Reply to Den Boer

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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 noise[8].

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 data[9] 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the density dependence as crucial for the populations to persist within reasonable limits (J. Latto and M. P. Hassell, unpublished).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 mite[10]. 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 eliminated[11].

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 models[12]. 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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