invaded) patches → empty patches. The

invasion rates of predators and prey are taken to be proportional to the number of patches they currently occupy (implying that all patches are equally accessible from all other patches and that interpatch dispersal is instantaneous). The two models differ in that the first assumes a negative exponential distribution of the predator–prey interaction period whereas the second assumes that this interaction period has a fixed length.

The first model is described by the system of differential equations:

$$\begin{aligned} \frac{dx}{dt} &= a(x + ey) - bxy \\ \frac{dy}{dt} &= bxy - dy. \end{aligned} \tag{1}$$

Here x denotes the number of prey patches and a the rate at which dispersing prey from an arbitrary prey patch found new colonies in patches which were still empty (note that x will increase exponentially in the absence of predators). The rate at which predators invade an arbitrary prey patch is given by by, where y denotes the number of predator patches and b a "reaction" coefficient. For an arbitrary predator patch there is a constant probability per unit of time d that first the prey and then the predators go extinct. Or, in other words, the interaction period following predator invasion is exponentially distributed with mean d^{-1}. Finally and most importantly, the rate at which prey dispersing from an arbitrary predator patch found new prey colonies in empty patches is given by ae. Hence, e indicates the contribution of a predator patch to the creation of new prey patches relative to the contribution of a prey patch. Note that $e > 1$ means that prey dispersal from predator patches is larger than from prey patches (which can be the case if the presence of predators enhances the tendency of the prey to disperse).

The system of differential equations (1) admits a non-trivial equilibrium,

$$x = d/b, \qquad y = ad/(b(d - ea)), \tag{2}$$

which is biologically relevant (i.e., positive) if and only if d exceeds ea (if $ea > d$ the number of prey patches will grow exponentially even in the presence of the predators). When $e = 0$ the system reduces to the familiar Lotka–Volterra system for which the equilibrium is neutrally stable. In other words, when $e = 0$ we are precisely at the edge of the stable–unstable transition. A straightforward analysis (see Appendix 1) shows that the equilibrium is stable (globally and exponentially) when $e > 0$. We conclude that prey dispersal from predator patches can act to stabilize populations of predator and prey at a large spatial scale.

For a set interaction period of length d^{-1} our variant of Hastings' model is described by the system

$$\frac{dx}{dt} = a(x + ey) - bxy$$
$$y(t) = b \int_{t-d^{-1}}^{t} x(s)\, y(s)\, ds. \tag{3}$$

The integral equation for y states that at time t the number of predator patches equals the sum of those prey patches which were invaded by a predator during the time interval $[t - d^{-1}, t]$. The non-trivial equilibrium of (3) is again given by (2). Using the methods outlined in the appendix of Hastings' 1977 paper, the local stability of this equilibrium can be investigated. It turns out that now the equilibrium is unstable when $e = 0$. However, when e is sufficiently large (depending on ad^{-1}) one obtains stability. The results are given in Fig. 1, while Appendix 2 gives an explanation of how they were derived. Again, we conclude that prey dispersal from predator patches has a significant effect on overall stability. Moreover, we note that, as expected, distributed interaction periods allow for a larger domain of stability than set interaction periods.

Finally, let us comment on the difference between the original Hastings models and our versions of them. The original models contain yet another stabilizing mechanism, viz., a possible lack of empty patches described by a logistic factor in the term corresponding to the creation of new prey patches. In the original version of model (2) one can also observe the

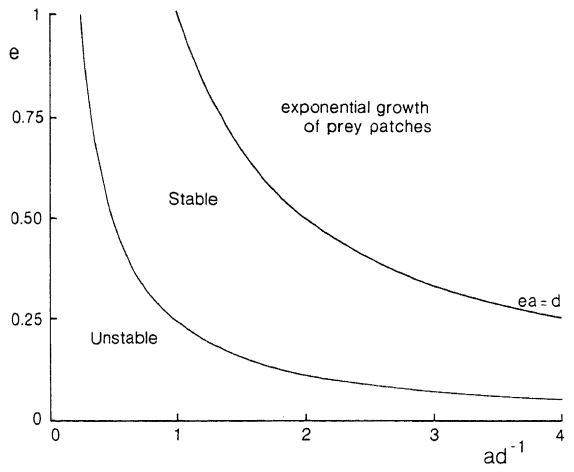

FIG. 1. Stability diagram of the model described by system (3) (see text).

stabilizing effect of prey dispersal from predator patches by noting that the stable region in the (a, b)-parameter plane is substantially larger when $e=1$ than when $e=0$ (see Fig. 1 in Hastings, 1978). We have eliminated the logistic factor in order to demonstrate that prey dispersal from predator patches *alone* (i.e., in the absence of any other stabilizing mechanism) can stabilize the equilibrium.

Admittedly, the assumptions underlying the models discussed above are simplistic and the relative importance of prey dispersal from predator patches as a stabilizing mechanism is yet to be assessed in more elaborate models. Nevertheless the results of the stability analysis presented in this paper are interesting in showing that a selectively advantageous property of the prey may confer stability to a predator-prey system that would be otherwise unstable.

Appendix 1

The Jacobi matrix corresponding to the linearization of (1) in the equilibrium (2) is given by

$$\begin{pmatrix} \dfrac{-ea^2}{d-ea} & ea-d \\ \dfrac{ad}{d-ea} & 0 \end{pmatrix}.$$

For a, d, $e>0$, and $ea<d$ the determinant is positive while the trace is negative. Hence both eigenvalues have negative real part and the equilibrium is locally exponentially stable. Global stability follows by applying Bendixson's criterion after the change of variables $x=\exp(u)$, $y=\exp(v)$ (see Knobloch and Kappel, 1974, p. 193; Hale, 1969, p. 63).

Appendix 2

The following scaling considerations facilitate the analysis of system (3). By taking dt as the new time variable we may put $d=1$ provided we change a into ad^{-1} and b into bd^{-1} while keeping e the same. The constant bd^{-1} now only governs the scale of x and y without affecting the dynamics (indeed, by scaling both x and y with this factor it disappears from the equations). Therefore, we study the system

$$\begin{aligned} \frac{dx}{dt} &= ad^{-1}(x+ey)-xy \\ y(t) &= \int_{t-1}^{t} x(s)\,y(s)\,ds \end{aligned} \tag{4}$$

and in particular the local behaviour near the equilibrium

$$x = 1, \qquad y = ad^{-1}/(1 - ead^{-1}). \tag{5}$$

If we linearize about the equilibrium, substitute an exponential trial solution, and do some algebraic manipulations we arrive at the characteristic equation

$$\lambda - \lambda K(\lambda) + CK(\lambda) + D = 0, \tag{6}$$

where by definition

$$K(\lambda) = (1 - \exp(-\lambda))/\lambda \tag{7}$$

and

$$C = \frac{ad^{-1}(1 - 2ead^{-1})}{1 - ead^{-1}}, \qquad D = \frac{e(ad^{-1})^2}{1 - ead^{-1}} \tag{8}$$

(notation in accordance with Hastings (1977)). The equilibrium will be locally exponentially stable if all roots of (6) have negative real parts and unstable if at least one root has a positive real part. Therefore the stability boundary in the (ad^{-1}, e)-parameter plane is (partially) characterized by the property that (6) has a root precisely on the imaginary axis. As Hastings observed, we can exploit the fact that (6) is linear in C and D to parameterize the stability boundary in the (C, D)-parameter plane by the position of the root on the imaginary axis. Indeed, putting $\lambda = iw$, splitting (6) into its real and its imaginary part, and solving for C and D we obtain

$$C = w\frac{\sin(w) - w}{\cos(w) - 1}, \qquad D = \frac{2\cos(w) - 2 + w\sin(w)}{\cos(w) - 1}. \tag{9}$$

Fortunately we can invert the transformation (8) from the (ad^{-1}, e)-parameter plane into the (C, D)-parameter plane. The inverse transformation reads

$$ad^{-1} = C + D, \qquad e = \frac{D}{2D^2 + 3CD + C^2}. \tag{10}$$

The stability boundary in Fig. 1 was computed by combining (9) and (10) and letting w traverse the interval $[0, 2\pi]$ (note that both C and D are even in w so that we get exactly the same curve for $w \in [-2\pi, 0]$; this corresponds to the fact that complex roots always occur in conjugate pairs). One needs additional arguments to make sure that this really is the stability boundary since, at least in principle, roots may return to the left

half plane with a higher value of w or curves corresponding to (9), (10) with $w \in [2k\pi,\ 2(k+1)\pi]$, $k \geqslant 1$, could enter the region labelled "stable equilibrium" in Fig. 1. In the present case, however, such possibilities can be excluded, but the proof will not be given here (available on request).

At the stability boundary a pair of conjugate roots crosses the imaginary axis and therefore the onset of instability is characterized by periodic behaviour (the so-called Hopf-bifurcation).

ACKNOWLEDGMENTS

We thank Hans Metz, Mike Hassell, and Kees Bakker for useful comments and all those joining the so-called Cannibalism meetings at the Institute of Theoretical Biology (University of Leiden) for stimulating discussions.

Note added in proof. More elaborate models of predator–prey–plant interactions in patchy environments are discussed in two forthcoming publications: DIEKMANN, O., METZ, J. A. J., AND SABELIS, M. W. 1988. *Experimental and Applied Acarology* **5** (extra issue; part 2). DIEKMANN, O., METZ, J. A. J., AND SABELIS, M. W. 1988. Proceedings of a Workshop on Selected Topics *in* "Biomathematics, IIASA," Laxenburg, Austria.

REFERENCES

CHESSON, P. L. 1982. The stabilizing effect of a random environment, *J. Math. Biol.* **15**, 1–36.

CROWLEY, P. H. 1978. Effective size and the persistence of ecosystems, *Oecologia* **35**, 185–195.

CROWLEY, P. H. 1981. Dispersal and the stability of predator–prey interactions, *Amer. Nat.* **118**(5), 673–701.

GURNEY, W. S. C., AND NISBET, R. M. 1978. Predator–prey fluctuations in patchy environments, *J. Anim. Ecol.* **47**, 85–102.

HALE, J. K. 1969. "Ordinary Differential Equations," p. 320, Wiley, New York.

HASSELL, M. P., AND SABELIS, M. W. 1987. Reply to Den Boer. *T.R.E.E.* **2**(3), 78.

HASTINGS, A. 1977. Spatial heterogeneity and the stability of predator–prey systems, *Theor. Pop. Biol.* **12**, 37–48.

HASTINGS, A. 1978. Spatial heterogeneity and the stability of predator–prey systems: Predator-mediated coexistence, *Theor. Pop. Biol.* **14**, 380–395.

HILBORN, R. 1975. The effect of spatial heterogeneity on the persistence of predator–prey interactions, *Theor. Pop. Biol.* **8**, 346–355.

HOGEWEG, P., AND HESPER, B. 1981. Two predators and one prey in a patchy environment: An application of MicMac modelling, *J. Theor. Biol.* **93**, 411–432.

HUFFAKER, C. B. 1958. Experimental studies on predation: Dispersion factors and predator–prey oscillations, *Hilgardia* **27**, 343–383.

HUFFAKER, C. B., SHEA, K. P., AND HERMAN, S. G. 1963. Experimental studies on predation: Complex dispersion and levels of food in an acarine predator–prey interaction, *Hilgardia* **34**, 305–330.

KNOBLOCH, H. W., AND KAPPEL, F. 1974. "Gewöhnliche Differential Gleichungen," p. 280, Teubner, Stuttgart.

MAYNARD SMITH, J. 1974. "Models in Ecology," p. 146, Cambridge Univ. Press, New York.

MEIJDEN, E. VAN DER 1979. Herbivore exploitation of a fugitive plant species: Local survival and extinction of the Cinnabar Moth and Ragwort in a heterogeneous environment, *Oecologia* **42**, 307–323.

MEIJDEN, E. VAN DER, DE JONG, T. J., KLINKHAMER, P. G. L., AND KOOI, R. E. 1985. Temporal and spatial dynamics in populations of biennial plants, *in* "Structure and Functioning of Plant Populations" (J. Haeck and J. W. Woldendorp, Eds.), Vol. 11, pp. 91–103, North-Holland, Amsterdam.

METZ, J. A. J., AND DIEKMANN, O. 1986 (Eds.). The dynamics of physiologically structured populations, Lecture Notes in Biomathematics, Vol. 68, p. 511, Springer-Verlag, Berlin/New York.

MURDOCH, W. W., CHESSON, J., AND CHESSON, P. L. 1985. Biological control in theory and practice, *Amer. Nat.* **125**(3), 344–366.

MURDOCH, W. W., NISBET, R. M., BLYTHE, S. P., GURNEY, W. S. C., AND REEVE, J. D. 1987. An invulnerable age class and stability in delay-differential parasitoid–host models, *Amer. Nat.* **129**, 263–282.

MURDOCH, W. W., REEVE, J. D., HUFFAKER, C. B., AND KENNETT, C. E. 1984. Biological control of Olive Scale and its relevance to ecological theory, *Amer. Nat.* **123**(3); 371–392.

ROFF, D. A. 1974. Spatial heterogeneity and the persistence of populations, *Oecologia* **15**, 245–258.

SABELIS, M. W., AND VAN DER MEER, J. 1986. Local dynamics of the interaction between predatory mites and two-spotted spider mites, *in* "Dynamics of Physiologically Structured Populations" (J. A. J. Metz and O. Diekmann, Eds.), Lecture Notes in Biomathematics, Vol. 68, pp. 322–344, Springer-Verlag, Berlin.

TAKAFUJI, A., TSUDA, Y., AND MIKI, T. 1983. System behaviour in predator–prey interaction, with special reference to acarine predator–prey systems, *Res. Pop. Ecol. Suppl.* **3**, 75–92.

ZEIGLER, B. P. 1977. Persistence and patchiness of predator–prey systems induced by discrete event population exchange mechanisms, *J. Theor. Biol.* **67**, 687–713.