

## The glass bead game

THE gap between theoretical and applied ecology seems to be widening. Indeed it is difficult to escape the worrying conclusion that some theoreticians are playing a version of Hermann Hesse's *Das Glasperlen Spiel*<sup>1</sup> or that they have little feeling for or understanding of biological problems. A particularly good example is the recent article by Gurney *et al.*<sup>2</sup> which attempts to provide a theoretical model to explain the oscillatory behaviour of laboratory populations of blowflies.

After reaching the esoteric conclusion that the blowfly cycles are "self-sustaining limit cycles" rather than "driven quasi-cycles", the authors proceed to use their model to explain the 'double-humped' nature of the cycles in terms of minimum population size ( $N_{\min}$ ) in relation to the size at which the population achieves maximum reproductive success ( $N_0$ ). The mathematics are correct, but in their zeal, the authors fail to notice Nicholson's own explanation of the 'double-hump' phenomenon (see Fig. 3 legend in ref. 3). He says "the lack of a clear inverse relation between the various low adult densities and the number of eggs produced is due to the fact that adults are mostly senile as the adult minima are approached, near the minima many are newly emerged and incapable of laying eggs, and subsequently highly fertile young individuals dominate". In other words, the fact that breeding occurred in 'quasi-discrete' generations is probably almost entirely a consequence of age-specific variation in the reproductive performance of the adult blowflies. As Gurney *et al.* ignore this variation their model must be seen as artefactual and spurious—a product of the 'game'.

Of less importance, but still worrying, is the promotion of "a satisfying qualitative fit" in the conclusions to "good quantitative agreement" in the abstract, and the failure to refer to similar published work<sup>4,5</sup>. In contrast, Readshaw and Cuff<sup>6</sup> have published a biologically realistic model of Nicholson's results which includes readily identifiable parameters. An age-specific version of the model would undoubtedly simulate the 'double-hump' but the data are not yet available.

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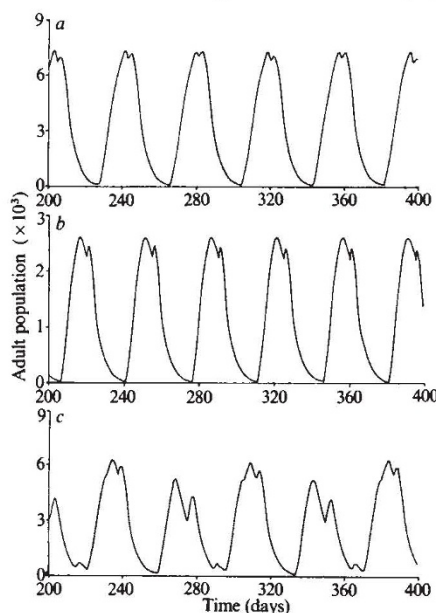
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GURNEY *ET AL.* REPLY—Readshaw raises three scientific objections to the model described in our recent article<sup>1</sup>. We shall deal with these in turn.

The question of the nature of the mechanism responsible for the observed cycles is very far from 'esoteric'. Any moderately repetitive fine structure exhibited by a limit-cycle type of fluctuation carries readily extractable dynamic information, whereas the fine structure of a driven quasi-cycle is mainly 'noise' which only serves to obscure our view of the underlying population dynamic. Thus our judgement that detailed investigation of the fine structure of the cycles observed by Nicholson is a worthwhile exercise hinges on our unambiguous demonstration that they are limit cycles.

It is clear from our work that if average future recruitment bears any kind of humped relationship to current adult population then cycles which have minima well below the population size at which maximum overall reproductive success is



**Fig. 1** Numerical solutions of Readshaw and Cuff's model equation<sup>1</sup>:  $n(t+1) = 0.8n(t) + R(n(t-\tau))$ . *a*, Adult food-limited case:  $R = 10n$  when  $n < 171$ ;  $R = 1,795 - 0.503n$  when  $171 < n < 3,569$ ;  $R = 0$  when  $n > 3,569$ .  $\tau = 15$  days. *b*, Larval food-limited case:  $R = 10n(1 - \exp\{0.154 - 109.9/n\})$  when  $n < 714$ ;  $R = 0$  when  $n > 714$ .  $\tau = 13$  days. *c*, Adult food-limited case with modified parameters:  $R = 2.49n$  when  $n < 600$ ;  $R = 1,795 - 0.503n$  when  $600 < n < 3,569$ ;  $R = 0$  when  $n > 3,569$ .  $\tau = 15$  days.

achieved, must be accompanied by a 'discrete generation' pattern of breeding activity. A clear implication of Nicholson's<sup>2,3</sup> batch culture results displayed in Readshaw and Cuff's paper<sup>4</sup> is that just such a relationship exists for *Lucilia cuprina*, and there is thus no shred of evidence for their *ex cathedra* statement that the double-humped egg-laying rate curves observed by Nicholson are entirely the product of the age structure-dependent fecundity changes noted in Fig. 3 legend of ref. 3. However, such effects do provide a very plausible explanation of the observation that in four out of seven cycles

shown the second peak of the double hump is considerably higher than the first.

The final objection of Readshaw is the claim that the fine structure predicted by our model must be 'spurious and artefactual' because their 'biologically reasonable' model predicts a limit cycle with no fine structure. This claim has no sound basis. Their model is effectively identical to ours except in the details of the functional form chosen for the recruitment rate function. In both experimental regimes considered the form chosen has a single hump with a maximum at a population size ( $N_0$ ) comfortably in excess of the observed minimum population and thus there seems every reason to suppose that careful numerical analysis will reveal that their model predicts population cycles with a fine structure very similar to that shown in Fig. 6 of our paper<sup>1</sup>. Figure 1*a, b* shows that this is indeed the case. Furthermore, in the adult food-limited case (Fig. 1*a*) note that there is no direct experimental evidence for the value of  $N_0$  implied by the parameters chosen by Readshaw and Cuff (171) and indeed that this value is considerably below the value of 600 that may be deduced from Nicholson's data (see Fig. 3 of ref. 3). If we abandon the attempt to force Readshaw and Cuff's piecewise linear approximation to the recruitment function to fit the behaviour of the population as  $N \rightarrow 0$  and instead place the maximum of the curve somewhere near the correct value (Fig. 1*c*), then the structure predicted by their model becomes very strong indeed.

We conclude that the very simple mechanism proposed in our original article captures much of the spirit of the population dynamics underlying Nicholson's blowfly cycles and is thus a contribution (rather than widening) the gap between theoretical and applied ecology.

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