

fashion (Fig. 4 of my article in *Trends in Ecology and Evolution*¹⁰).

Some still find the light better beneath the lantern of the logistic, but all indications are that the keys to ecology are to be found elsewhere.

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Detecting Density Dependence

Hassell's recent review¹ on the detection of density dependence is, in my opinion, based on faulty reasoning. In itself, the search for density dependence may be important, since it will often provide key information on an animal's way of life, as is clearly demonstrated by Hassell's other work². I agree with Hassell¹ that to detect density dependence from 'life-history tactics'³ it will be necessary to study the behaviour of individual animals within natural units of interaction (i.e. populations) – for instance, predator–prey interactions within a prey patch. I also agree that this spatial density dependence will only appear significant at the population level if the relevant processes run synchronously in the majority of patches. However, such synchrony will not often occur in heterogeneous and changeable natural environments, so that significant density dependence will not often be detected by traditional life table analyses, which is again in accord with Hassell¹. The reverse may also occur: density dependence at the population level may be more easily detectable because of stochasticity⁴. But even if density dependence is detectable at that level, it need not contribute to keeping density within limits, as can be shown in the winter moth of Wytham Wood⁵.

According to Hassell, different kinds of heterogeneity between patches and of asynchrony between processes will considerably promote stability¹. I completely agree with that, and about 20 years ago I called this phenomenon 'spreading of risk'⁶, which contributes to keeping density within limits (range stability*), and thus to persistence. But as soon as we appeal to heterogeneity and asynchrony in discussions on the role of density dependence, we partly or completely replace the deterministic principle of density dependence by the antagonistic, statis-

tical principle of spreading of risk⁷. We should carefully discriminate between these fundamentally different principles. If, because of heterogeneity, density dependence cannot be detected at the population level, it cannot be important at that level, and consequently cannot be the major cause of population persistence (you cannot have your cake, and eat it).

It has been shown, both with the help of simulation experiments⁸ and in field populations⁹, that different kinds of heterogeneity in the population or in the environment, as well as asynchrony between processes, can greatly promote range stability (= keeping density within limits). This increased stability occurs irrespective of whether any of the processes are basically density-dependent (e.g. within patches) or not. For instance, density-dependent movements of individuals between heterogeneous groups appear to contribute no more to the range stability of the population than density-independent exchange⁸. Apparently, in such cases it is not so much the nature of the processes that determines the contribution to the range stability of the population, but rather the degree of heterogeneity or asynchrony of these processes.

This is also illustrated by the interactions between the phytophagous mite *Tetranychus urticae* and the predatory mite *Phytoseiulus persimilis*¹⁰. After a predator invades a prey patch, the local predator population increases at the expense of the prey until the local prey

population is exterminated. Only then do the predators disperse in search of new prey patches. Stability, and thus persistence, of this system is promoted – in a stable limit cycle – by asynchronization of the local predator–prey cycles¹⁰. This kind of stability resembles that in the experimental systems of Huffaker¹¹, and is probably also at the base of the *Opuntia–Cactoblastis* interactions, which were described as 'hide and seek'^{12,13}.

All this does not mean that I consider density dependence to be an unimportant phenomenon. It may play a prominent part in the way of life of many animals and in the population dynamics of some. But persistence at the population level is not always served by persistence of the composing population units. In less stable environments especially, a high turnover (extinction/(re)founding) of population units can be a highly favoured way of life¹⁴. Therefore, to understand the persistence of natural populations we should not concentrate exclusively on density dependence and any resulting 'regulation' of numbers, and thus consider heterogeneity and asynchrony to be aspects of density dependence¹. These statistical phenomena should be judged on their own merits, as contributing to range stability and persistence⁷.

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*'Stability', in the sense of persistence, is not only promoted by processes that feed back upon the starting condition (norm) or some equilibrium value (regulation), e.g. by some kind of density dependence, but also by 'spreading of risk'⁶, i.e. statistical levelling of fluctuations, which may make a major contribution to 'staying longer within limits'^{7,8}. The latter kind of stability, in which feedback processes need not be involved, is here called 'range stability'.

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Reply from M. P. Hassell and M. W. Sabelis

The comments of den Boer reveal a strong desire to force the dynamics of natural populations into a single mould. In doing so, he makes unwarranted assertions and misuses specific examples. According to den Boer, populations are kept within limits due to processes contributing to the 'spreading of risk' of local extinctions. Density dependence is relegated to providing 'key information on an animal's way of life', and is perceived to be of little importance to population persistence. These statements are not only vague, but also obscure important questions for future research.

That populations can persist by processes promoting asynchrony of local population dynamics is not in question and has been clearly demonstrated in principle a number of times^{1–7}. To assume, however, that all populations persist solely by this means, without the action of density-dependent processes, is an act of faith and not supported by what information is available. In sweeping aside the regulatory role of density dependence, den Boer also misconstrues the problems in detecting density dependence. It is not that heterogeneity renders it impossible to detect density dependence so that it cannot be the major cause of population persistence; only that some conventional life table techniques using total population estimates are prone to overlook this density dependence. They fail to disentangle the signal from the noise⁸.

Den Boer gives two examples to support his views. The winter moth at Wytham Wood is quoted as a case where identified density dependence (pupal mortality in the soil) does 'not contribute to keeping density within limits'. On the contrary! Den Boer's analysis of the winter moth data⁹ is inappropriate in that he builds persistence into all his null models. A proper analysis clearly identifies the density dependence as crucial for the populations to persist within reasonable limits (J. Latto and M. P. Hassell, unpublished).

For his second example, den Boer leans heavily on the simulation results of a dynamic predator-prey model based on detailed laboratory studies of the interaction between a phytophagous and a predatory mite¹⁰. In this system local populations are transient either because rapid population increase of the prey leads to food depletion, or because the numerical response following predator invasion of a prey patch leads to elimination of the prey. Though locally transient, predator and prey populations persist on a regional scale due to processes that keep local cycles out of phase. The regional populations do not fluctuate randomly, but show stable limit cycles. The cyclic pattern appears to hinge upon the predators not dispersing from prey patches until after the prey are eliminated¹¹.

Why the cycles should be stable was not clear from the simulations, but they do not hinge upon the availability of host plants for the prey, on the aggregative response of the predator to (local) prey density, or on interpatch transit times and mortality of the dispersing predators. Most plausible is that the asynchrony between local cycles acts as a refuge in time whose net effect is density-dependent in a way analogous to that of other types of refuges in classical predator-prey models¹². Thus, the asynchrony not only promotes persistence, but also confers a pattern of stable cycles to a system which would otherwise fluctuate randomly. This would be of great importance in 'keeping density within limits', in the face of environmental vagaries in a finite space (J. K. Waage, M. W. Sabelis and M. P. Hassell, unpublished). In this example, therefore, den Boer has overlooked the possibility of a density-dependent mechanism important for promoting persistence on a regional spatial scale.

Population ecology is not well served by polarized stances in which the world is black or white. Future studies on particular systems should look for density-dependent processes

(in whatever guise), for factors promoting asynchronies between sub-populations, as well as for the causes of population fluctuation.

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