

GAMMA DISTRIBUTIONS OF ADULT NUMBERS FOR *TRIBOLIUM* POPULATIONS IN THE REGION OF THEIR STEADY STATES

BY R. F. COSTANTINO AND R. A. DESHARNAIS

Zoology, University of Rhode Island, Kingston, Rhode Island 02881, U.S.A.

SUMMARY

(1) A gamma steady-state probability distribution was established for adult numbers in continuously growing populations of the flour beetle *Tribolium*. The derivation of the distribution was based on a general stochastic model of population growth with three biological entities: adult inhibition of immatures, pupal productivity, and death-rate among adults.

(2) The hypothesis of a gamma steady-state distribution was tested using thirteen observed frequency distributions of adult numbers for *Tribolium castaneum* and *Tribolium confusum*. The data, in general, supported the gamma steady-state hypothesis.

(3) Using the theoretical gamma probability distribution an attempt was made to explain the *Tribolium* data and identify testable hypotheses. For instance, the observed differences in the mean and variance of the adult steady-state distributions for the genetic strains of *T. castaneum* and *T. confusum* were qualitatively consistent with the theoretical predictions based upon differences in cannibalistic rates, pupal productivity and adult death-rates. The expected effects of stochasticity on the mean and variance were also discussed.

(4) The stochastic differential equation of population growth was viewed using the Ito and Stratonovich definitions of stochastic integrals. Both procedures yielded gamma steady-state distributions; however, the conditions for the existence of the stationary densities were different. With stochastic variation in the death-rate among adults, the existence conditions for the Ito calculus was that the magnitude of the stochastic variance must be less than twice the difference between the number of pupae produced per parent and the death-rate among adults. For the stratonovich calculus, the stationary density always existed.

INTRODUCTION

Adult numbers in single species cultures of the graminivorous beetles *Tribolium confusum* Duval and *Tribolium castaneum* Herbst were observed by Park (1954) to achieve some stationary distribution after 360 days of continuous culture. In a stochastic, two age-class model for *Tribolium*, Leslie (1962) attempted to reproduce the type of frequency distributions observed in the experiments of Park (1954). The distribution of adult numbers predicted by the Leslie model was approximately Gaussian in form. However, the observed *Tribolium* distributions were all asymmetric and skewed to the right. While the model did not provide an adequate description of the experimental data (Leslie 1962, p. 14), the analysis did focus attention on this important aspect of the observed data.

Our objectives in this note are three-fold: (i) to establish that the theoretically expected steady-state distribution of adult numbers based on a general stochastic model of

population growth is a gamma distribution, (ii) to test this hypothesis with Park's (1954) data on the grouped frequency distributions of adult numbers analysed by Leslie (1962) and to test similar data reported in Park, Leslie & Mertz (1964) and Moffa & Costantino (1977), and (iii) to discuss the biological implications of the gamma steady-state distribution.

DERIVATION OF GAMMA PROBABILITY DISTRIBUTION

Population growth model

Our basic population dynamic model for adult number attempts to explain the changes in the size of the adult beetle population based on the association between the number of adults and the number of progeny produced by these adults. Let C be the probability that a single adult prevents a potential recruit from entering the adult population in some small time interval $(t, t + \Delta t)$. Assuming adults act independently, the proportion of potential recruits that become adults during this interval will be $(1 - C)^{A(t)} \doteq e^{-CA(t)}$ for small C , where $A(t)$ is the number of adults at time t . Defining X as the rate at which potential recruits are produced per adult and D as the adult mortality rate, we can describe the change in adult numbers during $(t, t + \Delta t)$ as

$$A(t + \Delta t) - A(t) = \Delta t A(t) X e^{-CA(t)} - \Delta t A(t) D.$$

Dividing through by Δt and taking the limit as Δt goes to zero we have

$$dA(t)/dt = A(t) X e^{-CA(t)} - A(t) D \quad (1)$$

as our model (Ricker 1954; Lloyd 1968; Desharnais & Costantino 1980). The equilibrium number of adults for this deterministic differential equation is $A^* = \log(X/D)/C$ and the equilibrium is stable if $X > D$, or equivalently if $A^* > 0$ (Desharnais & Costantino 1980). However, Park (1954); Leslie (1962); Park, Leslie & Mertz (1964) and Moffa & Costantino (1977) noted that continuously growing cultures of these graminivorous beetles did not assume a fixed equilibrium number of adults, A^* , but rather achieved some stationary distribution.

There are two principal methods of connecting our population dynamic model, eqn (1), with a diffusion equation and hence with an equilibrium probability distribution of adult number: the Ito and the Stratonovich. Both methods are applicable only when stochastic variation appears in parameters that are linear functions in the original model. In our case, these are parameters D and X . For a general discussion of Ito and Stratonovich calculi see Turelli (1977) and Roughgarden (1979, p. 379). For the moment, we shall deal exclusively with the Ito calculus.

Stochastic variation in death rate among adults

Assuming that D is subject to fluctuations of the white noise type, we obtain the stochastic differential equation

$$dA/dt = A[X \exp(-CA) - (D + \sigma R(t))] \quad (2)$$

where $R(t)$ is standard white noise and $\sigma > 0$ is a parameter measuring the amplitude of the fluctuations. To obtain a steady state probability distribution of adult number we used the distribution

$$f(A) = \frac{K}{v} \exp \left[2 \int \frac{m}{v} dA \right] \quad (3)$$

based on the Kolmogorov equation (see Roughgarden 1979, p. 69, Crow & Kimura 1970, p. 371 and May 1973, p. 114 for a review). For the Ito calculus with D stochastic, the mean, m , is the deterministic analogue of eqn (2) and the variance v , is $A^2 \sigma^2$. K is a normalization constant. Substituting m and v into eqn (3) it can be shown (see Appendix for details) that the approximate steady state probability distribution is

$$f(A) = K[A]^{(2(X-D)/\sigma^2)-2} \exp [-[2C(D - X)/\sigma^2 \log (D/X)] A]. \tag{4}$$

This equilibrium density function is a gamma distribution provided

$$\sigma^2 < 2(X - D). \tag{5}$$

K is the normalization constant making the integrated probability unity. The expectation of $f(A)$ is

$$M(A) = \left[\frac{\log (X/D)}{C} \right] \left[\frac{2(X - D) - \sigma^2}{2(X - D)} \right] \tag{6}$$

and the variance of $f(A)$ is

$$V(A) = \left[\frac{\sigma^2 (\log (X/D))^2}{C^2} \right] \left[\frac{2(X - D) - \sigma^2}{4(X - D)^2} \right]. \tag{7}$$

Stochastic variation in recruitment rate

Assuming that X is subject to stochastic fluctuations we can write

$$dA/dt = A[(X + \sigma R(t)) \exp (-CA) - D] \tag{8}$$

where $R(t)$ is standard white noise and $\sigma > 0$ is a parameter measuring the amplitude of the fluctuations. To obtain a steady state distribution, we again used eqn (3) but with the mean $m = XA \exp (-CA) - AD$ and the variance $v = A^2 \sigma^2 \exp (-2CA)$, so that we obtained the steady-state probability distribution

$$f(A) = K[A]^{(2(X-D)/\sigma^2)-2} \exp \{-[2C(X - D - \sigma^2 \log (X/D))]/\sigma^2 \log (X/D)\} A \tag{9}$$

which is an approximation to the exact distribution arising from the above model (see Appendix). K is the constant that makes the integrated probability equal to one. The expectation of $f(A)$ is

$$M(A) = \left[\frac{\log (X/D)}{C} \right] \left[\frac{2(X - D) - \sigma^2}{2(X - D - \sigma^2 \log (X/D))} \right] \tag{10}$$

and the variance of $f(A)$ is

$$V(A) = \left[\frac{\sigma^2 (\log (X/D))^2}{C^2} \right] \left[\frac{2(X - D) - \sigma^2}{4(X - D - \sigma^2 \log (X/D))^2} \right]. \tag{11}$$

This equilibrium density function is also a gamma distribution, however, to have a positive mean and variance of $f(A)$ we must have

$$\sigma^2 < \min (2(X - D), (X - D)/\log (X/D)). \tag{12}$$

The equilibrium probability distributions established by considering the Ito calculus with D or X stochastic are gamma density functions. They are different and we shall say more about these distributions in a later section. Our central concern, at this time, is that this excursion into theory provides us with a testable hypothesis, namely, that the variate, adult number in *Tribolium*, follows a gamma distribution.

EXPERIMENTAL OBSERVATIONS

We shall examine thirteen observed frequency distributions of adult numbers when the species were fluctuating in the region of their equilibrium levels. These data were obtained from four separate publications. In general, the experiments were conducted as follows: At the outset, young adult beetles were paced in a vial containing a wheat flour medium. These vials were then maintained in incubators for a specified time interval (14 or 30 days) after which the cultures were censused. The larvae, pupae, and adults were counted and all living stages were returned to fresh medium. This 'census-incubation-census' routine was then repeated for $1\frac{1}{2}$ – $2\frac{1}{2}$ years. The recorded adult numbers for the individual replicates, after the steady-state was achieved, were used to generate the frequency distributions. Standard *Tribolium* culturing techniques were used in each study, however, some differences in laboratory procedures were employed. A description of the latter is beyond the scope of this note and readers are referred to the original data sources for specific details.

Statistical method

Our procedure to check on the validity of the gamma was as follows: The random variable adult number A is said to be distributed as the gamma distribution (Feller 1966) if its density is

$$f(A; \alpha, \beta) = (1/\Gamma(\alpha + 1) \beta^{\alpha+1}) A^\alpha \exp(-A/\beta) \quad 0 < A < \infty \quad (13)$$

$$= 0 \quad \text{elsewhere.}$$

This family of distributions has the two parameters

$$\beta = \sigma^2/\mu \quad (14)$$

$$\alpha = (\mu/\beta) - 1 \quad (15)$$

where μ and σ^2 are the expected mean and variance of adult numbers. The parameters were estimated using the method of maximum likelihood (Johnson & Kotz 1970, p. 189). The expected numbers were calculated using the gamma distribution with the parameters set equal to their estimated values. The chi-square test of goodness-of-fit was employed to make a comparison between the actual and the expected number of observations. Class intervals which had expected numbers less than one were not included in the analysis to avoid inflating the test statistic (Ostle 1963). All statistical tests were made at the 0.01 level of probability.

Data of Moffa & Costantino (1977)

Adult census data were collected at 2 week intervals for 68 weeks on thirty-seven cultures of *T. castaneum* initiated with twenty adults (Fig. 1). It is the adult data from week 20 to week 68 (861 observations) that we suggest may be characterized by the gamma distribution. In Fig. 2, the smooth curve is the gamma distribution with the parameters obtained from the maximum likelihood procedure. The critical chi-square value which must be exceeded to reject the gamma at the 0.01 level of probability is 37.6. The calculated chi-square value, based on twenty-three class intervals (Fig. 2), was 18.9. Therefore, the data of Moffa & Costantino (1977) support the hypothesis of characterizing the steady state probability distribution of adult numbers in continuously growing populations of *T. castaneum* as a gamma distribution.

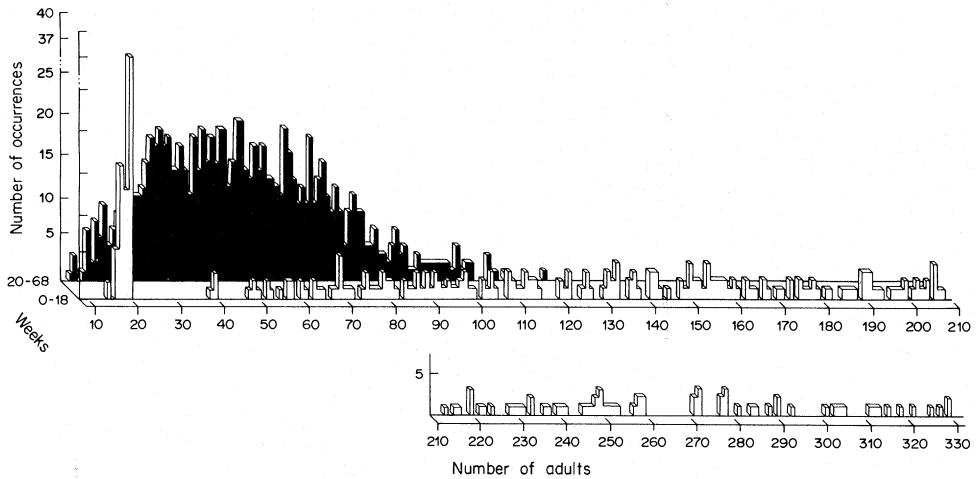


FIG. 1. The number of times that particular adult numbers were recorded for thirty-seven cultures of *T. castaneum* observed by Moffa & Costantino (1977) during the intervals 0–18 weeks (□) and 20–68 weeks (■).

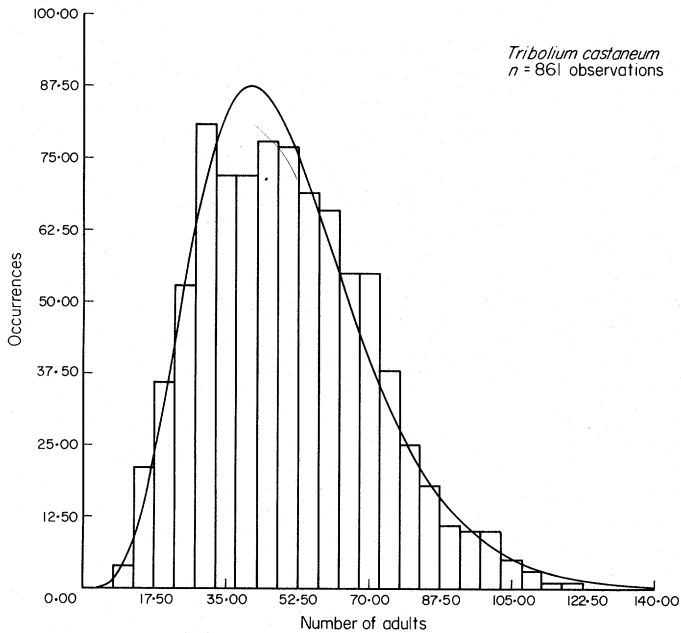


FIG. 2. The grouped frequency distribution of the adult numbers from weeks 20–68 recorded by Moffa & Costantino (1977). The smooth curve is the gamma density function with parameters (α , β) obtained by the method of maximum likelihood.

Data of Park (1954) published in Leslie (1962)

Professor Park provided Leslie with data on *T. confusum* and *T. castaneum* for his treatment III (29 °C, 70 RH) and his treatment V (24 °C, 70 RH) (Park 1954). The observed frequency distributions of Park together with the predictions from Leslie's model are given in Table 9 of Leslie (1962). The four grouped frequency distributions were based on adult numbers recorded at day 360 onward to day 720 at 30 day intervals.

The observed frequency histograms for these two species cultured at 24 °C and 29 °C are presented in Figs 3(a)–(d). The smooth curves are the gamma distributions with the parameters set equal to their maximum likelihood estimated values. In both data sets for *T. confusum*, the hypothesis that the data fit a gamma distribution was accepted. For *T. castaneum* cultured at 24 °C the hypothesis was also accepted, however, at 29 °C the hypothesis of a gamma distribution was rejected.

In Figs 3(e) and (f), the computed gamma distributions reveal that for both species the mean adult number was higher at 29 °C than at 24 °C and that the variance of the distributions was larger at the higher temperature. We shall suggest an interpretation of these data in the next section.

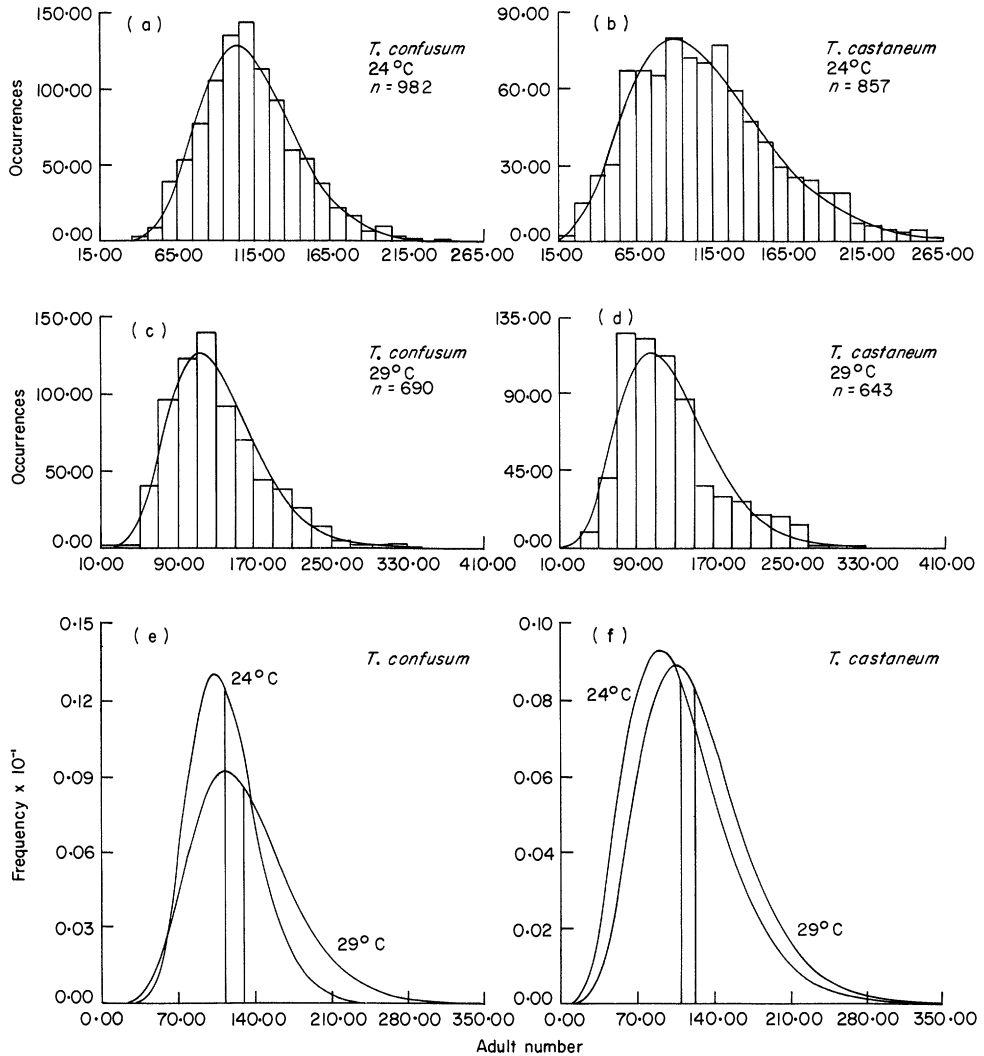


FIG. 3. Observed grouped frequency distributions of Park (1954) published in Leslie (1962) together with the expected gamma distributions: *T. confusum* cultured at (a) 24 °C and (c) 29 °C and *T. castaneum* cultured at (b) 24 °C and (d) 29 °C. The computed gamma density functions for *T. confusum* are sketched in (e) and for *T. castaneum* in (f). N is the number of observations.

Data of Park, Leslie & Mertz (1964)

Four genetically different strains of *T. confusum* and four genetic strains of *T. castaneum* single species cultures were maintained for 870 days. Our data source was the grouped frequency distributions of the adult numbers from day 360 onward which were presented in Appendix Table N in the original publication.

The observed and gamma expected distributions for the four strains of *T. confusum* are presented in Figs 4(a)–(d). For strains 2 and 4, the gamma was accepted at the 0.01 level of probability. For strains 1 and 3 the gamma hypothesis was rejected. Figure 4(e) is a composite illustration of the four computed gamma distributions. We shall discuss these data in the next section.

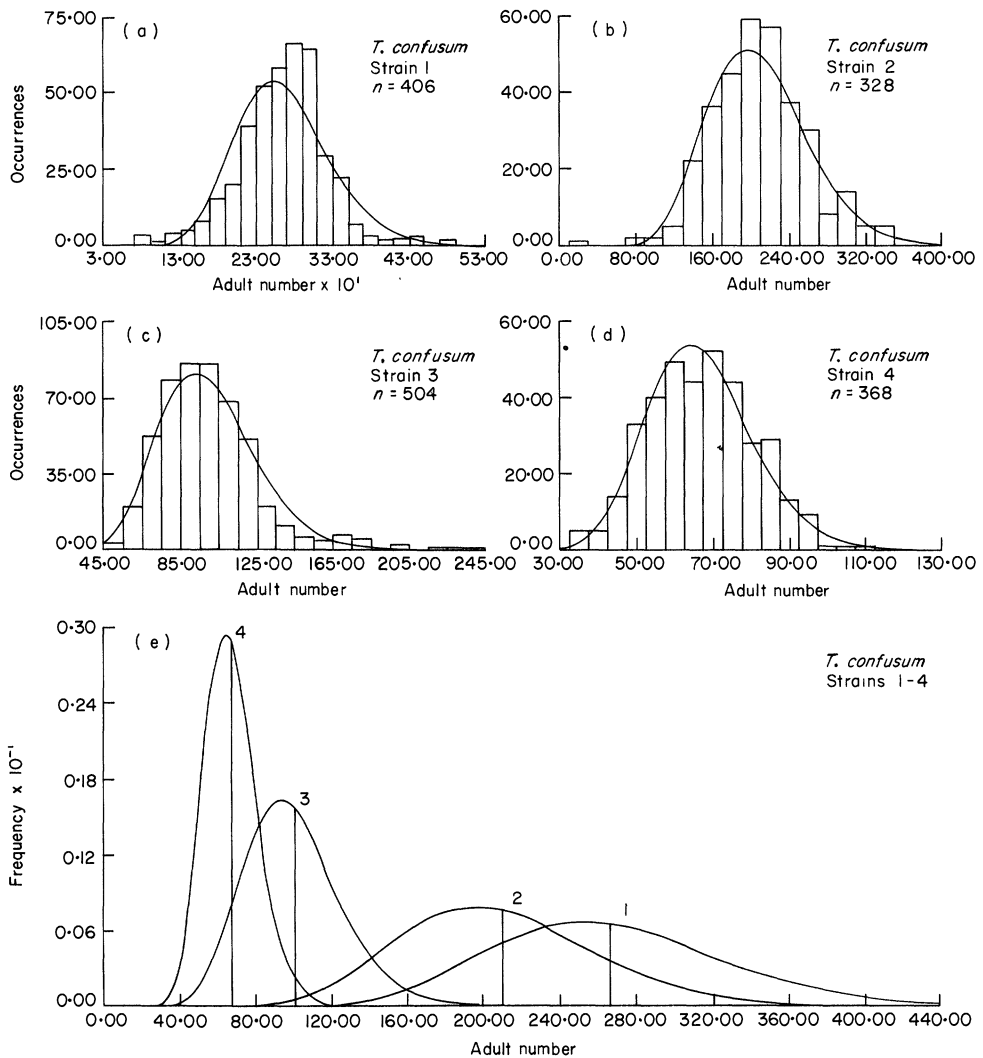


FIG. 4. *Tribolium confusum*. Observed grouped frequency distributions published in Park, Leslie & Mertz (1964) together with the expected gamma distributions. The gamma densities of all four strains are drawn in (e). N is the number of observations.

For the *T. castaneum* strains, the observed and expected distributions are sketched in Figs 5(a)–(d). For strains 3 and 4 the gamma hypothesis was accepted. In the cases of strains 1 and 2, this hypothesis was rejected. The composite illustration of the computed gamma distributions presented in Fig. 5(e) shall be discussed in the next section.

BIOLOGICAL INTERPRETATION OF STEADY STATE DISTRIBUTIONS

The incorporation of stochasticity into the deterministic *Tribolium* population growth model (1) was mathematically tractable and yielded a gamma steady-state probability distribution with the mean and variance defined in terms of X , C , D and σ^2 . Our objective

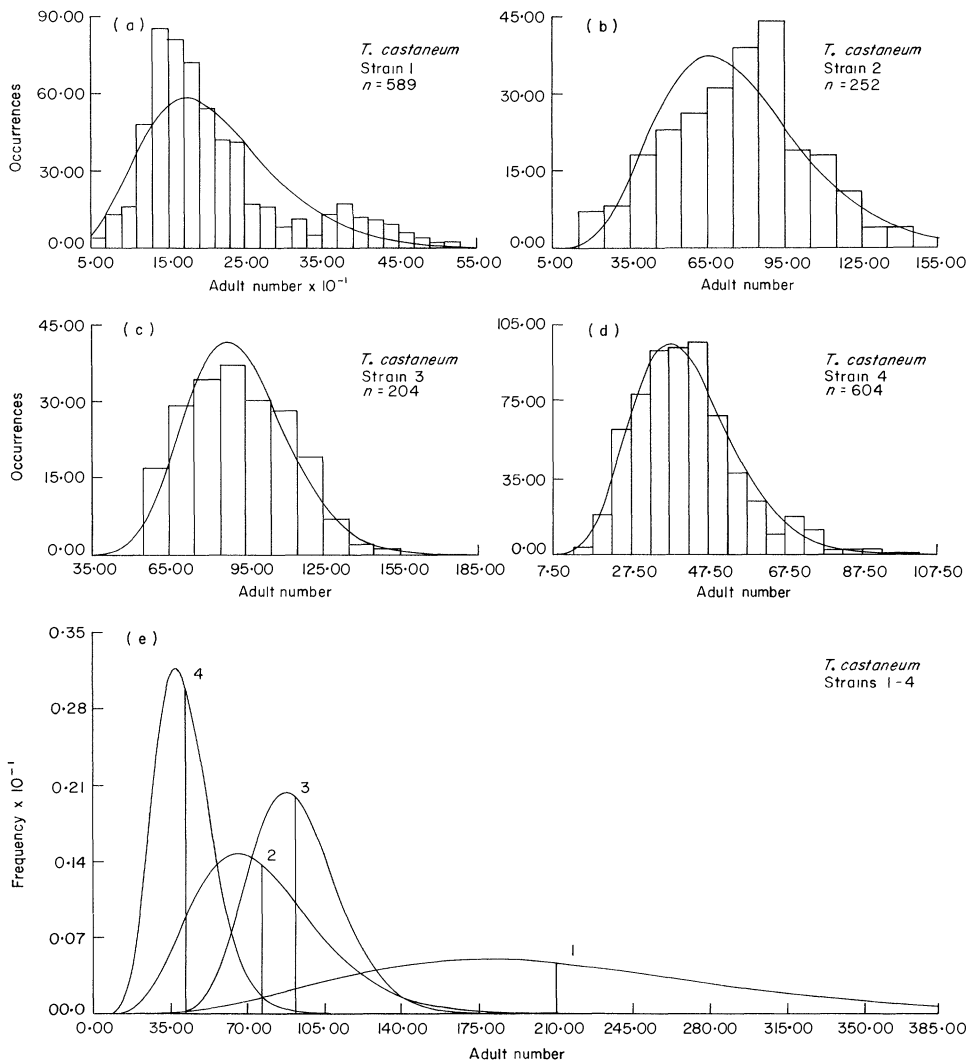


FIG. 5. *Tribolium castaneum*. Observed grouped frequency distributions published in Park, Leslie & Mertz (1964) together with the expected gamma distributions. The gamma densities of all four strains are drawn in (e). N is the number of observations.

now is to identify the biological properties of the gamma density function, with D or X stochastic, and thereby suggest an interpretation of the *Tribolium* data.

Stochastic variation in death rate among adults

The steady-state distribution of adults, $f(A)$, with D stochastic is given in eqn (4). The expectation of $f(A)$ (eqn 6) can be increased in several ways: (i) by an increase in X , the number of pupae produced per parent, (ii) by a decrease in C , the probability of cannibalism, (iii) by a decrease in D , the death rate among adults, or (iv) by a decrease in σ^2 , the variability of the random element. This latter observation is consistent with May's (1973) finding that white noise introduced into the carrying capacity term of the logistic model results in a reduction of the average population size. On reflection, these are all plausible effects on the mean value of $f(A)$ (see Fig. 6).

The variance of $f(A)$ is also quite informative. Unless X is very large relative to D , a decrease in X decreases the variance. As D or C decrease, the variance of $f(A)$ increases. Some findings are not intuitively obvious. The variance of $f(A)$, eqn (7), is a quadratic function of the stochastic variance so that an increase in σ^2 leads to the anticipated increase in the variance of $f(A)$ for $\sigma^2 < (X - D)$. For values of $\sigma^2 > (X - D)$, the variance actually decreases. Furthermore the steady-state distribution is gamma for $0 < \sigma^2 < (X - D)$; however, at $\sigma^2 = (X - D)$, $f(A)$ is a special case of the gamma, namely, an exponential distribution (Fig. 6, see curve #2). Stochastic variation at or beyond $2(X - D)$ yields no steady-state distribution.

To examine the steady-state distribution generated by our population growth model, we did a Monte Carlo simulation using the discrete time analogue of eqn (1), namely,

$$A_{t+1} = [1 + X(1 - C)^{A_t} - D]A_t \tag{16}$$

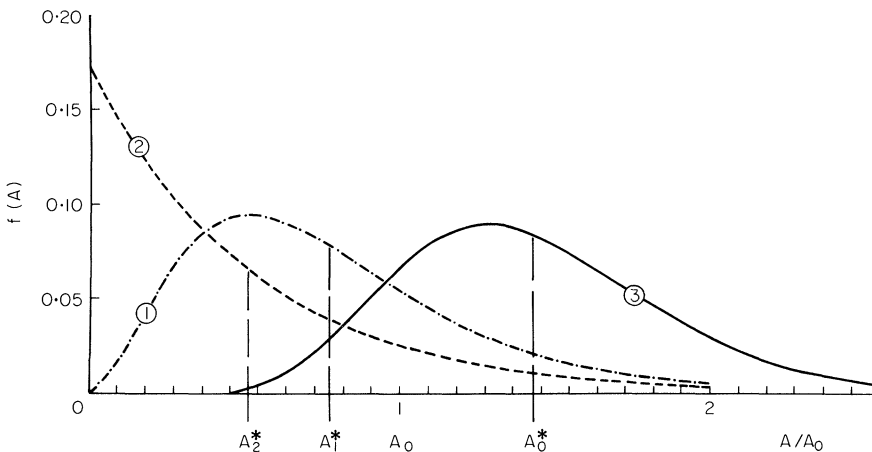


FIG. 6. Gamma equilibrium probability distributions for adult number, A , whose dynamics are described by eqn (1) with a stochastic component associated with the death-rate among adults. The distributions are displayed as the ratio of adult number to the deterministic equilibrium adult number, A/A_0 . The parameters for curve #1 are $X = 0.2$, $C = 0.044$, $D = 0.1$ and the death rate variance $\sigma^2 = 0.05$. The expectation of $f(A)$ has been reduced to $0.75 A_0$. Curve #2, with the same numerical values as #1 except that the variance is increased to $\sigma^2 = 0.1$, shows a further reduction in the mean value to $0.50 A_0$ and is a special case yielding the exponential density. Curve #3 is identical to #1 except that the number of pupae per parent is increased from $X = 0.2$ to $X = 0.4$. The expectation of $f(A)$ is increased as compared to the deterministic equilibrium number of curve #1, i.e. $1.37 A_0$.

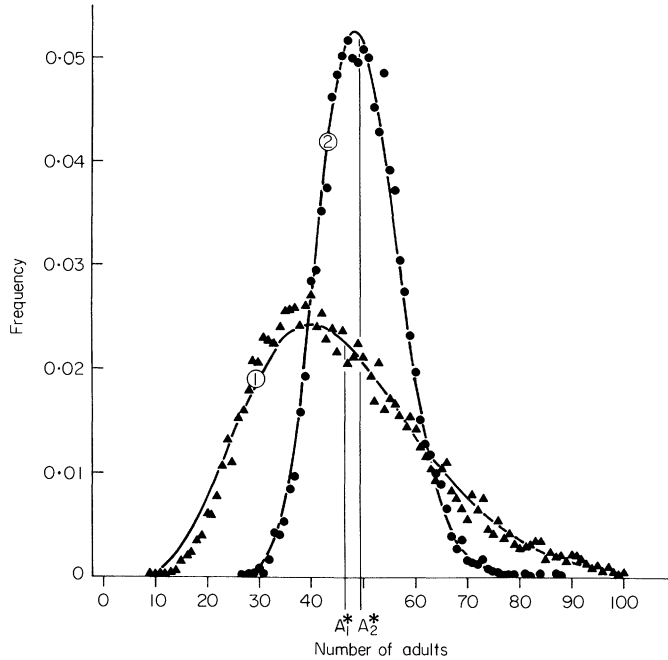


FIG. 7. Frequency distributions generated by the numerical analysis of eqn (16) with $C = 0.014$, $X = 0.71$ and D randomly chosen from a normal distribution with mean and variance (0.35, 0.05) in #1 and (0.35, 0.01) in #2. The smooth curve gamma distributions were calculated with the parameters (α, β) set equal to their sample estimates.

and allowed the death rate parameter D to be randomly chosen from a normal distribution with specified mean and variance. For each numerical example, 10 000 iterations of eqn (16) were performed and a frequency distribution of the numerically generated adult numbers was computed beginning with iteration 100, so that each distribution was based on 9901 'observations'.

In all of the many numerical examples we have evaluated, the computed frequency distribution was gamma. (Two typical examples are presented in Fig. 7.) In addition, the pattern of change in the mean and variance of $f(A)$ was consistent with the derived gamma (eqns 6 and 7): as the stochastic variance, σ^2 , decreased (from 0.05 to 0.01) the mean of $f(A)$ increased (from 46.5 to 49.4) and the variance of $f(A)$ decreased (from 305.6 to 58.5). These results indicate that although the derivation of the gamma distribution (4) was approximate, it is accurate and essentially correct.

We shall now examine the observed *Tribolium* data of Park (1954) published in Leslie (1962). As noted in Figs 3(e)–(f), the observed mean and variance of the adult distributions for both species increased when cultured at 29 °C as compared to 24 °C. The model suggests several explanations: first, a decrease in the probability of the adult inhibition of the immatures, second, a decrease in the death rate among adults or third, an increase in the rate that pupae are produced per parent at the higher temperature. Leslie (1962, p. 8) pointed out that the mean length of time from egg to adult is approximately twice as long as 24 °C than at 29 °C. This observation is consistent with the third explanation.

The observed gamma steady state distributions for the data of Park, Leslie & Mertz (1964) reflect the considerable differences that exist among these genetic strains of *T.*

confusum and *T. castaneum*. The authors of that study seem quite certain that cannibalism, C , is an important characteristic for predicting adult densities. In general, for *T. confusum* strains 3 and 4 were much more cannibalistic than strains 1 and 2 (Park, Leslie & Mertz, p. 150). Our interpretation of the distributions for *T. confusum* (Fig. 4(e)) is as follows: (i) stochasticity in X or D is present with $\sigma^2 < (X - D)$ which yields a gamma density, and (ii) the probabilities of cannibalism among the four strains are $C_4 > C_3 \gg C_2 > C_1$. The model predicts that the mean of adults will be $A_1^* > A_2^* \gg A_3^* > A_4^*$ and that the variances of adult numbers will be $V_1 > V_2 \gg V_3 > V_4$. These qualitative statements agree with the experimental data.

The equilibrium distributions for the *T. castaneum* data (Fig. 5(e)) may be interpreted as follows: (i) $\sigma^2 < (X - D)$ as before, and (ii) the probabilities of cannibalism (from Park, Leslie & Mertz 1964, p. 150) among the strains are $C_1 > C_4 > C_2 > C_3$. For the mean number of adults, the model predicts that $A_3^* > A_2^* > A_4^* > A_1^*$. The qualitative agreement between the theory and data is correct for strains 3, 2 and 4 but is completely wrong for strain 1 which had the largest mean number of adults and not the smallest as predicted. The model also predicts that the variances of adult numbers will be $V_3 > V_2 > V_4 > V_1$. Strain 1 did not have the smallest observed variance but the largest followed by strains 2, 3 and 4 in that order. A single biological parameter is not sufficient to explain these data. For example, while strain 1 does have a high C value, in addition, it has maximal fecundity and maximal fertility when compared to the other strains (Park, Mertz & Petruszewicz 1961). The equilibrium distribution of strain 1 may be a consequence of high C , high X (number of pupae produced per parent) and moderately low D (death rate).

Stochastic variation in recruitment rate

When the rate that pupae are produced per parent, X , is stochastic the situation is more complex than when D is stochastic. However, the parameter C plays the same role in both cases; consequently, the previous interpretation of the *Tribolium* data invoking C is also appropriate for X stochastic and will not be repeated.

The mean and variance of $f(A)$ with X stochastic (eqns 10 and 11) are similar to those when D is stochastic (eqns 6 and 7) except for the term $\sigma^2 \log(X/D)$ that appears in the denominator of both the mean and variance. Consequently, our analysis of the family of distributions with X stochastic will focus on the impact of the stochastic element, σ^2 , on the mean, $M(A)$, and the variance, $V(A)$, of the steady state distribution for four magnitudes of the ratio X/D : (i) $1 < X/D < \sqrt{e}$. The ratio of pupal production to adult mortality is slightly greater than unity. This case is the same as D stochastic. $M(A)$ is a monotonically decreasing function of the stochastic variance and $V(A)$ is a quadratic function. (ii) $X/D = \sqrt{e}$. In this case, $V(A)$ is a monotonically increasing function of the stochastic variance and at $\sigma^2 = (X - D)$, $f(A)$ is an exponential distribution. The mean is unchanged by the magnitude of σ^2 . (iii) $\sqrt{e} < X/D < e$. The ratio of pupal production to mortality is considerably larger now. Perhaps surprisingly, the introduction of stochastic variance in X actually increases the mean number of adults. $V(A)$ is a monotonically increasing function of σ^2 . The distribution again is exponential at $\sigma^2 = (X - D)$, however, a new lower limit on the magnitude of the stochastic variance is established at $(X - D)/\log(X/D)$, rather than at $2(X - D)$, (note eqn 12). For σ^2 beyond this boundary no distribution is expected. (iv) $X/D \geq e$. If pupae are produced at rates greater than or equal to 2.7 times adult mortality, the mean and variance both increase with the introduction of stochasticity in X . Only a gamma distribution is expected (no exponential) and the upper limit on stochastic variance is $(X - D)/\log(X - D)$. Beyond this point no distribution is realized.

Ito and Stratonovich calculi

In the evaluation of the stochastic differential equations of population growth (2) and (8) we used the Ito calculus. When we used the Stratonovich calculus the steady-state distribution was still gamma, but the conditions for its existence were quite different. As an example, if the parameter D is subject to white noise we can write eqn (2). For the Stratonovich calculus, the mean is $m = XA \exp(-CA) - DA + (\sigma^2/2)A$ and the variance is $V = A^2 \sigma^2$ which gives us the exact probability distribution

$$f(A) = K[A]^{(2(X-D)/\sigma^2)-1} \exp [(2X/\sigma^2) \sum_{n=1}^{\infty} (-CA)^n/nn!]. \tag{17}$$

This gamma density is to be compared to the gamma given in eqn (A1) in the Appendix. Using the approximation in (A4) the steady state distribution is

$$f(A) = K[A]^{(2(X-D)/\sigma^2)-1} \exp [-[2C(D - X)/\sigma^2 \log (D/X)]A]. \tag{18}$$

This density is to be compared to eqn (4). Both are gamma densities, however, the density in (18) exists provided $X > D$; there is no requirement on the relationship among σ^2 , X and D . Recall that for the Ito calculus this condition was $\sigma^2 < 2(X - D)$. From (18) we obtain the stationary expected adult number to be

$$M(A) = \log (X/D)/C \tag{19}$$

and the variance of $f(A)$ is

$$V(A) = \left[\sigma^2 \frac{(\log (X/D))^2}{C^2} \right] \left[\frac{1}{2(X - D)} \right] \tag{20}$$

Similar qualitative differences to those that we have obtained from eqn (2) with these two calculi have been noted by Feldman & Roughgarden (1975) for the logistic equation in a form proposed by May (1973) with stochastic variation in the carrying capacity term, k_0 . The stationary probability density for population size was, as in our case, gamma for both calculi. However, the existence condition for the Ito calculus was $\sigma^2 < 2k_0$, whereas, for the Stratonovich calculus the density always existed.

The question of which stochastic calculus is preferable to model population growth in *Tribolium* is a difficult one. Feldman & Roughgarden (1975) suggested that an important factor should be the meaning associated with our eqns (2) and (8). Brauman (1979) has recently proposed that either calculi can be used as long as the same method is employed in the entire analysis including the estimation of the parameters. In our case, the estimation of D must be examined to correctly interpret the conclusions of these calculi. For the Ito method, representing the expected value by E ,

$$E[dA(t)/dt] = A(t) X e^{-CA} - DA(t)$$

and D_I (subscript I for Ito) can be estimated using

$$D_I = E[\int_0^t A(y) X e^{-CA(y)} dy - A(t) + A(0)]/E[\int_0^t A(y) dy]. \tag{21}$$

For the Stratonovich method,

$$E[dA(t)/dt] = A(t) X e^{-CA(t)} - DA(t) + \frac{\sigma^2}{2} A(t)$$

and D_S (subscript S for Stratonovich) is

$$D_S = D_I + \sigma^2/2. \quad (22)$$

As $t \rightarrow \infty$ the asymptotic distribution of adult numbers for the Ito and Stratonovich methods are the same when D is defined as in (22) using the exact distributions in (A1) and (17).

Concluding comments

The gamma distribution may be of widespread interest to population ecologists. In general, any model of the form

$$dN/dt = N[b \exp(-cN) - d]$$

where b = birth rate (can include survival to maturity), d = death rate, c = parameter which specifies the intensity with which population size lowers the birth rate and N = population size (reproductives) will yield a gamma distribution if either the death rate or the birth rate is made stochastic. May (1973) has shown that stochasticity in the popular logistic model of population growth also yields a gamma steady-state distribution. Unlike a symmetrical distribution, the gamma is skewed to the right—away from extinction and towards larger population size.

The *Tribolium* data, in general, supported the hypothesis of characterizing the steady-state distribution of adult numbers in continuously growing populations as a gamma distribution. On the other hand, several of the observed distributions did not fit the gamma so that alternative models do warrant study. In this regard, the time-series information present in these data but which was not available to us in the published work of Leslie (1962) and Park, Leslie & Mertz (1964) may be of value.

Finally, it should be pointed out that the observed frequency distributions do not allow us to distinguish between X stochastic or D stochastic; in either case, the theoretical prediction of $f(A)$ is a gamma density function. Nor can we obtain estimates of the number of pupae produced per parent, the death rate among adults, or the adult inhibition of immatures from the observed distributions. However, the theoretical statement of $f(A)$ does allow for an interpretation of the observed distributions in terms of plausible biological entities and, perhaps more importantly, we can now make predictions concerning the steady state of single species cultures.

ACKNOWLEDGMENTS

We especially thank Andrea Moffa-White for allowing us to use her *Tribolium* data and Carlos Braumann for making his work on the Ito and Stratonovich calculi available to us. We also want to thank Joel E. Cohen and the reviewers for their helpful comments. During an extended visit at Purdue University, R. F. Costantino is grateful for the hospitality of Professor A. E. Bell and his staff at the *Tribolium* laboratory. The illustration (Fig. 1) was prepared by Kathy Shuster. We also appreciate the skilled typing assistance of Ruth Saunders, Peggi-Joan Barbour and Sandra Koerner.

APPENDIX

In this appendix we derive the approximate steady-state probability distributions given in eqns (4) and (9) in the text.

For the Ito calculus with D stochastic, substituting the mean $m = XA \exp(-CA) - AD$ and the variance $v = A^2 \sigma^2$ into eqn (3), we have

$$f(A) = \frac{K}{A^2} \exp \left[\frac{2}{\sigma^2} [X \int (\exp(-CA)/A) dA - D \int (1/A) dA] \right].$$

Now we note that

$$\int [\exp(-CA)/A] dA = \log A + \sum_{n=1}^{\infty} (-CA)^n / nn!$$

which gives us the exact probability distribution

$$f(A) = K[A]^{(2(X-D)/\sigma^2)-2} \exp [(2X/\sigma^2) \sum_{n=1}^{\infty} (-CA)^n / nn!]. \tag{A1}$$

The series in (A1) was approximated by substituting $A^* = \log(X/D)/C$ into the higher order terms of the series to obtain

$$\sum_{n=1}^{\infty} (-CA)^n / nn! \doteq -CA [1 + \log(D/X)/2 \cdot 2! + (\log(D/X))^2 / 3 \cdot 3! + \dots]. \tag{A2}$$

The series enclosed by brackets in (A2) is nearly

$$[(D/X) - 1] / \log(D/X) = 1 + \log(D/X)/2! + (\log(D/X))^2 / 3! + \dots \tag{A3}$$

Substitution of (A3) into (A2) yields

$$\sum_{n=1}^{\infty} (-CA)^n / nn! \doteq -CA [(D/X) - 1] / \log(D/X). \tag{A4}$$

The steady state probability distribution in (A1), using the approximation in (A4), yields the distribution given in eqn (4).

For the Ito calculus with X stochastic, substituting the mean $m = XA \exp(-CA) - AD$ and the variance $v = A^2 \sigma^2 \exp(-2CA)$ into eqn (3) we have

$$f(A) = \frac{K \exp(2CA)}{A^2} \exp \left[\frac{2}{\sigma^2} [X \int (\exp(CA)/A) dA - D \int (\exp(2CA)/A) dA] \right]. \tag{A5}$$

In this case we note that

$$\int [\exp(CA)/A] dA = \log A + \sum_{n=1}^{\infty} (CA)^n / nn! \tag{A6}$$

and

$$\int [\exp(2CA)/A] dA = \log A + \sum_{n=1}^{\infty} (2CA)^n / nn! \tag{A7}$$

which gives us the exact probability distribution

$$f(A) = K[A]^{(2(X-D)/\sigma^2)-2} \exp \left[(2X/\sigma^2) \sum_{n=1}^{\infty} (CA)^n / nn! - (2D/\sigma^2) \sum_{n=1}^{\infty} (2CA)^n / nn! + 2CA \right] \tag{A8}$$

The two series terms in (A8) were approximated, as in eqn (A1), by substituting A^* into the higher order terms to obtain expressions similar to eqns (A2) and (A3). For the first integral we have

$$\int (\exp (CA)/A) dA \doteq \log A + CA [(X/D) - 1]/\log (X/D). \quad (\text{A9})$$

and for the second integral

$$\int (\exp (2CA)/A) dA \doteq \log A + CA[(X/D)^2 - 1]/\log (X/D). \quad (\text{A10})$$

Substitution of (A9) and (A10) into (A8) gives the approximate steady state distribution in eqn (9).

REFERENCES

- Braumann, C. A. (1979). *Population growth in random environments*. Unpublished Ph.D. thesis, S.U.N.Y., Stony Brook, New York.
- Crow, J. F. & Kimura, M. (1970). *An Introduction to Population Genetics Theory*. Harper & Row, New York, U.S.A.
- Desharnais, R. A. & Costantino, R. F. (1980). Genetic analysis of a population of *Tribolium*. VII. Stability: Response to genetic and demographic perturbations. *Canadian Journal of Genetics and Cytology*, **22**, 577–589.
- Feldman, M. W. & Roughgarden, J. (1975). A population's stationary distribution and chance of extinction in a stochastic environment with remarks on the theory of species packing. *Theoretical Population Biology*, **7**, 197–207.
- Feller, W. (1966). *An Introduction to Probability Theory and Its Application*. Wiley, New York.
- Johnson, N. L. & Kotz, S. (1970). *Continuous Univariate Distributions—1*. Houghton Mifflin, Boston.
- Leslie, P. H. (1962). A stochastic model for two competing species of *Tribolium* and its application to some experimental data. *Biometrika*, **49**, 1–25.
- Lloyd, M. (1968). Self-regulation of adult numbers by cannibalism in two laboratory strains of flour beetles (*Tribolium castaneum*). *Ecology*, **49**, 245–259.
- May, R. M. (1973). *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, New Jersey, USA.
- Moffa, A. M. & Costantino, R. F. (1977). Genetic analysis of a population of *Tribolium*. VI. Polymorphism and demographic equilibrium. *Genetics*, **87**, 785–805.
- Ostle, B. (1963). *Statistics in Research*. Iowa State University Press, Ames, Iowa.
- Park, T. (1954). Experimental studies of interspecies competition. II. Temperature, humidity, and competition in two species of *Tribolium*. *Physiological Zoology*, **27**, 177–238.
- Park, T., Leslie, P. H. & Mertz, D. B. (1964). Genetic strains and competition in populations of *Tribolium*. *Physiological Zoology*, **37**, 97–162.
- Park, T., Mertz, D. B. & Petruszewicz, K. (1961). Genetic strains of *Tribolium*: Their primary characteristics. *Physiological Zoology*, **34**, 62–80.
- Ricker, W. E. (1954). Stock and recruitment. *Journal of the Fishery Board of Canada*, **11**, 559–623.
- Roughgarden, J. (1979). *Theory of Population Genetics and Evolutionary Ecology: An Introduction*. Macmillan Publishing Co., New York, U.S.A.
- Turelli, M. (1977). Random environments and stochastic calculi. *Theoretical Population Biology*, **12**, 140–178.

(Received 4 August 1980)