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Additional Comments on Reproductive Strategies and Population Fluctuations in Microtine Rodents

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Notes and Comments

ADDITIONAL COMMENTS ON REPRODUCTIVE STRATEGIES AND POPULATION FLUCTUATIONS IN MICROTINE RODENTS [1]

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Recently, Schaffer and Tamarin (1973) proposed a model relating changes in reproductive effort (RE) to fluctuating densities in microtine rodents (lemmings and voles). They assumed (and presented data supporting this assumption) that the major effect of increased crowding would be a reduction in survival among prereproductives, thereby lowering the effective fecundity (Schaffer and Rosenzweig 1977) of their parents. As a consequence, Schaffer and Tamarin argued that the optimal reproductive expenditure, $\hat{E}(N)$, should decline with increasing population size, N. They also deduced the shape of the zero-growth isocline, $N^*(E)$, for differing levels of RE and plotted both $\hat{E}(N)$ and $N^*(E)$ on a graph whose axes are reproductive expenditure and population density (Fig. 1a).

In the case of continuous time models, which are appropriate for microtines given their extended breeding seasons and short gestation periods, Schaffer and Tamarin's graphical analysis suggests two conclusions: (1) In the absence of time lags (e.g., May 1973) in the population's growth equation, and if the equilibrium point ($\hat{E}$, N^*) is constant in time, RE and density will approach equilibrium. This assumes that individuals adjust their reproductive output in the direction of maximizing Darwinian fitness, i.e., in the direction predicted by Schaffer's (1974, Schaffer and Rosenzweig 1977) model of optimal reproductive expenditure. (2) In the case of fluctuating environments, in which the equilibrium point shifts back and forth between two or more points on the graph, the point $[E(t), N(t)]$, i.e., RE and density taken together, should trace out a clockwise trajectory circumscribing the various equilbria (Fig. 1b). Notice, however, that in the absence of environmentally induced fluctuations in equilibrium, a clockwise trajectory will still be obtained if the population's growth equation contains a sufficiently large time lag, T (e.g., May 1973, 1976; for discussion, see also Stenseth 1977).

In their 1973 paper, Schaffer and Tamarin analyzed previously published data for six species of lemmings and voles and showed that in each case plotting the best available measure of RE against density yielded a clockwise trajectory.

More recently, Rose and Gaines (1978) conducted an extensive study of *Microtus ochrogaster* in eastern Kansas. Since the mean litter sizes during the prepeak, peak, and postpeak phases of the cycle were 3.04, 3.69, and 3.70 young per female, they concluded that the inverse relationship between reproductive rate and density predicted by Schaffer and Tamarin did not occur in the Kansas voles. However, further consideration shows that this conclusion is not necessarily correct. First, since pregnancy rates often vary dramatically during the course of microtine cycles (Keller and Krebs 1970), litter size by itself is an inadequate estimator of average reproductive expenditure. (In the Kansas voles there was statistically significant heterogeneity in pregnancy rates during population fluctuations due to a midsummer breeding depression.) Second, the clockwise trajectory in Fig. 1b reveals that data supporting the Schaffer-Tamarin model would be unlikely to show an inverse relationship between RE and density. Although the optimal expenditure, $\hat{E}(N)$, declines with population size, the population's inability to respond instantaneously to changes in N can produce a roughly circular path, which will generate a correlation coefficient between $E(t)$ and $N(t)$ approximately equal to zero.

As a result of these considerations, we have re-analyzed the Kansas vole data to determine whether or not successive measures of reproductive effort and density fit a clockwise trajectory. The results are given in Fig. 2. Here, reproductive effort was estimated by multiplying mean litter size by pregnancy rate. Densities were estimated from the numbers of individuals caught per hundred trap nights. Each point represents the average of a 4-mo interval. As predicted by the Schaffer-Tamarin model, the path connecting successive estimates of (N,E) is clockwise.

We therefore now agree that the Schaffer-Tamarin model may be of heuristic value to microtine biologists. First, the model offers an adaptive explanation for the changes in reproductive output observed during the course of most microtine cycles. In particular, Schaffer and Tamarin were able to show that reproductive rate varied with changes in juvenile and adult
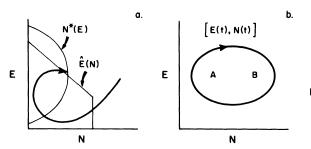
Fig. 1. a. Optimal reproductive expenditure $E(N)$ and zero growth isocline $N^*(E)$ generate partial oscillations which converge to the equilibrium point (E, N^*). b. If the equilibrium point moves between two values A and B, for example, seasonally, the point $[E(t), N(t)]$ describes a clockwise trajectory enclosing both equilibria.
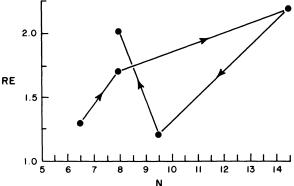

Fig. 2. Phase plane diagram of reproductive effort vs. density for Kansas prairie voles. Each point represents the average of a 4-mo interval. See text for details.

death rates in the manner predicted by their model. That is, when the ratio of juvenile to adult mortality declined, so did the average population reproductive rate. This prediction is amenable to further testing in the field. Second, together with May's (1976) work, the Schaffer-Tamarin model emphasizes the advantages of considering microtine cycles from a dynamical viewpoint (see, for example, May 1973, Levins 1975). The need to consider microtine cycles as a problem in dynamics also supports the multifactorial approach to population cycles advocated by Lidicker (1973). This is because any number of recurrent factors can displace the population from equilibrium, if the latter is stable, or cause the equilibrium point itself to shift. In either case, oscillations will result. Furthermore, if environmental factors which thus "reset" the cycles are widespread in their effect, synchrony between local populations (Krebs and Myers 1974) can thereby be achieved.

The Schaffer-Tamarin model also has some problems. First, Schaffer and Tamarin do not specify the immediate factor or factors responsible for the increase in juvenile mortality which they propose to be associated with increased crowding. Accordingly, their model fails to identify the proximate causal mechanisms for the cyclical patterns of ≈3–4 yr which are so often seen in microtine populations. The same restriction also applies to May's time delay model. Second, the Schaffer-Tamarin model is a qualitative one which will only generate the predicted pattern of simultaneous changes in density and reproductive output given the right values of intrinsic rate of increase, r, the magnitude of the shift in the equilibrium point, and the rate at which the population responds to changes in optimal reproductive effort.

Quantitative extensions of the model sufficient to extend the number of possible field tests would appear difficult to come by since this would require estimating the partial derivatives $(\partial N/\partial E)$ and $(\partial N/\partial N)$.

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