in regard to its slope, but it does not cease to be a function solely of numbers. It should be added that alteration of environmental capacity can be absolute, that is, independent of the organisms concerned, as when weather favours or retards the growth of vegetation for food or shelter ; or it can be relative, that is, due to modification of average individual needs brought about, for example, by weather increasing and decreasing activity, or by some change in age-distribution or genetical composition of the population[3]. Mr. Solomon did not counter the above argument to my satisfaction.

Solomon now says[1] : "I do not believe that *factors* perfectly dependent on density exist except at a high level of abstraction. In Nature, the actions of all factors are presumably variable and inexact." [The italics are mine.]

In that statement it is interesting to note (1) a plurality not present in my thesis (cp. "factors") ; and (2) an indirect admission that I am correct in holding enemies to be at best imperfectly density-dependent factors. I would suggest also that the "high level of abstraction" has actually existed for a long time in the unwitting ascription of perfect density-dependence to enemy action as in Nicholson's popular theory of natural control of population.

It is also interesting to note Solomon's adherence to another abstraction, namely, the 'inverse' density-dependent factor. This factor was a tentative proposition by Howard and Fiske[5], of which, as Allee *et al.*[6] point out, Smith[4] "made little". The proposition is on a par with the erroneous idea prevailing until recently[2,3] that a density-independent factor killed a constant proportion of the population in Nature. I put it to Mr. Solomon that there is no field evidence of 'inverse' density-dependence which will stand up to stringent ecological and statistical analysis (and that includes so-called 'sexual isolation').

Again there seems to me little point in distinguishing between factors the density-dependent action of which is (1) immediate ('direct') or (2) delayed ('alternate') simply because enemy reproduction is not immediate. I think it more useful to regard delay in action as contributing to the imperfection I ascribe to the density-dependence of enemies.

I should go further than Varley[7] (though for different reasons) and say there is no advantage in adopting Solomon's classification of density-dependent factors.

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[1] Solomon, M. E., *Nature*, **181**, 1778 (1958).
[2] Milne, A., *Canad. Entom.*, **89**, 194 (1957).
[3] Milne, A., *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 253 (1957).
[4] Smith, H. S., *J. Econ. Entom.*, **28**, 873 (1935).
[5] Howard, L. O., and Fiske, W. F., *Bull. U.S. Bur. Ent.*, No. 91 (1911).
[6] Allee, W. C., Emerson, A. E., Park, O., Park, T., and Schmidt, K. P., "Principles of Animal Ecology", 331 (Saunders, Philadelphia and London, 1949).
[7] Varley, G. C., *Nature*, **181**, 1780 (1958).

I OBJECTED to Dr. Milne's proposed term "perfectly density-dependent" because neither intraspecific competition nor any other factor to be observed in the field is likely to preserve (in the words of his definition[1]) "an exact linear (or curvilinear) relationship between increasing action of the factor and increasing density of the species". The logic of his argument can be made clearer by re-stating it as follows.

If all causes of variation were removed, there would be a simple and exactly maintained relationship between the intensity of intraspecific competition and the population density. Let us relegate all sources of variation to a category for which we shall borrow the term environmental capacity. Then we are left with a perfectly density-dependent factor, intraspecific competition.

I see no objection to this argument as an exercise in logic or as a step in the development of a simplified mathematical theory. I only wish to point out that the perfection achieved in this way bears little relationship to what we can expect to find in studying the dynamics of actual populations, and that therefore the term seems inappropriate for use by the practical ecologist. It should perhaps be added that, by a similar process of abstraction, the relationships expected to hold between a parasite or predator population and the density of its host can also be made to appear simple and regular, as in the mathematical theories, although imperfect in Milne's sense.

Milne's remark about Nicholson's theory refers to a point already dealt with by Varley[2] in these columns.

Milne objects to the idea of inverse factors because "there is no field evidence of 'inverse' density-dependence which will stand up to stringent ecological and statistical analysis". But since, unfortunately, we have very little field information of this quality on density relationships of any sort, we can scarcely attach special significance to the lack of it in this case.

As to "the erroneous idea prevailing until recently that a density-independent factor killed a constant proportion of the population in Nature", in fact the idea that the action of density-independent factors varies in intensity is, of course, neither new nor at all unfamiliar. It is true that Howard and Fiske[3] wrote of catastrophic factors that "the average percentage of destruction remains the same, no matter how abundant or how near to extinction the insect may have become", and Smith[4], in re-naming these factors 'density-independent', described them as "destroying a constant percentage regardless of the abundance of the insect". But it seems obvious that their intention was to argue that the percentage effect of density-independent factors did not vary in response to changes in population density, not that they necessarily produced a mortality-rate which did not vary in time. In a discussion[5] published nine years ago, I unhesitatingly adopted the former view, and have seen no protest on this score. Milne's claim implies that ecologists have hitherto believed that mortality due to weather factors is constant.

Although Milne sees no advantage in my proposed classification of density-relationships, some ecologists may do so. It has at least the advantage of making no assumptions about particular types of factors in advance of our knowledge of them. This discipline is likely to be valuable for some time to come, even if the categories I suggested are augmented, subdivided or replaced by others.

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[1] Milne, A., *Canad. Entom.*, **89**, 193 (1957).
[2] Varley, G. C., *Nature*, **181**, 1780 (1958).
[3] Howard, L. O., and Fiske, W. F., *Bull. U.S. Bur. Ent.*, No. 91 (1911).
[4] Smith, H. S., *J. Econ. Entom.*, **28**, 873 (1935).
[5] Solomon, M. E., *J. Anim. Ecol.*, **18**, 1 (1949).

[This correspondence is now closed.—Editors, *Nature.*]