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Spatial heterogeneity and the dynamics of parasitoid-host systems

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This paper considers the dynamics of coupled host-parasitoid interactions where the hosts are distributed amongst discrete patches over which the parasitoids search. While it is well known that density dependent patterns of parasitism from patch to patch within such a setting can be important in promoting the stability of the interactions, only recently has it been appreciated that inverse patterns of parasitism can be just as important. Furthermore, it is now clear that even where there is no spatial density dependence of any kind, the distribution of parasitism can still play a crucial part in promoting stability as long as the probability of hosts being parasitized is sufficiently variable from patch to patch. Distinguishing between different spatial patterns of parasitism is thus not a reliable means of identifying those foraging behaviours that promote population persistence. A possible alternative approach is briefly described which involves measuring the variance in the distribution of parasitism. In simple models at least, this can be simply related to the stability of the interactions.

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1. Introduction

The early models of predator-prey (including insect parasitoid-host) interactions were either neutrally stable (Lotka 1925, Volterra 1926) or had an unstable equilibrium around which the populations oscillate with increasing amplitude (Nicholson 1933, Nicholson & Bailey 1935). These basic models are not in themselves, therefore, much help in explaining how predator-prey interactions persist in nature. One possibility is that predation does indeed promote instability in natural systems and that the interactions only persist in the real world by grace of other stabilizing processes such as a density dependent rate of increase of the prey. This would be an unlikely explanation in the face of the ubiquity of predation in natural systems.

Several aspects of predation that were omitted from early models and promote the stability of interactions have been widely discussed in the literature (e.g. sigmoid functional responses (Murdoch & Oaten 1975, Hassell et al. 1977), mutual interference (Hassell & Varley 1969, Hassell 1978) and density dependent parasitoid sex ratios (Hassell et al. 1983)). Most attention, however, has been focused on the effects of patchy, heterogeneous environments in which prey and predators are spatially distributed, since in this setting, more than any other, predation emerges as a plausible and powerful stabilizing mechanism in its own right. It was the classic laboratory experiment of Huffaker (1958) involving predatory and prey mites feeding on oranges that first drew wide attention to this role of heterogeneity. Only with a complex system of many oranges and a variety of barriers and aids to dispersal did coexistence occur in the form of sustained predator-prey cycles (but see Taylor, this issue).

Surprisingly, there have been few attempts since then to demonstrate this phenomenon with other laboratory systems. One clear-cut example, however,

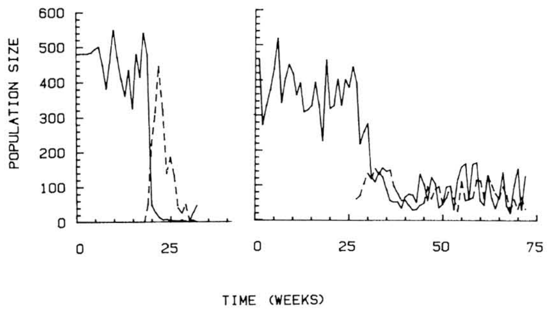

Fig. 1. Population dynamics of the bruchid beetle, *Callosobruchus chinensis* (——) feeding on black-eyed beans, and its pteromalid parasitoid, *Anisopteromalus calandrae* (- - - -), in a laboratory system. Left: 'non-patchy' – 50 beans uniformly distributed on floor of arena. Right: 'patchy' – 50 beans each in an individual container with restricted access to both hosts and parasitoids. In both cases the parasitoids were introduced to the arena once the host population was fluctuating around its carrying capacity (V. A. Taylor & M. P. Hassell, unpublished).

is shown in Fig. 1 using the bruchid beetle *Callosobruchus chinensis* (L.) feeding on black eyed beans, and its pteromalid parasitoid, *Anisopteromalus calandrae* (Howard). In a relatively homogeneous environment — an arena with 50 beans renewed weekly — the interaction is clearly unstable (Fig. 1a). This is in sharp contrast, however, to the stable host-parasitoid interaction shown in Fig. 1b where the 50 beans are each within a plastic cup, which neither host or parasitoid can leave after entering (V. A. Taylor & M. P. Hassell, unpublished).

While real examples of patchiness promoting persistence, even in the laboratory, are very few indeed, there is certainly no shortage of theory striving to show how this may come about. There are two main strands to this literature.

(1) Models, often in continuous time, where patches can pass from being empty, to being colonized by prey, to being found by predators, to becoming empty again following the extinction of prey by the predators. In such systems (reviewed in detail by Taylor, this issue) asynchronies in the state of the different patches clearly have the potential to promote the persistence of the system as a whole (e.g. Maynard Smith 1974, Roff 1974, Hilborn 1975, Zeigler 1977, Hastings 1977, Crowley 1979, Chesson 1981).

(2) Models in discrete time with explicit patches and predators, or more usually parasitoids, roaming over these, often with an emphasis on the details of the foraging strategy adopted by the natural enemy (see Hassell (1978) for a review). Models of this second kind will form the basis of this paper, with the aim of emphasizing just how pervasive is the stabilizing effect of predation in a patchy environment.

2. A basic model

Let us consider a habitat containing *n* patches (e.g. plants) serving as food for the larvae of an univoltine insect population. The adult insects in a given generation are the dispersing stage and each female lays her complement of eggs on the plants. The resulting larvae are hosts for a parasitoid whose poulation is coupled to that of the host. We will also assume that the host density is kept below the level where competition is important. This serves to keep the model simpler and makes easier the clear demonstration of the dynamic role of patchiness in the interactions. This now leads to the model discussed in detail in Hassell & May (1973, 1974), namely:

$$N_{t+1} = FN_t \sum_{i=1}^{n} [\alpha_i \exp(-a\beta_i P_t)] \qquad (1a)$$

$$P_{t+1} = N_t \sum_{i=1}^{n} [\alpha_i (1 - \exp(-a\beta_i P_t)]. \qquad (1b)$$

Here, N and P are the host and parasitoid populations, respectively, in generations t and $t+1$, F is the finite net rate of increase of the hosts, α_i is the fraction of hosts in the ith patch and β_i is the corresponding fraction for the parasitoids (such that $\Sigma\alpha_i = \Sigma\beta_i = 1$). Thus, the surviving hosts and parasitoids are redistributed amongst the n patches in each generation according to (α_i) and (β_i). ($\beta_i = 0$ corresponds to an even distribution of searching parasitoids, while at the limit $\beta_i \rightarrow \infty$ all the parasitoids are in the patch of highest host density leaving the remainder as refuges.) Parasitism of hosts within a patch is defined by the familiar Nicholson-Bailey expression where a is the per capita searching efficiency of the parasitoids. Thus, exploitation of hosts *within* patches is random and handling time is assumed to be negligible. Any stability in the model, therefore, cannot stem from the within-patch functional response and must depend in some way on the between-patch variability in parasitism.

The central conclusions from this model are straightforward. With an even distribution of parasitism, the system collapses back to the unstable Nicholson-Bailey model exhibiting expanding oscillations around an unstable equilibrium. Stable populations can easily be obtained, however, if the parasitoids cause direct, *or inverse,* density dependent patterns of parasitism from patch to patch. Both of these generate the pseudo-interference effect of Free et al. (1977), in which the per capita searching efficiency measured over the whole host population falls with increasing parasitoid density as a result of the uneven distribution of parasitism from patch to patch (Hassell, 1978).

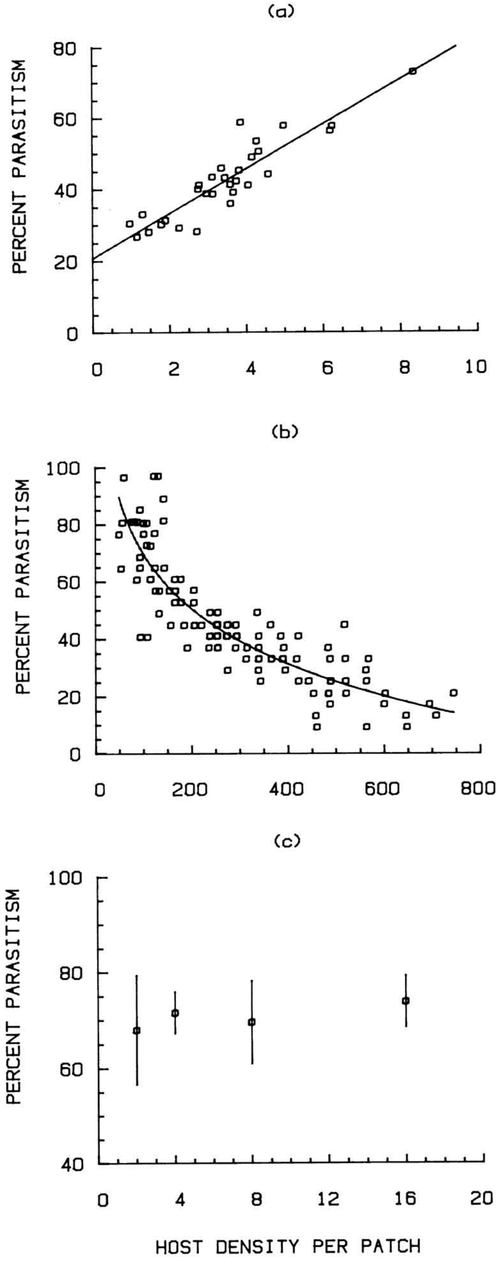

Fig. 2. Three field examples of different patterns of parasitism from patch to patch. — (a) Parasitism of the scale insect, *Fiorinia externa* Ferris, by the eulophid parasitoid, *Aspidiotiphagus citrinus* (Craw.) on the lower crown of 30 hemlock trees. Fitted line: $Y = 20.45+6.26X$ ($P<0.001$) (from McClure 1977). — (b) Parasitism of Gypsy moth (*Lymantria dispar* (L.)) eggs by *Ooencyrtus kuwanai* (Howard) (Encyrtidae). Fitted line: $Y = 197.57-63.92(\log_{10}(X)$ ($P<0.001$) (from Brown & Cameron 1979). — (c) Parasitism of *Plutella xylsotella* (L.) larvae on brussels sprouts plants by *Diadegma* spp. (Ichneumonidae) (from Waage 1983).

3. Patterns of parasitism from patch to patch

The theoretical interest in the dynamics of interactions in patchy environments has prompted many workers to look for signs of density dependent parasitism from patch to patch, culminating recently in reviews cataloguing the incidence of different patterns (e.g. Lessells 1985, Stiling 1987). These show that while there are many examples of spatial patterns of parasitism that are directly density dependent, there are just as many showing quite the opposite (inversely density dependent), and even more showing no relationship at all (Fig. 2). At first, and guided by the theoretical work of that time, the general interpretation of these examples was that only the direct density dependent patterns promoted stability. Later it became clear that inverse density dependent responses could be equally effective. Which is more important — direct or inverse — depends on the details of the host's distribution (Hassell 1984).

What has not been widely appreciated to date is that even where there is *no* pattern of density dependence between patches, the spatial distribution of parasitism, if sufficiently variable, can still be playing a crucial part in promoting stability for just the same reasons as outlined above. Let us consider the very simple example of an environment of *n* patches on which the hosts are distributed. We will take the situation least likely to be stable — of hosts evenly distributed from patch to patch and, similarly, parasitoids not discriminating between patches so that they, too, tend to be evenly distributed. This reverts to the unstable Nicholson-Bailey model as described above, except we now add one extra ingredient — the parasitoids in any one generation only succeed in finding some of the patches (chosen randomly). The remainder form an obvious refuge which, if sufficient, can stabilize the interaction. The important point here is not that refuges may promote stability — this is well known (e.g. Bailey et al. 1962, Hassell & May 1973, Maynard Smith 1974, Hassell 1978) — but that the spatial pattern of parasitism is now independent of host density from patch to patch and yet is still the key to stability. Clearly, some other measurement is needed to assess this effect of parasitism on dynamics (see below).

These examples indicate that distinguishing between different spatial patterns of parasitism is not a reliable means of identifying those foraging behaviours that promote persistence of the interactions. Both direct and inverse patterns as well as density independent ones can all be important to stability in leading to some hosts being less at risk from parasitism than others (a kind of 'proportional refuge effect'). This is much the point recently stressed by Chesson & Murdoch (1986).

4. Incomplete host and parasitoid mixing

While some hosts and parasitoids, particularly univoltine species, do indeed redistribute themselves amongst patches each generation, others show less complete mixing, with some of the hosts and parasitoids tending to remain within the patch from which they originated. Scale insects, for example, develop colonies over a number of generations, with only a fraction of progeny dispersing each generation. Amongst parasitoids, some, particularly egg parasitoids such as *Trichogramma* spp., are weak flyers and may often tend to remain on the plant on which they developed.

Let us consider, therefore, the picture of some hosts and/or parasitoids staying in the particular patch from which they emerged, while the remainder behave as previously and enter a 'pool' to be redistributed anew in the next generation. There is thus a continuum from complete host mixing to no host mixing, and complete parasitoid mixing to no parasitoid mixing. To keep things simple, we will consider only the four obvious limiting cases:

(1) complete host and parasitoid mixing: $x_i = 1$, $y_i = 1$,

(2) no host or parasitoid mixing: $x_i = 0$, $y_i = 0$,

(3) complete host mixing, but no parasitoid mixing: $x_i = 1$, $y_i = 0$, and

(4) no host mixing, but complete parasitoid mixing: $x_i = 0$, $y_i = 1$,

where x_i and y_i are the fraction of hosts and parasitoids, respectively, leaving the *i*th patch to enter a 'pool' for subsequent redistribution in each generation (full details will be given elsewhere (M. P. Hassell & R. M. May, unpublished)). We will also assume for simplicity that the probability of leaving a patch for dispersal is not density dependent, that there is no mortality associated with the movement and that those parasitoids that do disperse in cases (1) and (4), redistribute themselves evenly over the patches irrespective of host density per patch. The populations of hosts and adult parasitoids in the *i*th patch, N_i and P_i respectively, are now given by

$$N_i(t+1) = F\left[S_i(1-x_i) + \alpha_i\left(\sum_{i=1}^{n} S_i x_i\right)\right] \qquad (2a)$$

$$P_i(t+1) = N_{ai}(1-y_i) + \beta_i\left(\sum_{i=1}^{n} N_{ai}\, y_i\right). \qquad (2b)$$

Here S_i is the number of hosts surviving from parasitism in the *i*th patch, N_{ai} is the number of hosts parasitized ($N_i - S_i$), once again obtained from the Nicholson-Bailey expression for random parasitism, and α_i and β_i are as defined in Eq. (1).

Of the four cases listed above, case (1) is the same as Eqs. (1a, b) and case (2) is trivial in that each patch now contains separate and isolated populations making no contact with others. Case (3), however, is different and, interestingly, is stable for some parameter combinations despite the absence of any behavioural response by the parasitoids. The populations in each patch are now given by:

$$N_i(t+1) = \alpha_i\left(F_i \sum_{i=1}^{n} N_i \exp(-aP_i)\right) \qquad (3a)$$

$$P_i(t+1) = \alpha_i N\,[1-\exp(-aP_i)]. \qquad (3b)$$

Let us assume a simple host distribution where there is a single patch of high host density containing a fraction (α_0) of the total hosts, and the remaining (n–1) patches each with a fraction $(1-\alpha_0)/(n-1) = (\alpha_1)$. Two conclusions stand out.

(1) If the host rate of increase, F, is below a threshold, F_c, defined by

$$F_c = \frac{1}{1-\alpha_0\left[1-\exp\left(\dfrac{1-F(1-\alpha_0)}{\alpha_0 F}\right)\right]} \qquad (4)$$

the parasitoids become extinct in all but the single high density patch, making the remaining patches

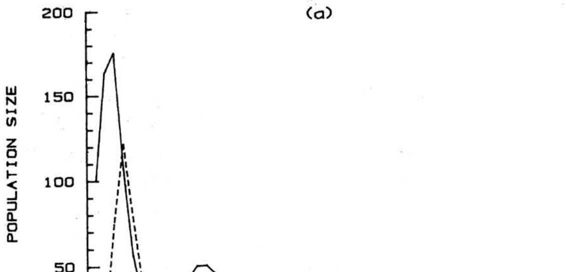

Fig. 3. Two numerical examples of the model in Eqs. (2a,b) with complete host and no parasitoid mixing (case 3: $x_i = 1$, $y_i = 0$; see text). Host population (——); adult parasitoid population (- - - -). — (a) A stable interaction obtained when $n = 5$, $a = 0.1$, $F = 2$, and $\{\alpha_i\} = 0.6;0.1;0.1;0.1;0.1$. — (b) A locally unstable interaction showing limit cycles when $F = 1.2$ and the other parameters as in (a).

complete refuges from parasitism. The system is now stable provided that the fraction of hosts in the high density host patch (α_0) is not too large (too few hosts in the refuge) in relation to F (Fig. 3a). The precise stability condition is given by:

$$1 > \left(\frac{F}{F-1}\right)[1 - F(1-\alpha_0)] \ln\left(\frac{\alpha_0 F}{1 - F(1-\alpha_0)}\right). \quad (5)$$

When $\alpha_0 > 0.5$, the system can become locally unstable if F is sufficiently small, and the populations then show stable limit cycles instead of a point equilibrium (Fig. 3b).

(2) Once, however, the host rate of increase becomes larger than the threshold, F_c, the parasitoids can persist in all the patches, and the interaction is locally stable as long as F is not too large. The end result in this model is thus much the same as from case (1) (complete mixing of both hosts and parasitoids), except that now the parasitoids accumulate in the patches of high host density *by virtue of their numerical responses* rather than any behavioural responses.

Of course, some relaxation of the constraints of complete host and no parasitoid mixing still permits stable interactions, and these become progressively easier if the dispersing parasitoids, instead of distributing themselves evenly, show some tendency for density dependent aggregation.

The examples so far discussed in this section assume that a patch of high host density in one generation remains so in the next. This allows the numerical build-up of parasitoids within these patches. In the real world it is likely that the location of the high host densities will vary amongst the available patches from generation to generation. Parasitoids that disperse little (or not at all) are thus faced with a 'moving target' of high host density which they can only exploit heavily if by chance the same patch has a high host density for enough generations for the numerical response of the parasitoid to be effective. Let us consider, therefore, the example where the location of the single high host density patch containing $\alpha_0 N$ hosts is chosen randomly. Coexistence of host and parasitoid is now inevitably less easy, but numerical examples show that, although ultimately unstable, the populations can persist for long periods showing erratic fluctuations (Fig. 4).

Finally in this section, we turn to the opposite situation of no host mixing, but very active parasitoids moving freely from patch to patch (case 4). The particular example discussed here assumes an initial host distribution that is completely even and no aggregation by the dispersing parasitoids. Such an interaction will always be unstable. However, a refuge effect sufficient for the system to persist can easily be introduced. For instance, Fig. 5 shows a numerical example of an interaction where the parasitoids in any one generation fail to find all the patches (see above). Although locally unstable, the populations still persist for many generations, and it now only takes a small amount of host mixing or parasitoid aggregation to ensure that the interaction is stable.

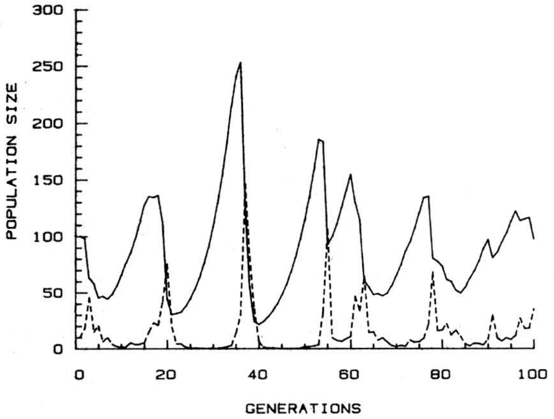

Fig. 4. A further numerical example with the same parameters as in Fig. 3a, except that now the location of the high host density patch is chosen randomly.

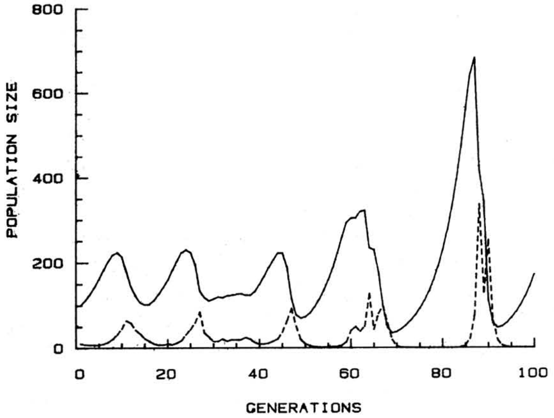

Fig. 5. A numerical example of the model in Eqs. (2a,b) with no host and complete parasitoid mixing (case 4: $x_i = 0$, $y_i = 1$; see text) and the added constraint that the parasitoids only locate 60% of the patches in any one generation (chosen randomly) amongst which they distribute themselves evenly. Parameter values: $a = 0.1$, $F = 1.2$, $n = 5$.

5. Conclusions and an alternative approach

It is hard to envisage any natural situation where all hosts in a patchy environment will have the same probability of being parasitised. Given such variability, models such as those described above point clearly to the stabilizing effect of this kind of heterogeneity (Chesson & Murdoch 1986). The problem remains, however, of identifying what should be measured to assess the contribution of natural enemies to persistence in a patchy environment. The current practice of seeking density dependent patterns of parasitism from patch to patch runs the risk of overlooking important heterogeneities in the distribution of parasitism that may be significant in the persistence of the interaction. A possible alternative approach is described briefly in this section — a fuller treatment will be given elsewhere (M. P. Hassell & R. M. May, unpublished).

Let us consider the particular example where the hosts are distributed among a large number of patches following some nonuniform distribution. The parasitoids likewise are distributed with the fractions of total parasitoids per patch drawn from some distribution that is uncorrelated with that of the hosts. This now gives Eqs. (1a,b) with the added constraint of no covariance between host and parasitoid distributions. If we now assume as a particular case that parasitoids are distributed according to a gamma distribution, it can be shown that stability requires that

$$(CV)^2 > 1 \qquad (6)$$

where CV is the coefficient of variation in the distribution of parasitoids and hence closely related to the distribution of parasitism. This result is sensitive to the chosen distribution (in this case the gamma distribution). However, at least in the limit of $F \rightarrow 1$, condition (6) approximates in general quite well to the condition needed for local stability.

Such an elegant solution is unlikely to apply well enough in natural systems to be useful as a measure the dynamic role of the natural enemies to population persistence. It does hold out the hope, however, that some criteria can be found that will both achieve this and still be easily measurable in the field.

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References

Bailey, V. A., Nicholson, A. J. & Williams, E. J. 1962: Interaction between hosts and parasites when some host individuals are more difficult to find than others. — J. Theor. Biol. 3:1–18.

Brown, M. W. & Cameron, E. A. 1979: Effects of dispalure and egg mass size on parasitism by the gypsy moth egg parasite, Ooencyrtus kuwanai. — Environ. Ent. 8:77–80.

Chesson, P. L. 1981: Models for spatially distributed populations: the effect of within-patch variability. — Theor. Pop. Biol. 19:288–325.

Chesson, P. L. & Murdoch, W. W. 1986: Aggregation of risk: relationships among host-parasitoid models. — Amer. Nat. 127:696–715.

Crowley, P. 1979: Predator-mediated coexistence: an equilibrium interpretation. — J. Theor. Biol. 80:129–144.

Free, C. A., Beddington, J. R. & Lawton, J. H. 1977: On the inadequacy of simple models of mutual interference for parasitism and predation. — J. Anim. Ecol. 46:543–554.

Hassell, M. P. 1978: The Dynamics of Arthropod Predator-Prey Systems. — Princeton University Press, Princeton.

—"— 1984: Parasitism in patchy environments: inverse density dependence can be stabilizing. — I.M.A. J. Math. Appl. Med. Biol. 1:123–133.

Hassell, M. P., Lawton, J. H. & Beddington, J. R. 1977: Sigmoid functional responses by invertebrate predators and parasitoids. — J. Anim. Ecol. 46:249–262.

Hassell, M. P. & May, R. M. 1973: Stability in insect host-parasite models. — J. Anim. Ecol. 42:693–726.

—"— 1974: Aggregation in predators and insect parasites and its effect on stability. — J. Anim. Ecol. 43:567–594.

Hassell, M. P., Waage, J. K. & May, R. M. 1983: Variable parasitoid sex ratios and their effect on host-parasitoid dynamics. — J. Anim. Ecol. 52:889–904.

Hassell, M. P. & Varley, G. C. 1969: New inductive population model for insect parasites and its bearing on biological control. — Nature 223:1133–1137.

Hastings, A. 1977: Spatial heterogeneity and the stability of predator-prey systems. — Theor. Pop. Biol. 12:37–48.

Hillborn, R. 1975: The effect of spatial heterogeneity on the persistence of predator-prey interactions. — Theor. Pop. Biol. 8:346–355.

Huffaker, C. B. 1958: Experimental studies on predation: dispersion factors and predator-prey oscillations. — Hillgardia 27:343–383.

Lessells, C. M. 1985: Parasitoid foraging: should parasitism be density dependent? — J. Anim. Ecol. 54:27–41.

Lotka, A. J. 1925: Elements of Physical Biology. — Williams and Wilkins, Baltimore (Reissued as Elements of Mathematical Biology. — Dover 1956).

Maynard Smith, J. 1974: Models in Ecology. — Cambridge University Press, Cambridge.

McClure, M. S. 1977: Parasitism of the scale insect, Fiorina externa (Homoptera: Diaspidae), by Aspidiotiphagus citrinus (Hymenoptera: Eulophidae) in a hemlock forest: density dependence. — Environ. Ent. 6:551–555.

Murdoch, W. W. & Oaten, A. 1975: Predation and population stability. — Adv. Ecol. Res. 9:2–131.

Nicholson, A. J. 1933: The balance of animal populations. — J. Anim. Ecol. 2:132–178.

Nicholson, A. J. & Bailey, V. A. 1935: The balance of animal populations. Part 1. — Proc. Zool. Soc. Lond. 1935:551–598.

Roff, D. A. 1974: Spatial heterogeneity and the persistence of populations. — Oecologia 15:245–258.

Stiling, P. D. 1987: The frequency of density dependence in insect host-parasitoid systems. — Ecology 68:844–856.

Volterra, V. 1926: Variazioni e fluttuazioni del numero d'individui in specie animali conviventi. — Mem. Acad. Lincei. 2:31–113 (Translation in: Chapman, R. N. 1931. Animal Ecology 409–448. MacGraw-Hill, New York).

Waage, J. K. 1983: Aggregation in field parasitoid populations: foraging time allocation by a population of Diadegma (Hymenoptera, Ichneumonidae). — Ecol. Ent. 8:447–453.

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

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