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FORUM

Reaction to J. Latto and C. Bernstein

Regulation in natural insect populations: reality or illusion? (*)

P.J. den Boer

Biological Station LUW, Kampsweg 27,
9418 *PD WIJSTER, The Netherlands*

First of all I welcome the continuation of the discussions on population regulation. In this way it must be possible, in my opinion, to reach agreement on essential points. Latto and Bernstein at least contribute to bringing this possibility nearer.

Their point about delayed density dependence is especially clarifying. It explains why DEN BOER (1986) found smaller *LR*-values than with the density dependence of k_5. But it also shows that the conclusion of Den Boer (l. c.), that the density dependence of pupal predation destabilizes density fluctuations to a certain extent, was right. I cannot judge the result from the 3,000 shuffled data sets with nine runs of like sign, because I do not know how this was reached. Anyway, if 90 sets out of 3,000 had a smaller *LR* than the field set, $P = 0.03$ (90/3001, compare REDINGIUS & DEN BOER, 1989: 3) and not < 0.01. I further wonder whether it is relevant to artificially keep the fluctuation pattern at nine runs (if I understand the procedure of Latto and Bernstein well), because the model of LATTO & HASSELL (1987) was already the result of simulations in which all mortalities, except k_5 which was density-dependent, were independent random variables. DEN BOER (1988) showed that — apart from random variables being not very adequate in this case — changing so many factors at the same time let the model deviate too far from reality, by which LATTO & HASSELL (1987) uncoupled all *k*-factors from each other, whereas DEN BOER (1986, 1988) tried to keep as much of the field data intact as possible. Regrettably, I don't see a simple method to both maintain the correlation between k_1 and k_5 and make k_5 density-independent (as it is desired by Latto and Bernstein: Discussion), without also changing other features. Each null model is a compromise between desirabilities and possibilities that will not always satisfy everyone. Although Latto and Bernstein make some critical notes to the null models of DEN BOER (1986, 1988) they do not present a

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workable alternative. Nevertheless, I agree that the coupling of different k-factors may significantly determine the fluctuation pattern. But does it also contribute to the survival chance of the population? On the contrary, it causes the low number of turning points and the connected wide logarithmic range observed, which will not promote survival.

The definition of "regulation" of Latto and Bernstein is a weak one, because it depends on what are considered "low densities" and what "high densities". If it is their intention that these are related to the "equilibrium density", as defined in Methods and Results, we are running into circular reasoning, because density dependence is already included in their "equilibrium density". Also their definition of "limitation" is inconsistent, insofar it is responsible for the statement "Any factor that correlates with the density or with the growth rate of a population is limiting the population". For instance, in poikilothermic animals egg production is positively correlated with temperature, which often appears to result in a significant correlation with the growth rate of the population (see VAN DIJK, 1983). Is temperature thus "limiting" population growth? I imagine that they did not want to suggest that. Their definitions apparently led them to the statement (in the Discussion) that, "the overall densities which the (winter) moth reached were influenced by density dependence". When the authors would insist on this, further discussions are useless. But if we test this statement with the randomization test of POLLARD *et al.* (1987), which is especially geared to answering this question, this appears not to be significant: $P = 0.415$ (larvae) and $P = 0.274$ (adults) respectively (DEN BOER & REDDINGIUS, 1989, table 2). Therefore, it is not true either (in the Discussion), that "Constraining the overall population to fluctuate from the first observed value to the final observed value in the null model, as in the original model of DEN BOER (1986), mistakenly includes the effects of density dependence and so renders the model useless (LATTO & HASSELL, 1987)", because the test of Pollard *et al.*(l. c.) is exactly asking whether the observed track followed by the population between first and last density was consistent with the assumption of overall density dependence, and this appeared not to be the case. Hence, according to the authors, by randomly permuting the net reproduction values of a series of census data we would include effects of density dependence? Where and how is this proposition proved? Does it not stem from the conviction that only significantly density-dependent — i. e. "regulating" — processes can keep density in the neighbourhood of these two values during that number of generations?

Of course, Latto and Bernstein are right in saying that extrapolating from the pattern of fluctuation as observed between 1950 and 1968 is speculative (in 3), but science cannot progress without speculation. In the present case this extrapolation was principally meant as a warning, and not as a highly probable prediction. Leaving out some observed values from a series, as is proposed by Latto and Bernstein, is as speculative (or "misleading") as extrapolation; both have an illustrative value. Also, the models presented in their figure 2 are highly speculative, but are used both by Den Boer and by Latto and Bernstein to give new impulses to the discussion. Moreover, I wonder whether an average decrease of the population of log 0.05 or 11 % "in itself has little meaning"! It is either significant and then most probably will result in rapid extinction of the population, or it is not significant and then should not be called a decrease.

To conclude: in spite of valuable trials in that direction Latto and Bernstein do not show that the conclusions of DEN BOER (1986, 1988), that pupal predation of the winter moth at Wytham Wood, Oxford, between 1950 and 1968 did not regulate population density, were wrong. I have the impression that Latto and Bernstein, possibly as a result of their somewhat deviating definitions of "regulation" and "limitation", are not yet sufficiently released from the conviction that significant density dependence in a particular population process, e. g. pupal predation in the winter moth, implies overall density dependence, in spite of stating the reverse in the Introduction. Not only does the test of Pollard *et al.* (above) show that this does not apply in the present case, but neither does the first test of Bulmer, which examines the time series for density dependence in a way that closely approaches the definition of "regulation" of Latto and Bernstein, give significant results (DEN BOER & REDDINGIUS, 1989, table 3); see also REDDINGIUS and DEN BOER (1989). Moreover, the observed sequence of net reproduction values does not keep density between limits: permutation test (DEN BOER & REDDINGIUS, 1989, table 3). The latter effect is partly due to the low number of turning points in the time series, as was rightly noticed by Latto and Bernstein , but this can hardly be turned into an argument favouring "regulation".

Therefore, for the time being I don't see any conclusive reason to consider the winter moth population of Wytham Wood to be regulated by density dependence.

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