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ON THE APPLICABILITY OF CURRENT POPULATION MODELS TO THE GROWTH OF INSECT POPULATIONS

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Since most models of population growth assume a stable age distribution, it is interesting to know which populations this may be relevant to and which not. In an environment in which fecundity and survivorship rates are constant, almost all populations will achieve a stable age distribution no matter what their original age distribution (Lotka, 1922). The problem with most insect populations, particularly in highly seasonal environments, is that the time when a population can grow is limited. This corresponds roughly to the growing season. So I asked, within the constraints of a normal growing season in the temperate zone, which insect species would be able to reach a S.A.D.?

I. **Methods.** My methods are straightforward and proceed through four steps. Full elaboration of this work has been presented elsewhere (Taylor, 1977).

1. **The physiological time axis.** The growth and development rates of insects depend upon temperature. Generally, these rates increase with temperature to the point where high temperatures have a deleterious effect. Thus, during mid-summer, insect populations would appear in normal clock time to grow faster than in spring and fall. In physiological time, development rates are approximately constant over a fairly broad range of temperatures. On this scale, then, the population growth rate does not vary so much with temperature. Below, a degree-day scale (Stinner, et al., 1974) has been used to overcome the problem of fluctuating temperature during the season.

2. **The equation for population growth.** I used Lotka's renewal equation to take into account age-dependent birth and death rates:

$$B(t) = \int_0^{\beta} B(t-a)\, m(a)\, l(a)\, da + G(t).$$

Only females are considered. This model includes the effects of the three basic ingredients in population growth: (i) births due to an *initial age distribution* occur in the $G(t)$ expression; (ii) *age-specific mortality*

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occurs in $l(a)$; and (iii) *age-specific fecundity* appears as $m(a)$. Thus, the integrand represents births due to females of age a.

The solution of this equation looks like:

$$B(t) = Q_1 e^{r_1 t} + Q_2 e^{r_2 t} + Q_3 e^{r_3 t} + \cdots. \tag{1}$$

There are a couple of important points for the following argument. (a) There is one real root, r_1, often called the intrinsic rate of increase. (b) This root is greater in magnitude than the real part of any complex root. After some time, then, growth will be purely exponential dominated by r_1. At this time, the population has assumed the S.A.D. If $r_2 = u_2 + iv_2$ is that complex root with the largest real part, equation (1) becomes:

$$B(t) = Q_1 e^{r_1 t} + e^{u_2 t}\,[A \cos v_2 t + B \sin v_2 t] + \cdots, \tag{2}$$

where A and B are real-valued constants.

3. **Criterion for convergence on the S.A.D.** From equation (2), $Q_1{}^{r_1 t}/Ae^{u_2 t} = W$ gives a reasonable measure of convergence on the S.A.D., where A is the larger of A or B in (2) and W is given a value for the desired closeness to convergence. It is given a value of 20 here. Coale (1972) estimated Q_1/A at 2.0 for human populations and this value will be assumed here. Hence,

$$t = \frac{\ln(W/2)}{r_1 - u_2}$$

estimates the time to convergence given values for r_1 and u_2 from $m(a)$ and $l(a)$ data.

4. **Length of growing season.** We have a measure of the time to convergence. Now we require a context into which to fit it. From a few studies carried out in the Midwest, a reasonable estimate of length for the entire growing season between hard frosts is 2500 degree-days.

II. **Results.** Using a length for the season of 2500 degree-days, 18 out of 30 species I considered would converge to the stable age distribution.

Notice, however, that it requires considerable effort to get the sort of data needed for my calculations. Thus, there has been a tendency to choose fast-growing species. Also, many species are further limited in time by the availability of resources to a period of growth that is considerably less than the entire growing season. A more reasonable time limit for such species might be 1000 degree-days. Only 9 of the 30 species achieves a stable age distribution in 1000 degree-days. This includes five aphid species, two mite species, a dermestid beetle, and *Drosophila melanogaster*.

III. **Conclusion.** I conclude from the above analysis that many, possibly most, insect species growing in seasonal environments, never experience a stable age distribution. This means that most population models in current use do not apply to these species and that new models should be developed.

References

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