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the "number-of-factors" model of Reddingius and den Boer is unrealistic. As any careful reader will have noticed, we were pretty well aware of this lack of realism, and we offered some arguments to suggest that this did not really matter. For example, the "factors" f_i in the model need not be "real" factors such as temperature or humidity, but they might well be transformations of these such as "the cubic root of the difference between environmental temperature and the optimum temperature." To show this, we did not merely run a series of computer simulations, but we proved a theorem. This theorem asumes something about expectations, variances, and covariances of hypothetical influences on net reproduction; it assumes nothing about the relationship between net reproduction and temperature.

In my opinion, den Boer's spreading-of-risk theory is still highly speculative, but it does have heuristic value. The question under what conditions the assertions of this theory are true and under what conditions they are not is worth a thorough discussion. Most of the points raised by Roff (1974) and Levandowsky (1974) do not seem to bear on this question at all.

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AN ANSWER TO THE COMMENT OF ROFF

Reddingius and den Boer (1970) chose extreme values of net reproduction (r_{max}, r_{min}) "unrealistically" high and low for a lepidopterous insect. Since the probability that all factors attain their extreme values in the same direction within the same generation must be very low (more so when

the number of factors is large), we concluded that r usually varied within more or less "realistic" bounds. Hence, the question of whether only one factor will set the absolute limit on r is not very interesting to our model which represents the kind of situation in which populations persist for some time. Of course, there are places where one or more "factors" will often reach extreme values, but such populations generally will not be able to persist for more than a few generations. Nevertheless, let us look briefly at Roff's (1974) numerical examples. Let the two factors of Roff be factors 6 and 2 of table 1 in Reddingius and den Boer (1970); that is, factor 6 = total evaporation in April, and factor 2 = number of hours of sunshine during May.

One may imagine factor 2 to influence number of eggs deposited and factor 6 to influence survival of winged adults. Roff supposes factor 2 reaches an extremely high value (with the result that great numbers of eggs are deposited per female in May) and factor 6 reaches an extremely low value (with the result that mortality of winged adults is very high in April). He is dissatisfied with r having about the same intermediate value as when both factors have intermediate values.

I cannot see how the result could differ from this, even in nature. This is not to say that our model is "biologically realistic," for—like all models—it simplifies reality; we only hope that our simplifications do not invalidate the point we wanted to make about populations in nature. In any case, Roff does not question such unwarranted simplification.

Roff does not seem to realize that our "r" is thought to be the result of life histories of individuals of a population during a whole generation and that each life history is composed of a sequence of encounters with more or less dangerous "factor values." An individual that escapes one source of mortality must encounter another and thus will have another risk of succumbing but also another chance to reproduce. Hence, our r is R_o of Andrewartha and Birch (1954, p. 41) and *not* the "innate capacity for increase" (r_m) or "finite rate of increase" as used by Birch (1953) and Andrewartha and Birch (1954, p. 47–54).

Our opinions do not seem to contradict views of Andrewartha and Birch (1954), who among others (p. 53) stress the point that in certain places some "factor" may reach such extreme values that it limits the distribution of the species concerned. However, our model is concerned with the pattern of fluctuations in places where conditions are less severe.

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A FURTHER COMMENT ON THE MODEL OF REDDINGIUS AND DEN BOER

The model by Reddingius and den Boer (1970) assumes that net reproductive rate $r(t)$ varies between a maximum and a minimum greater than zero, and that its logarithm $y(t)$ is a monotonic linear function of a number of environmental factors f_i. These assumptions appear unreasonable, even in a first approximation:

A reasonable model needs to allow r to fall to zero at the upper and lower extremes of any f_i. Thus, a typical plot of r versus temperature has the general form shown in figure 1.

Therefore r, or log r, is not a monotonic function of the f_i.

Since $y = \log r$ is not monotonic or identically zero, it is not linear. For high values of r, log r is usually a "smoother," or more linear, function. But for many natural populations, net reproductive rate fluctuates near one, and taking logs does not have this smoothing effect; further, log r fluctuates wildly when r varies near the origin, since $\log r \to -\infty$ as $r \to 0$.

However, both the model and the above criticisms are a bit artificial, in ignoring interactions of the effects of environmental factors. These are known to be quite important in microbial ecology (Smayda 1963; Brock 1966), where range limits of one variable are conditioned by values of others.
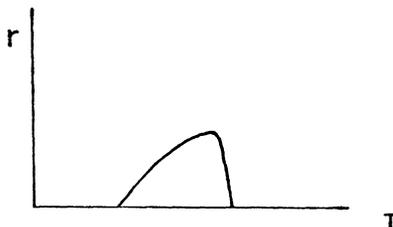

FIG. 1.—Form of relation between growth rate (r) and temperature (T) found in many microorganisms. For specific examples see Hansen (1933).