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NON-LINEAR INTERACTIONS OF POPULATIONS AND THE IMPORTANCE OF ESTIMATING PER CAPITA RATES OF CHANGE

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SUMMARY

(1) We derive a computational formula for estimating the per capita rate of change in experimental cohorts when detailed schedules for reproduction and survival during the reproductive period are impractical to obtain. For experiments that manipulate densities, this calculation can provide estimates for the unlimited population growth rate (r_m), the equilibrium carrying capacity (K), and the intensity of interspecific interactions.

(2) These methods are applied to life history data for treehole mosquitoes to underscore the potential shortcomings of analysing separate life-history features in testing the adequacy of simple linear models of population growth. We demonstrate that non-linearities which arise when survivorship and fecundity are treated separately may cancel when gathered into a well-behaved estimate of population growth.

INTRODUCTION

Experimental tests of central ecological hypotheses, such as the importance of higher order effects in both intraspecific and interspecific interactions (e.g. Wilbur 1971, 1972, 1977a,b; Smith-Gill & Gill 1978; Moore & Fisher 1969; Wilbur & Collins 1973) will depend critically on the method used to assess population performance. Herein we develop practical methods for obtaining robust estimates of population growth, with a view to sharpening the current debate over the existence of higher order interactions (Abrams 1980; Pomerantz 1981; Case & Bender 1981). In particular, we aim to demonstrate how simple linear models of population growth may be robust to non-linearities which may arise from the analysis of separate components of the per capita rate of change.

The ideal measurement for quantifying population performance is the per capita rate of change (r):

$$1 = \sum_x e^{-rx} l_x m_x. \quad (1)$$

However, for even the simplest experimental systems, the data required for computing this statistic are usually prohibitive, and the problem becomes magnified in complex replicated experiments. Not only must detailed mortality and natality schedules be constructed

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separately for each replicate population, but the task must be multiplied by the factorial combinations of experimental treatments involved.

Most investigators have side-stepped this logistical barrier by focusing on a single life-history trait that is easily measured, such as clutch size, survival to a particular age or developmental stage, time required to attain a given stage in development, or time required for 50% mortality (e.g. Wilbur 1972, 1977a,b; Nekrasova 1976; Barbosa, Peters & Greenough 1972; Gromko, Mason & Smith-Gill 1973; Moore & Fisher 1969; Moore & Whitacre 1972, Sullivan & Sokal 1963). These life-history features are presumed to correlate with the per capita rate of change; however, they may not bear the same functional relationship (e.g. linear) as r would to density. Beyond such arguments about the details of this relationship, contradictory conclusions may arise, depending on which life-history trait is chosen for analysis. For example, if early and high mortality permit the survivors to achieve more rapid development, a trend indicated by a mortality measure might oppose a trend obtained from a correlate of fecundity.

Efforts toward a more complete analogue of the per capita rate of change have combined pairs of life history traits into single indices of individual fitness. Measurements of individual rates of biomass accumulation and various estimates of larval growth rates, including the Smith-Gill & Gill (1978) index composed of the cube root of the volume of metamorphosing larvae divided by the natural logarithm of time to metamorphosis, combine aspects of both generation time and eventual fecundity. However, in all of these composite measures, the relative weights given to size and development time are arbitrary, and none of them incorporate survivorship. Therefore, such indices should not in general scale linearly with the per capita rate of change. This is significant especially when testing for the importance of non-linear growth with density. Therefore, previous studies which point to the inadequacies of the Volterra equations may not have a solid footing because they have relied on incomplete correlates of (dN/Ndt) .

In this paper we describe a simple method to estimate the per capita rate of change when experimental populations are established as cohorts and when fecundity and mortality schedules are not readily available for the period of reproduction. Our estimate, which may be modified into a well-behaved index of performance, combines easily obtained indirect information on cohort survivorship, fecundity and generation time to construct estimates of (dN/Ndt) for organisms with type III mortality, i.e. high larval mortality and negligible adult mortality through the reproductive period. We apply our methods to data on experimental mosquito populations to demonstrate that misleading conclusions about the importance of higher order interactions can be reached through the analysis of incomplete correlates of the per capita rate of change.

AN ESTIMATE OF THE PER CAPITA RATE OF CHANGE

For many populations, this rate can be approximated with the equation

$$r = \frac{\ln R_0}{\tau}, \quad (2)$$

in which the net reproductive value, $R_0 = \sum_x l_x m_x$, is the expected number of offspring per newborn individual, and the cohort generation time, $\tau = \sum_x x l_x m_x / \sum_x l_x m_x$, is the mean

age at reproduction. The restrictions and assumptions of this equation are discussed by Laughlin (1965) and May (1976).*

Because of the impracticality of computing the per capita rate of change from detailed $l_x m_x$ schedules, especially in experiments with multiple treatments, we seek a simpler method of calculating eqn (2) from indirect estimates of the quantities R_0 and τ . As in much of the experimental work on higher order effects, attention here will be restricted to organisms with high larval mortality and negligible adult mortality through the reproductive period. We take advantage of the fact that in such organisms much of the information required to calculate R_0 and τ can be gathered during the period of emergence into adulthood. In particular, R_0 may be estimated from knowledge of the fraction of the original cohort maturing on day x and the future net fecundity of that fraction.

In a cohort with an initial number of females, N_0 , the fraction that survives to and matures on day x may be denoted A_x/N_0 , where A_x is the number of new adult females produced at time x . This expression estimates the joint probability of surviving to age x and maturing on day x , and may be thought of as the per capita production of adult females at time x . Notice that because of the lack of adult mortality through the reproductive period, the terms A_x/N_0 will contain all the important mortality information for the cohort.

These data may then be used to calculate the net reproductive rate as follows:

$$R_0 = \sum_x \frac{A_x F_x}{N_0}, \quad (3)$$

where F_x is the future net fecundity of those individuals maturing on day x . In practice, the value of F_x can frequently be predicted from a knowledge of the average size of the new adult females emerging on day x :

$$F_x = f(\bar{w}_x). \quad (4)$$

Here average female size, \bar{w}_x , can be expressed in dry weight or by a linear measure of size, such as wing length, and the generalized function $f(\bar{w}_x)$ can be determined empirically. An example will be given below to show how $f(\bar{w}_x)$ is a simple relationship for a mosquito population. In this case then, R_0 may be computed simply as

$$R_0 = \frac{1}{N_0} \sum_x A_x f(\bar{w}_x). \quad (5)$$

Notice that the terms in the summation of eqn (5) are analogous to l_x and m_x . A_x contains survivorship information and $f(\bar{w}_x)$ measures fecundity; however, A_x also includes information on maturation rate and $f(\bar{w}_x)$ is the future net fecundity of the average individual maturing on day x .

We turn now to the estimation of generation time, τ . If a constant period, D , is required before adults can reproduce after emergence, τ can be calculated as the weighted mean time to maturity plus D :

$$\tau = D + \frac{(\sum_x x A_x f(\bar{w}_x))}{\sum_x A_x f(\bar{w}_x)} \quad (6)$$

* The major assumption involves a brief duration of the reproductive period relative to the total life span, which results in a small error in the estimation of generation time. Departures from these conditions become particularly important at high values of R_0 . Laughlin (1965) estimates that a reproductive span which occupies 30% of the maximum reproductive age will result in less than a 3% deviation of the estimated r from the actual value when R_0 is less than 10^3 . The error in the estimate declines to zero as R_0 approaches unity.

A constant delay period may be reasonable for many experimental insect populations (Roff 1981).

Collecting these remarks on R_0 and τ leads to the following operational estimate of the per capita rate of change, which we denote as r' :

$$r' = \frac{\ln \frac{1}{N_0} \sum_x A_x f(\bar{w}_x)}{D + \frac{\sum_x x A_x f(\bar{w}_x)}{\sum_x A_x f(\bar{w}_x)}} \quad (7)$$

This rate is a far easier to determine than the conventional measure which requires a separate set of detailed information on l_x and m_x for each independent observation. To use eqn (7) one only needs to observe the cohorts during the maturation period in order to obtain measurements of the number of newly emerged adult females and their average size. If differences in fecundity in the various experimental regimes are obtained primarily from differences in female adult body size (e.g. Livdahl 1982), the relationship between size and fecundity, $f(\bar{w}_x)$, need only be determined once and should not have to be determined separately for each experimental treatment level. This seems reasonable for most experimental regimes using organisms with type III survivorship.

In some cases, it may not be possible to ascertain $f(\bar{w}_x)$ and D directly. If reproduction cannot be observed directly, the delay between maturity and reproduction cannot be estimated either. In these instances, if one is willing to assume that D is small compared to the mean time to maturity, and a positive and roughly linear relationship between fecundity and body size, at least within the range of observed values of body size, then it is possible to construct the following well-behaved index of relative per capita performance:

$$I = \frac{\ln \frac{1}{N_0} \sum_x A_x \bar{w}_x}{\frac{\sum_x x A_x \bar{w}_x}{\sum_x A_x \bar{w}_x}} \quad (8)$$

This index is a complete performance measure that combines information about survivorship and fecundity in a way that mimics the computation of the per capita rate of change. Although this index lacks the power of r in predicting population dynamics, it is nonetheless useful in comparing the success of experimental populations. In particular, under the conditions stated above (mean maturation time $\gg D$), both I and r' should behave similarly in detecting the importance of higher order interactions.

EXAMPLE

We will use the data of Livdahl (1982) from *Aedes triseriatus* to illustrate the utility of the methods presented here (see Livdahl 1984 for other applications). *Aedes triseriatus* larvae are divided into discrete cohorts by temporally distinct hatching stimuli which follow heavy rains.

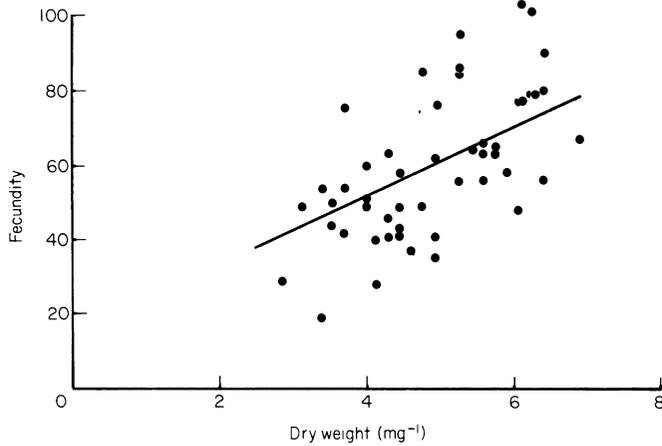


FIG. 1. The relationship between fecundity and female dry weight for the treehole mosquito, *Aedes triseriatus*. The least squares line is shown.

The relationship between fecundity and female size in *Aedes triseriatus* appears in Fig. 1. The linear function, $f(\bar{w}_x) = 7.13 + 45.85\bar{w}_x$, is obtained by dividing the coefficients of the least squares line by 2, providing the number of female offspring expected from a female of a given weight. We emphasize here that this function is only an approximation of the reproductive capacity of individuals in the field. We know, for example, that there is the potential for individuals to produce more eggs per lifetime than the linear function predicts, and we also know that a certain amount of pre-reproductive adult mortality occurs.

Table 1 provides a sample calculation of r' for one experimental cohort. To complete the calculation, it is necessary to assume that forty of the initial eighty larvae were females ($N_0 = 40$) and that a female requires approximately $D = 7$ days after emergence to mate, find a bloodmeal and oviposit. Both of these estimates can be adjusted if more detailed information becomes available, and if a more precise estimate of the per capita rate of change is desired.

This computation was applied to each of fifty-four experimental cohorts reared in field

TABLE 1. A sample calculation of r' , using the linear function obtained in Fig. 2,

$$f(\bar{w}) = 7.13 + 45.85 \bar{w}.$$

x (days)	\bar{w}_x (dry mg)	A_x	$A_x f(\bar{w}_x)$	$x A_x f(\bar{w}_x)$
19	0.340	1	22.72	431.66
26	0.535	1	31.66	823.15
28	0.437	5	135.83	3803.30
30	0.430	9	241.61	7248.29
31	0.388	11	274.12	8497.65
32	0.465	3	85.35	2731.22

$$\sum_x A_x f(\bar{w}_x) = 791.29$$

$$\sum_x x A_x f(\bar{w}_x) = 23\,535.28$$

$$D = 7$$

$$N_0 = 40$$

$$r' = \frac{\ln(791.29 \div 40)}{7 + (23\,535.28 \div 791.29)} = 0.08$$

containers at three levels of initial density, three levels of concentration of natural treehole fluid, and in the presence or absence of a second cohort introduced 7 days after hatching. For this discussion, the treatments are labelled 'density', 'food', and 'cohort structure.' Values of r' were inspected in a 3-way analysis of variance, summarized in Table 2. Other correlates of cohort success, including mean female development time per culture, mean female dry weight per culture, and the fraction of initial larvae that emerged as adults were given the same statistical treatment, also summarized in Table 2.

TABLE 2. Summary of analyses of variance for correlates of success in experimental cohorts of *Aedes triseriatus*. Experimental treatments of density, food, and cohort structure are respectively abbreviated D, F and CS. Significance levels appear within the table (N.S., $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$)

Correlate	D	F	CS	D × F	D × CS	F × CS	D × F × CS
r'	***	***	N.S.	N.S.	N.S.	N.S.	N.S.
Female	***	***	N.S.	N.S.	*	*	N.S.
Development Time							
Female Dry Weight	***	**	N.S.	N.S.	N.S.	N.S.	N.S.
Survival to Adulthood	***	***	N.S.	N.S.	N.S.	N.S.	*

Inspection of separate life-history traits suggests a deep internal complexity in which non-linearities and higher order effects abound. The apparent effect of competition within the first cohort is actually moderated by the presence of the second cohort when development time and survival are examined separately. Such complexity notwithstanding, the composite index of success, r' , reveals a remarkably simple overall picture of the total effects of density, food and a late larval cohort on per capita population growth. As can be seen in Figs. 2 & 3, the relationship is surprisingly linear ($r^2 = 0.66$), and projects the

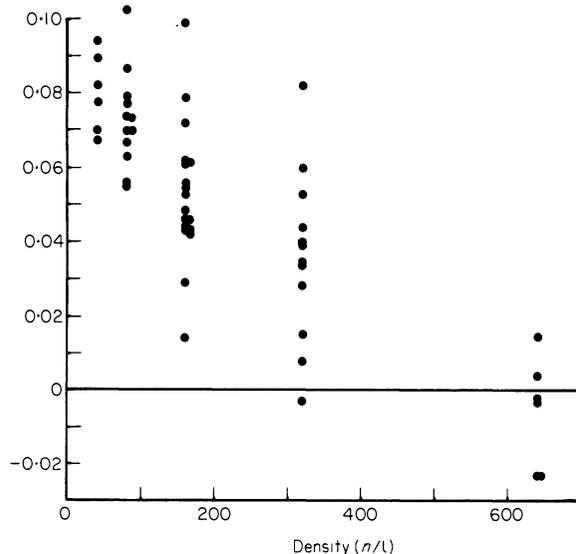


FIG. 2. The response of r' , an estimate of the per capita rate of change, to density per unit food for cohorts of *Aedes triseriatus* reared at three initial densities and three concentrations of natural fluid. Density per unit food is expressed as the initial number of larvae divided by the initial volume of treehole water which was used to initiate the cohort (prior to dilution or concentration).

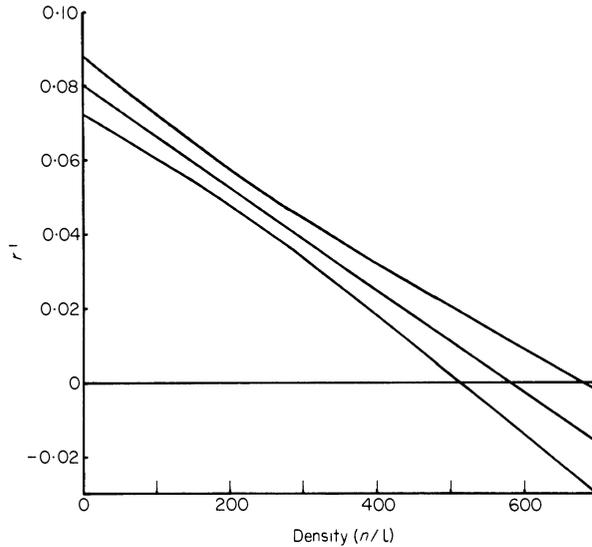


FIG. 3. The least squares line for the data of Fig. 3, accompanied by 95% confidence intervals of predicted r' values for given densities.

following parameter estimates: $r_m = 0.080 \pm 0.008$ per individual per day; $K = 580$ initial larvae per litre of unaltered treehole fluid (95% C.I.: 513–679). K and r_m are estimated from the x and y -intercepts of the least squares line, respectively.

Obviously, one should not advocate the use of eqn (7) or (8) when actual survivorship and fecundity schedules are available. However, for most populations, including the example presented, it is most unlikely that traditional methods of life table analysis could be used to produce the estimates of Fig. 3.

Our example demonstrates the potential dangers in the use of separate correlates of the per capita rate of change to judge the importance of higher order interactions, particularly in examining the adequacy of classical models of population dynamics. Whereas analyses of separate components of the per capita rate reveal a complex and very non-linear picture of growth, these complications appear to cancel when the components are gathered into a single well-behaved analogue of the per capita rate of change. This appears to lend credence to the simple linear feedback set forth in the logistic or Volterra equations. We suggest, therefore, that previous claims of the inadequacy of the classical models of population dynamics should be viewed with caution.

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