

Stabilization or regulation: What is the difference?*)

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Although Berryman (1990) does not want to "belabor the semantic arguments surrounding the meaning of regulation and density dependence which burdened the ecological literature for decades" it appears necessary to once again say something about this, because it is at the root of the misunderstanding of Wolda (1989) by Berryman. For instance, when Berryman states that "equilibria are properties that may emerge from the operation of a dynamic system" he evidently has stability and not equilibria in mind. Den Boer (1968) and Reddingius & Den Boer (1989) consider "stabilization" to be the often supposed, but less often observed, tendency for populations to stay for some time between relatively narrow limits. Such a stabilization of numbers may emerge from two quite different sources: (1) it may be the result of the operation of an effective "negative feedback mechanism", i.e. a power that in most generations sufficiently corrects densities that deviate from some supposed norm value, equilibrium value, "Sollwert", or whatever it may be called. Only in that case we can speak of "regulation of numbers"; (2) it may result from the improbability of any of the factors that affect density to more than incidentally dominate the change of numbers from generation to generation, by which the fluctuations of numbers are relatively restricted (Den Boer 1968; Reddingius & Den Boer 1970; Reddingius 1971). The latter situation usually is the outcome of spreading of the risk of reaching extreme densities, either over differently directed environmental influences, or over the possibilities to survive and reproduce of individuals with different properties or of mutually connected groups of individuals living under different conditions.

Berryman seems to be unable to appreciate the second source of

stability, probably because it leads to a random walk of densities and eventually to extinction. But each population, also an evident regulated one eventually becomes extinct. Therefore, the only relevant point in this discussion is how long a random walk of densities can keep a population between safe limits. Reddingius (1971) showed that the claim of regulationists that only regulated populations would persist is unwarranted, because in the field population processes cannot be purely deterministic. On the other hand, Den Boer (1985, 1989) not only demonstrated that many local (carabid) populations will survive a random walk of densities for some decades and sometimes for a few centuries, but also showed that among the fluctuation patterns of the field populations studied a random walk of densities was the pattern that most prolonged survival. In other words, it was the best pattern observed in the field, although -as could be expected- nearly all populations showed some trend of numbers in time ($E(\ln R) \neq 0$, see Den Boer 1985: Fig. 5). Moreover, the deviations from $\text{mean}(\ln R) = 0$ were exactly what could be expected: in 90% of the 64 species $\text{mean}(\ln R)$ reached values between +0.3 and -0.3 (in 84% between +0.2 and -0.2). For, as soon as $\text{mean}(\ln R)$ exceeds $|0.3|$ the survival time of a population randomly fluctuating according to the frequency distributions of R (=net reproduction)-values found in the field (Den Boer 1985: Fig. 1, 1989: Table 1) will survive for a few years only. These observations of Den Boer make perfectly clear that we cannot reject the null hypothesis that many field populations would fluctuate about randomly, the more so because in this way they can survive even longer than the maximum observation period that an ecologist is allowed.

However, not being able to reject a null hypothesis does not mean that the alternative hypothesis, in this case "regulation of numbers", should be false. So easy as it is to mathematically construct regulation models, so difficult is it to show something comparable in field populations. In our opinion this difficulty mainly results from the fact that "density" is an abstraction: in

most cases individuals are distributed quite irregularly and are usually clustered to highly varying and continuously changing degrees. Therefore, density-dependent processes are not only necessarily imperfect (by definition), but also vary in an unpredictable way, because, what kind of density effect we may imagine, it will not exactly follow the changes of the contagious distribution of individuals. This applies to at least the same extent to a possible norm or equilibrium value, for, this is supposed to be a special density value. As far as an imperfect feedback on an unpredictably varying norm can still "regulate" something, it will be difficult to show its effect, because it is taken up into and thus importantly modified by other effects. Moreover, the feeding back of some density effect on density takes time during which the start situation, and even the equilibrium (whatever that may be in a real population) will have changed again.

In short, the only thing we can do to test a regulation hypothesis is trying to detect in a proper way (Reddingius 1971) a significant relationship between succeeding mean densities or between mean density and the next population change. Adequate tests are discussed by Pollard et al. (1987) and by Reddingius & Den Boer (1989), and applied to suitable census data by Den Boer & Reddingius (1989). Only the Eupalus-population of Klomp (1966) scored significantly, but Den Boer (1990) could show that most probably this has little to do with "regulation of numbers". Such test results give interesting hints for further research, but not necessarily point to underlying causal processes. Neither can we extrapolate from density effects that are observed in separate patches (Hassell 1986), because such processes do not run synchronously in all patches, and in many patches will not occur at all (see Den Boer 1987). For the population as a whole the most probable outcome is the kind of risk spreading that for the first time was described by Huffaker (1958). Therefore, negative correlations between mean density and the next net reproduction do

not necessarily imply causality, let alone the operation of some "mechanism". Summarizing, the reasons of Wolda (1989) to reject the equilibrium concept for use in field populations are sound. In the field we simply cannot do much with these cybernetic concepts that are adopted from technology and physiology (see e.g. Wilbert 1971). We will have to develop our own concepts that will have to be based on extensive, careful and unbiased field observations during sufficiently long periods (see Reddingius 1971).

Equilibrium models for field populations or systems, e.g. those of May (1973, 1979), are based on unprovable assumptions and do not simulate anything general we can observe in the field. In studies of field populations we should either directly study the vicissitudes of the individuals and integrate these properly (without heavily leaning on theoretical concepts from unrelated sciences) into simulation models (e.g. Van den Bos & Rabbinge 1976; Dempster & Lakhani 1979; Sabelis & Laane 1986), or study the course of numbers through time and as far as possible extrapolate the observed fluctuation patterns into the future. As it is already unknown whether we may consider the present environmental conditions stationary, it is wise not additionally to diminish the reliability of our predictions by introducing unrelated concepts in our models. Therefore, to get at expected survival times of different kinds of populations Den Boer (1981, 1985, 1989) prefers it to directly extrapolate from the fluctuation patterns and density limits as these were observed in the field. In the first species in which so far this expectation could be tested the survival times actually found nicely fitted the predictions (De Vries & Den Boer 1990), which is another reason not to reject the null hypothesis that many field populations fluctuate about randomly in numbers.

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